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Culture in whales and dolphins

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Abstract: Studies of animal culture have not normally included a consideration of cetaceans. However, with several long-term field studies now maturing, this situation should change. Animal culture is generally studied by either investigating transmission mechanisms experimentally, or observing patterns of behavioural variation in wild populations that cannot be explained by either genetic or environmental factors. Taking this second, ethnographic, approach, there is good evidence for cultural transmission in several cetacean species. However, only the bottlenose dolphin (*Tursiops*) has been shown experimentally to possess sophisticated social learning abilities, including vocal and motor imitation; other species have not been studied. There is observational evidence for imitation and teaching in killer whales. For cetaceans and other large, wide-ranging animals, excessive reliance on experimental data for evidence of culture is not productive; we favour the ethnographic approach. The complex and stable vocal and behavioural cultures of sympatric groups of killer whales (*Orcinus orca*) appear to have no parallel outside humans, and represent an independent evolution of cultural faculties. The wide movements of cetaceans, the greater variability of the marine environment over large temporal scales relative to that on land, and the stable matrilineal social groups of some species are potentially important factors in the evolution of cetacean culture. There have been suggestions of gene-culture coevolution in cetaceans, and culture may be implicated in some unusual behavioural and life-history traits of whales and dolphins. We hope to stimulate discussion and research on culture in these animals.

Keywords: Animal culture; cetaceans; coevolution; cognition; cultural transmission; dolphins; evolution of culture; imitation; teaching; whales

1. Introduction

The presence of cultural processes in nonhuman animals is an area of some controversy (de Waal 1999; Galef 1992). In this target article we attempt to fuel the debate by reviewing the evidence for cultural transmission in whales and dolphins (order Cetacea), a group that has so far received almost no attention from students of animal culture. Studies of cetaceans have uncovered a number of patterns of behaviour and vocalizations, which some cetologists have ascribed to cultural processes. Here we review these results from the perspectives used in research on cultural transmission in other animals.

Theoretical investigations suggest that cultural transmission of information should be adaptive in a broad range of environments (Boyd & Richerson 1985), but it is quite rarely documented outside humans (but see Slater 1986; Whiten et al. 1999). This discrepancy has yet to be explained (Laland et al. 1996). When stable over generations, culture can strongly affect biological evolution, in both theory (e.g.. Findlay 1991) and practice – much of human behaviour is determined by a broad range of cultural processes, and there is good evidence for gene-culture coevolution in our species (Feldman & Laland 1996). In contrast, among nonhuman animals culture is much simpler, rarer, and, except possibly in the case of bird song (Grant & Grant 1996), thought not to have the stability necessary to make a substantial impact on genetic evolution (Feldman & Laland 1996; Laland 1992).

The logistical difficulties of studying wild cetaceans make the study of culture difficult, and often give rise to information that is incomplete and poor in detail. Nonetheless, we feel it is timely to introduce cetaceans into the wider debate surrounding animal culture for a number of reasons. First, there is growing evidence of cultural transmission and cultural evolution in the cetaceans, some of which is strong, some of which is weaker, but which when taken as a whole make a compelling case for the detailed study of cultural phenomena in this group. Although culture and cultural transmission have been briefly discussed in the context of cetaceans by a number of authors (Felleman et al. 1991; Ford 1991; Norris & Dohl 1980; Norris & Schilt 1988; Norris et al. 1994; Osborne 1986; Shane et al. 1986; Silber & Fertl 1995), no synthesis has been attempted. Second, the evidence now available describes some interesting and rare (in some cases unique outside humans) patterns of behavioural variation in the wild, likely maintained by cultural transmission processes. Third, there is growing evidence that in the complexity of their social systems – the only nonhuman example of second-order alliances (Connor et al.

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1998) – and their cognition – data suggest that dolphins can use abstract representations of objects, actions and concepts to guide their behaviour (Herman et al. 1993; 1994) – some cetaceans match or exceed all other non-human animals. Since complex social systems and advanced cognitive abilities have been suggested as good predictors of animal culture (Roper 1986), it is pertinent to ask whether these factors are reflected in the cultural faculties of cetaceans. Finally, cetaceans provide an interesting contrast to the study of culture in humans and other terrestrial animals, since they inhabit a radically different environment and perhaps represent an independent evolution of social learning and cultural transmission.

The study of animal culture is heavily influenced by perspective. Hence, before we review culture in cetaceans, we discuss the differing approaches that have been taken to the study of nonhuman culture. We then review evidence for culture in cetaceans from the two principal perspectives, ethnographic patterns and the experimental study of imitation and teaching, comparing the results with the most similar phenomena described in other groups of animals. After trying to reconcile the evidence from these two approaches, we consider the evolution of cultural transmission in cetaceans, gene-culture coevolution, and the possibility that cultural processes may explain some unusual behavioural and life-history patterns of whales and dolphins.

2. Perspectives on culture

Clearly our review of culture in cetaceans will depend heavily upon our idea of what culture is. There is little consensus on this issue; the term *culture* is defined in an array of subtly different ways within the literature, some of which we have listed in Table 1. We have not included definitions that make culture a trait only humans show. These were considered by Mundinger (1980) in his review of cultural theory. We agree with him in both respects, that is, that there is "no empirical evidence" supporting such a cultural dichotomy between humans and other animals, and more general concepts of culture are more likely to advance understanding. The work of Boyd and Richerson (1985; 1996) has been crucially important in giving the study of cultural transmission and cultural evolution a sound theoretical basis (Bettinger 1991, p. 182). Thus the definitions of culture that they found useful are particularly important, and have heavily influenced our decision on which definition to adopt:

> Culture is information or behaviour acquired from conspecifics through some form of social learning. (Boyd & Richerson 1996)

Whiten and Ham (1992) list a range of "social processes" as supporting cultural transmission, and in the definition of culture we use, the phrase "some form of social learning" refers to these processes. These comprise exposure, social support, matched dependent learning, stimulus enhance-

Table 1. *Some definitions of culture.*

Source	Definition
Aoki (1991)	The transfer of information between individuals by imitative or social learning.
Bonner (1980, p. 163)	I have defined culture as the transfer of information by behavioural means.
Boesch (1996)	The key to culture is not so much the precise transmission mechanisms, as we saw that many of them could be at work, but a permanence-guaranteeing mechanism.
Boesch et al. (1994)	A behaviour is considered cultural only if differences in its distribution between populations are independent of any environmental or genetic factors.
Boyd & Richerson (1985, p. 33)	Culture is information capable of affecting individuals' phenotypes, which they acquire from other conspecifics by teaching or imitation.
Boyd & Richerson (1996)	We define cultural variation as differences among individuals that exist because they have acquired different behaviour as a result of some form of social learning.
Feldman & Laland (1996)	Culture is treated as shared ideational phenomena (ideas, beliefs, values, knowledge).
Galef (1992)	. . . defined as an animal tradition that rests either on tuition of one animal by another or on imitation by one animal of acts performed by another.
Heyes (1993)	. . . a subset of traditions in which the focal behaviour has been formed through the accumulation of modifications through time.
Kummer (1971, p. 13)	Cultures are behavioural variants induced by social modification, creating individuals who will in turn modify the behaviour of others.
Mundinger (1980)	Culture is a set of [behavioural] populations that are replicated generation after generation by learning.
Nishida (1987)	Cultural behaviour is thus defined here as behaviour that is (*a*) transmitted socially rather than genetically, (*b*) shared by many members within a group, (*c*) persistent over generations, and (*d*) not simply the result of adaptation to different local conditions.
Russell & Russell (1990)	The culture of a society may be defined as behaviour common to a substantial proportion of its members, socially transmitted within and between generations.
Slater (1986)	Cultural transmission is the phenomenon whereby features of behaviour pass by learning from one individual to another.
Tomasello (1994)	The concept of culture was specifically formulated to describe group differences in human behavior, and, thus, behavioral traditions of humans provide the proto-typical case of cultural transmission.

ment, observational conditioning, imitation, and goal emulation as listed and defined in Whiten and Ham (1992).

In contrast to this broad definition, some scientists have insisted that cultural transmission only takes place under two types of social learning: phylogenetically homologous (to humans) imitation and teaching (Galef 1992; Tomasello 1994). This restriction is justified on the grounds that these processes seem to be vital elements of human culture (Galef 1992), and also that, unlike other forms of social learning, they allow complex cultures to be constructed by successive modification (Boyd & Richerson 1985). While we reject this narrower view of culture for reasons discussed next, we recognize that teaching and imitation are particularly important forms of social learning when considering cultural transmission.

The empirical study of cultural processes in animals is generally approached in two major ways: controlled laboratory experiments on social learning mechanisms and field descriptions of behavioural variation (Lefebvre & Palameta 1988). The first follows from the restriction of culture to imitation and teaching and emphasises process – is imitation and/or teaching taking place? – and the second, espoused by those accepting a generally broader definition of culture, emphasises product – cultural patterns. Both make important contributions to our understanding of culture.

The first approach focuses on experimental study of the cognitive processes underlying cultural transmission. In general, controlled laboratory experimentation is the preferred methodological tool; this gives the approach the advantage of controlled conditions and hence less chance of ambiguity in the interpretation of data. However, the studies do not necessarily relate to what occurs in the wild, and care must be taken to establish that such studies are not simply measuring what McGrew (1992, p. 21) calls the "socio-ecological validity of the captive environment" rather than the true abilities of the animals under scrutiny.

The second approach is field-based, involving the systematic assimilation of data on the behaviour of individuals and groups often over large temporal and spatial scales. Here culture is deduced from patterns of behavioural variation in time and space, which cannot be explained by environmental or genetic factors (Boesch 1996; Boesch et al. 1994; Nishida 1987; Whiten et al. 1999). This approach has been likened to ethnography in the social sciences (Wrangham et al. 1994). The strength of this approach is that it is firmly rooted in what the animals actually do in the wild, with the unavoidable weakness that results can be more ambiguous than those derived from controlled experiments. However, such studies cannot usually tell us much about which specific social learning processes are involved in producing the observed behavioural variation.

These two approaches have interacted in different ways in the study of culture and cultural transmission in different taxonomic groups. Culture in humans is studied largely from an ethnographic perspective, although some experimental work has been done (e.g., Meltzoff 1996; Tomasello et al. 1993). In the study of the cultural evolution of birdsong, the two approaches have generally integrated cooperatively with laboratory and field studies complementing each other in a stimulating and progressive way (see Baker & Cunningham 1985). In non-primate mammals there exists an impressive body of work concerning the social transmission of feeding behaviour, based mainly on an experimental approach (see Galef 1996), with little reference to variation in the wild (for a notable exception, see Terkel 1996). It is in the discussion surrounding culture in nonhuman primates that the most severe dichotomy between these two perspectives is apparent. A lack of laboratory evidence for imitation has led to the persistent denial of culture in chimpanzees (*Pan troglodytes*) from some (Galef 1992; Tomasello 1994), while others, drawing on field evidence of variation in behaviour such as nut-cracking, which cannot be explained by ecological or genetic factors, maintain that wild chimpanzees *do* have distinctive and complex cultures (Boesch 1996; Boesch et al. 1994; McGrew 1994; Whiten et al. 1999).

We strongly believe that research on cultural processes is best served by an approach that integrates the sometimes opposing process- and product-oriented perspectives, as well as the laboratory and field approaches, taking good data from each. This cannot be achieved unless both perspectives are understood, and so we shall approach cetacean culture from both in turn. Following this, we will bring our own perspective, as field biologists heavily influenced by evolutionary ecology, to an attempted integration.

3. Culture in cetaceans: Ethnographic patterns

The ethnographic evidence for cetacean culture is remarkably strong, given the substantial difficulties of studying whales and dolphins in the wild. In only four (of ~80) species of Cetacea have more than a handful of papers on behaviour been published (Mann 1999): the bottlenose dolphin (*Tursiops* spp.), the killer whale (*Orcinus orca*), the sperm whale (*Physeter macrocephalus*) and the humpback whale (*Megaptera novaeangliae*). However, studies of each of these species have been carried out in different ocean basins and over time periods of ten years and more. In many attributes, these four species span a wide range. For instance, their sizes range from 2 m (bottlenose dolphins) to 16 m (sperm whales), their habitat from protected coastal lagoons (bottlenose dolphins) to deep oceanic waters (sperm whales), and trophic levels from partial planktivores (humpback whales) to top predators (killer whales). The four species have diverse social systems: humpback whales live in loose fission-fusion societies (Clapham 1993); both sexes of killer whale generally remain within their natal matrilineal group (Baird 2000); female sperm whales live in largely matrilineal groups from which males disperse to lead quite solitary adult lives (Whitehead & Weilgart 2000); in bottlenose dolphins, males can form stable alliances, whereas females possess a network of more labile relationships (Connor et al. 1998). Although the four well-studied cetacean species are socially diverse, they are likely to be unrepresentative of all cetaceans. For instance, the pelagic dolphins, beaked whales, and river dolphins may have quite different social systems (Connor et al. 1998) and cultural faculties. From the ethnographic perspective cultural transmission is deduced from spatial, temporal or social patterns of variation in behaviour that are not consistent with genetic or environmental determination or individual learning. It should be noted that from this perspective, no attempt is made to deduce what particular *form* of social learning underlies the observed patterns. We will consider three types of pattern:

1. Rapid spread of a novel and complex form of behaviour through a segment of the population, indicating a largely

horizontal – within-generation (Cavalli-Sforza & Feldman 1981) – cultural process.

2. Mother-offspring similarity in a complex form of behaviour, indicating vertical – parent-offspring (Cavalli-Sforza & Feldman 1981) – cultural transmission.

3. Differences in complex behaviour between stable groups of animals that are hard to explain by genetic differences, shared environments, or the sizes or demographic structure of the groups. Such patterns could arise through vertical or oblique – learning from a nonparental model of the previous generation (Cavalli-Sforza & Feldman 1981) – transmission within strictly matrilineal groups, or through a combination of vertical, oblique, and horizontal within-group transmission in a system with conformist traditions – individuals aligning their behaviour with that of other group members (Boyd & Richerson 1985) – within more labile groups.

We will refer to these as *rapid-spread, mother-offspring*, and *group-specific* behavioural patterns, respectively. Our categories are not discrete, as the same cultural phenomenon (such as behaviour learned primarily from the mother) could be inferred in more than one way (mother-offspring or group-specific if groups are matrilineal). However, there is a distinction between rapid-spread patterns, which are likely to be primarily due to within-generation transmission, and the other categories, which are likely to incorporate a significant between-generation transmission component. This distinction is important from an evolutionary perspective since it is between-generation transmission that has the most profound evolutionary effects (Feldman & Laland 1996; Laland 1992; Russell & Russell 1990). Here, we review examples of each pattern in cetaceans, and compare what has been found with results from other animals. We consider cases where environmental and genetic causation can be ruled out, and also those where such causes are theoretically feasible but practically unlikely.

3.1. Rapid spread of novel behaviour

When new behavioural variants spread through much of a population over time scales of less than a generation, then genetic causation can be excluded, but environmental change plus individual learning must be considered as an alternative to social learning. If behavioural change is continuous, then an environmental causative factor should vary over a similar temporal scale. The spread of a single novel behaviour through a population over a short period could be caused either by environmental change and then individuals learning the appropriate behaviour independently, or by social learning (culture). Distinguishing between these alternatives requires either observation of individual or social learning (which is very hard for cetaceans, see following paragraphs), or a consideration of the likelihood that a new environmental factor could have triggered a bout of independent individual innovations.

On their winter breeding grounds, male humpback whales produce songs, structured sequences of vocalizations cycling with a period of about 5–25 min (Payne & McVay 1971). At any time, all males in a breeding population sing nearly the same song, but the song evolves structurally over time, changing noticeably over a breeding season, substantially over periods of several years, but remaining stable over the largely nonsinging summer months (Payne & Payne 1985). Males sing virtually identical songs on breeding grounds thousands of kilometres apart, and the songs on these different grounds evolve as one. For instance, songs from Maui, Hawaii, and Islas Revillagigedo, Mexico (4,500 km apart) are similar at any time but change in the same way over a two-year period (Payne & Guinee 1983). While the mechanisms underlying this process are not fully understood, horizontal cultural transmission almost certainly plays an important role in maintaining song homogeneity as there is no conceivable environmental trigger for such a pattern of variation (Cerchio 1993; Payne & Guinee 1983) – it may be that the oceanic deep sound channel (Payne & Webb 1971) plays a role in facilitating this transmission.

Superficially, this pattern of rapid change is similar to the cultural evolution of song in yellow-rumped caciques (*Cacius cela*) (Feekes 1982; Trainer 1989) and village indigobirds (*Vidua chalybeata*) (Payne 1985), but there are important differences. Humpback song is homogenous over entire ocean basins compared to the sharp variation over short distances in both bird species, and thousands of individual humpbacks share the same song compared to the colony- or locale-specific birdsongs (Cerchio 1993). Thus it is hard to see how the changes in humpback song could be driven by imitating a few dominant males as has been suggested by Trainer (1989) for birds showing similarly rapid change – some other cultural process must be acting. Cerchio (1993) suggests that evolving humpback song may constitute dialects in the time domain, and that conformity to the current dialect may be socially significant in the same way that conformity to the local dialect is in birds (we take as our definition of dialect that of Connor [1982] – variation in the vocal behaviour of different but potentially interbreeding groups). Nevertheless, the differences in scale make humpback songs a so far unique instance among nonhumans of a continuously evolving conformist culture in a large and dispersed population.

Bowhead whales (*Balaena mysticetus*) of the Bering Sea stock also sing during their peak mating season. While their songs are simpler than the humpbacks', bowhead songs also change from year to year and all males on a given migration sing the same general song (Clark 1990; Würsig & Clark 1993). Bowheads have been observed apparently imitating conspecific calls (Clark 1990), hence horizontal cultural transmission also likely maintains song homogeneity in this species. However, as much less data are available for comparisons between areas and over time than with the humpbacks, the characteristics of this system await further recordings from different populations.

Cultural innovations can also spread quite rapidly on humpback feeding grounds where they spend the summer months. In the southern Gulf of Maine, a novel complex feeding technique, "lobtail feeding," was first observed in 1981, and by 1989 had been adopted by nearly 50% of the population (Weinrich et al. 1992). This feeding method is apparently a modification of "bubble-cloud" feeding, a complex but common form of feeding in humpbacks in which prey schools are enveloped in clouds of bubbles formed by exhaling under water (for the diversity of humpback feeding techniques, see Hain et al. 1982); the behaviour is modified by slamming the tail-flukes onto the water (termed *lobtailing*) prior to diving. The spread of the behaviour is known in some detail since it was recorded over a nine-year period in individuals known from photo-identification, and in these details are clues to the transmission process (Weinrich et al. 1992). The increase in the numbers of animals showing lobtail feeding was due primarily to animals born into the study population using the technique (many of these had mothers that did not show the technique, thus genetic determination is unlikely), although some adults also adopted the method. Figure 1 shows that this pattern of spread strongly suggests social learning, given that it is best represented by an accelerating function, as would be expected under social learning (Lefebvre 1995), although a series of independent individual learning events cannot be entirely ruled out (Weinrich et al. 1992). Although the innovation of lobtail feeding followed a shift in diet accompanying a change in the distribution of prey species (Weinrich et al. 1992), the change was in proportional use of different food sources, not the introduction of a novel environmental element. Given that the technique is a modification of preexisting methods, these observations suggest the potential for a "ratchet effect" (Tomasello 1994) in culturally transmitted feeding behaviour.

The spread of novel feeding methods through a population has been documented for a number of terrestrial and avian species (Roper 1986). Two of the most famous cases are milk-bottle top opening by birds in Britain (Fisher & Hinde 1949), and washing sweet potatoes by Japanese macaques (*Macaca fuscata*) (Kawai 1965). In both cases, the spread was thought to be due to imitation, but more recent work has cast doubt on this (Sherry & Galef 1984; Whiten 1989). Rates of spread of the innovations were similar to those observed for the lobtail-feeding humpbacks: Milk-bottle opening took 20 years to spread across London and potato washing spread through almost all the band of macaques in nine years.

3.2. Mother-offspring similarity

When mother and offspring have similar, but characteristic, patterns of complex behaviour, this suggests vertical cultural transmission through imitation, teaching, or other forms of social learning. However, genetic determination or shared environments leading to parallel individual learning are also potential explanations in some cases. The limitations of current field studies on cetaceans mean that only seldom are mother-offspring relationships known among adults.

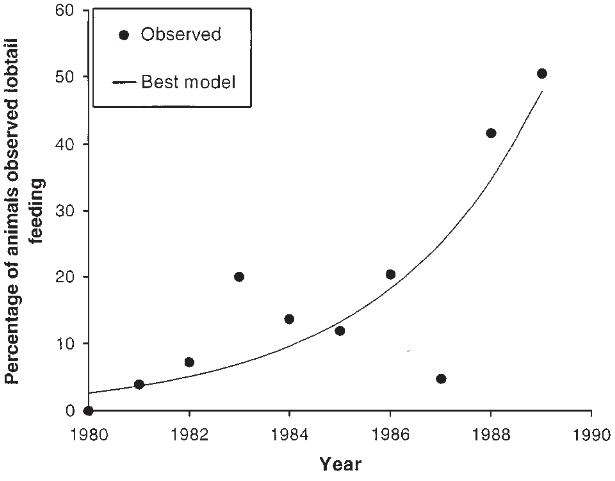

Figure 1. Number of animals lobtail feeding as a percentage of all animals observed feeding over a 10 year study (data from Weinrich et al. 1992). We applied the exact methodology of Lefebvre (1995) to this dataset, comparing the fit of several models (linear, exponential, logarithmic, logistic, and hyperbolic sine) using Akaike's information criterion. The lowest AIC value, and hence best fit, came from the exponential model (AIC $= -16.72$, $y = 0.02e^{0.32x}$) which is consistent with social learning and is plotted here. This fits the data better than a linear model which would indicate individual learning (AIC $= -15.10$).

Genetic and photo-identification studies have shown that young beluga (*Delphinapterus leucas*) and humpback whales follow their mothers on initial migrations between breeding and feeding grounds, and then repeat them faithfully throughout their lives (Katona & Beard 1990; O'Corry-Crowe et al. 1997). In both species, the segregation of mitochondrial DNA haplotypes by migration routes suggest strong maternal migratory traditions (Baker et al. 1990; O'Corry-Crowe et al. 1997) (a haplotype being any given DNA sequence – individuals with the same mitochondrial haplotypes have the same DNA sequence in their mitochondrial genome; mitochondrial DNA is found not in the nucleus but in the mitochondria, and is inherited through the maternal germ line). In humpbacks this hypothesis is supported by photo-identification data showing calves returning to their mother's feeding grounds, even though several feeding stocks apparently intermingle on breeding grounds – making genetic inheritance unlikely (Clapham & Mayo 1987). These cases have obvious parallels in the migratory behaviour of some birds (e.g., Healey et al. 1980).

Bottlenose dolphins in Shark Bay, Australia, carry sponges on their rostra (Smolker et al. 1997). The exact function of "sponging" is not known; it is thought to be a foraging specialisation (Smolker et al. 1997), but could carry little obvious adaptive significance, making it directly comparable to stone-handling in Japanese macaques (Huffman 1996). What is interesting from a cultural perspective is that in a population of over 60 individuals known from the 150 km^2 study site, only five sponge regularly; it was been observed only four times in other individuals over a six-year study period (Smolker et al. 1997). The sponging dolphins are also unusual in their social behaviour; all female, they are markedly more solitary in their habits than the other dolphins in the population and were not observed in any large social groups during the study period. While sponging is only seen in sandy parts of the mixed sand – sea grass habitat, all members of the population experience the same mixed habitat, so ecological explanations for this behavioural variation can be discounted. Other members of the population are seemingly aware of the technique, as evidenced by the occasional observations of sponging in other individuals, but they do not fully adopt it; thus variation is unlikely to be due to any genetic ability. However, the calf of one of the regular spongers itself sponges, suggesting vertical cultural transmission. Dolphins in Shark Bay also show another "foraging specialisation" – feeding by humans at Monkey Mia beach – in which not all of the population takes part. This variation also appears to be maintained by vertical cultural transmission, since most of the dolphins taking advantage of the feeding are offspring of females which were themselves fed (Smolker et al. 1997); hence the so-called specialisation is likely learned while swimming with the mother.

The transmission of feeding specialisations from parent to offspring is fairly common in other animals. For example, it has been documented in oyster catchers, *Haematopus ostralegus,* (Sutherland et al. 1996), rats, *Rattus rattus,* (e.g., Terkel 1996), and chimpanzees (Nishida 1987; Whiten et al. 1999), although the remarkable diversity of feeding specialisations in bottlenose dolphins both within and between areas (Shane et al. 1986; Würsig 1986) is comparable only with chimpanzees.

Mother-offspring similarity in feeding behaviour is also known from killer whales, particularly the dramatic case of intentional stranding on beaches to catch pinnipeds (Baird 2000). This behaviour has been sufficiently well studied that it provides good evidence for teaching, and so is discussed below under transmission mechanisms.

3.3. Group-specific behaviour

The principal ethnographic approach to the study of culture has been the contrasting of behavioural patterns between stable social groups of animals (e.g., Whiten et al. 1999). However, social groups, especially in primates, usually occupy distinct habitats and are genetically related, leading to criticism that such ethnographic patterns may be the results of individual learning in different environments, or may have been caused by genetic differences (Galef 1992). Primatologists address such arguments by examining correlations between presumed cultural variants and environmental features or phylogenetic relatedness (Whiten et al. 1999). In the two species of cetacean with matrilineal social systems where group-specific behavioural patterns have been explicitly studied, killer and sperm whales, environmental causation is easily dismissed as groups showing distinctive behavioural patterns are often sympatric, sharing the same habitat and frequently interacting (Baird 2000; Whitehead & Weilgart 2000). We use the term *group* here *sensu* Connor et al. (1998) – a set of animals with consistently stronger associations with each other than with other members of the population over periods of months to decades.

Addressing potential genetic causation of behavioural differences between groups is more complex, as some presumed cultural traits in the matrilineal groups of these species seem to be sufficiently stable that they can show occurrence patterns that are very similar to parts of the maternally inherited mitochondrial genome (Whitehead et al. 1998, Fig. 2). However, except in the case of the different forms of killer whale (see below), mating appears to occur across behavioural variation boundaries (Baird 2000; Ohsumi 1966). Thus, stable group-specific behavioural traits, if genetically determined, would have to lack paternal inheritance, as conventional biparental genetic transmission via the nuclear genome would lead to hybrid behaviour and scramble group-specific patterns (Whitehead 1999a). It is unlikely in the extreme that mitochondrial DNA would code for behaviour. It is theoretically possible for behavioural variants to be encoded in the nuclear genome and give rise to the observed patterns if the encoding genes were subject to some form of genomic imprinting, where only the alleles from one parent, in this case the mother, were expressed (see Barlow 1995; Spencer et al. 1999). However, such genomic imprinting systems are typically involved in embryonic development and are thought to be the result of genetic conflict for developmental resources (Spencer et al. 1999); it is hard to see how such a system could have evolved in the case of group specific behaviour. Vertical (or oblique within matrilines) cultural transmission is an obviously analogous process to the maternal inheritance of mtDNA, which could easily lead to strong mtDNA-behaviour correlations.

Several species of cetaceans live in stable social groups (Connor et al. 1998); of these the best known is the killer whale, particularly those that live around Vancouver Island. There are at least two different forms of killer whale in this area, which are sympatric but can be distinguished by diet, morphology, behaviour, social structure, and genetics (Baird 2000). Although they are known as *residents* and *transients,* this terminology does not really reflect the habits of the two forms (Baird & Dill 1995). Best known is the fish-feeding, resident, form. Residents live in highly stable matrilineal *pods* averaging 12 animals (Bigg et al. 1990); there is no known case of individuals changing pods in over 21 years of study (Baird 2000). In contrast, transients live in smaller pods, averaging three animals (Baird 2000), which appears to be the more typical case for killer whales worldwide (Boran & Heimlich 1999). Transient killer whales do occasionally leave their natal pods and travel temporarily with other transient groups. The study of this species off Vancouver Island and in other areas has produced evidence for considerable behavioural variation among social groups.

The strongest evidence lies in the vocal dialects of resident pods; each pod has a distinctive set of 7–17 *discrete* calls (Ford 1991; Strager 1995). These dialects are maintained despite extensive associations between pods. Some pods share up to 10 calls (Ford 1991), and pods that share calls can be grouped together in acoustic *clans* (Ford 1991), suggesting another level of population structure. Ford (1991) found four distinct clans within two resident communities, and suggested that the observed pattern of call variation is a result of dialects being passed down through vocal learning and being modified over time. Thus, given the lack of dispersal, acoustic clans may reflect common matrilineal ancestry, and the number of calls any two pods share may reflect their relatedness (Ford 1991). So how reasonable is the assumption of vocal learning in the face of the alternative hypothesis that dialects are genetically based? Although the question has not been directly addressed, there is some evidence that killer whales are capable of vocal learning, (Janik & Slater 1997 and see sect. 4.1). In a fine scale analysis of call variation over time within pods, Deecke (1998) showed that individual call types accumulated modifications over a 12-year period within two pods, and that these modifications did not result in a divergence between the two pods, implying that some mechanism is preventing divergence while modification takes place (the most likely is horizontal cultural transmission); both of these findings are evidence against genetic determination of dialect in killer whales. Finally, for genetic determination of pod-specific dialects when most mating appears to take place between pods (Baird 2000), some highly unusual genetic system without paternal inheritance would be needed (as discussed previously).

Between-pod variation is also evident in other aspects of killer whale behaviour, particularly foraging. Baird and Dill (1995) found strong variation in the use of their study area by transient pods – some pods were seen primarily during the harbour seal (*Phoca vitulina*) pupping period, apparently specialising on foraging around haul-out areas during the pupping season, while others were seen foraging away from haul-outs all year round. There are strong indications that different sympatric resident pods specialise on different salmon species (*Oncorhynchus* spp.), evidenced by correlations in the abundance of different salmon species and killer whale pods at various locations. It has been suggested that accumulated knowledge of salmon distribution results in the traditional use of specific areas by different pods (Nichol & Shackleton 1996). Resident predation on marine mammals is extremely rare compared to transients, but interestingly, of the handful of observations of resident killer whales "harassing" marine mammals, all but one (10/11 combined observations from Osborne [1986] and Ford et al. [1998]) were by a single pod, L01. In a study of Norwegian residents and their interaction with herring (*Clupea harengus*), Similä et al. (1996) reported pod-specific variation in migration patterns as indicated by area use, while Similä and Ugarte (1993) describe a cooperative hunting technique (carousel feeding) not seen in any other killer whale population. The feeding techniques of killer whales are as variable and adaptable as those of the bottlenose dolphin; in addition to the techniques we describe here, they also take a wide variety of other cetaceans (Jefferson et al. 1991), pinnipeds (e.g., Smith et al. 1981), and elasmobranchs (Fertl et al. 1996; Visser 1999), using a range of often complex and cooperative hunting techniques. This variability and adaptability in feeding techniques has also allowed killer whales to take advantage of new anthropogenic food sources as they become available, – for example the discards of trawlers (Couperus 1994). In the Bering Sea, killer whales take fish from long lines (Yano & Dahlheim 1995); of 19 known pods in the Prince William Sound area, only two are known to take fish in this way (Yano & Dahlheim 1995), another example of sympatric behavioural variation.

Other behavioural patterns vary among higher-level groups of killer whales. Off Vancouver Island, there are community-specific "greeting ceremonies" observed when resident pods of one community meet (Osborne 1986); the two pods line up facing each other and stop in formation for 10–30 seconds before approaching and mingling. Some pods of another community engage in "beach-rubbing," and again there is variability between pods in the preferred locations for rubbing (Hoyt 1990). All of this variation should be considered in the context of the markedly low genetic variability within the resident and transient communities (compared to other cetaceans) found by Hoelzel et al. (1998).

Sperm whales make distinctive, stereotyped patterns of 3 to >12 clicks called *codas*, which are thought to function in communication (Watkins & Schevill 1977). Distinctive coda dialects (consisting of very different proportional use of about 30 different types of coda) are a feature of partially matrilineal, but interacting, groups of about 20 female sperm whales (Weilgart & Whitehead 1997). Given the wide-ranging movements of these animals – on the order of 1,000 km (Dufault & Whitehead 1995) – these dialects are effectively sympatric. Among six sperm whale groups, there was a strong and significant correlation between intergroup dialect similarity and the similarity of their mitochondrial DNA (mtDNA) haplotypes – groups with similar coda dialects also had similar mtDNA (Whitehead et al. 1998, and see Fig. 2). The existence of this correlation implies that mitochondrial haplotype and coda dialect are transmitted by analogous processes through the female line and show a similar order of stability. However, it also presents a conundrum as sperm whale groups are not themselves particularly stable, often consisting of two or more largely matrilineal units that swim together for periods of days (Christal 1998; Richard et al. 1996; Whitehead et al. 1992). These social units may themselves split or merge (Christal et al. 1998). How then can the groups possess highly stable dialects? Possible resolutions (Christal 1998; Whitehead 1999a) include the possibility that the coda repertoire of a group is largely determined by its numerically dominant social unit; the fact that the results on non-matrilineality of sperm whale units are based on studies of just a few units in Galápagos and Ecuadorean waters that may have been fragmented by intense whaling from Peru; the transfer of individuals between units may occur within larger, currently unrecognized, cultural trait groups (such as the acoustic clans of killer whales, Ford 1991); transferring individuals may have low reproductive success; and

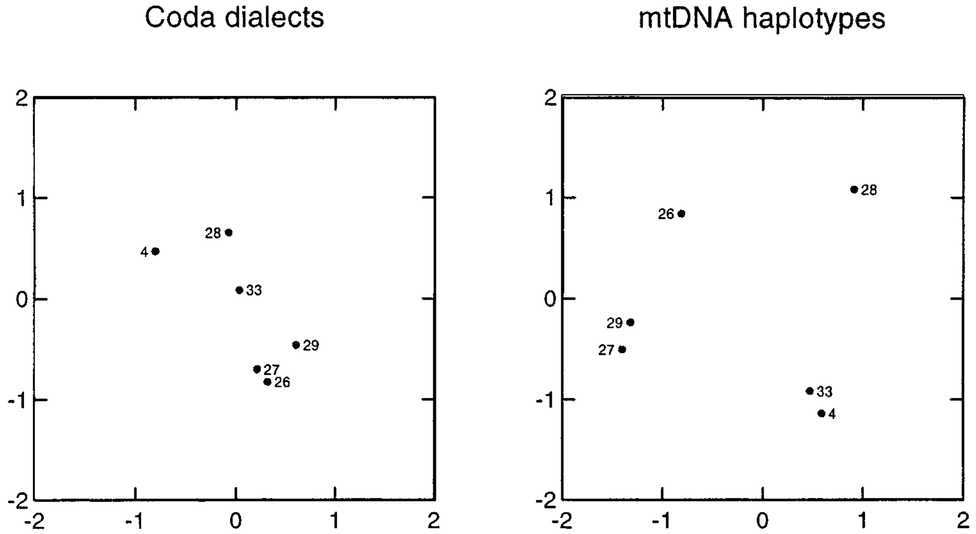

Figure 2. Non-metric multidimensional scaling plots of coda type and mitochondrial DNA dissimilarities for six sperm whale groups; the numbers next to the points indicate group identity in the analysis. The two dissimilarity matrices upon which these plots are based were significantly correlated (Mantel test $p = 0.01$), showing that groups with different mitochondrial DNA also have different coda repertoires. Neither matrix showed any significant correlation with geographic distance (from Whitehead et al. 1998).

conformist traditions maintain cultural stability within groups in situations when groups frequently interact (see next paragraph).

There are also indications of nonvocal group-specific behaviour in sperm whales. Group identity accounted for an estimated 40% or more of the variance in 6/18 measures of the visually observable behaviour of sperm whales off the Galápagos Islands when environmental and temporal variation had been considered (Whitehead 1999b). These measures were mostly (5 out of 6) concerned with how the groups used space: heading consistency, interanimal distance, and straight-line distance moved in daylight. The results of this study should be interpreted cautiously for a number of reasons (Whitehead 1999b). For instance, in only one measure (straight-line distance moved in 12 hours) was the group-specific effect statistically significant at $P < 0.05$ following corrections for multiple comparisons, although statistical tests for group-specific effects had little power (group identity had to account for $>\sim 65\%$ of the variance in a measure to produce a significant effect at $P < 0.05$).

In a study spanning the South Pacific, there were significant differences in the number of predator-inflicted marks on the tails of sperm whales between matrilineal groups (Dufault & Whitehead 1998). As with coda repertoire, the marks possessed by a group were correlated with the group's predominant mitochondrial haplotype (Whitehead et al. 1998). One explanation for this surprising result is that, like coda repertoire, methods of communal defence against predators are passed down culturally in parallel with the mitochondrial genome (Whitehead et al. 1998): Sperm whale groups have been observed to defend themselves against killer whale attack in some instances by forming a tight rank and keeping their heads and jaws toward the killers (e.g., Arnbom et al. 1987), and in others by putting their heads together and allowing their bodies to radiate outward in a wagon-wheel formation so that their tails face the predators (e.g., Pitman & Chivers 1999) – although there is no data available on whether groups consistently use one or other strategy. Groups adopting the wagon-wheel formation would tend to accumulate tail markings much more readily than those that defended with their jaws.

In addition to these group-specific patterns of killer and sperm whales, there are some local behavioural patterns of cetaceans that do not live in such stable groups. Bottlenose dolphins at Laguna off the coast of Brazil have an unusual group-specific feeding technique which seems to date from 1847 and have been transmitted within a matrilineal community since at least three generations of dolphin are involved (Pryor et al. 1990). The 25–30 dolphins and local fishers follow a strict protocol – involving no training or commands from the fishermen – that allows the humans and dolphins to coordinate their actions. The dolphins drive fish into the nets of human fishermen, indicating as they do so by performing a distinctive rolling dive when the humans should cast their nets. The humans can also pick up from how much of the body comes out of the water on this roll an idea of how many fish are present – it is entirely unclear whether this cue is given intentionally or not – and then feed off the fish that are stunned or missed by the net (Pryor et al. 1990). There are other bottlenose dolphins in the area that do not participate in the cooperative fishing and sometimes try to disrupt it (Pryor et al. 1990); hence, again, behavioural variation is sympatric. Only young adults whose mothers took part in the fishing later adopted it themselves, although not all the offspring of fishing mothers did so (Pryor et al. 1990). There are several other accounts of such cooperative fishing on different continents (Pryor et al. 1990). For example, Irrawaddy dolphins (*Orcaella brevirostris*) in the Ayeyarwady River, Myanmar, have a similar, generations-old, cooperative relationship with local fishers (Anderson 1879; Smith et al. 1997).

Group-specific, culturally transmitted behavioural patterns have parallels in other animal taxa, but in some respects these cetacean cultures, in particular those of the killer whale, appear unique outside humans. Within a number of primate species, including macaques and chimpanzees, bands have characteristic cultures, which include diet, familiarity with a home range, social signals, relationships, and, in the case of chimpanzees, tool use (Russell & Russell 1990; Whiten et al. 1999). Similarly, populations of birds of a single species sing different dialects of the species-specific song (Baker & Cunningham 1985). However, these dialects and cultures are geographically based: Animals in one place behave in one way, and those in another behave differently. In contrast, different cultural variants of killer and sperm whales, as well as the cooperative fishing traditions of bottlenose dolphins, are sympatric, and animals with different cultures often interact. Thus, members of these species are repeatedly exposed to a wide range of cultural variations but maintain their own group-specific culture. Somewhat similar phenomena have been observed in the flock-specific calls of some birds (e.g., Feekes 1982; Mammen & Nowicki 1981). However, these flocks are not stable for more than a few months and hence do not support persistent cultures. Greater spear-nosed bats (*Phyllostomus hastatus*) modify their screech calls to establish and maintain differences between stable social groups that share caves (Boughman & Wilkinson 1998), hence demonstrating sympatric cultural variation. However, this variation is based only on modifications of a single call and so does not approach the complexity of group-specific behaviour seen in killer whales. Another contrast is that the behavioural complexes seen in killer whales appear to encompass both vocal *and* physical behaviours; such complex multicultural societies where culture encompasses both the vocal and motor domains are otherwise known only from humans. However, it should be noted that in no cetacean example is there evidence of such broad suites of cultural behaviours as have been found in chimpanzees, where 39 behaviour patterns have been shown to vary culturally (Whiten et al. 1999).

A second remarkable attribute of some of the group-specific cultural traits of cetaceans is in their stability. Killer whale dialects are highly stable, known to persist for at least six generations, and it has been suggested, much longer (Ford 1991). To give rise to the strong dialect – mtDNA correlations that seem to be present in sperm whales – vocal culture must be stable over many generations (Whitehead 1998). Such stability is not a feature, as far as is known, of comparable cultures outside humans (Feldman & Laland 1996). Some songbird dialects last over 10 years, but these are apparently not related to stable social groups (e.g., Trainer 1985).

4. Cetacean culture: Transmission processes

What kinds of social learning are cetaceans capable of? Some scientists (e.g., Galef 1992; Tomasello 1994) will only admit culture when it can be shown that behavioural patterns are being transmitted between animals by either imitation or teaching, and not by other types of social learning such as stimulus enhancement (in which individual learning is enhanced when one animal directs the attention of another toward a stimulus). While we do not subscribe to this particular view, we do think that understanding process (cultural transmission) is crucial to our understanding of the product (culture) – for example, some forms of cultural transmission may be more likely to produce cultures capable of feeding on themselves, producing the "ratchet effect" (Tomasello 1994) – and so it is appropriate to ask whether cetaceans are capable of higher-order social learning such as imitation or teaching.

In the wild, cetaceans are mostly underwater and out of view, while only the smaller species, such as bottlenose dolphins, can be kept in captivity for more than a short period. Even then, the social and ecological environment of the captives is far from natural. Therefore, there is little concrete evidence for imitation or teaching by cetaceans. For instance, it has not been experimentally proven that maturing killer whales learn their group-specific call dialects (Tyack & Sayigh 1997); only cross-fostering experiments could establish this, and given the expense and difficulty of raising killer whales in captivity even without cross-fostering, these experiments are not likely to be performed, regardless of the ethical issues involved. We are also limited by the fact that the vast majority of experimental work has been performed on a single species – the bottlenose dolphin. Despite these substantial difficulties, there is some good evidence that cetaceans can imitate and teach.

4.1. Imitation in cetaceans

Bain (1986) describes a captive killer whale from Iceland learning, over a three-year period, the vocal repertoire of its tank-mate from British Columbia, while Ford (1991) presents evidence for interpod call mimicry in the wild – both suggesting that killer whales are capable of vocal learning. Bowles et al. (1988) followed the ontogeny of vocal behaviour in a single captive killer whale. During the study, the calf was housed with its mother, another female companion, and a young male; the calf never had any contact with its father. By 398 days, the calf's output was dominated (90% of output) by the one call type that distinguished its mother's repertoire from that of the female companion (the two adult females shared other call types), even though 82% of all the calls recorded from the tank were not of that type. Bowles et al. (1988) suggest that this is due to selective learning by the calf. However, they recognise that their study cannot exclude genetic effects, although there was no trace of the father's dialect in the calf's repertoire, hence no evidence for the hybrid dialect expected under genetic determination. When viewed as a whole, the combined evidence clearly points to imitation as the transmission mechanism of vocal repertoire. Hence, it seems very likely that killer whale call dialects are, as Ford (1991) suggests, cultural institutions, even from the perspective of those who believe cultural transmission should be restricted to teaching and imitation.

There is less direct evidence for social learning in the other good example of group-specific cetacean dialects, the sperm whale coda repertoire. However, in the remarkable *echocodas,* two animals precisely interleave their click patterns, giving rise to two overlapping codas, identical in temporal pattern to within a few milliseconds, offset by about 50–100 msec (Weilgart 1990). This duetting suggests that sperm whales may be matching codas in a similar way to bottlenose dolphins matching signature whistles (see Tyack 1986b); such matching would require imitative learning in some form.

Experimental work on the learning abilities of cetaceans has been largely confined to a single species, the bottlenose dolphin, mainly because this species makes up the vast majority of the captive population. A number of studies have shown that this species is clearly capable of vocal and motor imitation (Bauer & Johnson 1994; Kuczaj et al. 1998; Richards 1986; Richards et al. 1984). Anecdotal examples include the imitation of the movements and postures of a pinniped by a dolphin sharing the same tank described by Tayler and Saayman (1973). Imitative abilities include *simple* imitation, called "action level imitation" in the terminology of Byrne and Russon (1998) and "copying" in Heyes (1994), and *true* imitation, called "goal emulation" in Whiten and Ham (1992) and "program level imitation" in Byrne and Russon (1998). An example of the former is the imitation of motor patterns (for example, shaking the head from side to side) described by Bauer and Johnson (1994); of the latter, the imitation of functional tool use described in Kuczaj et al. (1998). Such examples are deserving of more recognition than they have previously been given in discussions of animal imitation; evidence for imitation in dolphins is a consistent "thorn in the side" (Byrne & Russon 1998) of those who deny imitation in nonhumans (e.g., Galef 1992; Tomasello 1994). The grey parrot (*Psittacus erithacus*) rivals the bottlenose dolphin in social learning ability, being capable of both vocal and movement imitation (see Moore 1992; 1996); however, it has yet to be shown whether parrots are capable of program level imitation. Thus, to our knowledge, bottlenose dolphins are the only nonhuman animal for which *both* vocal imitation, *and* motor imitation at both action and program level, have so far been demonstrated (Herman 1986; Kuczaj et al. 1998).

4.2. Observations of teaching in killer whales

Killer whales in the Crozet Islands and off Punta Norte, Argentina, swim ashore to capture pinnipeds (Guinet 1991; Guinet & Bouvier 1995; Hoelzel 1991; Lopez & Lopez 1985). In the clearest descriptions of the social learning process in wild cetaceans, Guinet and Bouvier (1995) describe young killer whales learning from their mothers, and sometimes other animals, the feeding technique of intentional stranding on pinniped breeding beaches. This method of feeding is profitable but risky; one of the calves in Guinet and Bouvier's (1995) study was found permanently stranded and facing death until observers returned it to the water. As the behaviour of adult killer whales towards juveniles during intentional stranding appears to (unusually for nonhumans) fit definitions of teaching (Baird 2000; Boran & Heimlich 1999), the details bear repeating here. We take Caro and Hauser's (1992) definition of teaching as modifying behaviour at some cost or lack of benefit only in the presence of a naïve observer such as to encourage, punish, provide experience, or set an example, such that the observer acquires a skill more rapidly than it might do otherwise, or may not ever learn. While Caro and Hauser (1992) considered the evidence for teaching in killer whales weak, this was before the publication of Guinet and Bouvier's (1995) study. The evidence now is considerably stronger, although it is based on observations of only two calves, so we are unaware of how widespread the process may be.

Adult killer whales have been observed pushing their young up the beach, then back down the beach, directing them toward prey, helping them out when they become stuck by creating wash, helping them back to deep water after a successful capture (Guinet & Bouvier 1995), and throwing prey at juveniles (Lopez & Lopez 1985) – hence they modify their behaviour in the presence of naïve observers. Adults are more successful at hunting in the absence of juveniles (Hoelzel 1991); at the extreme, they throw away already captured prey (Lopez & Lopez 1985) – hence there is a demonstrable cost. Pushing juveniles onto beaches and pushing them toward prey is clearly encouragement. As to whether observers learn better with or without instruction, consider Guinet (1991) and Guinet and Bouvier's (1995) studies in the Crozet Islands. They followed the development of hunting by intentional stranding in two killer whale calves, A4 and A5. At the start of the study, the calves estimated ages were 4 and 3, respectively, and they were observed taking part in *beaching play* (stranding, with their mothers and/or other adults, on beaches devoid of elephant seal, *Mirounga leonina,* prey); occasionally they would also strand during predation attempts by adults. Both calves were observed to strand alone for the first time at age 5. Near the end of the three-year study calf A5, then aged 6, was observed successfully catching a seal pup. A4, although a year older, had not been observed hunting successfully by the end of the study. This difference between the calves is very interesting; during beaching play, A5 stranded exclusively with its mother, while A4 stranded only twice in 35 observations with its mother (Table 2). A4's mother rarely took part in beaching play, and was not observed hunting in this way. In contrast, A5's mother closely supervised its strandings. The mother was observed pushing the calf up the beach and stranding onshore in order to push the calf back into the water, accompanying the calf on unsuccessful hunting attempts and finally assisting in the first successful capture by pushing the calf toward the prey and helping the calf to return to the water following capture. Hence, the behaviour of A5's mother seems to have enabled her calf to learn the hunting technique at least one year earlier (aged 6) than A4, who received very little "instruction," so the behaviour apparently results in a skill being learned more rapidly than it otherwise would. It is not known whether A4 ever learned to hunt successfully this way; interestingly, A4 was the previously mentioned calf found permanently stranded and facing death, suggesting a severe fitness cost for mothers who do not give their calves much attention. Clearly, according to accepted definitions, killer whales teach. Caro and Hauser (1992) point out the rarity of such overt encouragement in other animals.

5. The question of cetacean culture

Does the evidence we present here legitimately allow us to attribute culture to cetaceans? We recognise that how one defines culture will inevitably affect how one attributes it, and we also recognise that we have chosen a broad definition of culture. However, we think there are good reasons for choosing such a definition, which we will attempt to explain here.

From our evolutionary perspective, the important questions surrounding culture in humans and animals concern how cultural faculties and the behavioural complexes to which they give rise (which we would call cultures by our definition) vary in extent and form within and across species, and how this may be related to evolutionary ecology. Along with Mundinger (1980), we find that there is no "empirical evidence for any qualitative difference that would support a basic human/nonhuman dichotomy." Many social learning processes apparently play an important role in supporting human culture (Boesch 1996; Midford 1993; Olsen & Astington 1993; Plotkin 1996; Rogoff et al. 1993), but there are also animals, including bottlenose dolphins, that are capable of sophisticated social learning, in particular imitation. Hence, we cannot support any definition that renders culture *by definition* as something only humans can have. Surveying cultural transmission in nature, one finds what approaches a continuum among animals that acquire only a single behavioural pattern culturally (e.g., bluehead wrasse, *Thalassoma bifasciatum,* mating sites, Warner 1988), through animals that acquire suites of behaviours by cultural processes (including chimpanzees and, data strongly suggest, killer whales), to humans where culture has enabled us to radically alter our own environment. Given this continuum, it seems to us that the question of culture is more likely a question of extent: Just how much of the behavioural repertoire must be culturally determined before a population can be said to show *culture*? We would maintain that drawing a line on this continuum and labeling one side *culture* and the other *not culture* is essentially an arbitrary exercise, leading to the current variability in attributions of culture to nonhumans. Instead, we adopted a definition that has allowed significant progress to be made in developing a theoretical basis for understanding culture and is not tied to any particular species or any particular form of culture. Such a broad definition allows us to concentrate on comparing cultures across species, and relating these comparisons to ecology.

We have rejected an exclusively process-centred definition of culture. Such a stance contains a number of serious weaknesses. Culture has been incorporated into theoretical models in a way that is essentially process independent. Though, the transmission process will affect the parameters of cultural evolution (for example the speed of acquisition of a novel trait, or the stability of resultant traditions) as long as information is transferred between individuals extragenetically, then, it does not affect the basic coevolutionary process. To define culture in terms of the transmission mechanisms upon which human cultures depend (see Tomasello et al. 1993) is from an evolutionary perspective counterproductive and anthropocentric (de Waal 1999). We concur with Plotkin's (1996) assertion that "dual inheritance can be, and almost certainly is, served by more than one form of social learning"; Whiten and Ham (1992) explicitly list a range of social learning processes from exposure to goal emulation as supporting cultural transmission. Human cultures depend on human cultural learning; teaching and imitation may be unique to humans (although there is good and growing evidence that it is not, and cetaceans are a group that has given rise to some of the strongest evidence, as presented here), and hence culture as a human trait has unique properties, the material evidence of which surrounds us. However, to then define culture as a general trait in terms of human transmission processes is, in our view, a mistake; it is akin to defining locomotion as a general trait in terms of walking on two legs; this is how humans move, but other animals achieve the same effect (moving from A to B) with a huge variety of different locomotion processes, some of which are energetically more efficient, or quieter, or faster than others (de Waal 1999 independently gives a similar argument). Clearly it is wrong to say that animals do not show locomotion if they do not move using a bipedal gait; in our view it is equally wrong to say that animals showing stable behavioural variation independent of ecology and genetics and transmitted through social learning do not show culture if that behavioural variation is not transmitted using teaching or imitation. We cannot agree with Tomasello's (1994) argument that since "behavioral traditions of humans provide the prototypical case of cultural transmission" (p. 302), then human culture should be the benchmark against which all else is compared. Instead, we concur with Boesch (1996) that "it seems rather arbitrary to single out one process of information transmission as the only one able to produce culture" (p. 258).

We see other weaknesses in the process-centred definition. Concentrating on process reduces the issue of culture to a question of whether or not a species can imitate or teach in an experimental setting, as opposed to other social learning mechanisms, such as stimulus enhancement. However, there is much conceptual confusion surrounding imitative and nonimitative social learning; it is not clear how the bewildering taxonomy of terms (e.g., Galef 1988) for various social learning mechanisms relate to each other, nor that the underlying conceptual approach is really satisfactory – many of the categories are based on unobservable and ill-defined mechanisms, are not mutually exclusive, and give little or no information regarding conditions for occurrence or functional significance (see Heyes 1994). The "cross-talk and confusion" (Heyes 1996) surrounding the taxonomy of social learning processes, up to and including various forms of imitation, weakens the process-centred approach to culture; the different approaches of Heyes (1994), Zentall (1996), Tomasello et al. (1993), and Byrne and Russon (1998) have yet to be resolved into a coherent understanding of social learning. This becomes serious if, as tends to occur, observational learning (and hence culture) is rejected as an explanation for field observations until and unless all other social learning mechanisms are experimentally excluded (Boyd & Richerson 1996); we do not accept this to be a really sound approach, given the lack of consensus surrounding social learning. Moreover, the implicit assumption that behaviour is culturally acquired in humans and that it *is not* in nonhumans (McGrew 1992, pp. 14, 197, 217) leads to different null hypotheses for considering culture in humans and animals; the apparent lack of culture in animals may be due more to the placement of the burden of proof than anything else, leading to the criticism that "a double-standard is being applied" in this human-centred approach (Boyd & Richerson 1996), and a heuristic weakness has led this approach "down paths of steadily decreasing interest to the rest of the community of life scientists" (Galef 1992, p. 158).

Until and unless cetacean traditions are proven experimentally to rely on teaching or imitation, those who restrict culture to imitation and teaching will deny culture to these animals. The final weakness of such an approach is that the necessary experiments will likely *never* be performed given the expense and difficulty of keeping, let alone raising, most cetaceans in conditions that are both sufficiently controlled for valid experiments and sufficiently naturalistic so that the animals may show realistic social behaviour. For instance, social groups of sperm whales will never be kept in captivity; the logistics are simply not feasible. Ethnographic data and field observations are all that are, and likely ever will be, available for such species. Here is the central problem with an experimental approach to cetacean culture: It can freeze the question by demanding that which will never occur (i.e., experimental studies). In our view, it is not reasonable to postpone discussion on this semipermanent basis, because other rigorous and conceptually sound approaches are available. This is not to say that the study of social learning mechanisms is not important – as we have already stated. Human culture shows extraordinary characteristics when compared with animal culture, in particular, concerning its linguistic, material, and symbolic extent, and it is likely that the mechanisms by which it is propagated contribute to this uniqueness. For example, accumulating modifications over time, the so-called ratchet effect (Tomasello 1994) may be greatly facilitated by enhanced observational learning abilities in humans (Boyd & Richerson 1995; 1996; Henrich & Boyd 1998).

The field-based approach to culture is exemplified by Boesch et al.'s (1994) and Whiten et al.'s (1999) work on chimpanzee culture, Grant and Grant's (1996) work on Darwin's finches and Warner's (1988) work on bluehead wrasse. The approach is clear; systematic field observation (and manipulation of natural populations in Warner 1988) enables the elimination of ecological and genetic factors potentially causing behavioural variation; what is left must be cultural. The resulting conclusions are weak in that the transmission process remains unproven but strong in that they are firmly rooted in how the animals actually behave in the wild. Since cultural learning is *social* learning, we can only fully appreciate its complexity and functional usage in animals when it is studied in a naturalistic *social* setting. The cultural hypothesis is strengthened if the behaviour under scrutiny varies nonadaptively or arbitrarily (Boesch 1996) since both ecological and genetic factors are more likely to produce adaptive variation, whereas culture can produce maladaptive behaviours (Boyd & Richerson 1985) or influence otherwise selectively neutral variation in behaviour (e.g., bird song, Baker & Cunningham 1985).

This ethnographic perspective heavily influences our approach to culture. Our review suggests that at least some cetaceans are adept social learners (see also Boran & Heimlich 1999). It seems to us most likely that these abilities, and not genetic or environmental causation, have given rise to the conspicuous patterns of rapid-spread, mother-offspring similarity, and group-specific behaviour listed in Table 2. In a few cases, such as sponge feeding and the use of human provisioning by bottlenose dolphins, it is possible to envisage scenarios of environmental change and individual learning giving rise to the observed patterns. However, the continuously evolving songs of humpback and bowhead whales have no conceivable environmental or genetic cause, and if the characteristic dialects and behaviour of the matrilineal groups of killer and sperm whales were genetically determined, there would have to be little or no pater-

Table 2. *Numbers of self-strandings observed and the percentage in which the mother was present for two killer whale calves (data from Guinet & Bouvier 1995)*

Calf		Year 1988	1989	1990	1991
A4	Estimated age (yrs)	4	5	6	7
	No. self-strandings	6	23	0	6
	% with mother	**0**	**4.3**	—	**16.7**
A5	Estimated age (yrs)	3	4	5	6[1]
	No. self-strandings	1	20	12	20
	% with mother	**100**	**100**	**100**	**100**

[1] The only successful capture by a calf during the study was by A5 in 1991.

nal inheritance, a highly unusual process. Thus, from the ethnographic perspective, we believe that most, if not all, of the patterns listed in Table 3 can be ascribed to cultural transmission.

In the case of the killer whale, there are strong indications that groups possess suites of distinctive, interlocking cultural characteristics, so far described only for humans and chimpanzees (Whiten et al. 1999). However, one obvious difference between these cultures is that there is no evidence at all for preservable material culture in cetaceans compared to both humans and chimpanzees (cf. McGrew 1992). Human culture is intimately linked to both language and symbolism, but there is currently no empirical basis for discussing the role or nonrole of language and symbolism in cetacean culture – bottlenose dolphins have been taught artificial "languages" (e.g., Herman et al. 1993), but such work tells us little about the role of communication in the natural situation (Tyack 1993). Cetacean cultures do appear to possess attributes that have otherwise been restricted to humans. In particular, we are aware of no phenomena outside humans comparable to the distinctive, stable, and sympatric vocal and behavioural cultures that appear to exist at several levels of killer whale society.

6. The evolution of cetacean culture

Some cetaceans, then, seem to have evolved cultures that closely parallel those found in chimpanzees and humans. What is perhaps surprising is that all four of the best studied cetacean species show strong evidence, from either the experimental or ethnographic approach, for social learning. Why? It is true that they possess those biological attributes that Roper (1986) suggests favour social learning: long lifetimes (~20–90 years), advanced cognitive abilities, and prolonged parental care (Herman et al. 1994; Marten & Psarakos 1995; Tyack 1986a). However, while there probably is a minimum cognitive capability required for social learning, the relative success of those individuals within a given species that are better than average at social learning likely depends ultimately on the ecological situation in which those individuals must make a living. Thus it is more important to look to ecology when attempting to explain species differences in social learning (Lefebvre & Palameta 1988). We think that ecological factors may have a strong role to play in explaining the social learning abilities and culture to which they give rise in cetaceans. Whitehead (1998) suggests that the structure of the marine environment may have favoured the evolution of cultural transmission in cetaceans. Here we explore this suggestion in more detail.

Compared with life on land, marine ecosystems are more likely to switch into alternate states over time scales of months or longer (Steele 1985). This increased low-frequency temporal variability of marine systems may significantly increase the adaptiveness of culture to cetaceans, as the benefits of cultural transmission, relative to individual learning or genetic determination, are thought to be strongly related to environmental variability (Boyd & Richerson 1985; 1988; Laland et al. 1996). The scale of spatial variation may also be important; spatial autocorrelation in oceanic ecosystems weakens at ranges of about 500 km (Myers et al. 1997), so that one way to deal with radical changes in the environment in any place is to move a few hundred kilometres. Many marine organisms are adapted to particular environments in which they can flourish, but also have long-range dispersal of large numbers of eggs, larvae, or juveniles, which allow them to colonize suitable distant ocean areas and so to persist when conditions deteriorate in any one place (Steele 1985). Long-lived marine animals with low reproductive rates similarly can use migration to avoid unfavourable conditions (Whitehead 1996). Compared to terrestrial mammals, but not birds, cetaceans have the advantage of much lower travel costs (Williams et al. 1992), and few substantial barriers. Many oceanic cetaceans do appear to use movement over hundreds of kilometres to improve environmental conditions (e.g., Whitehead 1996). For instance, the mean monthly displacement of a female South Pacific sperm whale – ~350 km – is roughly 10 times that of members of a particularly mobile population of a particularly mobile terrestrial mammal, the African elephant, *Loxodonta africana* (Thouless 1995; Whitehead, in press). The efficiency of these movements could be greatly enhanced by cultural transmission of desirable movement strategies vertically from mother to offspring, horizontally among animals in the same region, or, perhaps especially, between generations within stable groups (Whitehead 1996). Moreover, if the primary benefits of culture accrue from accelerated adaptation to changing circumstances or more rapid expansion into new niches relative to individual learning or genetic change (Boesch 1996; Boyd & Richerson 1996), then these benefits will be accentuated in environments that are more variable, and also in which movement into new habitats is likely or easy, conditions that are both true for cetaceans. For example, chimpanzees live in quite stable ecological situations and have a limited migratory potential, and hence the adaptive advantage of culture may not have been as strong as in nomadic hominids (Boesch 1996); perhaps also this is why the evolution of culture seems to have progressed further in some directions among cetaceans than in nonhuman primates.

Extensive mobility, while often primarily a function of the need to reduce variation in one key environmental variable (usually food intake, availability of water, or temperature), tends to increase variance in other aspects of an animal's environment, including its social environment. Tyack and Sayigh (1997) argue that the relatively greater mobility of cetaceans may be one reason why they show extensive capabilities for vocal flexibility and vocal learning, while terrestrial mammals do not. Consider group-living species:

Table 3. *Ethnographic patterns suggesting cetacean culture*

		Causation:		
Species	Phenomenon	Ecological?	Genetic?	Common
Humpback whale	Songs	No	No	Continuously evolving in large and dispersed population
	Lobtail feeding,	Unlikely	No	Rapid spread through population
	migration	No	Unlikely[1]	Calf repeats mother's migration
Bowhead whale	Songs	No	No	Continuously evolving; some evidence for imitation
Beluga whale	Migration	No	Unlikely[1]	Calf repeats mother's migration
Bottlenose dolphin	Sponging	Unlikely	Unlikely	A few animals in one study site, seem to be passed from mother to female offspring
	Use of human provisioning,	?	Unlikely	Recent phenomenon in one site
	human-dolphin fishing cooperative	Unlikely	No	Complex coordinated behaviour pattern of both species has persisted for generations
Killer whale	Intentional stranding,	Unlikely	Unlikely	Teaching process described
	resident call dialects	No	Unlikely[1]	Sympatric dialects are quite stable but show small coordinated changes
	Pod-specific foraging specializations,	No	Unlikely[1]	Consistent specializations of both resident and transient pods, sometimes sympatric
	pod-specific migration patterns,	No	Unlikely[1]	Sympatric
	community-specific greeting ceremonies	Unlikely	Unlikely	Not sympatric
Sperm whale	Group-specific coda repertoires,	No	Unlikely[1]	Sympatric, partially matrilineal groups have stable dialects
	group-specific movement patterns	Unlikely	Unlikely[1]	Sympatric groups show evidence of characteristic movement patterns
	Group-specific communal defence methods	?	Unlikely[1]	Indirect evidence
Irrawaddy dolphin	Human-dolphin fishing cooperative	Unlikely	Unlikely	Complex coordinated behaviour pattern of both species has persisted for many generations

[1] For these patterns to be genetically determined the inheritiance would have to be entirely or principally from the mother; as discussed in the text, this is unlikely.

There are substantial advantages for individual cetaceans living in groups, be it through cooperative foraging (Similä & Ugarte 1993), food sharing (Hoelzel 1991), or communal defence (Arnbom et al. 1987), but there is also the risk of sharing food with, or being injured in defending, individuals who are not members of the same group and hence are unlikely to reciprocate. Group signatures are one way to minimize this risk. However, as Tyack and Sayigh (1997) point out, when highly mobile animals regularly interact with conspecifics of different groups, signature systems need to be flexible and sophisticated, a demand that culturally transmitted dialects meet.

We can envision an evolutionary trajectory for cetacean cultural learning abilities similar to that proposed for psittacine birds by Moore (1992; 1996) of call learning being generalised to vocal mimicry through to more generalised imitative capabilities – although it must always be recognised that we know virtually nothing about the actual learning mechanisms cetaceans employ. Three of the four species we primarily discuss here are known or very likely to be vocal learners: the bottlenose dolphin, killer whale, and humpback whale. For sperm whales, the learning of codas, since it does not involve learning a new sound, only a pattern of known sounds (clicks), may involve contextual rather than strictly vocal learning (see Janik & Slater 1997). In addition, the link from vocal to motor mimicry through percussive behaviour proposed by Moore (1992; 1996) for birds may also be present in cetaceans – almost all species perform behaviour that involves striking the water surface (lobtailing, flipper slapping) and it is thought that these may sometimes function as acoustic signals (e.g., Norris et al. 1994). So the mobility of cetaceans may have created selection for vocal learning, providing the roots of sophisticated social learning, while the spatial and temporal variability of the marine environment made social learning highly adaptive as a cost-reducing adjunct to individual learning about new niches (see Boyd & Richerson 1995). In long-lived animals that form stable social groups, the opportunities for cultural transmission are greatly increased, and if most other group members are kin, such information exchange would also accrue inclusive fitness benefits – leading, perhaps, to the remarkable cultures of killer whales.

For the dialect-gene and dialect-ancestry correlations that seem to be present in sperm and killer whales, cultural transmission must be very stable, with cultural traits being passed consistently within matrilines, but very rarely between them (Whitehead 1998). How can this occur when cetacean matrilineal groups frequently meet, interact, and, in the case of sperm and transient killer whales, occasionally receive new members (Baird 2000; Christal et al. 1998; Connor et al. 1998b)? Conformist traditions within groups seem to be a vital element of human cultural evolution (Boyd & Richerson 1985); we actively adopt the prevalent cultures of the groups we are members of. Conformity is clearly advantageous to the group as a whole, and thus its members, when the culture refers to coordinated behaviour, such as communal foraging or within-group communication, and can lead to highly stable cultures (Cavalli-Sforza & Feldman 1981). One of the mechanisms with which cultural information could be secured is through *social norms* (Boesch 1996; Heyes 1993); this idea equates to Boyd and Richerson's (1985) *conformist transmission.* When group-specific behaviour is generally favoured, then conformist cultural markers of group membership may evolve, reinforcing the conformist transmission of other cultural elements (Richerson & Boyd 1998). Recent theoretical work points to the widespread conditions favouring conformist transmission and suggests a synergistic relationship between the evolution of imitation and conformism (Richerson & Boyd 1998); such an interaction could well have occurred, or be occurring, in killer and sperm whales.

7. The effects of culture: gene-culture coevolution and nonadaptive behaviour

The two features in which killer and probably sperm whale cultures seem to differ from those of virtually all other nonhuman animals, stability and multiculturalism, are prerequisites for cultural processes to have much effect on genetic evolution. To affect genetic evolution, cultures must usually be stable over many generations (Laland 1992), and if cultural variants rarely interact, they will generally have only local effects (Whitehead 1998). There have been two suggestions that substantial gene-culture coevolution has occurred in whales and dolphins; since both involve historical explanation, neither can be empirically proven. However, this is no different from posited cases of gene-culture coevolution in humans (Feldman & Laland 1996). Both Baird (2000) and Boran and Heimlich (1999) propose that culturally transmitted group-specific foraging techniques initiated the divergence of the forms of killer whale, which now show genetic and morphological differences, and may well be in the process of speciation given the apparent reproductive isolation of the two forms (Baird et al. 1992). This is a plausible explanation for the ongoing sympatric speciation; however, since the genetic differences between the two forms are now so evident (Hoelzel et al. 1998), it cannot be proven that culture was responsible for the divergence.

Mitochondrial DNA diversity in four matrilineal whale species (killer whales, sperm whales, and the two pilot whale species, *Globicephala* spp.) is about fivefold lower than it is in most other cetacean species (Whitehead 1998). Whitehead (1998) suggests that this may have occurred by means of "cultural hitchhiking" in which selectively advantageous and matrilineally transmitted cultural variants sweep through a population, incidentally reducing the diversity of analogously transmitted mitochondrial DNA. Such a process is theoretically analagous to molecular hitchhiking in which diversity in a neutral locus is reduced by selection at a linked, nonneutral locus (Kaplan et al. 1989). In the cultural hitchhiking proposed by Whitehead (1998), the non-neutral locus is a cultural trait, transmitted matrilineally between generations; selection is in the form of greater reproduction or survival for animals with certain cultural variants. Since mtDNA is also transmitted matrilineally between generations, alleles at neutral mtDNA loci will track the spread of ("hitchhike on") successful cultural traits – as successful traits spread in the population, the mtDNA alleles associated with that matriline will also spread, giving rise to the reduced mtDNA diversity now observed in the matrilineal odontocetes. Other theoretically tenable explanations for the low mtDNA diversity of the matrilineal odontocetes are population bottlenecks (Lyrholm & Gyllensten 1998), group-specific population dynamics (Amos 1999; Siemann 1994), or group-specific environments (Tiedemann & Milinkovitch 1999). However, all of these alternative explanations make assumptions or predictions that do not seem to be consistent with what we know of the biology of the matrilineal whales (Whitehead 1998; 1999a).

Conformist traditions can lead to cultural group selection (Boyd & Richerson 1985). Group conformity increases both homogeneity within groups and heterogeneity among groups and thus elevates variation in behavioural phenotype to the group level (Boyd & Richerson 1985; Richerson & Boyd 1998); hence we would expect selection on behavioural phenotype to act at this level. For species that forage cooperatively, particularly within kin-based groups (e.g., killer whales), competition for resources may occur largely between rather than within groups, which would significantly increase the adaptive value of conformist traditions, reinforcing the whole system. Similarly, predator-prey arms races can be a potent driver of both genetic evolution (Dawkins & Krebs 1979) and, as is very apparent in human history, cultural evolution. For most whales and dolphins, the most formidable and important natural predator is another cetacean, the killer whale (Jefferson et al. 1991), and the predatory techniques of killer whales appear to be largely determined by cultural processes. Thus, it is possible to envisage cultural arms races between killer whales and their cetacean prey.

Theoretical studies also suggest that during the evolution of group-specific cultures behaviour that is not adaptive can easily arise (Boyd & Richerson 1985). There is one behavioural pattern seen in group-living cetaceans that is individually maladaptive but could have arisen within a system of conformist traditions: mass stranding. Cetaceans of several species fatally strand en masse. In contrast to individual strandings, most of the animals involved in these mass strandings appear healthy, but when individually pulled back to sea, turn around and restrand (Sergeant 1982). A simple, genetically mediated, aggregation response is unlikely to produce such behaviour as it is so individually maladaptive. This phenomenon is seen as indicative of extreme social cohesion in the species that mass strand (Norris & Schilt 1988), with the usually adaptive strategy of remaining with the group proving fatal when one member makes a mistake or becomes debilitated through disease. There is evidence from pilot whale strandings that larger (presumably older) animals have a strong influence on the behaviour of the group (Fehring & Wells 1976). We suggest that cultural group conformity in movement strategies may play an important role in mass strandings; such phenomena might then be an example of the maladaptive effects of conformist cultures.

Culture may also have had effects on the evolution of life history. Menopause is known in killer and short-finned pilot whales (*Globicephala macrorhynchus*), and there are indications of its occurrence in other cetacean species (Marsh & Kasuya 1986; Olesiuk et al. 1990). Like humans, and unlike any other mammal, female killer and short-finned pilot whales may live decades after the birth of their last offspring (Table 4). Within-group cultural processes may have played a part in this phenomenon, if, for instance, the role of older females in cultural transmission is very important. Menopause could be highly adaptive if the role of older females as a source of information significantly increases the fitness of her descendants, and reproduction toward the end of her life decreases survival (Boran & Heimlich 1999; see also Norris & Pryor 1991). Guinet and Bouvier (1995) note that the juvenile killer whales they observed learning the difficult and dangerous technique of self-stranding in order to catch pinnipeds spent at least six years closely associated with their mothers; one calf was not observed to capture prey itself until it was six years old, and even then required assistance in handling the prey. They contrast this with observations near Vancouver Island where juvenile resident killer whales rarely spend more than three years in such close association with their mother and feed on salmon, which they learn to catch within a year of birth (Haenel 1986). We suggest that the long time required to learn the culturally transmitted (and highly adaptive) self-stranding technique may be driving an incipient divergence in life histories, with the by-product of extended parent-offspring contact providing the opportunity for more cultural transmission. Such interactions between culture and development may closely parallel early human evolution.

Russell and Russell (1990) point out the link between maternal care and cultural transmission in early humans and other primates, and it is interesting that the cetacean species for which gene-culture coevolution has been suggested are also those with matrilineally based societies. This potential link produces a testable hypothesis: Other, less studied, matrilineal cetacean species should show group-specific traditions. Preliminary evidence suggests that short-finned pilot whales, almost certainly a matrilineal species and also a species showing menopause (Kasuya & Marsh 1984), do indeed have group-specific dialects (Scheer et al. 1998). If our ideas on gene-culture coevolution in cetaceans and cultural influence in the evolution of menopause are correct, then further investigation of this species and its congener, the long-finned pilot whale (*Globicephala melas*) – also matrilineal (Amos et al. 1991) – would strengthen this link.

8. Conclusions

Although it has not been experimentally demonstrated in any case, observations of cetaceans in the wild strongly suggest that cultural transmission is important in some species.

Table 4. *Life-histories of some primates and cetaceans. Only humans, killer whales, and short-finned pilot whales show significant post-reproductive lifespans. (Data from Whitehead & Mann 1999)*

Species	Age at sexual maturity (yrs)	Age at reproductive senescence (yrs)	Lifespan (yrs)	Post-reproductive lifespan (yrs)
Macaque (*Macaca* sp.)	~5	~25	~25	0
Gibbon (*Hylobates* sp.)	~8	~30	~30	0
Chimpanzee (*Pan troglodytes*)	~11	~40	~40	0
Human (*Homo sapiens*)	~17	~45	~70	~25
Short-finned pilot whale (*Globicephala macrorhynchus*)	~10	~40	~63	~23
Killer whale (*Orcinus orca*)	~12	~45	~70	~25

The lack of evidence in other species could well be due simply to lack of study. In the case of killer whales and possibly other matrilineal species, this transmission gives rise to stable cultures, which are in some respects unique outside humans. Our ethnological perspective, and hence our conclusions, are unlikely to be shared by all. However, our approach is internally consistent, and its conclusion is that culture should be attributed to cetaceans. We hope to stimulate a research effort which, even if it should disconfirm some aspects of our assertion, will give us a much better insight into the role of cultural transmission in the behavioural development of cetaceans. Given that there are over 80 species in the group, the possibility for comparative work is exciting.

We have suggested several aspects of the natural history of whales and dolphins that may have promoted the evolution of these complex cultures. Of these, mobility may largely account for the apparently greater complexity of some cetacean cultures than those found in some nonhuman primates, whereas greater group stability and cognitive ability may be important in the differences between the cultures of cetaceans and birds. These ideas have relevance to our understanding of human prehistory. Theoretical work indicating the widespread adaptiveness of culture coupled with a dearth of empirical examples suggest there are important obstacles to the evolution of cultural transmission, obstacles which both humans and some cetaceans appear to have overcome. What ecological and social factors were common in the histories of both groups to enable this evolutionary leap? Our review suggests stable matrilineal groups as an important social factor, and environmental variability and mobility (c.f. Boesch 1996) as important ecological factors. While cetaceans are intrinsically more mobile than humans, humans have been able to use cultural innovations to become progressively more proficient travelers, overtaking first cetaceans, then birds, and so accelerating the spread and evolution of our other cultural forms.

None of the observations of cetacean culture summarized in this paper come from research directly on cultural transmission – they are by-products of observational studies of behaviour, vocalizations, or populations. Yet, together, they constitute strong evidence that, from the ethnographic perspective, these animals do have culture. Thus, there is a clear case for studying the cultural transmission of information directly as parts of the research agendas of the long-term field studies of whales and dolphins.

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Culture and hyperculture: Why can't a cetacean be more like a (hu)man?

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Abstract: Human hyperculture appears to have been produced by the amplification of the kind of normal culture shared by cetaceans and other animals and presumably by our ancestors. Is there any possibility that cetaceans could be subject to these amplifying processes, which may include: sexual selection; within-group moral behavior; culling of low-cultural-capacity individuals through predation or self-predation; and reciprocal positive feedback between culture and the capacity for culture.

If cetaceans (and many other animals) have what can be termed "normal culture," perhaps we should call what *Homo sapiens* has "hyperculture." Rendell and Whitehead review a literature establishing that culture in cetaceans is in many ways similar to that of terrestrial species; along the way, they argue that there are no qualitative differences between human and animal culture. Let us begin with that "along the way." There are indeed many similarities between human and nonhuman culture, but there are also dissimilarities (and reasons for discussing them that have nothing to do with quaint claims for human uniqueness). Human culture is not just socially transmitted information, it is an immense pool of different categories of data (Barkow 1989). Some categories seem to be fairly stable across generations (e.g., the grammar of a language), other kinds alter with considerable rapidity (e.g., allocation criteria for relative standing). Presumably, different kinds of information are acquired/conveyed through different cognitive mechanisms, so that the "transmission" term itself is more metaphor than explicit process. Individuals use the "cultural" information for many purposes, and frequently struggle to edit, revise and add to it in ways that may further their own interests rather than those of others. The cetacean cultures the authors describe are far simpler than any human hyperculture: they may be limited to a group dialect, for example, or to a socially transmitted foraging strategy. Though research limitations have probably obliged the authors to understate the extent of cetacean culture, there seems little doubt that it is a "normal" culture and therefore of far less scope and complexity than human "hyperculture." Thus the question arises: why are not cetacean cultures more like our own?

Various "amplification" processes appear to have been involved in the transformation of the presumably "normal culture" of our ancestors into hyperculture. (1) For Boyd and Richerson (1996; Richerson & Boyd 1998; 1999), one such process was that of "cultural group selection" in which groups that were able to create moral codes that transcended mere kinship overcame others (cf. Waddington 1960 for a similar argument). (2) For Miller (2000) it was a matter of sexual (rather than "survival") selection for the language and other "genetic indicator" abilities that permit us to develop and transfer cultural information in the way that we do. (3) For Alexander (1971; 1975; 1979) and others, it was a matter of self-predation. The less intelligent and socially cooperative would have been culled out by conspecific predators. (4) A similar selection pressure could have resulted from culling by other predator species, but there is no evidence for this (Barkow 2000). (5) For Dobzhansky (1963), Geertz (1962), and Spuhler (1959), our hyperculture was produced by a reciprocal positive feedback between the genetic capacity for culture and the adaptive culture being invented and transmitted (a process that would have led to an exponential growth in culture and brain size and complexity that is apparently not reflected, unfortunately, by the fossil and archaeological records). It is possible that all of these hypothetical processes contributed to the generation of human culture and capacity for culture, during some periods of our evolutionary history. For present purposes, however, the question is: Are any of these five processes occurring among cetaceans? Could they even in principle occur, and so result in the evolution of a hypercultural species of dolphin or whale in some ways similar to ourselves?

Does the fact that cetaceans are not terrestrial have any bearing, here? As the authors point out, aquatic life favors both efficient movement and efficient vocal communication, and culture can permit rapid adaptation to the changing environments and potential new niches made possible by the resulting cetacean "extensive mobility." These factors may have non-obvious implications for the development of hyperculture.

While there is thus far no evidence for a hyperculture cetacean species, the evolutionary possibility of one merits thought. To the various interesting questions R&W already raise, therefore, let us add the following: (1) What is the relationship, if any, between socially transmitted information and sexual selection, among cetaceans? (2) Is there any evidence of a predation or self-predation process affecting cultural capacity? That is, do individuals and/or groups get culled out if they are less successful in transmitting/acquiring social information than others in the face of predation or conspecific conflict? (3) Is there any socially transmitted information that has to do with "moral behavior," that is, behavior having to do with how individuals in a group treat one another, rather than simply how they transmit vocalizations or foraging strategies? Finally (4), If aquatic environments are conducive to the evolution of normal culture, could it be that they may provide novel ways for normal culture to become hyperculture?

A sound approach to the study of culture

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Abstract: Rendell and Whitehead's thorough review dispels notions that culture is an exclusive faculty of humans and higher primates. We applaud the authors, but differ with them regarding the evolution of cetacean culture, which we argue resulted from the availability of abundant but spatially and temporally patchy prey such as schooling fish. We propose two examples of gene-culture coevolution: (1) acoustic abilities and acoustic traditions, and (2) transmission of environmental information and longevity.

The faculty of culture has long been argued as one of the last features to set us humans apart from other animals, but, as Rendell and Whitehead (R&W) have shown, once more our cultural pedestal is crumbling badly, forcing us to assume our place as one cultural animal among many. That the latest assault on human cultural supremacy should come from the field of cetacean studies is not surprising, given the advances in this field since Mundinger (1980) acknowledged the vocal traditions of some "whales" (he fails to mention the species) as cultural institutions. What is surprising is the glacial speed with which findings from the field of cetacean science have diffused into the study of cultural transmission, and we hope that R&W's thorough review will help to remedy this problem. As researchers of vocal variation and patterns of gene-culture coevolution in killer whales, we are excited at the prospect of a renewed, more vigorous scientific discourse between the fields of cetacean science and cultural evolutionary theory.

Determining the extent to which the expression of certain behaviours is based on innate or learned factors is the first challenge in field studies of animal culture. The second challenge is to distinguish between social learning (via cultural transmission) and experiential learning, as R&W point out. The problems and pitfalls that students of social learning face in studies of terrestrial species are compounded when they turn their attention to cetaceans. It is naïve to think that the nuances of social interactions can be untangled by surface observers: with a few exceptions (e.g., the learning of high-risk stranding behaviours by killer whales) social learning in cetaceans must be inferred from rapid intra-populational changes, mother-offspring similarities, and inter-populational differences in readily observed behaviours such as prey capture or migration, as the authors discuss. However, there is a bright side to the study of behaviour in cetaceans. Many species produce highly variable vocalisations, and although water makes visual observations difficult, it is an excellent conductor of sound. Furthermore, the transmission mechanism of vocal behaviour is likely more direct than that of other behaviours, because an animal perceives the sounds of other individuals and its own sounds in the same sensory modality. Not surprisingly, then, many (and, we would argue, the most convincing) of the examples of cultural transmission in cetaceans described by R&W involve sound.

One of the points in which we differ from R&W is in the role of environmental variability in the evolution of culture. The authors note that marine ecosystems change state over relatively short time periods compared to terrestrial ecosystems, and that cetaceans generally compensate for change by moving. Culture, they argue, is seen as an efficient mechanism for transmitting learned movement strategies. While terrestrial ecosystems do not switch between ecological states in the same manner as marine ecosystems, they are subject to much greater variation in temperature and to catastrophic events such as floods, droughts, hail or ice storms, fires and the like – all of which could presumably be better survived by species with a cultural memory of similar events. And yet, as the authors acknowledge, the best example of a non-human cultural primate, the chimpanzee, comes from one of the most stable terrestrial ecosystems. The authors also observe that the development of culture is likely enhanced in species that are long-lived and live in stable social groups. These conditions are most likely to arise under environmental conditions that favour low adult mortality and groups of constant size. We therefore suspect that culture has evolved in cetaceans because they are able to survive ecosystem changes, rather than vice versa.

We believe that the evolution of culture in cetaceans is more closely linked to super-abundant but spatially and temporally patchy prey than to state changes in ecosystems. Terrestrial ecosystems have few equivalents of schooling or aggregating marine species such as krill, forage fish, and squid, which support vast suites of large predators. It is the availability of such aggregated prey, we argue, that makes it possible for species such as killer, pilot, and sperm whales to live in stable groups, and for migratory species such as humpback whales to congregate seasonally on their feeding grounds. The fundamental requirement of such species is to be able to find patches of such prey, and to feed on them efficiently. Cultural transmission of information regarding prey distribution will increase the average fitness of group members. Likewise, cultural transmission of feeding techniques, including cooperative foraging methods such as "bubble-netting" in humpback whales (Jurasz & Jurasz 1979) or carousel-feeding killer whales (Similä & Ugarte 1993) would seem to have obvious advantages.

R&W limit their discussion of gene-culture coevolution to the evolution of menopause and protracted juvenile dependence in certain cetaceans. We feel it is worth adding the remarkable acoustic facility of many cetaceans to this list. Almost all mammals, including our primate relatives, are poor vocal copiers. The notable exceptions are humans and cetaceans. The similarities cannot be explained by common ancestry. How then can we account for this convergent evolution? Sociality alone is not a satisfactory answer; many mammalian species are highly social but have not evolved the ability to produce and imitate complex sounds. We propose that the propagation of successful traditions by cultural transmission creates selection pressure for reliable mechanisms to signal group identity. In other words, culture preceded and selected for vocal variation and vocal copying, which in turn enhanced the development of traditions. Similarly, culture may select for longevity since senescent individuals may increase the fitness of their offspring and relatives by transferring knowledge to them, and longevity in turn promotes further culture. Elders are valued in many human societies for precisely this reason, and it is not unreasonable to imagine that very old individuals are tolerated in killer whale groups (Bigg et al. 1990) for similar reasons.

In conclusion, we feel that the case for cultural transmission of traditions in cetaceans, particularly acoustic traditions, has been well established for many years. R&W correctly point out that this message has been slow to reach researchers working on other species (including humans). We believe that their methodical marshalling of the evidence is long overdue and will help to bring about a more general appreciation of the central role that culture plays in the lives of certain cetaceans.

The mimetic dolphin

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Abstract: Rendell and Whitehead note the necessary, complementary relationship between field and laboratory studies in other species, but conclude their article by de-emphasizing the role of laboratory findings in cetacean research. The ambiguity in field studies of cetaceans should argue for greater reliance on the laboratory, which has provided much of the available research supporting the hypothesis of cetacean culture.

Rendell and Whitehead (R&W) recognize the benefits of integrating laboratory and field studies for investigating culture. Paradoxically, they also suggest that study of imitation and teaching in laboratory settings is not a productive approach. Not withstanding their reservations, evidence of imitation in laboratory settings provides strong indications of the cognitive skills necessary for cetacean culture. A more thorough review of the literature on imitation (including yet to be published data), a clarification of the status of social learning in cetaceans, and a look at some lines of future research suggest that laboratory studies make essential contributions to understanding culture.

Ostensibly solid examples of cultural transmission in more easily observed terrestrial animals, such as potato washing in Japanese macaques, lend themselves to alternative interpretations (Galef 1992). Laboratory research on transmission processes provides substantive evidence to support the more ambiguous evidence of culture that arises from the difficult observational conditions in the wild.

Many researchers report vocal imitation in trained dolphins (Caldwell & Caldwell 1972; Evans 1967; Lilly et al. 1968; Richards 1986; Richards et al. 1984; Sigurdson 1993). Dolphins also copy spontaneously without external reinforcement. Wild dolphins appear to imitate each other's signature whistles (Janik 1997; 2000). Captive dolphins often copy their poolmates' signature whistles (Janik et al. 1994; Janik & Slater 1997; Ralston et al. 1987; Tyack 1986b). Mimicry of the secondary reinforcer "bridge" whistle used by trainers is also reported (Tyack, 1986b; personal observations). In a study in which two mothers and their male calves were presented with the opportunity to use a keyboard, which led to electronic whistle-like emissions, which the two young males spontaneously imitated after a short exposure (2–19 emissions) to the sounds (Reiss & McCowan 1993). Young dolphins' repertoires appear to change over the first year (McCowan & Reiss 1995), and young dolphins often share whistles with their adult companions (McCowan & Reiss 1995; Sayigh et al. 1995). One dolphin isolated at age 1–2 years (and for 7 years thereafter) was exposed to a large number of recorded and electronic whistles. His repertoire became large and included copies of these sounds (Caldwell et al. 1990).

Experimental studies also confirm that dolphins mimic familiar actions of other dolphins (Bauer & Johnson 1994) as well as imitate novel behaviors performed by their conspecifics (Xitco 1988; Xitco et al. 1998; see Herman, in press, for a review). Two recently wild-caught 2-year-old dolphins successfully imitated novel behaviors performed by human models (Harley et al. 1998). An older dolphin with more experience in captivity also imitated two novel behaviors demonstrated by a human (Herman, in press). Anecdotes of interspecies imitation include imitation by a false killer whale of a pilot whale (Brown et al. 1966), by a bottlenose dolphin of a spinner dolphin (Brown et al. 1966), and by a bottlenose dolphin of a Cape fur seal (Tayler & Saayman 1973), and so on. (See Herman 1980, for a review.) Dolphins can also learn to replicate behaviors presented to them via television (Herman et al. 1993) and to "repeat" the last behavior they themselves produced, which could potentially be an imitation of their own actions (Mercado et al. 1998).

In arguing the problematic nature of laboratory evidence, R&W note the disputes over differentiation of various social learning processes, for example, true imitation (learning a new behavior by observation) versus alternative, putatively primitive, processes such as stimulus enhancement, social facilitation, and matched dependent behavior (cf. Roitblat 1998). This is an unnecessarily cautious interpretation of the literature. A wide range of processes contributes to cultural transmission of information (Whiten & Ham 1992). A thorough explication of the role(s) of these processes in the development of culture is an active area of research. To dismiss this exploration is to confuse the details (processes and mechanisms) with the empirical demonstration of social influence and learning in cetaceans. The fact is that bottlenose dolphins have demonstrated mimicry of complex, novel behaviors, performed by a variety of species, over delays of time, and under degraded stimulus conditions (Herman, in press). They have shown a sophisticated, flexible ability to imitate that could provide the foundation for culture in natural environments.

Although the capacity and flexibility of cetacean mimetic abilities is clear, laboratory studies can go much further in exploring these foundations of culture. Research on imitation in general has been limited by Thorndike's (1965) heritage of denying imitation by animals, an influence that is rapidly attenuating. Research on a broader range of species has been limited by an availability bias favoring the bottlenose dolphin. An effort needs to be made to reduce this bias in order to investigate the range of mimetic abilities across cetaceans. Blackmore (1999) hypothesized that imitation not only supported culture in humans, but also promoted brain size increases. Comparison of brain size and mimetic performance among the cetaceans might provide an interesting test of her hypothesis. The facility of imitation by young dolphins (Harley et al. 1998; Xitco 1988) suggests that developmental factors need to be explored. Numerous observers have commented on the pronounced synchrony of dolphin behavior, and a recent study of a captive mother/calf pair (Fellner & Bauer 1999) indicates that behavioral synchrony is exhibited from shortly after birth and maintained at a high level (over 90% of the time) throughout early infancy. An interesting hypothesis is that imitation might evolve from this apparently innate characteristic, that is, synchrony might provide a model or foundation for a more flexible skill – imitation. Differences among studies suggest that social factors may play a role in elicitation of imitation, that is, social roles may determine the models and imitators.

Size might be an obstacle to captive study of the large cetaceans, but the majority of toothed whales can be studied in captive settings. The carefully controlled studies of the numerous smaller species that the laboratory allows will contribute strongly to the understanding of cetacean culture.

Social learning by observation is analogue, instruction is digital

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Abstract: Social learning in the strict sense is learning by observation or instruction. Learning by observation appears to be an analogue process while learning by instruction is digital. In evolutionary biology this distinction is currently thought to have implications for the extent to which mechanisms can function successfully as an inheritance system in an evolutionary process.

Rendell and Whitehead's impressive review of the evidence of culture in whales and dolphins is persuasive and it, along with Boran and Heimlich's (1999) recent review, allows us to firmly place cetaceans alongside the other mammals and birds for which similarly persuasive evidence is available. I agree with the authors that the existence of culture in nature is most usefully recognized by the kinds of field methods employed in the research they review – independent of the details of the social learning mechanisms involved – despite the fact that mechanisms are not irrelevant for specifying what could reasonably be called culture. To be relevant to the concept of culture, as a minimum, mechanisms must be both social (independent individual learning is excluded) and have the effect of maintaining or increasing similarity. Matched-dependent individual learning in which reinforcement is conditional on "matching" another's behavior meets these minimal criteria; hence some, including Whiten and Ham (1992), consider it relevant to the concept of culture. We should not be surprised, however, by the scepticism with which the concept of animal social learning in the more strict sense (sometimes called imitation) can be greeted by psychologists. Recall that from roughly Thorndike at the turn of the last century until Bandura in the 1960s and 1970s, as incredible as it may now seem in retrospect, the existence of social learning in this sense was widely denied by psychologists in humans as well! Albert Bandura, developing his interest in the effects of television violence on children, first showed that as a practical matter, most social learning in humans cannot be explained by individual learning mechanisms such as matched-dependent learning. Bandura experimentally demonstrated social learning without concurrent performance, without at least overt rewards, and with long-time delays between learning and performance (see discussion and references in Blute 1981). This led to the common definition of social learning in the strict sense as learning by "observation" (in any sensory modality) or "instruction" (the communication of strings of symbols, among people; normally, sentences in a natural language). While many other distinctions can and have been drawn subsequently, learning by observation is social learning whether the learning is about stimuli, responses, associations, or consequences; whether purely behavioral or cognitive; whether modelling is passive or active, and so on; which brings me to my second point.

Observational learning appears to be an analogue (continuous) process while instructional learning by means of human language is, like the genetic code, digital (discrete). As a consequence, observational learning would appear to be subject to the cumulative degradation of information characteristic of any analogue copying mechanism (Dawkins 1995 Ch. 1; Woolfson 2000 Ch. 8). In the short run, collapsing continuous input into discrete categories loses information. Over the longer run, however, it provides periods of stability making possible the evolution of complexity (e.g., by analogy in the ordinary language sense, i.e., over-duplication and divergence to serve new functions and by symbiosis). In the still longer run, discrete information too is subject to error, but it is also amenable to the evolution of error-correcting mechanisms. Knowing as little as we do about the origin and early evolution of life, it is unclear whether the limitations of analogue copying mechanisms affect their ability to function as inheritance systems in evolutionary processes as much in practice as they are thought to do in theory. Perhaps the study of observational learning and cultural evolution will shed some light on this.

Maynard Smith and Szathmary (1995) have stated flatly that among living things, beyond nucleic acid molecules, the only hereditary replicators capable of supporting the inheritance of an indefinitely large number of distinct states are language and music. What fascinates so much about whales and dolphins is that those notes, phrases and themes of humpback songs and the clicks, whistles, and pulsed calls of killer whale vocalisations (Boran & Heimlich 1999a) are so language-like in appearance (varying elements, in which repetition and order can matter, with hierarchical structure, i.e., grammar possible, etc.). Perhaps a decade from now, we will be reading another review in *BBS* of evidence for the evolution of language in cetaceans.

Sacrileges are welcome in science! Opening a discussion about culture in animals

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Abstract: The sacrilegious proposition of the existence of cultures in whales and dolphins should open the discussion of cultures in other animals, allowing us to find what is unique in human cultures. The ethnographic approach used by all anthropologists is the key in this investigation and revealed that cultural differences are present in animals and could result from different learning mechanisms.

Animal cultures? This sounds as a heretic combination of words to some social and cultural anthropologists. Here, the authors combine the word culture with whales and dolphins. This sounds like a stronger sacrilege than to use it with chimpanzees. Some sacrileges in science should be welcomed, and I welcome that one with the hope that it will lead to a thorough discussion of the evidence and improve the study of culture in non-human animals. Any claim of uniqueness within a species of a behaviour can be confirmed only if we can show that effectively it is absent in other species. In fact, the discussion about culture being uniquely human has been often clouded by anthropocentrism and misreading of the evidence. Rendell and Whitehead's claim of culture being present in whales and dolphins is eye opening, for most of the readers are probably not aware of the complexity of the behaviour in aquatic mammalians. I allow myself to follow their heretic proposition by discussing two important aspects about how to study culture in animals, including humans.

Social anthropologists were the first to concentrate their study on describing human cultures in many different societies. If we follow Rendell and Whitehead's terminology, all their approach was ethnographic. The overwhelming outcome of this approach was that all human societies possess large differences in feeding, housing, clothing habits, in rules of kinship, marriages, in knowledge about their environment, group members and foreigners, and in what they believe, feel, and share. The key method used to arrive at this result was comparing these aspects in many different human societies. This scientific method is in animal behaviour a luxury. This fact may explain the difference we see between humans and other mammals, because only in a small minority of species do we have observations on more than one group. Thus, by definition, comparisons between societies are not yet possible for most species and cultures, therefore, cannot be detected.

We have observations on more than one social group for a few animal species only, for example, on some great apes, a few primates, a few carnivores, some birds, and cetaceans, and evidence increased slowly about behavioural differences between populations. That is the moment when psychologists entered the arena and proposed that the ethnographic approach used in animals does not answer the question of culture and that only the transmission mechanism counts to attribute culture to a species (Galef 1990; Tomasello 1990). Beside the intrinsic interest of studying the mechanism of social transmission of information within a species, the problem with this argument is the double standard it sets. No one seems to require human cultural differences to be acquired only through imitation or teaching. The reason being simply that this data do not exist (Boesch & Tomasello 1998).

1. Ethnographic versus the transmission process approach. Since the ethnographic approach has been the main one for studying human cultures, we are perfectly justified to use the same approach to study animal cultures. However, an awareness of the transmission mechanism has led scientists working on culture in non-human animals to emphasise the social component of cultural transmission and require that the behaviour should not be influenced by either genetic nor ecological factors. This criteria is more stringent than what has been used by social anthropologists, that never excluded a behaviour from being cultural if it was affected by ecological factors such as climatic conditions.

The main criteria for attributing cultures is that we observe differences between social groups that have a pure social origin. What qualifies as culture is the result of the interactions within the group that is independent of the transmission mechanism that produced this result. In fact, anthropologists have almost never studied the acquisition of a behaviour or a ritual in humans; and applying a transmission approach to humans would disqualify most human cultures.

2. Culture cannot be defined only through the transmission mechanisms, as a behaviour seen in all humans would never qualify as cultural whatever the transmission mechanism. Hard-liners have proposed that human cultural traits are learned only by imitation or teaching and therefore this should be proved in animals before attributing them cultural abilities (Galef 1990; Heyes 1994a; Tomasello 1990). However, no evidence has been provided for this proposition. Many studies have been done with animals on the transmission mechanisms during the acquisition of different behaviours (Galef & Heyes 1996; Tomasello & Call 1997; Whiten & Custance 1996) that provided evidence of how, for example, chimpanzees learn to throw sand, to rake food, to open artificial boxes containing food, or how rats learn to push bars. These observations are very interesting when we want to understand social learning in animals. But our present interest is in cultural learning and not the learning of any behaviour. Thus, these studies tell us nothing about cultural learning in animals, since nobody proposed, for example, sand throwing to be a cultural behaviour.

The few studies about the acquisition of cultural behaviours in humans and chimpanzees show that many transmission mechanisms are at work. For example, observational learning is a major practice in learning complex weaving techniques in different human societies, a practice that is partly complemented by facilitation and stimulation from an expert during later phases of the acquisition process (Greenfield 1984; 1999; Rogoff 1990). More specifically is shown that when maintenance of a traditional way is important, learning by observations and shaping by scaffolding prevail, whereas when innovation is valued, learning by trial and error dominates (Greenfield 1999). The only existing study of the acquisition process in a cultural behaviour in chimpanzees is on the nut-cracking behaviour in the Taï forest (Boesch & Boesch-Achermann 2000) and shows that observational learning is important but mothers interfere with the learning of their offspring every five minutes by stimulating and facilitating their attempts and correcting errors when necessary. Thus, when known, the learning of cultural behaviour can be very similar in humans and chimpanzees.

In conclusion, I would like to thank the authors for opening a thorough discussion about culture in animals. I suggest that culture is a dynamic process reaching different complexities, and this will allow us to understand the uniqueness of cultures in different species, including humans.

Genomic imprinting and culture in mammals

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Abstract: Genomic conflicts are potentially involved in the evolution and maintenance of culture. Maternal genes contributing to neocortical development could influence biases in the acquisition of information. Specifically, relatedness asymmetries due to multiple paternity are expected to lead to an increased reliability and receptivity of matrilineally-transmitted information. This view complements the gene-culture coevolutionary model adopted by Rendell and Whitehead.

Rendell and Whitehead (R&W) offer an indispensable ethnography furthering the case for an evolutionary convergence of cultural capacities between aquatic and terrestrial mammals. This particular convergence implies that natural selection acted upon neural systems mediating culture (the social transmission of information or behaviour). In this commentary, I suggest that genomic imprinting may be a significant factor in the evolution of culture.

Genomic imprinting is the inactivation of a particular allele dependent upon the sex of the parent from which it was inherited. The genomic conflict hypothesis proposes that multiple paternity favours the differential expression of maternal and paternal alleles so that (1) paternal alleles increase the cost to the offspring's mother; and (2) the maternal alleles reduce these costs. Haig (1999; 2000) suggests that genomic conflict applies to all fitness costs imposed on a mother that benefit offspring (not just offspring size). Moreover, the genomic conflict hypothesis applies to all interactions between relatives with different maternal and paternal coefficients of relatedness (Haig 1997). In terms of social learning, the decision rules to adopt a cultural practice for helping relatives may be costly to paternal genes (or maternal x-linked genes). Maternal genes in daughters could benefit from decision rules filtering the costly noncooperative preferences sometimes induced by paternal genes.

R&W assume that traditional inclusive fitness calculations are sufficient for explaining the benefits of culture. When one considers "relatedness asymmetries" (Haig 1997) the information transmitted between siblings may have different levels of reliability. Cultural transmission between siblings could be detrimental to maternal genes. R&W "downplay" genomic conflict's connection to "group-specific" behaviour (i.e., culture). They state that genomic imprinting is restricted to conflicts over resources during embryonic development. Although it is true that imprinting is implicated in growth, there are also influences on behaviour via the differential expression of paternal and maternal genes in the mammalian brain (Isles & Wilkinson 2000). In mice, maternal genes are expressed in cells found in the neocortex (involved in decision-making) and paternal genes are expressed in the cells of the hypothalamus, involved in homeostasis (Allen et al. 1995; Isles & Wilkinson 2000; Keverne et al. 1996).

R&W adopt Richerson and Boyd's (1998) model that culture is the conformist acceptance of transmitted information. However, since signal-receptor systems are particularly susceptible to superstimulation (Ryan 1990), cultural transmission may provide opportunities for sensory exploitation (Rice & Holland 1997). Animals likely filter information that is designed to cause them to deviate from their optimum behaviour.

The "cultural hitchhiking" hypothesis (Whitehead 1998) endorsed by R&W may be bolstered by a genomic conflict approach. Any heritable unit (mtDNA or cultural information) transmitted with high fidelity from mother to daughter can lead to tight social networks due to high maternal relatedness. Relatedness asymmetries, genomic imprinting, and paternity are factors favouring matrilineal sociality (Haig 2000). The imprinted expression of genes predisposing cooperation are favoured when recipients in the social group have different probabilities of sharing the donor's maternally and paternally derived alleles (Haig 2000). Under conditions of multiple paternity it is predicted that maternal genes predispose offspring to learn from mother (vertical transmission) compared to other siblings (horizontal transmission). There can be inclusive fitness costs to maternal genes that treat all information as equally reliable. Conflict over the transmission and reception of information between (and within) individuals is possible (Trivers 2000). For example, nonpaternally related sibs could encourage behaviours costly to the learner or discourage behaviours detrimental to the "teacher." This places a premium on the reliability of information, and maternal genes may benefit from suppressing misleading information transmitted between sibs.

When there is male-biased dispersal, as in sperm whales *Physeter macrocephalus* (Lyrholm et al. 1999), sibling paternal coefficients of relatedness are low and the likelihood of genomic conflict is high (Haig 2000). Male-biased dispersal creates groups bounded by matrilineal kinship bonds. The degree of patrilineal kinship will depend upon the mating system (e.g., number of sperm donors). Even when males do not disperse, as seen in killer whales *Orcinus orca* and pilot whales *Globicephala melas* (Connor et al. 1998), it is possible that females mate multiply, given the molecular evidence for multiple paternity in humpback whales *Megaptera novaeangliae* (Clapham & Palsboll 1997). The evolutionary predictions regarding conflicts are simple when siblings have higher maternal than paternal relatedness. That is, maternal information may be designed to inform maternally related kin or suppress misleading information provided by paternal genes. However, when one or several males dominate paternity, the sources of conflict may change. Specifically, high coefficients of relatedness in male sex-linked genes among daughters could also favour tight social networks among daughters. This is because a father's x-linked allele is always transmitted to daughters and stays within the group for more than one generation given male-biased dispersal. However the probability that daughters share the x-linked allele inherited from mother is 1/2 (the same as autosomal genes). When homogametic (xx) offspring of a heterogametic (xy) parent share an entire sex chromosome subject to genomic imprinting, there should be a predisposition toward cooperation among daughters with common paternity (Haig 2000).

Social navigation increased neocortex size in primates (Dunbar 1992) and potentially Cetacea (Connor et al. 1998). Misinformation may have selected for better filtering (Rice & Holland 1997) and/or fine-grained kin recognition mechanisms in the neocortex. Sperm whale maternal genes may be associated with the cross-modal neocortical processing referred to as "echolocation imagery" by Roitblat et al. (1995). Oelschlager and Kemp (1998) reported that there is a large proportion of auditory neocortex in sperm whales, which may be implicated in echolocation images of conspecifics. Maternal genes could benefit from echolocation imagery if it allowed for more reliable assessments of information in an aquatic environment where visual assessments are error-prone. "Acoustic signatures" found in sperm whale echolocation click trains (Andre & Kamminga 2000) may be particularly salient if the signal is an intrinsically unfalsifiable kinship marker. In conclusion, genomic conflicts are potentially important for cultural studies if genomic imprinting influenced the evolution of mammalian brain structure (Barton & Harvey 2000) designed to transmit and acquire information.

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Individual foraging specializations in marine mammals: Culture and ecology

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Abstract: Rendell and Whitehead argue persuasively that individual foraging specializations, if socially learned, are examples of cetacean culture. However, they discount ecological variation experienced by individuals within a population as a factor in such behavior. I suggest that ecological variation may play an important role in individual foraging specializations and describe several ecological parameters that may help us understand the high frequency of this interesting behavior in the marine habitat.

I consider foraging specializations to be differences in the types of food or methods used to procure food among two or more individuals that have overlapping home ranges. I am not interested in differences attributable to age, sex, reproductive state, or cases recorded during periods when a new behavior is spreading through a population (although if it spreads incompletely, the result will be individual foraging differences). Individual foraging specializations have now been described for a taxonomically diverse sample of marine mammals including bottlenose dolphins, sea otters, seals, and minke whales (Connor et al. 2000; Harwood 1990; Hoelzel et al. 1989; Riedman & Estes 1990; Smolker et al. 1997). Marine mammals may exceed their terrestrial counterparts in this regard.

At least four distinctive foraging specializations have been observed in Shark Bay, Western Australia. (1) "Sponge-carrying" is performed by a minority of females in 8–10 m channels (Smolker et al. 1997). Wearing cone-shaped sponges over their rostra, these females engage in otherwise typical behavior associated with foraging in deeper water, arching their peduncles, or lifting their flukes out of the water as they dive toward the bottom. The duration of sponge-carrying and observations of females with sponges near the bottom suggests that the sponge may protect the rostrum from abrasion during benthic feeding (Smolker et al. 1997). The same females have been observed carrying sponges for over 10 years. (2) "Kerplunking" occurs over shallow offshore seagrass beds (1.5–2.5 m). Individuals lift their peduncle high into the air before bringing their flukes down at a steep angle with respect to the water surface, driving their flukes into the water (Connor et al. 2000). The resultant cavitation produces a 3–4 m high vertical splash and accompanying pulsive sound that is thought to startle prey hiding in the seagrass. Kerplunking appears common on offshore seagrass beds east and northeast of but not in our core study area of 130 km^2 where we observed kerplunking only twice in 10 years. Seagrass beds in our core study area are not as extensive but appear otherwise similar, and we have extensive observations of dolphins foraging on them. (3) At the tip of Peron Pennisula in Shark Bay, there is an unusually steep beach with deep water access where a few female dolphins "hydroplane" in extremely shallow water and even beach themselves in pursuit of fish (Berggren 1995). As in the case of sponge-carrying, beaching appears restricted to a few females, and may be passed on to their calves.

(4) Associating male alliances in Shark Bay may have different favored foraging habitats (Connor, unpublished data). One alliance foraged preferentially in shallows, while two alliances they associated with preferred to forage in deeper water in the embayment plain.

Each of the four patterns described above is limited to a particular habitat type; sponging in deeper channels, kerplunking in shallow offshore flats, beaching on the beach at the top of the peninsula, and male alliance foraging in shallows or the embayment plain. It is also worth emphasizing that while some of these specializations may be limited largely to one sex, they are not general to members of that sex. Thus sponging may be a mostly female activity, but most females do not carry sponges.

What kind of model might help us understand the adaptive basis of Shark Bay foraging specializations? I suggest that social position, physical condition, and ecology might play a role. One sponge carrier is missing half her fluke but other spongers have no such handicaps so physical condition seems insufficient as a general explanation (Smolker et al. 1997). We do not know the degree to which individuals are excluded from particular foraging areas by rivals, but the importance of feeding competition in other mammals suggests that this possibility should not be neglected in dolphins. Rendell and Whithead (R&W) suggest that because "all members of the population experience the same mixed habitat," "ecological explanations for this variation can be discounted." While a dolphin's home and day range will be closely related to their foraging strategies it is also a certainty that the natal ranges of dolphins do not contain equal amounts of the different habitat types in Shark Bay. The most obvious example is the beach favored by the beaching dolphins. No such beach is within the home range of most dolphins in the study. It is also clear that the ranges of dolphins in our study differ significantly in the extent to which they contain offshore seagrass beds, embayment plains, or channels. Thus, the profitability of a particular foraging specialization will depend on the extent of the concomitant habitat type in a dolphin's range and that will differ to some degree for most dolphins whose ranges do not overlap exactly.

If the behaviors are socially learned, then the profitability of learning particular foraging strategies will be influenced by the available models from which the offspring can learn (e.g., what mom does) and the proportion of habitat types in the offspring's range. While one of these influences (learning models) might outweigh the other (habitat types) it would be wise to maintain both in our working model until the data tell us otherwise.

This conclusion is relevant for the broader consideration of what amounts to culture in cetaceans. I suggest that, in keeping with the actual definition of culture used by Rendell and Whitehead, the only important question is whether the behavior is learned socially. While rendering this question a more difficult one, ecological overlap is not incompatible with the definition of culture as are genetic differences or individual learning.

What ecological conditions might favor specialization in marine compared to terrestrial habitats? In hopes of furthering research into this question, I offer several possibilities.

Prey diversity. Marine mammals may enjoy greater diversity in prey and habitat types per unit area compared to their terrestrial counterparts.

Prey biomass. A higher standing biomass and replacement rate would allow marine mammals to meet daily foraging requirements on fewer species.

Practice rewards. Animals may be more likely to specialize in cases where practice of particular foraging methods leads to greater foraging efficiency. Shellfish must be extracted, and fish may have a variety of hiding places and escape responses that must be overcome. It is also possible that the number of foraging techniques required increases with the number of prey species faster in marine than in terrestrial habitats.

Mobility. Dolphins enjoy relatively lower travel costs than do the terrestrial mammals. Thus, for the same energetic cost, dolphins can range over a larger area that, if other factors are equal, contains more prey biomass than is found in the ranges of their terrestrial counterparts. The same dolphins could then meet their energetic needs from fewer species and thus specialization would be more affordable.

Seasonality. R&W relate the overall importance of culture in cetaceans to environmental variation over large temporal and spatial scales. I suggest that short term stability may be key to understanding the frequency of individual foraging specializations in the marine habitat. Reduced seasonality should translate into more dependable food sources upon which one can afford to specialize.

Validating cultural transmission in cetaceans

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Abstract: The evidence of high cognitive abilities in cetaceans does not stand up to close scrutiny under the standards established by laboratory researchers. This is likely to lead to a sterile debate between laboratory and field researchers unless fresh ways of taking the debate forward are found. A few suggestions as to how to do this are proposed.

As the evidence presented for culture in Cetaceans is largely a byproduct of other behavioural studies, we welcome Rendell and Whitehead's synthesis which rightly highlights the fact that whales and dolphins have been neglected by those studying animal social learning.

Psychological mechanisms and cognitive ability. Rendell and Whitehead (R&W) begin by stressing the virtues of a broad definition of culture that is not anthropocentric in restricting culture to that achieved through imitation and teaching. It is paradoxical then that they should devote much of their article to citing supposed examples of imitation and teaching in order to make a number of bold claims about the psychological capabilities of whales and dolphins. It is quite clear that many of these do not stand up to close scrutiny. For instance, the authors assert that according to accepted definitions, killer whales teach. Yet Caro and Hauser (1992), the only source they cite on the topic, clearly state that teaching cannot be inferred in an animal unless there is evidence that the "teacher" adjusts its behaviour and the "pupil" learns something as a consequence, and their example provides evidence for neither.

In addition the majority of the proposed evidence of imitation in cetaceans constitutes vocal learning. In fact vocal imitation is likely to be cognitively less complex than motor imitation (Thorpe 1961) as all animals are able to compare directly the sounds they produce to those produced by another. In the case of motor imitation, in contrast, there is generally no such process enabling a perceptual match between the observer's behaviour and that of the demonstrator. Contrary to the opinion of R&W the vocal imitation qualities of cetaceans do not provide evidence for any more cognitive sophistication or complexity of culture than that found in birds.

The high fidelity of cetacean cultures is regarded by the authors as unique and held up as further evidence of imitation and high cognitive ability. However, the widely held belief that imitation is correlated with high copying fidelity remains unproven and several nonhuman species have traditions over many generations without imitation. Consider for example, the highly stable tradition of milk-bottle opening of British birds which has been maintained since the 1930s (Fisher & Hinde 1949; Sherry & Galef 1990). Fidelity reveals nothing about cognitive capacity in the absence of knowledge of what exactly is being learned. Is it the motor pattern (imitation), the sub-goals of an action (programme level imitation), the ultimate goal (goal emulation), or learning about the features of the environment (stimulus enhancement)? It is the answer to this question that has implications for the cognitive abilities that may be inferred from such traditions and which determines whether R&W are justified in their claims of higher cognitive capacities in cetaceans. Yet if R&W's goal is truly to develop a nonanthropocentric approach to the study of cetacean culture then it does not matter whether whales and dolphins imitate or not. They would seem to be judging their study species according to the anthropocentric standards that they reject.

Much of the evidence for cetacean culture cited by R&W assumes that increasing incidence of behaviour implies that individuals have learned the trait. However, it is not necessary for all individuals in the population to learn a context-dependent, novel behaviour, for it to appear to increase in frequency in a population. For example, whilst some animals may learn to perform a behaviour in a particular environmental context, others may perform the same behaviour by schooling, response facilitation or through social facilitation, without having learned anything. Furthermore, in a spatially changing environment the phenotypic distribution may alter through unlearned developmental processes. Thus, one would observe apparent diffusion that is in fact entirely unlearned. Moreover, contrary to R&W's statement it is quite possible for noncultural behavioural traits to change in frequency rapidly if the variation strongly affects survivorship. Conversely, the expression of many selectively advantageous cultural traits will be strongly correlated with environmental resources. If the existence of culture can only be inferred by the independence of cultural traits and environmental factors then the incidence of culture is likely to be widely underestimated. Therefore the processes that R&W document are likely to be a misleading reflection of the extent of the cultural attributes of the animals concerned. While this is true for all taxonomic groups and not just cetaceans, the difficulties of observing cetaceans make this issue particularly problematic.

A way forward? We see little virtue in another polarised debate in which field researchers are willing to accept evidence for advanced cognitive processes in their animals that does not satisfy more exacting standards of experimentalists. The way past this impasse is by attempting to develop new methods for drawing inferences from field data. One avenue that we are currently exploring is whether it is possible to use the shape of a diffusion curve to infer something about the processes that led to the spread of the novel behaviour. This is likely to be considerably more complicated than the prevailing dogma that accelerating curves imply social learning, which is based on an inadequate theoretical foundation. Our analyses have found a number of scenarios in which asocial learning could generate acceleratory and sigmoidal patterns. For instance, a normal distribution in time to learn asocially would generate a sigmoidal cumulative pattern of diffusion. Nonetheless, preliminary findings suggest that it may shortly be possible to make probabilistic statements giving estimates of the likelihood that data described by particular mathematical functions were generated by social or asocial processes, and draw other inferences concerning the underlying processes.

A second approach would be to devise experimental methods that are indicative of social learning processes, but require only a single individual or a small number of captive animals. One promising line is the do-as-I-do procedure developed by Hayes and Hayes (see Whiten & Custance 1996). A second could emerge from the Bowles et al. (1988) report that a killer whale calf's vocal output was dominated by the one call that distinguished its mother's repertoire from that of a female companion. The appropriately timed introduction of an additional female with a repertoire that overlapped with the mother's in a different fashion would be sufficient to distinguish vocal imitation from alternative explanations. We urge R&W to give some thought as to whether cetacean researchers could devise a battery of such tests, to satisfy the sceptics.

Finally, the authors' account of the evolution of cetacean culture stresses that there are likely to be interesting interactions between migration and culture. We agree with this general perspective, and suggest a complimentary line of reasoning, developed more extensively elsewhere (see Laland et al. 2000 sect. 2.1.3). Through their activities and movements, countless organisms modify their selective environments, that is they engage in *niche construction*. Among both cetaceans and hominids their niche construction has generated selection that favoured cultural transmission. This has occurred because their movements (relocational niche construction) and, for hominids, their construction of artefacts and other environmental components (perturbational niche construction) damps out significant variation in their environments. This means that parent and offspring experience similar environments (e.g., similar prey, predators, climates, etc.) which results in the learned behaviour of the parents being of value to the offspring. This niche construction (of which mobility is just one component) can mediate cultural evolution.

Culture in cetaceans: Why put the cart before the horse?

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Abstract: Twisting definitions of a concept to serve one's purposes is rarely a fruitful exercise and the demonstration of culture is, necessarily, a two-step procedure: (1) documenting a behavioral difference between populations, (2) demonstrating that this difference has spread through the group by means of social learning. This will avoid putting the cart before the horse.

Whiten et al. (1999) published an updated and careful examination of behavioral differences between several populations of chimpanzees. Their organized report followed a similar endeavor by Tomasello (1990). Both articles drew upon four decades of careful uninterrupted or almost uninterrupted observations made by researchers in close contact with their subjects. These field reports were paralleled by five decades of experimental research on chimpanzee cognitive capabilities. Although, in a phylogenetic perspective, it is legitimate to study culture in chimpanzee to document the emergence of certain human traits, primatologists have waited all this time and accumulated all these data to present this report which is far from being totally conclusive. Other efforts to tackle the issue of culture in animals have been made another way by putting the emphasis on an underlying mechanism: social learning. Heyes and Galef (1996) published *Social learning in animals: The roots of culture*. Although the range of studied species was restricted to only few groups of animals (rats, primates, and birds), chapters put an emphasis on social learning and the methods that should be used to demonstrate social learning. In addition all these species had been heavily studied both in the field and in the lab. As honestly acknowledged by Rendell and Whitehead in the target article, this is not, and possibly will never be, the case for cetaceans. Instead they attempt, at any price, to document culture in cetaceans while failing to adopt the scientific rigor that many other authors dealing with culture in animals have favored. This makes their claim for presence of culture in cetaceans very weak, if not fruitless. I will consider two issues: choice of the definition for culture and cultural transmission within the context of social development.

Choice of a definition. As often acknowledged, starting an article by defining the concept under study is always a fruitful exercise, immediately advertising the authors' intentions. The most common definition of culture has two components: (1) behavioral differences between populations, and (2) evidence that these differences had spread within the populations by means of different forms of "social learning," including imitation and possibly teaching (see Nishida 1986). Taken separately, each part of the definition has its own interest, but together, and only together, they mean "culture." In the target article while the authors considered this two-component definition, they nevertheless favored one component over the other one, behaving as if the two components could be taken separately. They are victims of the "Cappuccino syndrome": the presence of steamed cream and coffee is necessary but not sufficient, and the order in which the two components are arranged, the cream on top of coffee makes the specificity of the cappuccino. Just so for the definition of culture. The "ethnographic approach" that the authors favored will not provide sufficient evidence to claim the presence of culture. A similar problem exists when establishing the origin of sex differences: observing males behaving differently from females, one could claim that it is a sex difference, genetically determined, only if the causal link between sex genes and the behavior is demonstrated by means of experiments, as Bernstein (1978) suggested and Goy (e.g., 1996) did. In humans, and in chimps to a lesser extent, the ethnographic approach for assessing the existence of culture is acceptable only because there is sufficient evidence that humans are capable of every form of social learning including imitation. But even implicitly, the two-component definition of cultural transmission is always applied to humans and not overlooked.

Socialization and cultural transmission. To imply that the spreading of a behavioral innovation occurs through social learning restricts culture to social species. Sociality is defined as a type of gregariousness with the specific feature of an interattraction between individuals of the same species (Deputte 2000). Sociality implies the permanence of groups of conspecifics showing a network of relationships between them. As a consequence, every individual born in a social group will develop within a social context. It has been demonstrated that the expression of species-specific behaviors, and possibly traditions as well, developed through social interactions: the richness of an individual repertoire is a function of the size of the social network of this individual and/or the richness of partners' repertoires (Deputte 2000). But it would be wrong to conclude that culture is a compulsory by-product of sociality because learning within a social context is not necessarily social learning. Social partners do represent the necessary context for an individual to express its species-specific potentialities (cf. isolation studies and "wild child" cases, such as Victor from Aveyron, in humans). But within a social context all forms of learning co-exist including individual forms, trial-and-error, associative learning . . . and social ones, like observational learning and its highest form: imitation. All these alternative forms of learning have to be considered as possible before jumping to the conclusion that it could only be cultural (social learning) transmission. Observational learning and possibly imitation have to be demonstrated in a species if one wishes to infer that they are mechanisms of transmission of innovative behavior (see Visalberghi & Fragaszy 1990).

If scientists wish to study how animals fly they will not take the chimpanzee as a model. If scientists wish to study how animals walk quadrupedally they will not take the rattlesnake as a model. If scientists wish to study culture, it is better to select social species where social learning has been demonstrated than many species of cetaceans for which the relevant data do not exist. There is no need to speculate desperately before these data become available. Let us put the horse before the cart.

So how *do* they do it?

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Abstract: While the evidence that cetaceans exhibit behaviours that are every bit as cultural as those recognised in chimpanzees is unequivocal, I argue that it is unlikely that either taxon has the social cognitive mechanisms required to underpin the more advanced forms of culture characteristic of humans (namely those that depend on shared meaning).

Rendell and Whitehead provide a convincing case for the claim that whatever it is that can be classed as culture in primates (notably great apes) must necessarily apply to cetaceans. They are right to draw attention to the fact that observationalists (mainly ethologically-oriented field workers) and experimentalists (mainly laboratory-based comparative psychologists) disagree fundamentally about what evidence they are prepared to accept for the existence of cultural behaviour. Indeed, humans would often fail the rather stringent criteria demanded by the comparative psychologists. The situation is an unsatisfactory one and urgently needs to be resolved in the interest of progress.

However, the roots of this dispute raise an interesting issue. If cetaceans do aspire to phenomena that we would be willing to call cultural in higher primates, what does this tell us about the cognitive mechanisms involved? Does dolphin cultural behaviour involve the same kinds of cognitive processes, supported by the same kinds of neurological mechanisms, as chimpanzee (and ultimately human) cultural behaviour?

The neuroanatomical evidence would initially incline us to answer "no," because dolphin brains (at least) are organised rather differently to primate brains: the dolphin neocortex is thinner and lacks some of the cellular layers present in primate neocortex (Morgane & Jacobs 1972). Nonetheless, it is perhaps possible that similar cognitive functions can be supported by somewhat different neurological mechanisms. What cognitive functions might be required? Social (imitative) learning must be one of these, but one suspects this is not a particularly advanced phenomenon, since there is good experimental evidence that even the lowly rat can manage this kind of transmission (Heyes 1994b; Laland & Plotkin 1992). Even though social learning must be important as the mechanism of inheritance for cultural phenomena even in humans, it is difficult to see how it can stand as the critical marker for true cultural behaviour.

A more plausible suggestion, perhaps, is that cultural behaviour depends on advanced social cognitive functions. At least in humans, adoption of cultural practices or beliefs often seems to depend on an implicit recognition that the cultural item has social significance. Cultural practices commonly identify us as belonging to some small subset of the population as a whole: cultural practices (including such phenomena as dialects) are badges of group identity (Nettle & Dunbar 1997). Such a definition of culture would lead us perhaps to look for evidence for mechanisms like secondary representation and meta-representation (or theory-of mind, ToM), and for behaviours like teaching that depend on these more advanced social cognitive processes.

I cannot speak for the latter (although claims of teaching have certainly been made in respect of chimpanzees). However, I can comment on the question of social cognitive processes like theory-of-mind, since in my lab we have attempted to test both chimpanzees and dolphins for ToM using the standard kinds of false belief task that developmental psychologists have identified as the crucial marker. The chimpanzees showed modest performance on such tasks (at least insofar as they significantly out-performed autistic humans), but their level of achievement was roughly equivalent to 3–4 year old children (Dunbar 2000; O'Connell 1996). However, subsequent tests failed to replicate even these results (Call & Tomasello 1999).

The initial tests of dolphins on false belief tasks looked promising, with the dolphins succeeding on a task that chimpanzees failed but children passed easily. However, there remain some questions about uncontrolled cuing in the experimental design that have yet to be fully resolved. A subsequent attempt to replicate these results in a different population (which controlled for at least three key sources of confound) produced negative results.

If we take these results at face value, we might be inclined to conclude that both taxa can aspire to something analogous to the kinds of secondary representation achieved by 3–4 year old children (i.e., those who are beginning to be able to use belief-desire psychology successfully in inferring simple mental states, but who have yet to develop the more sophisticated ability to understand the complexities of another's mind that is deemed to be characteristic of older children and normal adults). But, on present evidence, it seems unlikely that either taxa can aspire to full blown theory-of-mind (second order intentionality) and the prospect that either could run the more advanced levels of intentionality habitually exhibited by adult humans (on current evidence, fourth order intentionality: Kinderman et al. 1998) seems remote.

Without at least second order intentionality, it seems unlikely that either taxon could ever aspire to full human-like language, since the real cognitive burden of language probably lies in the mind-reading that listeners have to do in order to fathom out just what speakers mean rather than in the neural costs of syntax. It is even possible that full blown language depends on higher orders of intentionality beyond formal ToM.

More importantly, if human culture in its fullest sense does depend on shared meanings in a mental world, then it seems unlikely to me that either of these taxa could ever aspire to the levels of culture that we see in humans: these kinds of shared meanings often reflect metaphysical rather than superficial descriptions of the world, and this surely necessitates at the very least second (possibly third?) order intentionality because the individual has to be able to divorce itself from the immediacies of the world as experienced in order to be able to imagine that the world could be other than it is. In a word, it may be that only humans will ever aspire to religion and literature, because only humans have the required depth of reflexiveness that is necessary to make either of these things possible.

This is not to decry the evidence that both chimpanzees and dolphins (and whales!) exhibit forms of behaviour that we should recognise as cultural in its truest sense. But it is to suggest, perhaps, that there are levels of culturalness, and that the evidence so far suggests that perhaps only humans aspire to these more advanced forms.

Cetaecean culture: Philosophical implications

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Abstract: Culture among cetaeceans has important philosophical implications. Three receive attention here. First, these animals are more like humans than we had previously thought. Even so, we must affirm and respect their otherness. Second, only a fresh approach to research makes this kind of information available. Third, whales and dolphins should now be included with us in an extended moral community.

What if whales and dolphins had their own recognizable culture, as determined in accordance with a commonly acknowledged set of criteria for culture? What if they proved to be among those nonhuman animals (possibly including the great apes, elephants, and other species) of which this could be said? What would be the implications for human beings, and more specifically for our treatment of cetaeceans? These are the kinds of questions that must be faced in light of the research done by Rendell and Whitehead (R&W), and reported in this journal. The conclusion drawn by R&W seems indisputable, based on a wealth of empirical data and cautiously worded inferences: *whales and dolphins live and develop within their own unique species-specific, even group-specific cultural contexts.*

What should we make of these findings? What do these strange facts mean to the scientist and nonscientist alike? To begin with, let us observe that perhaps they are not all that strange, and we shouldn't be too surprised. The idea has been around for decades, if not longer, that dolphins not only have culture but also philosophies, perhaps even metaphysical theories and forms of spirituality far in advance of our own (Lilly 1975). This may have been wild fantasy or at best science fiction in the opinion of many. Nonetheless, while the truth may not turn out to be so glorious or dramatic as this, such speculations often prepare the way for a breakthrough in the way we see and think about things. Even apart from this, however, the intelligence, curiosity, complex communication, and other humanlike qualities of some cetaeceans have been well established both anecdotally and experimentally.

The major challenge is how we might best create a mental space in our outlook on nature that will accommodate cetaecean culture. To start with, animals with culture become even more like us than they seemed before the discovery or confirmation of this dimension of their existence. And they become less like beings whose behaviours are instinctually or genetically preprogrammed. This "becoming," of course, signifies a change that takes place in *our* perception, in *our* heads, not in their mode of existence, which remains what it always has been and which we have merely learned to decipher to a certain extent. We may be contemplating the obvious here, but it deserves saying nonetheless, for humans are used to evaluating animals in relation to how well the latter measure up to some human norm of ability or attainment. Well, it appears that whales and dolphins have, in any event, done this once again. But can we see beyond this limited perspective? Can we appreciate them in their own right as cultural beings? Let us hope so. We cannot expect that we shall be able to escape entirely from our anthropocentric locus of evaluation, however, since all definitions of culture are bound to be drawn in the first instance from human contexts. Yet even if this be true, we can understand and value what (for want of a better term) we may call "alien cultures" for their own sake – as having a point and purpose that is in no way instrumentally important to, or dependent upon, us and our parochial interests and needs. Such cultures of otherness flourish according to their own rhythms which we cannot merely assimilate to our own, no matter how hard we try. And for this reason, many of the practices that constitute them may be and remain incommensurable in relation to our understanding of the workings of our own culture and cultures similar to ours.

There are clear epistemological implications of the R&W research. First, as they assert, controlled experiments are out of the question by virtue of being both unmanageable and counterproductive. Therefore, a choice has to be confronted of either closing down access to research in this area, and hence meaningful discussion in regard to the possibility of cetaecean culture, or else accepting that the issue can be explored as best we can only within a vast natural marine environment. It takes a bold and imaginative investigative strategy to surmount this problem, which these authors have demonstrated. The data are out there, and it is we who must seek a way of gathering and processing them that will enable knowledge to be gained, rather than invoke a standard of certainty, a skeptical barrier, that prevents us from seeing something new. Second, R&W reach their conclusion by eliminating alternative hypotheses, leaving their own as the most plausible alternative. This is not an eccentric procedure, but rather one which fits the domain of data with which they are working and which reflects the pragmatic decision (just described) to pursue such studies along the best available avenue. Furthermore, the procedure is one that is (or ought to be) followed in other areas of science where controlled experiments are simply not on (one thinks here of cosmology or theories about the origin of life, for example).

Finally, there are ethical implications to be considered. Perhaps a minimal starting-point here is to affirm the principles first promulgated by Paola Cavalieri and Peter Singer in framing *A declaration on Great Apes* (Cavalieri & Singer 1993). Chimpanzees, gorillas, and orang-utans – also animals with cultures of their own – share with humans a common extended moral community, and this entails that each member has three basic rights: to life, individual liberty, and freedom from torture. I submit that we are now at the point, owing to the findings of scientists like R&W, where dolphins and whales should be seen as entitled to *their* own "Declaration" affording the same guarantees. If such basic moral rights were also reaffirmed by law, cetaeceans would then receive sanctioned protection from hunting, captivity, wounding, habitat threats, or invasive experimentation. This would be an enormous step forward – not only for cetaceans but also for human moral evolution.

With respect to how we ought to treat whales and dolphins, the handwriting has been on the wall, or shall we say on the waves, for some time now. But research aimed at bringing their cultural lives into focus seems to clinch the matter, so far as fundamental moral obligations are concerned. Like the great apes, we owe these magnificent sea-dwelling creatures something, if only the right to survive and flourish free from human interference (Fox 1996).

R&W deserve our thanks for their careful and objective investigations. What the rest of us have to decide is whether we are ready for the new world of interspecies communication, empathy, and responsibility that is now dawning on the horizon of human knowledge.

Communicative cultures in cetaceans: Big questions are unanswered, functional analyses are needed

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Abstract: Demonstrating cetacean communicative cultures requires documenting vocal differences among conspecific groups that are socially learned and stable across generations. Evidence to date does not provide strong scientific support for culture in cetacean vocal systems. Further, functional analyses with playbacks are needed to determine whether observed group differences in vocalizations are meaningful to the animals themselves.

Rendell and Whitehead (R&W)provide an important and timely review of studies suggesting culture-like processes acting on cetacean behavioral systems. The question of whether culture might influence behavioral variation in nonhuman animals offers an exciting, theoretically powerful area of current research. Interpretations of work in this area depend largely on one's view of "culture." For some, culture represents behavioral variants not attributable to genes, the physical environment, or individual learning – in other words, variants due to social learning. For others, imitation and teaching are the social learning processes required for behavioral variants to represent culture (Galef 1992). R&W take the former view. While this more liberal view is problematic (see Galef 1992), I accept it for the present purposes and instead focus on whether current evidence supports the authors' views. In particular, a major branch of the authors' argument is that systems of cetacean vocal communication represent culture. I argue that the scientific evidence does not support this view firmly enough. Cetacean vocal traditions probably fit the liberal definition of culture, but probably is not a particularly satisfying scientific answer. Much more work is needed.

Whether systems of behavior are culturally transmitted across generations is the question of utmost interest from an evolutionary perspective in studies of culture. To demonstrate cultural transmission of vocal systems experimentally, certain criteria need to be met (Freeberg 2000). Vocal traditions must be characteristic of groups, must be socially learned, and must be fairly stable across generations. With most cetaceans, as R&W point out, testing cultural processes experimentally is simply not possible. However, ethnographic approaches can provide answers.

Here I focus on how well the peer-reviewed journal literature supports the authors' assertions that cetacean vocal traditions represent culture. The calls of killer whales provide arguably the strongest data: there are group differences, the differences are probably due to social learning, and they appear stable across several years (Ford 1991; Stranger 1995). One way of demonstrating social transmission of vocalizations would be to show that calls are indeed transmitted across generations matrilineally. Thus, an individual's call types should be more like its maternal grandmother's than its paternal grandmother's (the reverse of paternal-line transmission in Darwin's finches – Grant & Grant 1996).

For sperm whales, statements similar to those made for killer whales above could be made, though perhaps less strongly (Weilgart & Whitehead 1997). However, as stated by R&W, "sperm whale groups are not themselves particularly stable, often consisting of two or more largely matrilineal units which swim together for periods of days." In the avian species the black-capped chickadee (Poecile atricapillus) flocks show group-distinguishing calls, but because chickadee flocks are stable for only several months the authors argue they "do not support persistent cultures." One wonders how the authors can argue, though they do, that the day-to-day groups of sperm whales can therefore support persistent cultures.

The evidence for song as culture in humpback whales seems the most difficult to interpret. There probably are worldwide group differences, although to my knowledge no systematic comparison of such large-scale group differences in humpback song exists. Songs are likely socially transmitted, with all group members sharing the same song type during a year (Payne & Payne 1985). Across years, however, the songs show progressive change to such an extent that after several years, little if any of the original song components remain. Thus, there is little documented evidence of group differences maintained across generations, a necessary criterion for vocal systems to represent culture.

One problem facing the interpretations one can make from much of this work is whether the vocalizations purported to be characteristic of the group are, in fact, representative of all the members or just one or two members. For culture this concern is fundamental, as reported "group" differences may be nothing more than individual differences. The question is, how do we know the entire group has been recorded, and not just one or two particularly vocal individuals? For humpback whales, no information on the extent of group sampling is provided. For sperm whales, individuals can be successfully tracked and recorded, using a calibrated three-microphone array (Watkins & Schevill 1977). In the sperm whale studies suggesting click coda differences by group, however, this recording methodology was not used, so determining how many individuals were sampled per group seems problematic. Weilgart and Whitehead (1993) report sampling different individuals, but do not indicate how that was known. For killer whales, largely from evidence with captive animals, the data supporting group sampling are stronger (Ford 1989), but one would still like better indication that groups in the wild are being sampled sufficiently.

Perhaps the major missing piece of information for the cetacean work suggesting communicative cultures is that, to my knowledge, there have been no functional tests of vocal differences. (This problem is not faced solely by cetacean researchers, as there have long been similar critiques of studies of song dialects in birds.) To determine whether vocal differences are functional differences, playback studies are needed. With fine-scale acoustic analyses of calls, click codas, and songs, researchers demonstrate that vocalizations of groups differ, but it is not known whether the whales themselves make those group-level distinctions. Just because we can measure differences does not mean the animals perceive or care about those differences. If one recorded the speech patterns of individuals from Fifth Street of some city and compared them to the speech patterns of individuals from Sixth Street of that city, a detailed acoustic analysis would likely find group differences – differences that might mean nothing to those individuals. The point is, we will not know whether observed vocal differences do mean anything – whether they represent meaningful cultural variants – unless we functionally analyze the vocalizations with playbacks, letting the animals themselves answer the question of communicative cultures.

Where's the beef? Evidence of culture, imitation, and teaching, in cetaceans?

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Abstract: Vocal imitation does not imply an ability to imitate nonvocal motor patterns. Exponential growth in frequency of a behaviour in a population does not imply diffusion by social learning. Distinguishing analogues from homologues of human culture will avoid confusion in discussion of evolution of culture. Original sources do not demonstrate social learning, imitation, or teaching of intentional beaching or lobtail feeding in cetaceans.

Below, I address very briefly three aspects of the target article. I apologize for the uncompromising exposition, which surely fails to do justice to the complexity of issues raised.

First, for at least 100 years it has been acknowledged that it cannot be inferred from evidence of vocal imitation in a species that species members imitate motor acts other than vocalizations. Consequently, the implication in the target article that, because cetaceans have vocal traditions, they can learn other motor acts by imitation, is not convincing.

Second, in the target article, culture is defined to include cases where local enhancement supports transmission of behaviour. On such a definition, problem-solving guppies (Reader & Laland 1999) are bearers of culture. Of course, culture can be defined many ways, but there are differences between, for example, guppy aggregations and classic French cuisine that should probably be acknowledged in discussing "culture." Often, group-specific behaviours in animals are analogues, rather than homologues of human culture. Analogues need to be distinguished from homologues (Galef 1992; 1998a) both to focus discussion of the evolution of culture on relevant examples and to avoid misleading the uninitiated by using a word in common usage in an unusual way.

Third, I agree that "patterns of behavioral variation in time and space, which cannot be explained by environmental or genetic factors" (target article) suggest culture. However, I am not comfortable with the rich interpretation of selected data apparently required to attribute teaching, imitation, ratchetting, and culture to cetaceans.

Questions that need to be answered are: (1) Do subpopulations of a species differ in their behaviour? [In cetaceans, the answer is clearly, yes.] (2) Do such differences in behavior reflect social learning of some kind? [In cetaceans, in some cases, the answer is, probably yes], and (3) What kind of social learning is involved? [In cetaceans, the answer seems to be, we do not know]. Only after such questions are answered, can it be decided whether observed variation is analogous or homologous with human culture.

Because space is limited, I discuss just the two observations of variation in cetacean behaviour on which the target article depends most heavily in making the case that cetaceans have culture in domains other than the vocal: that is, lobtail feeding by humpback whales and intentional beaching by killer whales. To put those two examples in context, however, R&W's Table 3 lists 16 cases of observed behavioural variation among cetacean populations. In none of the 16 do the authors consider it likely that ecological or genetic variation produces behavioural variation.

Humpback whales. First, I quote from the paper (Weinrich et al. 1992) used in the target article to support the conclusion that ecological changes are unlikely to account for spread of lobtail feeding in humpback whales.

> A major change in diet did occur for New England humpback whales immediately prior to the onset of our study. . . . When this shift occurred, sand lance became increasingly important in the diet of humpback whales. . . . sand lance . . . would react to external stimuli by clumping more readily than the larger, stronger herring (Pitcher & Wyche 1983), possibly favouring use of a disturbance such as that created by a lobtail . . . the increase of sand lance in dietary importance immediately prior to the onset of this study may have encouraged development of a new, efficient manner of exploiting that prey particularly among younger animals. (Weinrich et al. 1992, p. 1070)

I do not see this discussion as consistent with the assertion in the target article that ecological variables are unlikely to be important in diffusion of lobtail feeding. Further, there can be no evidence of "ratcheting" here, as bubble feeding, the basis of lobtail feeding, is not socially learned.

Second, the data in R&W's Figure 1, though consistent with the hypothesis that lobtail feeding was socially transmitted, is of limited value. Although an exponential equation provides the best fit for the data, it is a very poor fit indeed for years 1 to 7. More important, exponential increase in the number of animals exhibiting a behaviour can result if animals show a normal distribution in latencies to learn a behaviour individually. Consequently, exponential growth of frequency of a behaviour in a population does not demonstrate social learning of that behaviour.

Killer whales. The target article depends heavily on the observations of Guinet and Bouvier (1995) to show that: (1) young killer whales learn to beach by imitating adults and (2) adults actively teach their young to beach. For example, the authors of the target article assert "the behaviour of A5's mother seems to have enabled her calf to learn the hunting technique at least one year earlier than A4" (target article). However, the relative ages of A4 and A5 are not known with any certainty ["Both calves were first observed in 1986 . . . According to the linear regressions obtained for the two calves, and based on an average birth length of 2.36 meters . . . we estimate A4 was born in 1984, while A5 was probably born in 1985" (Guinet & Bouvier 1995, p. 29)]. Further, Hoelzel (1991) has reported greater success by a female (A1) when hunting in the surf zone with a single juvenile, than when hunting alone.

Yes, swimming into shallow water endangers young whales, and yes, adults do engage in activities which sometimes facilitate stranded pups' return to deep water. However, to suggest that this is evidence of teaching is misleading. Surely, you do not teach a child to swim by returning it to shore, should it start to drown. Life saving provides an environment where learning can occur, but it is not teaching.

Further, we do not even know whether juveniles are more frequently in company with adults when beaching than when engaged in other activities. Similarly, although adult killer whales push young up and down the beach and throw prey around, we have no systematic data on the frequencies with which such pushing and throwing increases or decreases juveniles' access to prey.

Conclusion. Rich interpretations of a subset of field observations, or for that matter of selected laboratory data, may suggest directions for further work, but show nothing. Assertion of knowledge, where no knowledge exists is as likely to prove counterproductive in the twenty-first century as it did in the nineteenth.

Do humpback whales learn socially to lobtail feed? Do killer whales teach their young to hunt pinnepeds in shallow water? I really do not know, but then neither does anyone else.

Laboratory evidence for cultural transmission mechanisms

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Abstract: The mechanisms for cultural transmission remain disputable and difficult to validate through observational field studies alone. If controlled experimental laboratory investigation reveals that a putative mechanism is demonstrable in the species under study, then inferences that the same mechanism is operating in the field observation are strengthened.

Rendell and Whitehead (R&W) have performed a valuable service in calling attention to the possibility of culture in cetaceans and by providing several lines of supporting evidence for four cetacean species. We believe, however, that R&W's definition of culture requires some revision, and their view of the importance of laboratory studies, expansion. Although noting that the process (cultural transmission) is crucial to the understanding of the product (culture), R&W define culture as "information or behavior acquired from conspecifics through some form of social learning" (adopted from Boyd & Richerson 1996). This definition emphasizes how culture is achieved rather than what culture is. Thus, culture is not the information or behavior acquired per se, but the product of that acquisition expressed by the members of a social group. Culture, in turn, affects and controls behaviors of the group members, behaviors that may extend well beyond those copied or taught. Furthermore, as noted by Wrangham et al. (1994), culture is not an all-or-nothing phenomenon, but requires a broad definition that encompasses "culture-like, pre-cultural, or protocultural manifestations" (p. 1).

In effect, R&W use a "reverse engineering" approach, identifying behaviors that appear to be common and unique to some subgroup, and then attempting to impute social mechanisms through which these behaviors may have been transmitted. Imitation and teaching are identified as the prime social mechanisms, as noted by most researchers, but R&W would like to include also other forms of social learning, such as stimulus enhancement (an animal's behavior is influenced by what a conspecific is attending to) or local enhancement (an animal's behavior is influenced by where the conspecific is located when it is performing a behavior). However, R&W offer no examples of these mechanisms as causative agents in any imputed cetacean cultural expression. R&W rightly point to the importance of both controlled laboratory studies and field studies to the understanding of culture in cetaceans. Nevertheless, in their emphasis on and zeal for the ethnographic approach, they fail to appreciate fully the important role of laboratory studies in verifying whether particular mechanisms may be available to the species under study. Laboratory findings, obtained through the rules of scientific evidence, can reveal whether dolphins are capable of a particular form of social learning. Positive findings may stimulate a search for similar capabilities among wild animals or be used with increased credibility to explain their observed behaviors. For example, laboratory findings of dolphin vocal mimicry (Richards et al. 1984) have impelled subsequent field studies of vocal imitation among wild dolphins (Tyack 1986b), as well as theories about the functional significance of such imitation (Janik 2000). The ethnographic approach favored by the authors, which relies primarily on observation or anecdote, cannot easily conclude whether imitative mechanisms are involved in an observed apparent cultural expression. However, the presumption becomes stronger if there is independent compelling laboratory evidence for imitative abilities.

What is the evidence for cetacean imitation? Actually, R&W seem a little confused on this matter, saying within the same paragraph "there is little concrete evidence for imitation or teaching in cetaceans," and then only three sentences later, they say "there is some good evidence that cetaceans can both imitate and teach" (sect. 2). In fact, a recent review of imitation in bottlenosed dolphins (Herman, in press) summarized a suite of laboratory studies, including both previously published and unpublished materials, demonstrating that imitative abilities in this species are far more robust than is indicated by the brief summary given by R&W. The bottlenosed dolphin may be properly called an *imitative generalist.* Its imitative abilities extend not only to vocal and motor mimicry, including novel acts and actions on objects during motor mimicry, but also to self-imitation, defined as the ability to copy one's own past behavior. Motor imitation of conspecifics as well as of human models was reported, both for behaviors illustrated live and for behaviors appearing only on a television screen watched by the dolphin. Immediate as well as delayed imitation was demonstrated. A key element in these studies was that in all three cases, motor-, vocal-, and self-imitation, imitation was carried out by the dolphin only if it was requested to do so through a symbolic abstract gesture given by the trainer (cf. Custance et al. 1996). Thus, the dolphin developed a broad concept of imitation. Inasmuch as a large variety of behaviors were demonstrated, and these varied from trial to trial, the dolphin had to maintain a mental representation of the behavior performed and update that representation as each new behavior occurred. Mental representation, as a cognitive trait, is in keeping with other extensive advanced cognitive and communicative abilities demonstrated in the bottlenosed dolphin (e.g., Herman et al. 1993). Cognitive traits likely working in concert with imitation during the process of cultural transmission include attention, perception, memory, and communication. Each of these traits has been addressed in laboratory studies with bottlenosed dolphins, revealing their functional characteristics and competencies (e.g., see reviews in Herman 1986). Although laboratory studies of imitation in cetaceans have been largely limited to bottlenosed dolphins, we would not be surprised to see similar capabilities revealed for killer whales if tested in laboratory studies.

Still on the topic of imitation, we feel it necessary to comment on R&W's statement that "the Grey parrot rivals the bottlenose dolphin in social learning ability, being capable of both vocal and movement imitation (sect. 2)." A strong distinction can be made, however, between the imitative capabilities of these two species. Whereas the dolphin can copy many different motor behaviors in real time, the parrot exhibits imitation of only a few motor behaviors and only after a long "incubation" period (months or years) of having observed the behavior multiple times (Moore 1992). Moreover, unlike the case for the dolphin, there is no evidence thus far on whether the parrot can understood motor imitation as an abstract concept.

In contrast to imitation, the data on teaching by animals (pedagogy) are scant and controversial (see reviews in Caro & Hauser 1992; Visalberghi & Fragasy 1996). Teaching implies an intention to convey knowledge or skills to the pupil, and an understanding that the pupil is deficient in those areas being taught (Cheney & Seyfarth 1990). Under this view, teaching requires a theory of mind, yet to be demonstrated in cetaceans or convincingly in other animal species. The anecdotal example of an Orca mother teaching beaching to her young is compelling, but we do not know whether the stated criteria were met. The mother's actions are described as a series of goal-directed behaviors, but some of these might be explained as a series of other independent mechanisms. For example, the calf accompanying the mother on the beach could be an imitative act, and the mother refloating the calf could be interpreted as succorant behavior. Here, the value of controlled laboratory studies becomes apparent again. Through such studies, we are more likely to reach a firm conclusion as to what aspects of pedagogy are or are not within the capabilities of a cetacean species. A positive finding would likely motivate careful study of wild populations for pedagogical behaviors.

Finally, we have a brief remark on song transmission in humpback whales. R&W, relying on work of Payne and Guinee (1983) comparing songs in Mexico and Hawaii, state that whale songs are virtually identical in these widely separated winter grounds and "evolve as one" (sect. 1). However, a more recent comparison of songs in Hawaii, Japan, and Mexico in the same year (Helweg et al. 1990) showed three themes common across these three winter grounds, but that other themes were either unique to a given ground or were shared by only two of the three. Although there is ample evidence for song convergence within a winter ground, the more likely mechanism for similarities across grounds may not be through the long-range SOFAR channel, as postulated by R&W, but through singing during common migration routes (e.g., Clapham & Mattila 1990), singing occurring in the summer grounds (albeit to a limited extent) (Mattila et al. 1987), and by the same whales visiting different winter grounds in different years (Darling & Juarasz 1983; Salden et al. 1999). Any of these mechanisms could initiate or produce commonalities across winter grounds.

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The use and abuse of ethnography

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Abstract: Human beings grow into cultural knowledge, within a social and environmental context, rather than receiving it ready made. This seems also to be true of cetaceans. Rendell and Whitehead invoke a notion of culture long since rejected by anthropologists, and fundamentally misunderstand the nature of ethnography. A properly ethnographic study of cetaceans would directly subvert their positivist methodology and reductionist assumptions.

As a nonspecialist, I find much of what Rendell and Whitehead (R&W) have to say about the activities of cetaceans quite fascinating. As a social anthropologist I have no qualms (as do many of my colleagues) about extending approaches to cultural understanding developed for the study of human societies to studying the societies of nonhuman animals. But I do object when the approach that is extended to nonhumans – in this case cetaceans – is one that is itself based on the crude and simplistic extension of models derived from animal behaviour studies to humans. And when this approach is described as "ethnography," my objection verges on consternation.

In the perspective favoured by R&W, what they call culture is brought in to account for the residue of behavioural variation that cannot be attributed to ecological or genetic factors. It apparently consists of elementary behavioural instructions, or "traits," that are transmitted across generations by one or another form of social learning. Admittedly, the idea that culture consists of transmissible particles of information, analogous to genes, once enjoyed some currency in anthropology, and still persists in some quarters. For the most part, however, it has been dismissed as incoherent, and its current resurrection within evolutionary ecology and psychology looks decidedly anachronistic. Part of the problem lies in the very logic by which social learning is distinguished from individual learning. The notion of cultural transmission – and the theories of gene-culture co-evolution that are based on it – ultimately depends on this logic. But its effect is to remove the sphere of the learner's involvement with others from the contexts of his of her practical engagement with the world. It is as though human beings first received their knowledge ready-made from predecessors, and subsequently imported it into the settings of practice. By and large this is not what happens, however. Rather, novices grow into the knowledge of their culture, within an environmental context furnished by the presence and activity of others. Judging from the evidence presented by R&W, the same may be true of cetaceans.

Moreover, the idea that culture is a third determinant of behaviour, after allowance has been made for environmental and genetic determinants, is perfectly absurd. Behaviour is the surface appearance of the activity of the whole organism in its environment; it is not an effect of cultural, ecological, and genetic causes. R&W might try applying their explanatory framework to an analysis of their own scientific practice. It would not take them very far. (If their practice were determined in this way, we would have no cause to take their arguments seriously – they would just be products of their genes, their environment, and their culture.) If the idea does not work for scientists, who are human, it should not work for any other humans. And if it does not work for humans, I do not see any reason why it should work any better for nonhumans.

Citing an article by Richard Wrangham and two fellow primatologists (Wrangham et al. 1994), R&W tell us that their way of inferring "culture" from the data of field studies may be "likened to ethnography in the social sciences." Wrangham et al., however, are not social scientists, and they do not know what they are talking about. For the best part of a century, ethnography has been the principal research method of social and cultural anthropology, and has also been adopted to an increasing extent by sociologists. It goes far beyond the mere recording of observed behaviour to achieve an understanding that is sensitive to the intentions and purposes of the people themselves, to their values and orientations, to their ways of perceiving, remembering, and organising their experience, and to the contexts in which they act – all of which add up to what anthropologists generally mean by "culture."

What R&W call ethnography is a million miles from what ethnographers, whether in anthropology or sociology, actually do. This is for the simple reason that the proper conduct of ethnography and its rationale rest on philosophical principles concerning the nature of knowledge and understanding that run directly counter to the positivist methodology and reductionist assumptions built into the research programme set out in this article. It would be exciting to see a *genuine* ethnographic approach being applied to research on – or rather with – nonhumans, though I am afraid that the results of such research would likely be dismissed, out of hand, as "unscientific" (in much the same way as has the very extensive knowledge of animal behaviour possessed by indigenous people). The least one would expect of anyone considering an ethnographic study of non-humans, however, would be that they were minimally conversant with the anthropological literature on the promises and pitfalls of the ethnographic method as applied to humans, its epistemological underpinnings, and the understanding of culture that it entails. To sideline this literature altogether, as is done here, seems inexcusable.

It is sad to see such rich empirical material, about such wonderful creatures, harnessed to such an impoverished theoretical agenda.

Is cetacean social learning unique?

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Abstract: Studies on captive dolphins have shown that they are capable of social learning. However, ethnographic data are less conclusive and many examples given for social learning can be explained in other ways. Before we can claim that cetacean culture is unique we need more rigorous studies which are fortunately not as difficult as Rendell and Whitehead seem to think.

A definition of culture that includes any information transmitted through social learning is very broad. Using it, we find culture not only in primates and cetaceans but also in other mammals (Box & Gibson 1999), birds (Catchpole & Slater 1995), fish (Helfman & Schultz 1984), and possibly even in cephalopods (Fiorito & Scotto 1992). However, despite the wide range of taxa that show social learning it is interesting that cetaceans display a high degree of versatility in social learning that is not quite as common. The best examples come from captive studies. Bottlenose dolphins are clearly capable of vocal learning (Richards et al. 1984) and observational data suggest that they are equally adept at copying other motor behaviour (Bauer & Johnson 1994; Herman 1980). Such versatility raises the question of how widely social learning is used in less studied species of cetaceans. However, the only convincing ethnographic evidence for social learning comes from humpback whales using learned songs. Humpback whale song and the abilities of bottlenose dolphins are impressive examples for social learning. But does this justify concluding that social learning is used as widely as Rendell and Whitehead (R&W) suggest? Extrapolating data from a few species to all other cetaceans is not a good approach to study culture. Currently, other explanations that do not involve social learning are still equally likely for most examples for social learning given in the target article.

Genetic constraints. R&W argue that group-specific behavioural traits among sympatric matrilineal groups are indicative of social learning. There are two problems with this statement. First, males may mate primarily with the same group of females over several seasons, which could result in group specific behavioral traits caused by genetic influence. Second, it is not clear whether sperm and killer whales primarily mate outside their pods. The references given by R&W do not suggest that either. Baird (2000) states that "genetic data are not yet available to positively confirm that mating occurs between resident pods." The second reference given by R&W does not exist. It seems to be a mixture of two papers by Ohsumi (1966; 1971), neither of which suggests in any way whether breeding occurs inside or outside of maternal pods.

In fact, there is a clear correlation between mtDNA and behavioral patterns in matrilineal groups of sperm whales (Whitehead et al. 1998). R&W state "it is unlikely to the extreme" that mtDNA encodes behavioral traits. However, direct encoding is not the only way in which genes can influence behaviour. Mitochondrial DNA encodes mitochondrial proteins. Differences in their effectiveness would affect the energetic budget of animals and is therefore likely to affect a wide range of behavioral patterns. Due to the respiratory role of mitochondria, direct selection on mitochondrial genes is a distinct possibility in a diving mammal and may explain low mtDNA variability in general, an argument that also questions the cultural hitchhiking hypothesis (Whitehead 1998).

Environmental variables. R&W dismiss environmental variables as an explanation for behavioural specializations like lobtail feeding in humpback whales and sponging in bottlenose dolphins. However, the target article acknowledges that a shift in the available prey species accompanied the emergence of lobtail feeding in humpback whales. Even in primates that use social learning in other contexts, subtle shifts in food quality can lead to changes in foraging strategies that do not involve social learning (Visalberghi & Addessi 2000). Furthermore, the exponential relationship plotted in Figure 1 relies heavily on the data from 1987, which is the year with the lowest sample size (Weinrich et al. 1992). Similarly, it is incorrect that sponging dolphins in Shark Bay are exposed to the same environments as their conspecifics in the area. Sponging animals spend a larger amount of time in deeper water with a different bottom structure than other individuals in the population (Janik & Mann, unpublished data).

Individual learning and social effects. Even though learning seems likely in some cases, it is important to look at what aspects are learned and how. The feeding interactions with humans in Australia and Brazil could have equally likely arisen out of individual learning. In each of these cases food is involved and dolphins are easily trained with food reward. Such training need not necessarily be apparent to the humans involved as long as there is a stereotyped sequence of actions that leads to a food reward. The only social aspect may be local enhancement for infants that travel with their mothers. Individual learning may also explain beach feeding by killer whales. The evidence here comes from two individuals that could have differed in various other aspects besides their exposure to beaching animals. Furthermore, differences between animals can also be caused by dominance relationships that exclude some groups or individuals from certain resources.

The "uniqueness" of cetaceans. This brief review shows that many causation cells in R&W's Table 3 should be filled with the word "unknown" (note that individual learning is not listed in this table even though it is often a possible explanation). Therefore, it is premature to claim that cetacean culture is unique among nonhumans. Claiming uniqueness also suggests that a truly exhaustive comparison across species has been conducted. But has it? Learned group-specific calls can be found in several bird species (Brown & Farabaugh 1997; Hausberger 1997) and the stability of cultural traits is impressive in sympatric groups of birds that live near sharp dialect boundaries (Catchpole & Slater 1995). Furthermore, social learning and its effects on behavioural variation have received little research attention in species that are likely to rely heavily on it such as elephants, parrots, or bats. For example, it is incorrect to conclude that vocal learning affects only one call type in greater spear-nosed bats, since it has only been studied in one call type.

R&W's pessimistic statements about what will be possible to study experimentally or not are astounding. Large whales have been studied in captivity (Ray & Schevill 1974; Watkins et al. 1988) and observations in the wild have already revealed aspects of the use of socially learned traits (e.g., Frankel et al. 1995; Janik 2000). Cetaceans are a promising group for the study of culture and some patterns like humpback whale song and bottlenose dolphin signature whistles may indeed be unique. However, comparative studies of social learning will be helped more if we increase our research efforts and keep using Occam's razor rather than speculate on probabilities.

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The promise of an ecological, evolutionary approach to culture and language

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Absstract: Dichotomous definitions of culture and language do not generate productive questions. Instead, more progress can be made by identifying components of each that other animals might plausibly possess. The evolutionary, ecological approach advocated by Rendell and Whitehead holds great promise for helping us to understand the conditions under which natural selection can favor similar capacities in differently organized brains.

Like culture, language has often been defined so as to turn questions about the linguistic capacities of nonhuman animals into either-or propositions: Either another species can acquire human language in all of its richness, or it cannot acquire language at all. I wholeheartedly agree with Rendell and Whitehead (R&W) that such dichotomizing definitions do not lead scientists to ask productive questions. Following similar logic, I have recently argued (Kako 1999) that research on the syntactic capacities of language-trained animals should be evaluated not against full human language, but against a set of "core properties" that one might plausibly expect another animal to possess: discrete combinatorics, category-based rules, systematic encoding of the relationship between events and their participants, and the use of grammatical elements to make meaningful distinctions (such as the difference between one and many). Under these criteria, three species – the African Grey parrot (*Psittacus erithacus*), studied by Irene Pepperberg (Pepperberg 2000); the bottlenosed dolphin (*Tursiops truncatus*), studied by Louis Herman (Herman 1987; Herman et al. 1984); and the bonobo (*Pan paniscus*), studied by Sue Savage-Rumbaugh (Greenfield & Savage-Rumbaugh 1990; Savage-Rumbaugh et al. 1993) – all show evidence of being able to acquire some of the properties of human language syntax (albeit to varying degrees). Moreover, these criteria, like those that R&W advocate for culture, suggest additional studies that might illuminate further precisely how much these animals have learned about syntax.

I share R&W's concern about the ecological validity of experiments conducted in captivity, especially in cases where little is known about the behavior of the species in the wild. The fact that the bonobo Kanzi can comprehend English about as well as a two-and-a-half year-old (Savage-Rumbaugh et al. 1993) is both impressive and puzzling: impressive because his competence outstrips that of all other apes previously studied (especially when we consider that his knowledge of English comes from naturalistic interactions with his trainers, unsupported by explicit training); and puzzling because bonobos do not appear to invent or combine word-like units in the wild. Nonetheless, I am more optimistic than R&W appear to be about the value of captive animal experiments. To suggest that many such studies measure only the "socio-ecological validity of the captive experiment" (in the words they quote from McGrew 1992) is to underestimate how informative these studies can be. Although it is true that the environments of captive animals exposed to a language-like system or to some form of culture differ markedly from their native environments, their successes and failures can nonetheless reveal a great deal about the "boundary conditions" of their cultural-linguistic capacities. No matter how much I expose my cats to language, or how hard I might try to train them with a system of rewards, they will not learn the meanings of any words, let alone how to interpret those meanings in combination. Yet the African grey parrot Alex has done just that (to nothing like a human level, of course – though the precise limits of his capacities are not yet fully known, Pepperberg 2000). To be sure, captive experiments on cetaceans are, for the reasons that R&W outline, mostly quite impractical. But when such experiments are feasible, I believe they should be actively pursued, despite the associated difficulties in interpretation.

This minor disagreement aside, I strongly endorse the evolutionary-ecological approach taken by R&W. I believe that this approach should be applied as widely as possible, so that we might better understand the environmental, social, and life-history conditions that favor the development both of cultural and of linguistic-communicative capacities. The alternative is to take a brain-centered approach, to assume that brains like ours are more likely than others to have these capacities. To be sure, the similarities between human brains and those of other apes increase the likelihood that their capacities may resemble ours. But we should not be so seduced by the idea that behavior depends on the specifics of brain structure that we neglect the exciting possibility that differently organized brains can be shaped by natural selection to perform similar functions. The fact that the African grey parrot and the bottlenosed-dolphin can both achieve some measure of syntactic competence cannot be attributed to their having "approximately human" brains. Nor can the fact that, as R&W have convincingly argued, several cetacean species show evidence of culture. For cultural capacities, the answer may well lie with the factors that R&W have identified, including environmental stability and the timing of menopause during the female life cycle. For linguistic competencies, I believe it lies at least in part in the similar cognitive demands placed upon African greys, dolphins, and apes by the complexity of their social environments (Kako 1999).

The question remains, of course, as to why cultural capacities manifest unassisted in the wild, while linguistic capacities do not. Whether this puzzle is real or illusory remains to be seen, as we know very little about how these animals communicate in their natural habitats. By applying to the study of communication the same evolutionary, ecological approach that R&W have so successfully applied to culture, we may learn a great deal about the physical, social, and life-history conditions that favor the development of linguistic capacities.

Does cultural evolution need matriliny?

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Abstract: Cetacean cultural transmission is associated with lengthened postmenopausal life histories and relatively stable matrilineal social structures. Although Homo erectus was not marine adapted, broadly comparable selection pressures, life history profiles, and social structures can be inferred.

My field of research is human cultural evolution. Palaeoanthropological strategic modelling (Tooby & DeVore 1987) requires generalised, cross-species research into how and why animals might pursue cultural strategies. With their excellent overview of the cetacean literature, Rendell and Whitehead (R&W) have contributed significantly to this endeavour.

Inevitably, definitions of culture have been rooted in anthropological rather than biological problems and concerns. Attempts to model the earlier phases of human evolution have correspondingly been plagued by conceptual habits and assumptions derived from theoretical linguistics, semiotics, hunter-gatherer ethnography, and similarly non-Darwinian fields. Contemporary human patterns have typically been projected back as explanations of supposed counterparts in the Plio-Pleistocene. A well-known example from the 1970s was the claim by archaeologists that Oldowan lithic traditions indicated modern hunter/gatherer-style food-sharing, cooperative hunting, cultural kinship, and even language (e.g., Isaac 1971; 1978). Although such ideas have since been repudiated within archaeology, in disciplines further afield, the damage was done. Evolutionary psychology to this day postulates an Environment of Evolutionary Adaptedness centred around a vaguely-defined cooperative hunter-gatherer lifestyle stretching back several million years (Bowlby 1969). Human cognitive architecture is said to have been irreversibly forged in this setting (Tooby & Cosmides 1992). The Chomskyan Language Faculty is correspondingly viewed as a Plio-Pleistocene adaptation enabling cooperative pooling of environmental information (e.g., Pinker 1994; Pinker & Bloom 1990).

Nonhuman cultural studies enable us to avoid working back from modern humans in this way, and instead work forward on the basis of generalised behavioural ecological principles and constraints. Human abilities for vocal imitation and learning lack plausible primate antecedents, but may be matched in songbirds and cetaceans. The cetacean literature documents complex group-on-group social dynamics and correspondingly flexible, sophisticated signature systems involving a measure of syntactical, combinatorial creativity – "phonological syntax" in Marler's (1998) terms. If signal evolution theory can elucidate the underlying principles and constraints, we may better appreciate how complex group-on-group signature and display strategies among our ancestors spurred the evolution of distinctively human phonological competences, without having to assume speech (Knight 1999; 2000). Cetacean greeting rituals and similar performances apparently serve group-bonding, trust-generating functions; it seems unlikely that syntactical speech – a low-cost, intrinsically unreliable system of communication – could have evolved in our own species independently of comparable confidence-building strategies and displays of social commitment rendering such signals worth listening to (Deacon 1997; Knight 1998).

In the case of killer whales and sperm whales, cultural transmission of dialects maps closely onto matrilineal social structures. We may well ask whether such elaborate vertical cultural transmission could occur at all if females were dispersing from natal groups, as happens among chimpanzees. Of course, evolving humans were at no stage adapted, as cetaceans are, to marine environments. The transition to *Homo erectus,* however, arguably brought with it analogous challenges and solutions. In the case of cetaceans, cultural transmission is associated with high levels of mobility, in turn resting on low travel costs. In *Homo erectus*, lowered travel costs and increased mobility were made possible by larger body sizes (McHenry 1994) and obligate, efficient bipedalism (Walker & Leakey 1993). It is plausible to suggest that in both cetacean and *Homo erectus* populations, reduced territorial restriction led to novel requirements for behavioural flexibility in response to habitat variability, this in turn prompting an increasing reliance on cultural transmission of key subsistence strategies.

In humans, post-reproductive females may enhance their fitness by provisioning daughters' offspring (Hawkes et al. 1997; 2000); cetaceans, too, have evolved long post-menopausal lifespans and pass on cultural knowledge within stable matrilineal clans. In their "grandmother hypothesis," O'Connell et al. (1999) argue that human-like life history profiles emerged with Homo erectus. As climate change in the Pleistocene deprived juveniles of accessible resources, senior females acquired novel responsibilities in provisioning children. A shift of foraging strategies toward carbohydrate-rich tubers enabled female-based kin-coalitions to congregate more densely and colonise a wider range of environments. Life history parameters in killer and pilot whales appear comparable to those of humans, but from the cetacean data it is unclear what role is played by senior female kin in helping offspring to survive. It would be instructive to know more about cross-species variability in cetacean life history parameters, enabling us to explore the conditions under which long post-menopausal life spans evolve.

This raises the question whether cultural transmission in the human case could have reached take-off point without the emergence of stable, female kin-bonded coalitions. Twentieth century social anthropologists (e.g., Lévi-Strauss 1969) have tended to assume male philopatry and female dispersal as the default human hunter-gatherer configuration, despite considerable variability among extant foragers. Some palaeoanthropologists (e.g., Foley & Lee 1989; Rodseth et al. 1991; Wrangham 1987) have made this the basis of their evolutionary models. Such writers typically invoke African ape precedents. But under wild-living conditions, and especially when compared with cetacean achievements, ape cultural transmission is puzzlingly patchy and restricted given these animals' impressive cognitive capacities. My own view (Knight 1998; 1999) is that the major obstacles to ape cultural transmission are political, the patchiness reflecting not cognitive deficits but the relative instability of male philopatric coalitions. In the light of the grandmothering explanation for the evolution of long postmenopausal lifespans, it seems likely that sophisticated cultural transmission in Homo evolved, as in the cetacean case, within female philopatric social structures (cf. Dunbar 1996; Knight 1991; 1997; Power 1997).

Cetacean culture: Slippery when wet

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Abstract: Cetaceans are likely candidates for social learning and culture. Meager experimental evidence suggests that some cetaceans possess the requisite cognitive skills for social learning. Equally sparse ethnographic data provide clues about possible outcomes of social learning. Although the available evidence is consistent with the notion of culture in cetaceans, caution is warranted due to the many gaps in the data.

As Rendell and Whitehead (R&W) suggest, cetaceans are likely candidates for culture, if culture is defined as behavior or knowledge acquired "through some form of social learning." They contrast the experimental approach and the ethnographic approach, and conclude that "excessive reliance" on the experimental approach is not productive in the study of culture in cetaceans. Of course, "excessive reliance" on any methodology is not productive, for so long as a methodology is productive it cannot be called excessive. Nonetheless, as R&W note, it is difficult to obtain appropriate experimental data on many cetaceans, which magnifies the importance of good observational data. In turn, however, this reliance on observational data should make us more cautious about the attribution of culture to these species. Overly rich interpretation of data is dangerous in any science, and the path advocated by R&W is potentially treacherous. The path need not be abandoned, but we should be careful where we step.

It is often difficult to specify the behaviors involved in social learning from ethnographic data, particularly when members of a species spend much of their life underwater (and typically out of view). R&W suggest that culture (i.e., social learning) can be "deduced" by ruling out genetic and environmental factors when behavioral variation within a species is observed. In order to validate such deductions, we need very good unambiguous data. However, observational data are rarely unambiguous. Indeed, R&W acknowledge that such data are often "incomplete and poor in detail."

The examples that R&W cite to support their conclusion that the "ethnographic evidence for cetacean culture is remarkable strong" illustrate the need for caution when fragmentary observational data are involved. For example, the notion that some bowhead whales imitate the calls of others demonstrates social learning only if we can be certain that imitation actually occurred. The simple observation that one animal produced a particular call after another animal has produced a similar call is not conclusive evidence for imitation. If the call already existed in the "imitating" animal's repertoire, the animal may have produced the call for reasons other than imitation. It is important to know why animals produce behaviors, not just that they do so.

Similarly, although the development of a novel feeding technique by humpback whales may reflect social learning, the possibility of independent individual learning cannot be ruled out. This is also true for the "sponging" behavior of dolphins. The fact that one calf of a sponging mother learned to sponge suggests social learning, but might also reflect independent individual learning. This dilemma also holds for dolphin calves' acquisition of cooperative foraging behaviors with human fishermen. The historical comparison of the initial and subsequent analyses of the spread of milk-bottle opening by blue tits and the dunking of sweet potatoes by Japanese macaques demonstrate that we must be cautious in the attribution of social learning based solely on observational data. What looks like social learning may in fact reflect other processes, which emphasizes the importance of attending to process as well as product.

A striking part of the humpback whale song story is that the songs of whales thousands of miles apart somehow "evolve as one." This is a problem for the notion of social learning rather than evidence for it. No matter how one tries to define social learning, the availability of a model or teacher to the learner is essential. It is hard to imagine how models or teachers become available at approximately the same times thousands of miles away from one another, which would be necessary in order to produce this simultaneous evolution.

The hypothesis that killer whales teach their young hunting skills is an exciting one, for such teaching would be a significant form of cultural transmission. However, it is not clear whether or not this "teaching" is intentional. Does the "teaching" whale intentionally provide models and learning opportunities for the "student"? Or is the "teaching" incidental, that is, the result of normal behaviors in which the "teacher" normally engages? This is an important consideration, and has considerable implications for the notion of cultural transmission in this species.

The vocal dialects of killer whales and sperm whales are consistent with the notion of social learning, but the analyses of these data are based on the group rather than the individual. Since the vocal repertoire of each individual in a pod is unknown, it is impossible to document cultural transmission.

Although I have emphasized the weaknesses of existing ethnographic data, I agree with R&W's hypothesis that cetaceans are capable of social learning (and therefore culture). The available experimental evidence suggests that at least some cetaceans possess the requisite cognitive abilities for social learning (e.g., Kuczaj et al. 1998; Xitco & Roitblat 1996). In addition, the available observational data provide valuable cues about possible outcomes of social learning. Such cues are invaluable, but limited. We have used observational data for cues about deception and empathy in cetaceans (Kuczaj et al., in press). These data suggest that cetaceans are capable of deception and empathy, but fall short of demonstrating these capabilities. Similarly, the *suggestion* of social learning is not the same as the *demonstration* of social learning.

In order to understand cetacean culture, we must gather considerably more experimental and observational data. Observations can provide additional insights into the products of culture that are important to cetaceans, as well as into the processes that might be involved. Experiments can help to define the nature and limits of these processes. It is essential that we keep open minds about both products and processes. For example, I would argue that stimulus enhancement is a process, and that limiting the notion of process to imitation and teaching ignores other potentially viable social learning processes. It seems likely that the evolutionary emergence of increasingly sophisticated cognitive abilities and the resulting behavioral plasticity made culture possible. Thus, a theoretical perspective on culture that minimizes or assumes process would be woefully inadequate.

Culture: In the beak of the beholder?

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Abstract: We disagree with two of Rendell and Whitehead's assertions. Culture may be an ancestral characteristic of terrestrial cetacean ancestors; not derived via marine variability, modern cetacean mobility, or any living cetacean social structure. Furthermore, evidence for vocal behavior as culture, social stability, and cognitive ability, is richer in birds than Rendell and Whitehead portray and comparable to that of cetaceans and primates.

Rendell & Whitehead (R&W) present a useful review of cetacean culture. We were stimulated by their analyses of a difficult topic, detailed descriptions of cetacean behavior, intriguing interpretations of cultural activity with respect to these behaviors, and attempted cross-species comparisons. We disagree, however, with R&W on two issues: evolutionary history and avian culture.

First, culture may be an ancestral state predating the cetacean split from their terrestrial ancestors. Based on evidence presented in the target article, cultural traits exist in each of the best-studied species of both cetacean suborders. Not enough is known about their behavioral ecology to estimate when in cetacean evolution culture arose, though parsimony suggests it is not independently derived within the order. Culture is as likely to have been a trait of terrestrial proto-cetacea and among the suite of changes that facilitated cetacea's submergence as to have been the evolutionary product of a marine lifestyle. Cetacean culture may thus be independent of R&W's proffered explanations: marine environmental variability, extensive modern cetacean mobility, or any living cetacean social structure. Possibly terrestrial variability, scaled appropriately to the life span and sociality of ancestral proto-whales, drove evolution of their culture.

Second, avian culture, especially regarding vocal behavior, is richer than R&W portray. Issues involve social stability, sympatric behavior and dialects, imitation, and advanced cognitive abilities. We discuss each in turn.

Social stability should incorporate some notion of scale relative to an organism's lifespan. R&W write "song-bird dialects . . . are apparently not related to stable social groups." Indigo bunting (*Passerina cyanea*) learned vocal elements, however, persist in shared male song long after an individual bird's lifespan (Payne 1996). Also, given many songbirds' short lifespans, interactions with the same individuals over multiple breeding seasons imply stable social groups (Godard 1991).

In comparing mammalian and avian vocal and behavioral cultures, R&W claim that avian cultural groups are not sympatric. Although birds may not exhibit the same population-level sympatry as resident and transient *Orca,* some birds – oscines with group territorial defense such as Australian magpies *(Gymnorhina tibicen;* Brown & Farabaugh 1997), white-browed sparrow-weavers (*Plocepasser mahali;* Wingfield & Lewis 1993) – do have sympatric overlap of social groups possessing within-group shared vocal cultures, which parallels R&W's dolphin and chimpanzee examples.

R&W treat motor and vocal learning independently. Vocal behavior is, however, motoric – muscles produce vocalizations. For whatever ecological and social reasons, vocal learning is evolutionarily rare: only cetacea, parrots, oscine songbirds, hummingbirds, humans, and a bat have vocalizations variable enough that learning can be experimentally established as contributing to the crystallized productions of mature animals. Experimental study of functional production of imitated vocalizations is rarer still, yet critical to the issue of imitative learning. Specifically, R&W appear unaware of the complexities of parrot imitative vocal behavior. Over 20 years of data demonstrate that, at least within the laboratory, Grey parrots' (*Psittacus erithacus*) learned vocalizations represent communicative motor behavior, and that these vocalizations are goal-directed (intentional), not simply stimulus-bound (Pepperberg 1999). Such functional use of vocalizations learned by imitation constitute program-level imitation in a nonmammal (Pepperberg, in press), contrary to R&W.

Given that socially-mediated learning is a cornerstone of culture, we expected R&W to develop more fully cross-species comparisons of the effects of social interaction on learning. Social interaction and/or social demonstrations of functional use are critical for acquiring vocal behavior in humans, dolphins, and birds. For children, certain aspects of social interaction clearly facilitate label acquisition (e.g., Baldwin 1993), and operant-based procedures often fail with developmentally delayed or otherwise dysfunctional children whereas socially-mediated training succeeds (Pepperberg & Sherman 2000). For dolphins, large numbers of trials of food-reinforced operant conditioning produced low-fidelity copies of target sounds (Richards et al. 1984) whereas socially- and functionally-oriented reward conditions yielded, in orders of magnitude fewer exposures, high-fidelity copies of similar computer-generated whistles (Reiss & McCowan 1993). The importance of social interaction for songbird learning was critically delineated in papers by, among others, Baptista & Petrinovich (1984; 1986). In training Grey parrots to produce referential copies of human speech sounds, both a socially-interactive training method (the model/rival technique) and functional use of vocalizations (referent as reward) are necessary (Pepperberg 1999; Pepperberg et al. 1999). Lacking either condition, training is either ineffective or activates simple mimicry but not referential communication (Pepperberg 1998).

Parrots, then, are capable of program-level imitation in vocal behavior and possibly in other motor skills (Moore 1992). Do free-ranging parrots use imitation to pass information culturally? Our work with wild Greys in Africa remains too incomplete to report, but we believe R&W conclude too hastily that only Orca and humans share "complex multicultural society" (i.e., socially learned vocal and nonvocal behavior). Amazona parrots maintain vocal dialects that distinguish neighboring roosts (Wright 1996). Thick-billed parrots (*Rhynchopsitta pachyrhyncha*) learn pine nut extraction and predator avoidance from adults (Snyder et al. 1994). Nomadic budgerigars (*Melopsittacus undulatus*) share flock-specific calls yet maintain individually unique vocalizations; the flock is a permanent structure from which young of both sexes disperse, and budgerigars adjust their contact calls towards those of the flock they enter (Brown & Farabaugh 1997; Farabaugh & Dooling 1996). Social structure within parrot roosts and functions of parrot vocalizations remain poorly understood, but in many social and ecological patterns, these large-brained, social birds may resemble large-brained, social mammals, including primates and cetaceans.

Finally, R&W conclude that cetaceans display greater social stability and cognitive abilities than birds. We disagree with these generalizations. With respect to parrots and corvids, for example, such claims about social stability are false or unknown and about cognitive ability, false or untested. Parrots' and corvids' lifespans are comparable to cetaceans (multiple decades), and research by, for example, Pepperberg (1999) and Balda and Kamil (1998) demonstrate avian cognitive abilities that compare favorably with both cetaceans and nonhuman primates and, on occasion, young children.

R&W bring deserved attention to cetacean culture; their broad view of culture is a fruitful approach. We have attempted to address a shortcoming in their treatment of avian social learning, aiming for a more detailed understanding of independently derived cultures and the roles of sociality and ecology in their evolution.

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Teaching in marine mammals? Anecdotes versus science

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Abstract: The use of anecdotes is not a viable research strategy to study animal culture. Social learning processes can often be documented with careful quantitative analyses of observational data. Unfortunately, suggestions that killer whales engage in teaching are entirely based on subjective interpretations of qualitative observations. Thus, "evidence" of teaching in killer whales cannot be used to argue for the occurrence of culture in marine mammals.

Rendell and Whitehead (R&W) wrote an interesting and stimulating target article about behavioral traditions in whales and dolphins. However, they acknowledged only two of many possible approaches to the study of animal culture and they sometimes equated the collection of anecdotal observations of behavior with what they refer to as the "ethnographic" study of behavioral variants in animal populations. This is particularly evident in their discussion of teaching in killer whales, where anecdotal observations are used as evidence for the occurrence of instruction. In this commentary, we argue that there are more research options for the study of animal culture than those discussed in the target article, but that the use of anecdotes is not one of them. After reexamining two of the main studies of "teaching" in killer whales cited by R&W, we conclude that there is no quantitative evidence for the occurrence of instruction in this species, irrespective of whether one emphasizes the intentional or the functional aspects of instruction.

R&W argue that there are two basic approaches for the study of animal culture: controlled laboratory experiments on social learning (where emphasis is on the cognitive processes) and field descriptions of behavioral variation (where emphasis is on their product: culture). In reality, controlled experiments on social learning can be conducted both in the field and in the laboratory, and behavioral traditions can be studied in both settings as well. Furthermore, processes of social learning and teaching can also be studied with observational data alone and without experimentation, if the observational data are collected and analyzed with careful quantitative procedures and if clear hypotheses are formulated and tested (e.g., Maestripieri 1995; 1996). Although we are sympathetic with the difficulties of conducting experiments with free-ranging marine mammals, we do not believe that such difficulties provide a valid justification for the use of qualitative/anecdotal observations of behavior as evidence for culture.

The limitations of this approach are exemplified by R&W's discussion of the evidence for teaching killer whales. Lopez and Lopez (1985) first reported that while killer whales hunted sea lions in Patagonia, they often pursued their prey near the shore and, as a result, became temporarily stranded on the beach. Regardless of their success at capturing prey, the adult killer whales were always able to arch their bodies, rock sideways, and swim back to sea. In their study encompassing 936 hours of observations and 568 observed incidences of hunting, Lopez and Lopez (1985) observed six hunting-related interactions between adults and juveniles. All the evidence of teaching provided by Lopez and Lopez (1985) is contained in the following statement: "Several times, an adult flung a captured sea lion toward a juvenile which had not caught its own prey, and the juvenile pushed the prey with its head or body, or captured it in its mouth. These observations with adults and juveniles interacting lead us to postulate that the adults may be teaching the young to hunt" (p. 182). Interestingly, Lopez and Lopez (1985) also reported that in some of these adult-juvenile interactions, an adult killer whale flung its prey toward a juvenile who had already caught its own prey. In these situations, "the juvenile did not catch the flung prey, but held on to the sea lion it had caught itself" (p. 182). These observations suggest that the behavior of the adult may have been accidental, and not motivated by intent to teach. According to R&W, the Lopez and Lopez (1985) study showed that adults throw away already captured prey while teaching their young, thus demonstrating that teaching has a cost.

R&W cited the study by Guinet and Bouvier (1995a) as providing the clearest description of teaching in killer whales. According to R&W, the behavior of adult killer whales described in this study fits the definition of teaching given by Caro and Hauser (1992), which involves "modifying the behavior, at some cost or lack of benefit, only in the presence of a naïve observer such as to encourage, punish, provide experience or set an example, such that the observer acquires a skill more rapidly than it might otherwise do otherwise, or may not ever learn." Guinet and Bouvier (1995a) observed four adults and two calves for 446 hours over a 5-year period. In this time period, the two calves performed 88 "intentional strandings," 81 of which took place when no elephant seals were present "and were thus regarded as beaching play events" (p. 30). No evidence was provided to support the notion that strandings were intentional or functionally related to hunting. Guinet and Bouvier (1995a) reported two observations of teaching. On one occasion, a stranded calf had difficulty returning to sea and could only do so with the help of its mother. On another occasion, after a calf began pursuing a seal pup, its mother "accompanied and pushed her offspring with her rostrum towards the seal pup. The calf grabbed the side of the seal while its mother positioned herself between the beach and her calf to prevent it from going too high up the beach" (p. 31).

In both the Lopez and Lopez (1985) and the Guinet and Bouvier (1995a) studies, the evidence of teaching in killer whales consists of the qualitative description of a few behavioral interactions between adults and juveniles and the authors' subjective interpretation of these interactions as teaching. It is not immediately apparent how these observations fit Caro and Hauser's (1992) definition of teaching or any other operational definition of this phenomenon. In our view, the observations reported by Lopez and

Lopez (1985) and Guinet and Bouvier (1995a) suggest that the hunting-related interactions between adult and juvenile killer whales are a potentially interesting phenomenon that warrants further quantitative investigation. However, they do not suggest that killer whales are capable of teaching anymore than they suggest that they are capable of solving differential equations. Whenever scientists use subjective interpretations of anecdotes as explanations for animal behavior, their explanations are no better than those of casual observers with no scientific training, who are seeing animals for the first time.

Cetacean culture: Definitions and evidence

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Abstract: Rendell and Whitehead have drawn attention to some striking cetacean behaviour patterns. However, the claims for "culture" are premature. Weak examples of cetacean social learning do not, in sum, provide strong evidence for culture. Other terms, such as social learning, vocal learning, imitation, and tradition may be applied in some cases without resorting to more complex and controversial terms.

What kind of scientific evidence is necessary to ascribe culture to non-human animals? First, culture must be adequately defined. Second, the observations or evidence should offer "culture" as the best or most appropriate explanation of a given phenomenon. Rendell and Whitehead (R&W) settle on a broad definition that culture "is information or behaviour acquired from conspecifics through some form of social learning." However, it is entirely unclear what then, the term "culture" *adds* to the concept of "social learning." As described, the implication is that all socially-learned behaviours represent some form of culture (and these terms are used loosely and interchangeably throughout their paper). By lowering the bar, the culture concept could apply to many animals. As such, cetaceans could not be considered "special" as the authors imply. Some cetacean species are adept social learners. Indeed, some of these socially learned behaviours *may* be transmitted to others, horizontally, vertically, or obliquely. These shared behaviours may qualify as conventions or traditions, without requiring the use of more loaded and complex terms such as culture. In their defense, the claims for culture have occasionally been exaggerated by primatologists and ornithologists alike. If vocal dialects can define bird cultures, then it would be only be fair to apply the same standards to whales. By diluting the definition of culture as roughly equivalent to social learning, the claim for cetacean culture becomes fundamentally empty.

Definitions of culture should not be tailored or repeatedly modified to exclude non-human animals as if there is some agenda (hidden or explicit) aimed at exalting humans above all other life. One could endlessly debate whether teaching or imitation (*sensu* Galef 1992) are essential to the definition of culture. I simply suggest that we use terminology that reflect, rather than exaggerate the actual observations. For example, terms such as vocal imitation, matching, social learning, convention, and even "tradition" (from the Latin of "handing over") would serve as appropriate and more accurate characterisations of the described behaviours.

R&W rightfully argue that long-term ethnographic approaches will continue to yield critically important information and some of the long-term studies do provide evidence for traditions. Ignoring the term "culture" for the moment, we can at least discuss evidence for some forms of tradition.

Bottlenose dolphin sponge-carriers in Shark Bay, Australia (my fieldsite) do appear to pass this foraging technique on to their offspring. The speculation that sponge-carrying is comparable to non-adaptive stone-handling by macaques is not supported. Sponge carrying females spend up to 95% of the day diving repeatedly and stereotypically with sponges on their rostra. Observations strongly suggest sponge-carriers are foraging (Smolker et al. 1997). Sponge-carriers associate with non-sponge-carriers, and males rarely use sponges. Six calves who took up sponge-carrying were born to sponge-carrying mothers and we know of no dolphins who adopted the technique independently (unpublished data). Individual learning and genetic explanations in isolation do not suffice. However, contrary to R&W's description, most sponge-carrying occurs in deeper channels (8–12 m) in specific areas (Smolker et al. 1997) that are not frequented by all memers of the population. Ecological explanations cannot account for sponge-carrying (non-sponging animals forage in the same channels) but are not irrelevant. We have never observed sponge-carrying in shallow water ($<$4 m, unpublished data). This particular behavior does appear to be a "tradition," vertically transmitted, but genetic influence cannot be excluded.

The provisioning case at Monkey Mia, Shark Bay (my fieldsite) where three matrilines of bottlenose dolphins visit a small strip of beach cannot be strictly attributed to social learning. Calves accompany their mothers into shallow water at the provisioning beach, but the begging gestures (head up, mouth open) may also be shaped, reinforced by the behaviour of tourists standing in knee-deep water. Although it seems likely that calves observe and copy their mother's gestures, other interpretations are possible. Similarly, it is not inconceivable that calves could individually learn the cooperative fishing with humans in Brazil. The development of this technique deserves further study.

The killer whale "teaching" example is supported by one observation of A3 pushing her calf, A5, toward a seal pup during an intentional stranding event. Otherwise, A3 assisted her calf in getting off the beach, not on. Nudging the calf towards the prey item is more likely to fit the definition of teaching than rescuing a stranded calf. A single event does not provide sufficient evidence for teaching in killer whales.

Other quibbles: (1) Contrary to R&W's assertion, the experimental literature on human social learning and imitation is huge, including entire fields of developmental and social psychology. "Social Learning Theory" is devoted to examining the mechanisms of social transmission, including imitation. (2) Bottlenose dolphins do use a diverse range of foraging tactics, but the claim that dolphin feeding specialisations are comparable only to chimpanzees requires clear documentation. (3) It is not clear that lobtail feeding was an "innovation" among humpback whales in the southern Gulf of Maine, nor that individual learning did not occur. The behaviour spread under specific environmental conditions and non-social learning explanations are also consistent with Figure 1. (4) R&W rightly indicate that the example of non-vocal group-specific sperm whale behaviour is weak (only one behaviour was statistically different between groups). Unfortunately, this gives the impression that adding weak data together makes a case stronger. It does not. (5) To suggest that menopause in whales could have been favored by cultural transmission is highly speculative and does not do justice to the wealth of theoretical and empirical treatments of this topic (e.g., Hawkes et al. 1998; Hill & Hurtado 1997; Packer et al. 1998; Williams 1957).

The data on vocal learning and imitation are strong for some species. Numerous reports suggest that dolphins are good at gestural and even program-level imitation. Dolphins have exceeded where our closest relatives have failed. Do such data warrant bold claims for "cetacean culture" or for calling a spade a spade?

Remarks on whale cultures from a complex systems perspective

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Abstract: The target article provides stimulating evidence for culture in cetaceans but does not provide a coherent theoretical framework. We argue that a complex, adaptive systems approach not only can provide such a framework but also can contribute advanced data analysis and simulation methods. For humpback whale songs, we suggest the framework of "small-world networks" to model the observed spatio-temporal dynamics.

Culture as emergent self-organized structure of a complex system. The authors give a list of published definitions and characterizations of the social phenomenon "culture" and argue that behavioral patterns observed in whale populations are best described by assuming that whales have developed cultures. It might prove useful for heuristic guidance to supplement elementary statistical analysis by theory-based numerical simulations – especially if the empirical data are as sparse as in the examples mentioned in the target article.

In the context of complex systems, cultures can be viewed as one manifestation of an emergent, self-organized structure of a complex, adaptive system (see for instance Haken 1987; Strogatz 1994). In this commentary we argue that the complex systems paradigm provides a coherent theoretical framework for data analysis and theory-building towards explaining the phenomena discussed in the target article.

Large-scale coherence of humpback whale song patterns. We pick as an example the singing behavior of humpback whales. Early claims that singers have reproductive advantages could not be confirmed in studies that clearly demonstrate that females are not attracted by singers (Mobley et al. 1988). Singers are also typically smaller than the male escorts who are believed to do the breeding (Spitz et al. 2000). Furthermore, there is evidence that singers do not optimize their depth for optimal transmission range (Mercado & Frazer 1999).

Music as collective memory. In cultures without written language, songs play an important role in preserving the community's collective memory. Without speculating about the semantics of humpback whale songs, we nevertheless can analyze the songs with respect to their information content. For instance, Tom Lehrer's song "The Elements" lasts 86 seconds and contains about 1 kb = 8,000 bits of information (Lehrer 1959). The upper limit of verbal information transmission for humans is of the order of 100 bits/sec. For the humpback whale songs, the stream of patterns distinguishable to us are significantly lower so that an upper limit of 200,000 bits for humpback whale songs seems reasonable. The mutual information content or redundancy between songs may be an appropriate statistic to track the spreading and evolution of the songs.

Work by K. Payne and others (see, e.g., Payne 1999) has identified recurrent structures and patterns in humpback whale songs that are similar to musical themes and motives in human songs. Therefore, the songs can be naturally mapped onto a symbolic representation with dynamics that evolve both in space and time. The similarity of songs is thereby potentially accessible to quantitative analysis with the help of symbolic dynamics, a tool from nonlinear dynamics that has been successfully applied to the study of human music, dance, and speech. A systematic study of song duration as a function of the time of the day or the day in the season has already revealed some fascinating regularities that can provide a rigorous foundation for a quantitative theory (Fristrup, pers. comm.). We anticipate that a systematic analysis of spatio-temporal humpback whale song dynamics would reveal valuable information about their social learning and cultural evolution beyond the singing behavior itself.

Spreading of song patterns. The phenomenon of rapid spreading of humpback whale song patterns may be aptly described as exhibiting the so-called "small-world" phenomenon (Milgram 1967; Newman et al. 2000; Newman & Watts 1999; Watts & Strogatz 1998), whereby the network of singing whales is hypothesized to exhibit both local clustering (e.g., in the breeding grounds) and a small "degree of separation" DS. For instance, if a singer has DS = 3, then this singer listened to a whale that had been listening to a singer that had been listening to any random humpback whale singer within the past season. As a comparison: For humans under the relation "is on a first-name basis with a person" the average degree of separation anywhere in the world is estimated to be no more than four. With this property, information travels very fast along the network – about as fast as on a random network if the degree of separation is small enough (i.e., there are enough shortcuts).

The theoretical challenge is to find an economical pathway connecting a singer in, say, breeding grounds in Hawaii with one in Japan and one in Mexico. Assuming social learning among singers, one asks how many degrees of separation exist between any two whales in any of the three Northern Pacific breeding grounds. A straight-forward statistical analysis could estimate the probability that singers visit new breeding grounds in consecutive seasons. In the small-world context, one would also expect to find "shortcuts" between clusters of singers concentrated in the three breeding grounds. The extra shortcuts could potentially be identified as "traveling minstrel" whales who visit more than one breeding grounds within the same season (Salden et al. 1999).

A back-of-the-envelope small-world calculation. Suppose there are 6,000 humpback whales, of which 1,000–2,000 are active singers. The five feeding grounds mentioned in the target article provide a potential location for traveling minstrels to act as shortcuts between the singers in the three clusters of breeding grounds.

In general, if the number of shortcuts is larger than a certain threshold, exponential transmission of information is expected because in this regime the DS is a logarithmic function of the number of whales. Below the threshold, the DS is a linear function of the number of whales, which implies a linear rate of information transmission.

If each singing whale has about 250 "listeners" among whales in the same breeding ground (i.e., before shortcuts are applied), then according to small-world models, the requisite number of shortcuts for exponentially fast information transmission could be as small as a few individuals.

Future directions. The target article mentions examples of social learning between humans and cetaceans. We expect that modern computer and communication technology will lead to more efficient interaction between the two most intelligent terrestrial and maritime species and new forms of global self-organization that might help to solve upcoming global problems (Mayer-Kress 1996; Mayer-Kress & Barczys 1995; Mayer-Kress et al. 2000).

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Experiments are the key to understanding socially acquired knowledge in cetaceans

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Abstract: We agree with Rendell and Whitehead that cetaceans acquire knowledge from caretakers and peers, and that a clear understanding of this process can provide insight into the evolution of mammalian cognition. The passive observational methods they advocate, however, are inadequate for determining what cetaceans know. Only by experimentally investigating the cognition of cetaceans can we hope to understand what they learn through social interactions.

Under the tutelage of extraterrestrial black monoliths, prehistoric man-apes learned a skill not possessed by any other animal, a skill that ultimately gave rise to the complex human societies of today.[1] According to science-fiction author Arthur C. Clarke (1968), this skill was the ability to identify and use tools. Others would suggest that abilities such as speech, imitation, self-awareness, or pedagogy were the key adaptations leading to human advancement (reviewed by Tomasello 1999). The human-specific evolutionary processes proposed by these cultural theorists are hardly less mysterious than alien interventions. Rendell and Whitehead (R&W) provide a welcome respite from such Kipling-esque tales of Renaissance apes. Their descriptions of cetacean behavior should serve as a wake-up call to those that believe primates are the only animals capable of acquiring knowledge from their caretakers and peers (see also Box & Gibson 1999).

Cultural research often focuses on identifying key differences between humans and other animals. These isolationist tendencies have been driven by philosophical arguments about the role of language/intention/awareness in thought (Macintyre 1999). Like R&W, we are dissatisfied with such anthropocentric approaches. Neuroscientific and behavioral evidence suggest many similarities between cognition in cetaceans and humans (reviewed by Schusterman et al. 1986). Like R&W, we want to understand why such cross-species similarities exist.

R&W suggest that cetacean culture can best be understood through passive behavioral observations in naturalistic social settings. Observational methods are useful for describing cetacean social structure and behavior, but less so for understanding what knowledge cetaceans possess, or how they acquire this knowledge. The ethnographic criteria proposed by R&W for what counts as evidence of culture (e.g., novelty, complexity, inexplicability) are highly problematic. Differentiating strategy shifts from innovations using observational methods is not possible and complexity lies in the eye of the beholder. How one might dissociate the influence of such interdependent factors as heredity, environment, and individual learning from that of social learning (which entails individual learning from perceived events that affect environmental conditions) is unclear. Many of the examples R&W provide as evidence of culture (e.g., vocal mimicry) do not require social interactions. Young cetaceans accompanying conspecifics (including mothers) will have opportunities to acquire similar knowledge, independent of whether those conspecifics know the youngsters exist.

R&W advocate ethnographic studies of cetacean culture on the premise that field observations provide a window into the real lives of cetaceans. Observing behavior in a natural setting does not, however, guarantee ecological validity (Hammersley 1992). Most of the observations reviewed by R&W were made by nearby humans. This invasion of privacy could affect behavior in unpredictable ways. A related concern is the proportion of cetacean behavior actually observed. Visual observations in the field are typically limited to opportunistic surface encounters occurring during the day. Behavior that occurs at night and/or underwater, in the absence of human observers, has scarcely been described. Drawing inferences from such grossly under-sampled observations of possibly observer-influenced behavior is probably not the best scientific approach to understanding cetacean culture.

Ethnographic studies of human culture usually involve participating observers. The human ethnographer, in addition to gaining a first-hand immersion experience, has the ability to interview subjects and determine whether they agree with her interpretations. Although this approach has succeeded in generating a large corpus of descriptions of human culture, it has produced only highly speculative theories about the evolutionary origins of human culture, and little understanding about how culture affects the behavioral development of humans. What then can we expect from the non-interactive ethnographic studies of cetaceans advocated by R&W?

R&W suggest that learning capacities demonstrated experimentally are not representative of natural abilities. Most data, however, indicate that mental abilities exhibited by animals in laboratory conditions are strongly predictive of their competencies in the wild (Balda et al. 1998; Moss & Shettleworth 1996). Social learning, in particular, appears to be enhanced by unnatural conditions rather than degraded, as evidenced by the cultural sophistication of humans who have created totally artificial environments within which to live. Similarly, cetaceans given the choice between living in a natural setting or an artificial one may voluntarily choose the latter (Pryor 1991). Innovation is most likely to occur when animals have less to worry about (Gardner & Gardner 1994). The reliability of food and safety available in enclosures may thus be more conducive to observations of innovations, and their subsequent spread through a social group, than natural conditions.

Experimentation does not necessitate captivity. Field experiments can be as informative as laboratory experiments. An experiment could be as simple as introducing interesting artifacts into cetaceans' habitats and observing if (and how) different species interact with them. With respect to social learning, it might be particularly interesting to introduce objects that might be useful or attractive to cetaceans (e.g., "snack" vending machines, vibrating massage stations, or shark-repelling enclosures). Assuming one or more cetaceans can discover the benefits of these artifacts (which would entail acquiring some new knowledge), one could measure the time it takes for other cetaceans to acquire this knowledge, and the conditions under which they do so.

Lorenz (1952, p.147) noted that, "It is only by living with animals that one can attain a real understanding of their ways." Cetaceans provide unique opportunities for such experimental approaches because of their willingness to interact socially with humans (Busnel 1973). Scientists can "participate to investigate" in several ways. One approach might be to live with cetaceans in a shared environment for several months, and see what happens (Lilly 1967). Alternatively, groups of animals could be housed in more conventional settings, and given daily opportunities for cross-species interactions across several years (http://www.dolphininstitute.com). More naturalistic shared environments (e.g., the shallow waters of Shark Bay, Australia) are also feasible (Conner & Smolker 1985).

Socially acquired knowledge may differ from other knowledge primarily in terms of the events that are learned about (Shettleworth 1998). Comparing cultural faculties across different species without knowing what those faculties are is like comparing some fruits with some other fruits. Experimental studies are more likely to increase our understanding of the cultural capacities of cetaceans than are passive observations.

NOTE

[1] See Clarke (1968) for the details of this fictional account.

Genetic relatedness in sperm whales: Evidence and cultural implications

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Abstract: Results of genetic analyses show that social groups of female and immature sperm whales are comprised of multiple matrilines as evidenced by the presence of multiple mitochondrial (maternally inherited) control region haplotypes. These data suggest: (1) a social environment in which the transmission of cultural information, such as vocal dialects, is more likely to be horizontal or oblique rather than strictly vertical (mother-offspring) and (2) lead us to question the data presented to support gene-culture coevolution.

Rendell and Whitehead (R&W) provide a compelling argument that culture should be attributed to cetaceans. One frequently cited example is the vocal dialects recorded from groups of female and immature sperm whales. The authors write that these dialects arise in a social environment that is largely matrilineal and that there are suggestions of gene-culture coevolution. Here, the traditional (matrilineal) view of sperm whale social structure is contrasted with the new view that is emerging from recent genetic analyses. The results are discussed in terms of the social environment in which vocal dialects, and other possible aspects of sperm whale culture, may be transmitted.

To be valid, interpretations of behavior must be soundly based on an accurate knowledge of the genetic structuring of social groupings. Premature conclusions of matrilineal structure can lead to biases in the interpretation of observable behavior (Christal 1998). At sea, female and immature sperm whales are typically found in cohesive "groups" of about 10–40 individuals which move and act together in a coordinated manner. These groups are the social entities in which calves are born and raised, individuals forage and in which mating take place. Members are known to reassemble if disrupted by whalers, to exhibit epimeletic (care giving) behavior, allomaternal care, communal nursing, and communal protection from predation (e.g., Caldwell & Caldwell 1966; Pitman et al. 2001; Whitehead 1996b). As discussed by R&W, these groups may also exhibit group-specific dialects (Weilgart & Whitehead 1997) and some groups show novel foraging techniques (e.g., following long liners; C. Matkin, unpublished data). Traditionally, these characteristics were easy to interpret as kin interacting with kin in stable matrilineal groups. Results from recent photo-identification studies and genetic analyses, however, show that these groups are neither particularly stable nor matrilineal, and these behaviors become more challenging and interesting to interpret.

Adult female and immature sperm whales of both sexes appear to live in a fission-fusion society with the observed "group" being temporary associations between more stable social "units" (Best 1979; Christal et al. 1998; Whitehead et al. 1991). In the Galápagos Islands, long term photo-identification studies by Whitehead and colleagues show that units consist of about 12 individuals who are constant companions over periods of several years (Christal et al. 1998; Whitehead et al. 1991). Although it is generally thought that females probably spend their lives in the same unit, there are known instances of the splitting and merging of units, transfers of individuals between units, and nonrelatives showing long-term relationships (Christal 1998). Both genetic analysis (two units) and photo-identification studies show that a unit may consist of two or more separate matrilines (Christal 1998; Christal et al. 1998). In the Galápagos Islands, units associate with one another for periods of about 6.5 days, although there seems to be considerable variation among years (Whitehead & Kahn 1992). Estimates of the mean size of "groups" have been made in different ocean basins by various researchers; most are about 25 individuals (e.g., Best 1979; Whitehead et al. 1991), or roughly two units. Genetic analyses of three groups from the Galápagos Islands showed the presence of multiple matrilines (Richard et al. 1996). In light of these findings, many of which are from Whitehead's own laboratory, it is surprising to us that the authors discuss sperm whale groups in the context of a matrilineal, or largely matrilineal, social structure.

We have used both mitochondrial (mtDNA) and nuclear markers to investigate social structure in a larger sample of "groups" from the Indian Ocean, North Pacific, and South Pacific oceans and in one "unit" known from long term photo-identification records (Galápagos samples from R&W). Our results also show that both types of social association generally consist of multiple matrilines, as indicated by the presence of multiple mitochondrial control region haploytpes (Table 1). All groups, except one, contained two to four mtDNA haplotypes. Because of the strikingly low mtDNA variation in sperm whales, a group with 4 mtDNA haplotypes contains about 17% of the mitochondrial diversity known in sperm whales worldwide (only 23 mtDNA haplotypes are known from over 750 individuals sampled from the Pacific, Atlantic, and Indian Oceans; the three most common haplotypes account for about 85% of sperm whales worldwide. (Dillon 1996; Lyrholm et al. 1996; Lyrholm & Gyllensten 1998; Mesnick et al., unpublished data). In a stranding of 10 adult females in Tasmania, a single mtDNA haplotype was present. However, this was the single most commonly found haplotype. Further analysis of nuclear loci reveal that this stranding consists of clusters of related individuals and a single adult female with no close relations to the other individuals in the group. In the Galápagos unit, two mtDNA haplotypes were present and no pair-wise comparisons between any of the five unit members sampled (of the nine in total) fell within the range expected for first order relations although they were known by photo-identification records to be long-term associates (Whitehead & Rendell, pers. comm.). To date, we know of no genetic evidence of a strictly or largely matrilineal unit or group of sperm whales. Rather, sperm whale "units" and "groups" appear to be comprised of clusters of related individuals and some may contain some individuals with no close

Table 1 (Mesnick). *Mitochondrial DNA diversity in one unit and 14 groups of female and immature sperm whales for which we have five or more samples. The number of samples analyzed from each group is shown in parentheses. Most groups were partially sampled (6% to 100%), thus the haplotypic diversity indicated below is a conservative estimate of the total diversity*

Social association	Number of mtDNA haplotypes
Groups	
Gulf of California stranding (7)	3
Gulf of California (8)	4
Central Eastern North Pacific (21)	3
Galapagos (10)	2
Gulf of California (10)	2
Gulf of California (11)	2
Tasmanian stranding (63)	2
Tasmanian stranding (10)	1
Tasmanian stranding (35)	4
Gulf of California (6)	2
West of Colombia (9)	3
West of Baja California (6)	3
West of Mexico (5)	2
West of Peru (15)	4
Unit	
Galapagos (5)	2

relations to any other individuals in the group. The clusters of related individuals may indeed be maternally related, but they are not strictly matrilineal, that is, the expected number of first order relations (e.g., mother-daughter) is not found. Relationships within these clusters often fall within the range expected for second order maternal relations, such as aunts/nieces and grandmothers/granddaughters. Some relationships indicate paternal relatedness, such as half brothers (see also Bond 1999).

This, as the author's point out, presents us with a conundrum: how do groups, which are neither particularly stable nor matrilineal, exhibit group-specific behaviors? If we are to attribute culture to these groups, then our results suggest a social environment in which the transmission of cultural information, such as vocal dialects, is more likely to be horizontal (within-generation) or oblique (from a non-parent relative or non-relative in the previous generation), than vertical (mother-offspring). Under this scenario, there is a larger role for social learning and perhaps conformist traditions in the transmission of cultural information in sperm whales.

In light of the genetic diversity found within both sperm whale units and groups, we must question the strength of the data presented to support a gene-culture connection. As mentioned above, a single sperm whale group may contain nearly 20% of the known mtDNA control region variation. In addition, because of the low mtDNA diversity in sperm whales, many individuals share common haploytpes. For example, the particular mtDNA haplotype mentioned in Whitehead et al. (1998) as being shared between two groups with similar dialects is the second most common haplotype worldwide. Not only these two groups, but 20% of our worldwide sample, share this haplotype. It may be premature to infer a gene-culture connection before analyzing the geographic range of codas, their stability over time and the relationships between individuals that use them. Perhaps the authors' alternative suggestion that social associations are made within the context of larger cultural trait-groups or acoustic clans, which correlate in some as yet unknown way with control region diversity, is possible.

Additionally, we would predict that social signals, such as vocal dialects, evolve much faster than the mitochondrial genome. Social signals are under strong selection as effective and efficient communication is vitally important in social animals (West-Eberhard 1983). Moreover, acoustic signals, in contrast to visual signals or other characters used in social display, may be particularly easy to alter, as changes in rhythm do not necessitate morphological change.

Lastly, the genetic data do not support the idea that an advantageous cultural trait that spreads rapidly can devastate mtDNA diversity. If, as the model asserts, nonmatrilineal transmission is greater than 0.5%, then mtDNA diversity is little reduced (Whitehead 1998). Sperm whale groups appear to be comprised of both related and unrelated individuals, at numbers significantly above this threshold. Moreover, if unrelated individuals co-occur within a group, then the transmission of advantageous information must be done in such a way that members outside a particular matriline are not privy to it (Mesnick et al. 1999).

There are striking examples of culture in sperm whales, all the more remarkable given a social environment comprised of both kith (close, but not related, companions) and kin.

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Cetacean science does not have to be pseudo-science

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Abstract: Rendall and Whitehead overstate the weak evidence for social learning in cetaceans as a group, including the current evidence for vocal learning in killer whales. Ethnographic techniques exist to test genetic explanations of killer whale calling behavior, and additional captive experiments are feasible. Without such tests, descriptions of learning could be considered pseudo-scientific, ad hoc auxiliary assumptions of an untested theory.

Cetaceans offer an exciting possibility for comparative studies of social learning, but genetic and environmental causes of behavioral variation have been ruled out in only a few species of this order (Janik & Slater 1997). Rendall and Whitehead (R&W) review a number of studies that fail to unambiguously reject genetic or environmental explanations, evidenced by the many cases of "unlikely" in Table 3. It is surprising that the authors rather uncritically disregard the shortcomings of those studies, fail to identify data needs, and thereby overstate the strength of the evidence for "culture" in cetaceans. Powerful tests of genetic and environmental explanations of behavioral variability are both feasible and necessary before descriptions of "culture" are attempted.

Consider the ethnographic evidence for vocal learning in *O. orca* from the perspective of Grant and Grant's (1996) field study of Darwin's finches (*Geospiza fortis*), cited by R&W as an "exemplary" ethnographic study. *G. fortis* males sing one species-specific song before and after finding a mate, so unfledged offspring are exposed to their father's song. By banding and observing the behavior of 95–100% of the males on a Galapagos Island over more than 13 years, Grant and Grant (1996) were able to compare songs of different males whose genetic relationship was known. They confirmed previous findings (Gibbs 1990) that songs of fathers and sons were similar, and calculated song feature heritability of 0.725. Father-son similarity could arise from genetic or cultural transmission, so they compared the songs of sons with both their paternal and maternal grandfathers. Across 136 son-paternal grandfather pairs they found a significant correlation near the expected value ($0.725^2 = 0.526$), but no correlation across 124 son-maternal grandfather pairs, revealing "that song is culturally and not genetically transmitted across generations" (Grant & Grant 1996).

In resident *O. orca,* the mother-offspring group has been shown to be a remarkably stable social unit, with no cases of dispersal over 20 years of observation (Bigg et al. 1990; Ford et al. 1994). Mother-offspring groups associate preferentially with each other in "pods." Recordings have revealed pod-specific calling behavior (Ford 1991), and similar but more subtle differences between mother-offspring groups within the same pod (Miller & Bain 2000). Because these groups are sympatric, an environmental cause of group-specific calling can be discounted. Based on field observations (Ford 1991) and recordings of individuals using array techniques (Miller 2000; Miller & Tyack 1998), group recordings appear to be representative of individual repertoires in the group. As with father-son song similarity in *G. fortis,* mother-offspring call similarity in *O. orca* could arise from genetic or cultural transmission of call features. As both sexes of *O. orca* produce calls, the approach of Grant and Grant (1996) can be replicated by comparing calls produced by offspring with those of their parents. Fathers can be identified using tissue samples taken from identified individuals and modern genetic techniques (Hoelzel 1998). Comparison of calls recorded from individuals (Miller & Tyack 1998) in mother-father-offspring triads could directly replicate the technique employed by Grant and Grant (1996). Low father-offspring call similarity across multiple individuals would contradict the explanation that genetic differences account for the pattern observed in the wild *sensu G. fortis* (Grant & Grant 1996). The captive study of Bowles et al. (1988) cited by R&W clearly documented this pattern, but a sample size of N = 1 is insufficient to reject a genetic explanation unambiguously and does not demonstrate a general phenomenon.

The key, therefore, is a description of the mating system based on identifying fathers. If mating occurs within pods, then father-offspring differences in calling behavior would be small and a genetic mechanism could not be ruled out. In fact, low genetic diversity in resident populations (Hoelzel 1998) and unusual levels of C-heterochromatin in O. orca chromosomes (Arnason et al. 1980) suggest high levels of inbreeding (Duffield 1986) consistent with within-pod mating. R&W cite Baird (2000) that "breeding is likely to occur between pods," but fail to cite Baird (2000) two sentences later, that "genetic data are not yet available to positively confirm that mating occurs between resident pods." The most detailed paternity analysis published to date concluded, "The preliminary paternity testing data we present here does not exclude the possibility of mating within the pod" (Hoelzel 1998).

R&W failed to inform readers that critical data to test genetic transmission of call features in *O. orca* are not yet available, devaluing the efforts of researchers actually collecting those data. An effort to obtain tissue samples from a large proportion of the resident population has been underway for many years, and should provide a broad paternity analysis. Initial reports from this data set are that mating is rare within pods, but common between different pods which share no calls (Barrett-Lennard 2000). If this finding is confirmed by peer review, then supported by the captive study of Bowles et al. (1988), a simple genetic explanation of call variability would be strongly contradicted. Vocal learning would be a likely developmental process to explain such a pattern, but only the poorly documented (Janik & Slater 1997) single animal cross-fostering study of Bain (1986; 1988) indicates vocal learning. There are currently at least 42 *O. orca* in captivity worldwide (NMFS 2000), providing ample opportunity for replication of the mimicry study that Richards et al. (1984) conducted with *Tursiops truncatus.* Sixteen of the 42 animals in captivity were transferred from another facility (NMFS 2000), suggesting that opportunities for additional cross-fostering experiments also exist.

Popper (1962) distinguished between "science" and "pseudoscience" by the criterion of falsifiability: "statements or systems of statements, in order to be ranked as scientific, must be capable of conflicting with possible or conceivable observations." It would be pseudo-science to assume cultural transmission without ruling out genetic and environmental explanations because few observations would conflict with diverse and flexible learning rules. In such a case, learning rules may not reflect what is actually occurring, but merely be "ad hoc auxiliary assumptions" (Popper 1962) of an untested theory of social learning. At this stage, good scientific progress can best be made by experimentally demonstrating social learning and conducting rigorous tests of genetic and environmental explanations of variability, although such tests may require development of new techniques.

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On not drawing the line about culture: Inconsistencies in interpretation of nonhuman cultures

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Abstract: Defining culture as social learning means that culture is present in many birds and mammals, suggesting that cetacean culture is not so special and does not require special explanation. Contrary to their own claims, Rendell and Whitehead present culture as having variant forms in different species, and these forms seem inconsistently applied and compared across species.

If culture is social learning by any means, it is common among nonhuman animals, even judging only from the examples provided by Rendell and Whitehead (R&W). Although R&W argue that drawing the line based on "how much" of a behavioral repertoire must be socially learned for culture to exist is counterproductive (sect. 5), much of the target article seems determined to show that cetaceans have more culture than other nonape nonhuman species. Indeed, R&W argue that similar ecological conditions of humans and cetaceans might have led to the evolution of culture in these species. But such a specific explanation is inappropriate, given that group-wide modification of a single call is enough to show culture in bats – rather, theory applicable to more species is necessary. If, as R&W state, no line should be drawn as to when culture begins, a theoretical explanation of culture as a general adaptation (Hall & Sharp 1978) must be applicable to all species which show social learning, not just those which show "more" culture than others.

Describing chimpanzee/human cultures and cetacean cultures as "closely parallel" is problematic. For example, chimpanzee cultures apparently show no group variation in vocal behavior or greeting and chimpanzees in a group do not always travel together, whereas killer whales show group-related vocal variation and greeting, and travel together. Two similarities exist: for both chimpanzee and killer whale groups, the same food items are eaten by group members, and both groups show maternal teaching. One of the strongest similarities between chimpanzee and human cultures – tool use variation – is apparently absent in killer whales. Similarly, the strongest similarity among human, cetacean, and avian cultures – vocal imitation – is absent in chimpanzees. Apparently culture is not monolithic, and I suspect (as do R&W) that this may have something to do with differing mechanisms. Indeed, R&W note a distinction between "vocal and behavioural cultures" (sect. 5), and suggest that birds and bats have only the former; and they describe cetacean but not bird groups as having "persistent cultures" (sect. 3.3). Yet why are these distinctions relevant for a general theory of culture in which no lines are drawn?

Oddly, evidence is viewed differently when produced by cetaceans and birds. For example, the fact that humpback song is homogeneous across "entire ocean basins," is presented as an important contrast to bird song's "sharp variation over short distances" (sect. 3.1), yet interacting groups of killer whales, dolphins, and sperm whales "maintain their own group-specific culture" even with short distances between them (sect. 3.3), and thus, like birds, show sharp variation over short distances. Such inconsistency makes me wonder if some of the seemingly remarkable aspects of cetacean culture will be found in other species when they are better-studied or, more likely, when scientists who study them connect their observations with culture theory (Slobodchikoff & Kiriazis 1997). Indeed, R&W's claims that dolphins' uses of abstract representations "match or exceed" those of "all other non-human species" (Introduction) are questionable (Schusterman & Gisiner 1997).

The interpretation of killer whale teaching (sect. 4.2) is conceptually problematic. Although A5's mother provided more encouragement or experiences for learning than did A4's, both mothers provided such facilitation; so the fact that A5 learned intentional stranding better and earlier than A4 is not evidence that A5 acquired the skill more rapidly than without the mother's behavior, as both mothers apparently showed facilitating behavior. Rather, evidence of more rapid skill development would only be present if A4 and A5 learned intentional stranding more rapidly than calves whose mothers had not exhibited encouragement or provided experiences to learn. Thus, although the evidence is suggestive, other evidence is required to support the interpretation of teaching. (Another conceptual problem is including the non-learned activity of "straight-line distance moved in 12 hours" as an instance of sperm whale culture.)

Still, as R&W note, some cetaceans show intriguing parallels with human and apes in their social learning, suggesting similar mechanisms (Mitchell 1994). Put a child, or an ape, in a human culture into which he or she was not born, and each takes on numerous aspects of that culture (Mitchell 1999). Similarly, in close interaction with humans and pinnipeds, Indian Ocean bottlenose dolphins acoustically and bodily imitated tool use and behavior (Tayler & Saayman 1973). One imitation by a young dolphin seems particularly striking. Through an underwater window, the young dolphin observed a human blow cigarette smoke, rushed to her mother, obtained milk, and returned to the window, spewing forth milk in what looked much like cigarette smoke. Although reliability measures are lacking, it is difficult to interpret this action as non-imitative. Indeed, dolphins' spontaneous imitations seem more obviously imitative than purported similarities between human bodily actions and subsequent actions of a parrot (Moore 1992) which so many experimentalists accept as imitation even without reliability. Such acceptance is particularly surprising given the difficulty in providing reliable discriminations for other bird species between similar behaviors using the same appendage (Mitchell, in press). Given dolphins' spontaneous imitations, their performance in experimental studies of imitation is generally poor (in comparison with humans and apes), in that they imitate familiar but not novel actions (Bauer & Johnson 1994; Mitchell, in press). Perhaps the impetus for enculturation can only occur when nonhumans are relatively free to participate in social group activities.

Parallels and contrasts with primate cultural research

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Abstract: The types of cetacean cultural behavior patterns described (primarily food-related and communication-related) reflect a very different research focus than that found in primatology, where dietary variation and food processing is emphasized and other potentially "cultural" patterns have (until recently) been relatively neglected. The lack of behavioral research in all but a few cetacean species is also notable, as it mirrors a bias in primatology towards only a few genera.

The authors are to be commended for a well-written and enlightening piece. Despite an impressive literature on social traditions across vertebrate genera going back many years, it is only recently that primatologists interested in nonhuman culture have recognized the need to look beyond the primates in their exploration of this phenomenon (i.e., McGrew 1998b). I expect that this paper will encourage primatologists to be more "taxa-inclusive" in future research and discussion of nonhuman culture.

As a researcher primarily interested in food processing techniques among wild primates, I found the types of cultural behaviors reported in the target article of particular interest. Of the 17 cetacean cultural patterns reported, 6 relate directly or indirectly to food acquisition, 5 relate to vocalizations or communication, while 4 relate to movement patterns or defense (see Fig. 1). The types of cultural patterns described for cetaceans seem to reflect a different research focus than that found in primatology, which tends to focus on aspects of foraging behavior, particularly tool use (i.e., McGrew 1992; van Schaik et al. 1999). In Whiten et al.'s (1999) cross-site comparison of chimpanzee populations, well more than half of the 39 cultural patterns relate to food acquisition or processing. While this has obviously been a rewarding approach for primate cultural research, the importance of other non-subsistence cultural patterns has (to some degree) gone unrecognized. For example, in chimpanzees, "dialectic" differences in vocalizations (Mitani et al. 1992) and forms of symbolic communication such as leaf clipping have been documented (Boesch & Tomasello 1998). In both chimpanzees and macaques, postural and grooming customs have also been identified (i.e., McGrew & Tutin 1978; Tanaka 1998, Whiten et al. 1999). Though in some cases the relevant behaviors have been known for many years, only recently have they begun to be incorporated into theories and discussions of primate culture (i.e., Boesch & Tomasello 1998; McGrew 1998b). If the target article is any indication, greater focus on the part of primatologists in such "non-subsistence" behavioral patterns could be at least as informative as the current focus on foraging and food-processing techniques, and would allow for more direct comparisons between primate and cetacean cultures.

The authors note the relative paucity of behavioral data available for most cetacean species. They report a bias toward only four of the ~80 cetacean species, which mirrors the focus in primatology toward a handful of taxa. As reported by McGrew (1998b), only five genera (Cebus, Gorilla, Macaca, Pan, and Pongo) account for 80% of genus-specific primate literature available from 1986 to 1997. Of these, 52% were from the chimpanzee (Pan troglodytes). As of this writing, four of these genera (Cebus, Macaca, Pan, and Pongo) have been identified as culture-bearers or potential culture-bearers (McGrew 1998b; van Schaik et al. 1999; Watanabe 1994; Whiten et al. 1999; Fragaszy & Perry, in preparation). To what extent could our current body of evidence for nonhuman culture be an artifact of our focus on such a small number of genera? For both cetaceans and nonhuman primates, it is clear that we need to expand our inquiries to include neglected taxa before we can speak with confidence about the prevalence of nonhuman culture in nature.

While as an anthropologist I would question the authors' claim that their methods can really be called "ethnological" (as opposed to ethological), I do not fault their conclusions. They have presented a substantial and compelling body of evidence for culture in cetaceans. As our understanding of these and other nonhuman cultures improves, so too will our ability to understand the similarities and differences between them, and their relationship to our own.

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Primate cultural worlds: Monkeys, apes, and humans

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Abstract: Monkeys and apes, inhabiting variable environments and subjected to K-selection, exhibit cultural behavior transmitted horizontally and vertically, like cetaceans. Behaviors enhancing better health and nutrition, predator avoidance, or mate selection, can affect differential reproduction.Furthermore, dominance hierarchies and social status not only affect the transmission and acceptance of new behaviors but they may also affect genetic inheritance.

There are many competing definitions of the term culture. Physical (biological) anthropologists generally grant cultural behavior to nonhuman primates and perhaps other mammals. However, many cultural anthropologists consider culture a human preserve – a defining element of human status. We think such restriction is an unwarranted, nonevolutionary approach to understanding culture. Because culture is not only learned but shared behavior, the notion of culture must include trans-generational transmission, without which behaviors learned in one generation disappear if not rediscovered anew. Cultural transmission requires intra-and inter-generational transmission of learned behaviors.

Culture might be an essential survival component for species exhibiting behaviors transmitted intra- and inter-generationally, a high brain to body size ratio, long lives, stable social groups, long migratory patterns, long-distance or stable communication systems, and variable habitats that change frequently and perhaps unexpectedly. In fact, these might be the elemental prerequisites for the developmental adaptation of culture.

Amongst primates cultural behaviors are passed horizontally (intra-generationally) and vertically (inter-generationally) – as in cetaceans. Most transmission of learned behaviors in nonhuman primates is from a mother to her offspring and within the matriline, perhaps through imitation and the modeling of behavior, with a few examples of direct teaching (Poirier 1973; 1993). Among nonhuman primates there are group-specific cultural patterns and matrilineal-specific behaviors (Poirier 1992). This occurrence complicates the analysis of species-specific behaviors because the behavior patterns of large and dominant matrilines can usurp a group's behavioral repertoire.

Culture can be an important survival tool for organisms undergoing K-selection, where environmental predictability is atypical and survival requires adapting to changing conditions. Potts (1998) cites variability selection (VS) as a strategy crucial to the survival of early human ancestors who encountered changing habitats (Poirier 1969; Poirier & McKee 1999). Perhaps the more unexpected or diverse the habitat, the greater role culture plays as a survival strategy. Culture aided early humans in leaving Africa and Eur-Asia. Animals, whose behavior is genetically patterned at birth where each generation encounters the same set of circumstances, are more fit in stable, unchanging environments.

Culture cannot exist without conformity and social norms. Fundamentally, culture is conformity and adherence to social norms. Those implementing culture change, the innovators, agents of change, have been little studied. At least among humans, these innovators might be shunned or expelled from the group. If they are too behaviorally different (culturally atypical), their genetic fitness might be negatively affected by being denied mating access. Agents of cultural change occur among nonhuman primates, and their behaviors are likely copied in direct measure to their hierarchical status, sex, age, and number of matrilineal relatives (Poirier 1992). Some animals behavioral patterns are followed while other animals are ignored. Do similar situations characterize cetaceans?

Young primates model their behaviors after their mother and perhaps role models, such as their close playmates. New behaviors are more likely to appear in expendable age and sex groups – younger animals and males. Reproductive females, the limiting resource to population growth, might be considered the behaviorally stable sex within a species, that is, the least expendable sex and possibly the least innovative. Amongst nonhuman primates, new behaviors passed from a mother to her offspring may not affect the rest of the group if the mother is low ranking and has few relatives within the group. However, if an alpha male exhibits a new behavior it may spread rapidly to the rest of the group. Do similar variables affect cetacean cultural expression? Are some ages, sexes, matrilines, or pods, more innovative than others and why?

If cetaceans, like chimpanzees, live in fission/fusion societies whose members may only see others of the group (pod for cetaceans) on an irregular basis, there may be strong selection for social intelligence to aid in remembering individuals and to elicit appropriate behavioral patterns with regard to social status (Dunbar 1996; Poirier 1993; Stanford 1999). If social intelligence is a reasonable construct, then a proximate link may be made that a larger and more complex brain is a likely prerequisite to culture.

Because primates learn their behaviors, behavioral patterns can change within and across generations. Behaviors enhancing better health and nutrition, predator avoidance, or mate selection affect differential reproduction. Those individuals who are more fit to their environment will pass on more of their genes to the next generation and, if there is a genetic basis for behavioral differences, it also will be inherited. Correlation between behavioral patterns and mtDNA sequences may simply be due to the matrilineal mode of transmission and may be the result of genetic drift. However, cultural adaptations that increase the fitness of a specific genotype in a specific environment may ultimately affect genetic evolution. The genetic make-up of any species can be seen as a record of the environmental adaptations of its ancestors (Cowley 1999). Species exploit their environment through biobehavioral adaptations. This may be how tool use and bipedalism took hold among early human ancestors. Tool users and bipeds might have exploited a wider ecological range and in essence were more fit, thereby contributing more of their genes to subsequent generations (Lovejoy 1981).

Accumulated knowledge and experience also can be important to a species survival. The grandmother hypothesis may explain why many primate females live long past their prime reproductive years. Essentially, although older females are eliminated from the effective population or gene pool, they actively contribute to the survival of individuals carrying their genes. For example, in human hunter-gatherers, foraging returns increase with age and experience enabling grandmothers to aid in the survival and reproduction of others carrying their genes (Diamond 1996). Not only primates and cetaceans, but also other long-lived mammals, like elephants, have females playing active (crucial) post-reproductive roles. Group matriarchs in elephant societies have an especially important role in coping with rare events, such as locating water holes during episodic droughts. Females in many species, not only cetaceans, are the font for group memory and the accumulated experiences they possess can affect their groups survival.

A whale of a tale: Calling it culture doesn't help

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Abstract: We argue that the function of human culture is to clarify what people value. Consequently, nothing in cetacean behavior (or any other animal's behavior) comes remotely close to this aspect of human culture. This does not mean that the traditions observed in cetaceans are uninteresting, but rather, that we need to understand why they are so different from our own.

One of the unsatisfying things about Hamlet's monologue on human nature is that it fails to specify why we are the paragon of animals. Equally unsatisfying is a monologue from some scientists who argue that we are not so special after all. Both views are wrong-headed. Hamlet was right in seeing us as paragons of a kind, but he simply failed to articulate an interesting theoretical account, and failed to see the logical flaw in creating an intellectual hierarchy among animals. Specifically, why should any particular mental quality be seen as superior when every species has been equipped with a brain that was designed to solve the unique problems that emerged in its evolutionary past. Conversely, those who see nonhuman and human animals as two qualitatively similar peas in an intellectual pod, have really missed out on what makes our own minds so different. If one can claim, without controversy, that dolphins echolocate and humans do not, why is it controversial to say that we have culture and animals do not? Sure, humans can *sort of* echolocate, and sure, dolphins *sort of* have culture, but "sort of" is only interesting if one can specify the constraints on what prevents the full blown capacity. In the following essay, we don't challenge the interesting observations synthesized by Rendell and Whitehead (R&W) in their target article, but rather, the interpretation of their data and the implications that such work might have for a theory of culture. We make four points: (1) Although we agree that culture must not be defined in such a way that it is uniquely human, we should use what we know about humans to motivate a theory of culture; in this sense, we adopt a position that is analogous to the debates about human language, and whether other animals do or do not have anything like it. (2) If it is not possible to conduct experiments on cetaceans in order to explore mechanisms of transmission, then perhaps the study of animal cultures should be left to other species; this argument has been made in several areas of animal behavior, including the quantification of life-time reproductive success, a topic for which dolphins are simply ill-suited. (3) We argue that the function of human culture is to clarify what people value, what they take seriously in their daily lives, what they will fight for and use to exclude or include others in their groups. (4) Based on point 3, we argue that nothing in cetacean behavior (or any other animal's behavior) comes remotely close to this aspect of human culture. This does not mean that the traditions observed in cetaceans are uninteresting, but rather, that we need to understand why they are so different from our own.

Like research on chimpanzees, R&W cite numerous examples from whales and dolphins which suggest cultural differences among populations. Although the authors acknowledge that they know little about the actual mechanisms of transmission, they are confident in their claim because neither genetic nor ecological factors can account for the variation between populations and the homogeneity within populations. But do such patterns warrant the conclusion that cetaceans have culture, even if the behaviors are nowhere near as complicated or varied as they are in human societies? More specifically, does the notion of culture in animals help us understand its evolution in humans, or is this a misleading metaphor that might actually block important progress on this problem?

The concept of culture is one of the more elusive concepts in the social sciences. In harmony with many other scientists working on animals behavior, Rendell and Whitehead define culture as any behavior that is transmitted over generations by social learning to become a population characteristic. This definition is problematic because it fails to specify the key mechanisms of cultural transmission, and consequently, fails to distinguish between trivial and non-trivial differences between populations. Second, a more meaningful theory of culture, and its evolution, must take into account the two key mechanisms – pedagogy and imitation – in order to show why some cultural differences are trivial while others are non-trivial.

Defining culture in terms of socially transmitted behaviors immediately runs into problems because some behaviors are little more than social practices, while others attain the status of culture. Driving on the right/left side of the road, beyond all doubt a socially transmitted practice, is a trivial behavior utterly lacking in social consequence. When on a given date and hour, Sweden changed its driving practice, Swedish culture did not change, and neither did the accident rate. On the other hand, if on the same date and hour, Sweden had discarded its Lutheran ministers, replacing them with Roman Catholic priests or Orthodox rabbis, Swedish culture would have changed dramatically.

Why is the religion Sweden practices incontrovertibly part of its culture, whereas the side of the road on which they drive is not? When culture is defined as "socially transmitted behavior," this question cannot even be properly addressed. To do justice to the concept of culture we need, not an operational definition, but a theory of culture, one that will, among other things, enable trivial behaviors to be distinguished from consequential socially acquired practices. Such a theory must be built in such a way that animal culture is at least possible.

No one disputes the self-evident distinction between genetically and socially acquired behavior, but it is not a distinction that will clarify the difference between human culture and animal "traditions." Social acquisition is a secondary property of culture, neither a sufficient condition for culture, nor probably even a necessary one. If an individual acquired a culturally important idea by himself, would that make the idea any less cultural?

Most work on animal culture does not do justice to the concept of social acquisition. It is our position that a theory of culture will require a clear exposition of how such acquisition mechanisms either facilitate or constrain the transmission of information from generation to generation. All significant human cultural practices are transmitted by pedagogy, or acquired by imitation. Animals, including whales and dolphins, do not engage in pedagogy, and with the exception of vocal mimicry, evidence for motor imitation is weak as well. In their article, R&W mention a review paper by Caro and Hauser (1992) in which it was claimed that evidence for teaching in killer whales was "weak," and then go on to say based on *two* additional observations that the evidence is "now considerably stronger." Even if we accept the point that two more cases help, the examples provided are readily explained by something other than teaching: differences in the acquisition of hunting skills between two individuals are due to individual differences in ability, not their parent's role in providing an opportunity to hunt. This example shows why it is necessary to use experiments and repeatable observations to explore why and how individuals acquire a particular behavior.

All socially-acquired behaviors in cetaceans (chimpanzees too!) appear to be of the trivial variety: carrying sponges on the head, lobtail fishing, beach-rubbing, wagon-wheel defense, and so on. All would-be cetacean cultural behaviors appear analogous to driving on one side of the road or the other. What, however, might constitute an important social practice in the cetaceans? The best candidates are likely to be found in the differences in greetings and vocal dialects. For example, it would certainly be nontrivial if groups only allowed migrants in if they immediately imitated their dialect or greeting gesture, or engaged in the same sort of cooperative hunting behavior. Similarly, it would certainly be nontrivial if females rejected the sexual advances of males who failed to speak their dialect. These consequential changes, though originating in acts that are trivial, might be found to develop slowly across generations. But long term observations of cetaceans have so far revealed nothing of the kind. Acts that begin trivial apparently remain trivial. They do not develop into attitudinal changes of a kind that could verge on culture.

We conclude that cetaceans (and chimpanzees) lack culture. This conclusion nonetheless raises many interesting questions for the future. How do humans and cetaceans differ so that, while both species have social practices, only humans have cultural practices? How do cultural practices differ from mere social practices? How much of the difference between them can be explained by language? These are difficult questions, ones that will only be answered by careful experiments investigating the psychological mechanisms guiding cetacean behavior, either in the wild or in captivity.

Cultural transmission of behavior in animals: How a modern training technology uses spontaneous social imitation in cetaceans and facilitates social imitation in horses and dogs

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Abstract: Social learning and imitation is central to culture in cetaceans. The training technology used with cetaceans facilitates reinforcing imitation of one dolphin's behavior by another; the same technology, now widely used by pet owners, can lead to imitative learning in such unlikely species as dogs and horses. A capacity for imitation, and thus for cultural learning, may exist in many species.

This is a wonderful target article, clear in its premises and argument, richly documented, and drawn from the findings of decades of meticulous and arduous field work. I of course agree with the authors' conclusions that some animals have social traditions that are learned by observation and maintained across generations, and that we may call this culture. These conclusions can be especially well demonstrated through studies of the killer whale, a charismatic animal whose true social behavior was unknown to us until recent times.

I will confine my additional comments to one topic central to the article, the question of animals learning by social imitation. I am amazed to learn from this article how tenaciously some academics still cling to the idea that no animals other than humans learn by true imitation. Let me start with the easy contradictory example, cetaceans. In captivity, learning by imitation of conspecifics is commonplace in dolphins, and relied on by marine mammal trainers.

Dolphins are customarily trained by a variant of Skinnerian operant conditioning, using a sound (the pip of a metal whistle, paired with food by classical conditioning) as a conditioned reinforcer. This marker signal identifies the precise action for which a reward will be given, as it is taking place. The procedure facilitates learning by imitation. One can instantly reinforce, at the moment it is happening, the act of copying another dolphin's movements. If you want dolphins (or any cetaceans) to perform a behavior in unison, therefore, most trainers shape the behavior in one animal, and then reinforce another who copies the first, until all the animals in the group are doing the behavior identically and simultaneously. My personal experience of using this technique has involved teaching unison behavior to groups of from two to six individuals of species including *Stenella attenuata, Stenella longirostris, Tursiops gilli, Steno bredanensis,* and *Pseudorca crassidens* (Pryor 1974).

Dolphins imitate each other with or without training. I have reported elsewhere on two rough toothed dolphins (*S. bredanensis*) that performed, spontaneously, most of each other's trained repertoires, learned only by watching through a gate as the other animal performed (Pryor et al. 1969). Imitation occurs even in behaviors that have no benefits or may be deleterious. I (and many others) have witnessed "fads" that spread among half a dozen tank mates, such as greeting human visitors tail first; playing with bubbles; "wearing" seaweed on flippers or forehead for hours or days at a time; and, at Sea Life Park in Hawaii, teetering out of the water on the tank edge even after some animals fell out and had to be rescued by humans (Pryor 1975).

Horses and dogs are universally assumed to be quite unable to learn by imitation. In fact, the literature, both lay and scientific, is forceful in stating that dogs can not learn in this way, but only respond similarly to stimuli other dogs are responding to; although, as far as I have been able to discover, only one small experiment involving two dogs was ever actually carried out. Repeated observations now suggest otherwise. Starting in the early 1990s, and fostered by the Internet, thousands of pet owners have been applying the dolphin trainers' operant conditioning methodology to dogs (*Canis familiaris*) and horses (*Equus equus*). Instead of traditional coercive control with leash or bridle, the trainer reinforces spontaneous behavior selectively, using a pocket clicker as the marker signal or conditioned reinforcer; hence the popular term for the process, "clicker training"(Pryor 1999).

Dog trainers customarily keep one or more dogs in wire or plastic crates while they train each in turn for shows or competitions. A crated dog familiar with the clicker, once released, may immediately demonstrate a behavior, such as negotiating an unfamiliar obstacle, that it has seen and heard being reinforced in a kennel mate. Horses in stalls also often begin offering behavior (such as lifting a foot, or lowering or nodding the head) that they have just watched another horse being clicked for in the barn aisle.

I suspect that the use of a marker signal assists this learning, as it clearly identifies, to the watcher as well as to the performer, the behavior being reinforced (Pryor 1981). However, the fact that successful imitation happens at all suggests to me that the capacity already exists in many species, and needs only the right environmental cues to make it apparent. Judging by the ease with which the general public is now producing the phenomenon of one dog or horse imitating another's operant behavior, learning by imitation could easily (and inexpensively!) be replicated in the laboratory in these species.

There are many long-lived social species, besides marine mammals and people, in which elderly (if not post-menopausal) females are high-ranking individuals whose body of knowledge is relied on and imitated: elephants, horses, and cattle come to mind (and I am curious about wildebeest). When longitudinal studies, field studies, and interactive studies become more the norm, I think we are going to find that learning by imitation, or true social learning, is not an either-or circumstance, but a continuum, ranging across species and environments from a little to a lot, but well within the capacities of many species besides just us. It is hard, however, to guess how long it will take theory to catch up to reality; we experience Galileo's dilemma.

Cetacean culture: Resisting myths and addressing lacunae

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Abstract: Assessments of cetacean behavior has been hampered by popular misconceptions and mythic imagery. Rendell and Whitehead argue persuasively for accepting the idea of cetacean culture. Approaches to "culture," however, must resist positivist approaches that reaffirm the observable. Culture is also comprised of "lacunae" when organisms choose to resist or avoid behavioral patterns.

It has been a curious phenomenon to trace the popular perception of dolphins over the last few decades. Initially embraced as a highly tractable performing animal, dolphins became emblematic, in the 1960s, of an intelligence that would deepen the moral consciousness of humans. Compounded by the notion, advanced by the unconventional scientist John Cunningham Lilly (1978), that there was a "dolphin language" – analogous to human speech – that might someday be interpreted, the misrepresentation of the species has endured. The popular image of the dolphin, the poster creature (if you will) for "new age" thinking, has hampered a serious consideration of issues related to advanced behavior in all cetaceans. Even now, cetaceans retain much of the mythic symbolism they have garnered over the last few decades.

The appeal of the dolphin has always been complex drawing on biological materialism (the dolphin's brain), and spiritual transcendency (its supposed "affinity" for humans), and a set of highly social behaviors. What is surprising and yet enduring, in so many arenas, is a fascinating reluctance to deal with the dolphin in pragmatic terms: the dolphin *qua* dolphin. Still, the work of so many animal behaviorists from Griffin (1984) to Seyfarth and Cheney (1990), has moved us considerably ahead in our ability to shift paradigms in our thinking about animal culture. Rendell and Whitehead's (R&W's) piece opens that dialogue even further by addressing the full complement of cetacean behavior within a scaffolding of strong ethological and behaviorist theory.

Following on the heels of Vincent Janik's (2000) recent work on whistle matching , which establishes important evidence for the possibility of the transferal of ideas in *Tursiops,* R&W offer a more broadly conceptualized rationale – drawing on definitions of culture – for establishing their own the idea of culture.

R&W's approach to the study of animal behavior and culture is as nuanced and sophisticated as any I have read. Their work complements a set of discourses that have allowed us to rethink "science" in ways that have enabled their subtlety and complexity. It is, I think, critical in this context to acknowledge the rise of the women's movement in the last few decades and the advent of feminist theory, such as the work of Haraway (1989; 1990), Keller (1983), and Longino (1990), in our understanding and appreciation of how animals "work." Needless to say, this includes the research of Goodall (2000) and many other women who relied more heavily on synthesis rather than reductive analysis as an enabling way of thinking about animals. The methodological and conceptual changes that have been incorporated into science have, of course, been critical to a general willingness to understand animals differently.

Other work in the cultural studies of science have allowed us to strip away the veneer of reductive empiricism, in an effort to reveal how science is "constructed." This approach, often vilified by scientists, has actually helped open science up by recognizing that the strict limits of objectivity can interfere if we seek to understand the intricate nature of biological processes. Whether we turn to the work of Latour (1987), Lewontin (1993), or Oyama (2000), we are all better practitioners if we understand the cultural constructions of our own modes of inquiry.

The work of cultural studies of science is not only useful in terms of understanding process, but also in evaluating content. It is a mode of thinking that addresses the lacunae of culture, reminding us that culture does not only exist in observable phenomena. As we begin to define cultural patterns in other groups of animals, particularly in cetaceans which are not easily observed for lengths of time, it is critical to resist the impulse toward positivist conclusions. Just as culture may be comprised of behaviors that are learned and transferred from one individual to another, it may also be marked by patterns of behavior that individuals (or groups) resist or avoid. By way of example, it may be instructive at least to look at the practice of breastfeeding – a physiological *and* a cultural practice – in American culture in recent decades. An intrinsically biological activity (with strong genetic and behavioral components), breastfeeding was *not* common practice among middle class women in the 1950s, 1960s, and even 1970s. But, of course, the withdrawal from the practice was not *outside* of culture. Quite the contrary, it reflected a strong, if localized, group-specific cultural movement in response to shifting community values. Interesting to note, a subsequent cultural shift, relying on cultural transmission of values and practices, has recently increased the frequency of breastfeeding within the very same social context.

In my own work on captive *Tursiops,* many years ago (1983), I noted a behavior I called "bottom sink" where an individual rests at the bottom of a pool for about a minute or more. Was this a "cultural practice" that pelagic animals learned from shallow-water peers? Is it a behavior that responds to the dynamics of an acoustically challenging concrete environment that the animals learn in captivity? The answers are unclear and more important elusive, given the difficulty of observing the *absence* of behaviors in a group or even the gradual acquisition of a behavior. But if we are interested in understanding the full complexity of culture, our questions must explore ideas of culture that may ask us to invert question of adaptive fitness. Such questions, particularly for animals that we study in captivity, are critical if we are to begin to understand the pragmatics of animal culture. R&W have extended the possibilities of that mode of understanding; their essay will be the springboard for the kind of sophisticated and nuanced treatment that cetacean behavior has deserved for decades.

Social learning and sociality

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Abstract: Sociality may not be a defining feature of social learning. Complex social systems have been predicted to favour the evolution of social learning, but the evidence for this relationship is weak. In birds, only one study supports the hypothesis that social learning is an adaptive specialisation to social living. In nonhuman primates, social group size and social learning frequency are not correlated. Though cetaceans may prove an exception, they provide a useful group with which to test these ideas.

Rendell & Whitehead (R&W) provide a timely review of cetacean culture, with compelling evidence for group-specific suites of socially learned behaviour patterns in sympatric populations. In particular, the association of vocal mimicry and motor imitation in cetaceans fits with a wide-ranging trend that includes parrots (Dawson & Foss 1965; Moore 1992), songbirds (Campbell et al. 1999; Lefebvre et al. 1997), and possibly humans (Iacoboni et al. 1999). In many ways, the evidence for cetacean cultures could be considered more compelling than that for apes (Whiten et al. 1999) because of the sympatric element, voiding geographical variation as an explanation for behavioural variation between groups. We agree that the ethnographic approach will often be the only feasible method of collecting social learning data in cetaceans. Determination of the precise social learning mechanism will be difficult, if not impossible, to ascertain in the field, but, as R&W argue, the exact mechanism of transmission has little relevance to definitions of culture (Heyes 1993b; Reader & Laland 1999a). It is important that ethnographic social learning data are collected, since cetaceans provide a valuable opportunity to study the evolution of cultural transmission, brain size, and cognitive capacities in a group both phylogenetically distant from humans and with a very different brain architecture to that of primates (Marino 1996).

However, we are concerned that a common theme of the target article, that stable social groups favour the evolution of social learning, reinforces an (often implicit) assumption that is becoming increasingly common in the social learning literature. R&W argue that the need to maintain group identity in the highly mobile cetaceans provides a selection pressure for vocal learning, which provides the roots of sophisticated social learning. Further, they argue that stable social groups increase the opportunities for cultural transmission and information exchange which could increase inclusive fitness if other group members are kin. R&W may be correct that, in cetaceans, the maintenance of group identity has favoured the evolution of social learning capacities: we do not have the comparative data to address this issue at present. Nevertheless, there are some relevant data available for other animal groups, and we note below that the evidence for a link between sociality and social learning is equivocal at best.

A number of authors have predicted a correlation between group living and an enhancement of the propensity or capacity to socially learn, with species that live a gregarious lifestyle predicted to rely more on social learning processes than solitary species (Klopfer 1959; Lee 1991; Lefebvre & Giraldeau 1996; Lefebvre

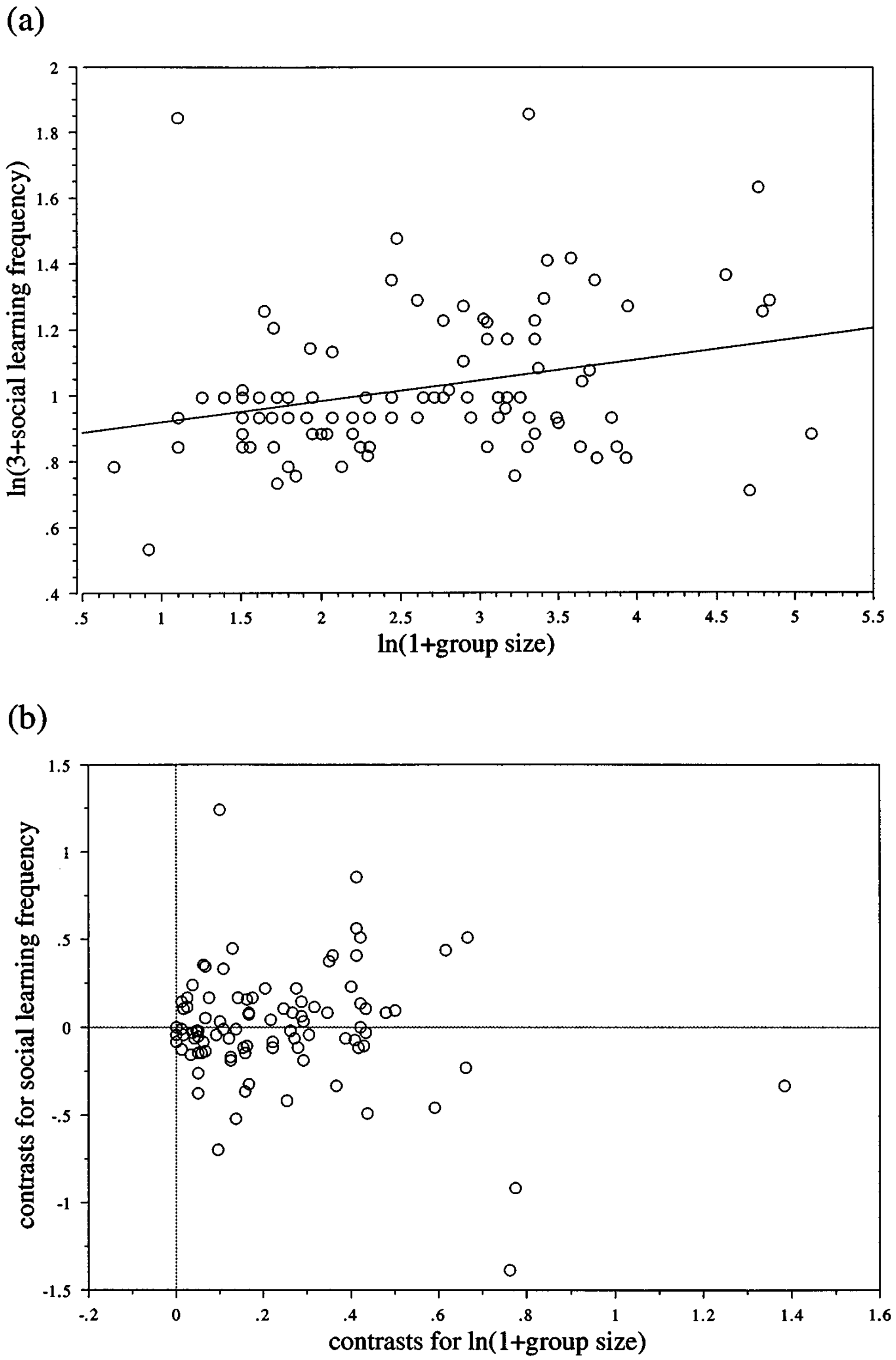

Figure 1 (Reader & Lefebvre). Social learning frequencies and social group size in non-human primates. (A) The raw data, with each point representing one species ($r^2_{adj} = 0.06$, $F_{1,103} = 7.33$, $p < 0.01$). (B) Independent contrast data ($r^2_{adj} = 0.00$, $F_{1,92} = 1.01$, $p > 0.1$). Frequencies are corrected for research effort by taking residuals from a natural log-log plot through the origin of social learning frequency against research effort. From Reader (1999).

et al. 1996; Roper 1986). Relevant to this discussion are the social (or Machiavellian) intelligence hypotheses (Byrne & Whiten 1988; Flinn 1997; Humphrey 1976; Jolly 1966; Whiten & Byrne 1997), which argue that the large brains of primates evolved as an adaptation to living in large, complex social groups. Social learning is often described as a core aspect of such social intelligence (e.g., Byrne & Whiten 1997).

What is the evidence for a link between social living and social learning? In birds, Templeton et al. (1999) found that the more social pinyon jay is better at social learning than individual learning, whereas the less social Clark's nutcracker performs similarly in both tasks. Templeton et al. (1999) argue that this supports the hypothesis that social learning is an adaptive specialization to social living. To our knowledge, this is the only study to show such a relationship after controlling for the possible confound of species differences in individual learning. Balda et al. (1997) describe a link between social structure and observational learning in corvids, but Lefebvre (2000) notes that the interspecific differences reported by Balda et al. (1997) parallel those found by Olson et al. (1995) on a nonsocial, nonspatial task, which may provide an alternative account for the results if individual learning is a confound. Similarly, interspecific variation in social learning parallels variation in individual learning and degree of urbanisation in the five Passerine species studied by Sasvàri (1979; 1985) and the two Columbid species studied by Lefebvre et al. (1996). There is thus currently little comparative evidence that social learning is an adaptive specialisation to particular environmental demands in birds (Lefebvre & Giraldeau 1996), beyond the study of Templeton et al. (1999).

In nonhuman primates, social learning frequencies have been estimated for 105 species by collecting reports of social learning from the published literature (Reader 1999; Reader & Laland 1999b). Mean social group size and social learning frequency correlate weakly when species are treated as independent data points, but when phylogeny was taken into account using independent contrasts this relationship was no longer significant (Fig. 1). Inclusion of relative executive brain size as an independent variable, the exclusion of the unusual orang-utan and the exclusion of captive studies and data where a human influence was suggested all produced similar findings. Hence we have no evidence for a correlation between group size and social learning frequency in nonhuman primates, once phylogeny or relative brain size are taken into account. However, it is also plausible that social group size may be a poor or inexact measure of social complexity, and that a better measure of social complexity would reveal an association with social learning.

Some authors view non-imitative forms of social learning as a subcategory of individual or asocial learning, perhaps sharing similar psychological mechanisms and neural substrates, and predict that social learning will co-vary with general behavioural plasticity (Galef 1992; Heyes 1994b; Laland & Plotkin 1992). Thus social learning per se may not be an adaptive specialisation, and selection for individual learning may also increase the propensity to socially learn. Others view asocial learning and social learning as different, domain-specific, special-purpose adaptive mechanisms (Giraldeau et al. 1994; Tooby & Cosmides 1989), with some authors suggesting or assuming a trade-off between these two abilities (e.g., Boyd & Richerson 1985; Rogers 1988). If the first group of authors are correct, a search for selection pressures specifically effect social learning may be misguided, and we may do better by focusing on the evolution of individual learning or general behavioural plasticity.

We have poor evidence at present that social learning is an adaptive specialisation to social living. It may be that, in cetacea, a reliance on social learning has more to do with feeding ecology than with social structure. Though there is an obvious confound in that the four cetacean species providing the best evidence for social learning are also the best studied, it is notable that all these species rely on diverse prey types and are partly carnivorous. Alternatively, if all cetacea are shown to exhibit similar social learning propensities, this may have more to do with common ancestry (that is, phylogeny), than the ecological explanations discussed by R&W. Like the target article authors, we urge researchers to study social learning in this interesting group, since data on social learning frequencies will allow tests of competing theories of foraging ecology, sociality, phylogeny, cognitive capacity, and dependence on parental care for the evolution of social learning.

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Can culture be inferred only from the absence of genetic and environmental actors?

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Abstract: Rendell & Whitehead's minimalist definition of culture does not allow for the important gaps between cetaceans and humans. A more complete analysis reveals important discontinuities that may be more instructive for comparative purposes than the continuities emphasized by the authors.

Although Rendell and Whitehead (R&W) choose a rather straightforward definition for culture, we think that this concept is insufficiently discussed in the target article. However, instead of debating about whether cetaceans have or have not a culture, we would rather like to concentrate in our commentary on the possible differences between cetacean culture and human culture.

A distinction is made by linguists and cognitive psychologists between performance and competence (Chomsky 1965). While performance refers to observable behaviors (e.g., spoken language as we hear it), competence refers to the set of rules and operations that make performance possible. This distinction can also be useful to critically examine R&W's approach because these authors seem to allude only to performance in discussing animal culture. We would like to focus on the interest of bringing up such distinctions in relation to culture in order to fully understand the nature and consequences of attributing a form of culture to cetaceans.

We start by pointing out some of the features that are associated with culture, in its full human sense. First of all, a single process of information transmission such as imitation cannot solely define culture. In this respect, and notwithstanding the controversies surrounding the definition of imitation (e.g., Galef 1998b), many animal species and even invertebrates such as octopuses (Fiorito & Scotto 1992) show evidence of fast learning by observing conspecifics performing a specific action. Now, would it be sufficient to state from this finding that octopuses have a culture? Certainly not. Concerning the definitions of cultural behaviors (e.g., R&W's Table 1), we note that all these definitions rely on some sort of social behavior (learning, modification, etc.), with or without reference to its likely mechanism (namely, some form of imitative behavior). But surprisingly, the proposed definitions do not mention competencies or processes related to culture for the organisms possessing it. In humans, some crucial features appear to be linked to culture either as necessary components or as by-products. Thus, language and more generally symbolic and intentional systems probably constitute the main features of human culture. But culture is hard to conceive outside a process of accumulation and complexification of knowledge over generations (e.g., Donald 1991; Tomasello & Call 1997). A starting point of culture is the establishment of social rules that have a commonly defined and conventionalized medium for which language is likely to be the best candidate. Moreover, it is likely that culture is organized as an autonomous system and thus presents similarities with linguistic organization. Each relation within this system is tied to other relations. In humans, this system has become independent from biology in such a way that the constraints acting for stabilization or for changes in a given culture are internal; and these features no longer require a parallel evolution of natural or genetic environments.

Let us briefly consider what could be equivalent in cetacean culture to the devices we just mentioned. First, according to R&W's minimalist definition, culture appears as soon as the behavioral repertoire is sufficiently broad to respond to environmental changes. From then on, a given species can develop specific traditions because learning abilities are flexible enough to make these behaviors possible. Is the existence of such flexibility sufficient to lead to culture or even to protoculture? We think it is not. In effect, cetaceans apparently have neither built artifacts nor accumulated cultural gains over generations. It is thus likely that the social repertoire of dolphins or whales have not changed over millions years because of this lack of accumulation whereby culture at time $t + 1$ would depend on culture at time t.

Second, we would like to challenge the idea that inter-group variations not based on environmental or on genetic factors should automatically yield culture. A more economical explanation could be provided by the authors for all examples concerning cultural behaviors. For example, acoustic variations observed in humpback whales can be explained without reference to necessary environmental or/and genetic changes (a similar argument could be made for the sponging by dolphins in the target article). They could simply reflect the play of random processes associated with the plasticity of learning mechanisms. Thus, whales at the beginning of the breeding season might produce various songs that end up converging toward a unique interpretation within the group. In this respect, the case of robots is interesting, since robots can also learn simply by interacting with other robots (e.g., Picault & Drogoul 2000). It could be said from the observed change in their learning abilities that robots in the B group have a different "culture" from that of robots in the A group. However, using the concept of culture in such a context would be purely metaphorical.

Third, we think that the interesting question to ask is why cetaceans which possess advanced cognitive abilities, a complex social life, long lifetimes, and extended mother-infant relations, have not developed a true culture, in the sense we referred to earlier?

Three main functions can be identified in relation to cultural behavior of humans. The first function concerns the ability to cope with different environments (relations to the world). The second function controls social regulations (through language and other media), while the third deals with the relations between the representations built by an individual and the universe (as expressed by several systems of shared values such as an aesthetic, and religion that Darwin (1871) called "spiritual agencies." It seems that only the first function is present in cetaceans and that its role is minimal: a dolphin born in captivity could probably survive in a more natural environment. The second and third functions are surely not fulfilled. If there are indeed some good evidence that dolphins can understand acoustic or gestural commands, it has not yet been shown that this kind of understanding is equivalent to human language (Vauclair 1996).

In brief, we think that considering the specificity of human culture lead to interpreting this concept when it is used in cetaceans in a more restricted and precise sense compared to the one used by R&W. In effect, cultural manifestations in cetaceans or in other animal species can only be punctual and express responses to environmental constraints. Because these cultural components are reactions, they cannot serve (as it is the case for humans) as stimuli for prompting other cultural elements. If animal culture obviously reflects a behavioral flexibility associated with sophisticated learning abilities, a cultural behavior is not embedded in a system. Consequently, because of the predominance of environmental pressures, there is no cultural drift as these pressures lead to maintaining behavioral stability; in this respect, animal culture is highly reliant on environmental features.

There's CULTURE and "Culture"

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Abstract: While cetaceans clearly show social learning in a wide variety of contexts, to label this as "culture" hides more than it reveals: we need a taxonomy of culture to tease apart the differences rather than hiding them in a catch-all category.

It is curious that the word culture, as defined by Boyd and Richerson (1996), and used by Rendell and Whitehead (R&W), covers a welter of different sorts of social learning, whereas in their earlier (1985) use they applied it only to cases where teaching or imitation were involved. I agree with R&W that the attempt by some to draw a contrast between humans and animals, reserving culture for the former, is a false one. But taking any instance of social learning as an example of culture pushes the concept far in the other direction. The only harm in this is that a wide variety of different phenomena are thereby placed under a single head and what they have in common (cultural transmission) may be less than what separates them. If we assume that all the phenomena are examples of the same thing, it may hinder us in getting to grips with what is involved in each case.

Let me take a single example: adaptiveness. There is no doubt that many examples of learning from others involve the spread of traits that enhance the inclusive fitness of the learner. Rats tend to eat what their companions have eaten (Galef 1996); small birds learn to mob predators they see others mob (Curio 1988); in the wonderful example cited by R&W killer whale calves learn to capture prey by beaching from their mothers (Guinet & Bouvier 1995a). But a quite different set of phenomena involves learning from others where adaptiveness is far from clear and the trait learned is somewhat arbitrary. Much vocal learning appears to be of this sort (Slater 1986). It happens to be from other individuals, and so involves cultural transmission, but beyond that the differences outweigh the similarities. In several examples of bird song, the evidence points to different song forms being very much equivalent to each other functionally, whether they become copied and spread in the population or drop in frequency to become extinct being a matter of chance (e.g., Lynch 1996; Payne 1996). Their transmission from one individual to another depends on learning but, beyond that, there is no need to postulate more than random processes to account for their distribution in time and space. Indeed, where innovation is involved, this appears more often to result from errors in copying rather than that advantageous new variants in behaviour have arisen.

While killer whales with different dialects may coexist in the same area, and this probably has no direct equivalent among birds, this difference may be the relatively trivial consequence of when and from whom they learn and patterns of movement thereafter. Perhaps with the exception of dolphin signature whistles (e.g., Janik 2000), a phenomenon to which R&W give little attention, I see no evidence of more profound differences between cetaceans and birds in vocal learning.

Where novel traits that clearly confer an advantage on their bearer spread through a population, there is little need to question why social learning, in whatever form, has evolved. But vocal learning in both birds and mammals is widespread in certain groups and non-existent in others (Janik & Slater 1997). Why? While many ideas have been put forward, notably that sounds may be thereby matched to those of neighbours (e.g., Payne 1982) or to the acoustics of the environment (e.g., Hansen 1979), none provides a satisfactory explanation of why vocal learning evolved in the wide range of species and situations in which it is found (Slater et al. 2000). Indeed, it has been argued that, once evolved, vocal learning may be maintained even if the learned trait ceases to be advantageous as such, because species become caught in a "cultural trap" (Lachlan & Slater 1999).

Social learning takes many forms, from one animal simply being attracted to another and so reacting to the same stimulus, to "true imitation," for which exacting standards of evidence are required so that it is quite hard to demonstrate. Whiten and Ham (1991) provide a useful taxonomy. Perhaps the whole concept of culture requires dissection in a similar way: while R&W provide a fascinating array of examples, they are divided by much and united only by the involvement in their development of that catch-all term "cultural transmission."

Marine versus terrestrial variability in relation to social learning

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Abstract: Rendell and Whitehead state that marine ecosystems are more variable than terrestrial ecosystems over time scales of months or longer. The marine environment is actually less variable than the terrestrial at these shorter time scales, and probably equally variable over centuries. This issue is important when considering claims that environmental variability affects benefits of social learning versus individual learning and genetics.

In section 5, Rendell and Whitehead (R&W) explore the possible role of ecological factors in the development of cultural transmission in cetaceans. The authors raise several interesting issues, some of which would benefit from clarification and correction. The authors assert that the increased "low-frequency temporal variability" of marine systems relative to terrestrial systems may increase the adaptiveness of social learning to cetaceans, as the benefits of social learning are strongly related to variability of the environment. There are two confusing issues raised here.

First, the marine environment is actually considered to be temporally less variable than the terrestrial at time scales of days to years (Steele 1985; 1991). Oceanic variability over these time scales is damped out by the large heat capacity of the ocean. In addition, the marine and terrestrial environments are probably equally variable over longer time scales. At time scales of centuries and longer, the ocean and atmosphere most likely respond as a single system (Steele 1991). Thus, it cannot be claimed that the marine environment is more variable than the terrestrial, either at the short time scales used for comparing benefits of individual learning and social learning, or at the longer time scales used for comparing genetics versus social learning.

Second, while the benefits of cultural transmission are indeed "thought to be related to environmental variability," the authors are unclear about the nature of this relationship. If, as the authors expect, the increased marine variability increases the adaptiveness of social learning to cetaceans, then one would infer that increased variability and social learning have a positive relationship. The authors also state that "if the primary benefits of culture accrue from accelerated adaptation to changing circumstances . . . then these benefits will be accentuated in environments which are more variable." This statement might also lead a reader to expect increased social learning in variable environments. However, the models referred to in the paper (Boyd 1988; 1996) show that as an environment becomes less predictable, the optimal amount of social learning versus individual learning decreases. For instance, in more variable environments, the most common behavior may not be the most adaptive, and it may be more beneficial to use individual learning than social learning (Boyd 1988). Thus, if the marine environment were truly more variable and less predictable than the terrestrial, as claimed by R&W, we might expect relatively less social learning, not more. In actuality, as the marine environment is generally more predictable than the terrestrial, we might expect relatively more social learning in the marine environment. This would agree with the authors' initial conclusions, albeit using a differing logical route.

Several caveats to these conclusions apply. Although the role of ecological factors in the development of social learning in cetaceans is interesting, one should also consider that the complex societies of many cetaceans may have generated their own pressures on social learning. In addition, when using broad generalities such as lumping all types of predictability in the environment, we should take our speculations with a generous grain of salt and use them as take-off points for future thought experiments and research and not as firm conclusions.

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Getting at animal culture: The interface of experimental and ethnographic evidence in dolphins

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Abstract: While supporting the claim for culture in cetaceans, I suggest that Rendell and Whitehead's argument is potentially incomplete if based solely on ethnographic evidence. The notion of cetacean culture can also be explored experimentally. I hope to complement the authors' assertion by discussing dolphin brain and behavioural research findings, thus contributing to a more holistic argument for culture in dolphins.

The question of animal culture is somewhat like a political debate, with the contestants divided into two main camps. The "liberals" are considered lenient in ascribing culture to animals (de Waal 1999; Rendell & Whitehead, target article), while the "conservatives" advocate a more reactionary position by reserving the term "culture" for exclusive human reference (see Bloch 1991; Tomasello et al. 1993). The above debate is often polarised in research, with the liberals drawing support from the ethnographic perspective, while the conservatives ratify their position on the basis of experimental evidence. One might argue that both approaches have their respective shortcomings.

In the liberal candidature, consider Whiten et al. (1999), who argue that cultural behaviours are continuously transmitted through a population by social or observational learning, with specific reference to single behavioural patterns in different animal species. This approach to culture, while of compelling interest, fails to address the critique levelled at it and therefore remains compromised. Specifically, consider the comments of Heyes (1993a), on the failure of such anecdotal evidence to account for the phenomena of coincidence, associative learning and inferential learning in explaining animal behaviour.

Representing the opposing view of the conservatives are those such as Tomasello et al. (1993), who propose, on the basis of their experimental findings, that the prerequisites for cultural learning (imitative, instructive, and collaborative learning) are definitive of humans. Just as the ethnographic school has limited application from an experimental perspective, the experimental school is also restricted by its primatocentric, if not anthropocentric, focus on evolutionary and comparative issues. It may be premature to restrict the phenomenon of culture to humans, after reflecting on the brain and behavioural evidence for social evolution in dolphins. The brain is energetically expensive to maintain, thus the argument that the evolution of a larger brain or the proliferation of neural structures must serve as some indicator of functional significance (Byrne 1995). Within the brain, the primary importance of the cerebral cortex to higher cognitive functioning has long been recognised (Martin 1981), providing the rationale for studying the extent of cerebral cortical evolution and neocortical evolution in different animal species (Dunbar 1992). Dolphin neuro-anatomy is impressive. The delphinids have large brains in absolute terms (Passingham 1982) and relative terms (Marino 1996) and have the most convoluted cortices of all animal species (Elias & Schwartz 1969).

Most significantly, dolphins have higher relative neocortex volumes than have all non-human primates, including chimpanzees, as well as all other mammalian species, including carnivores and insectivores (Tschudin 1999; Tschudin et al. 1996). What is the functional significance of extraordinarily large neocortex ratios in dolphins? Preliminary analysis indicated that in dolphins, the neocortex ratio was related to sociality (Tschudin et al. 1996), in what was initially thought to be a primate-specific relationship (Dunbar 1992; 1993; 1995). This relationship has since been verified for dolphins (Tschudin 1999) and extended to certain insectivores and carnivores (Dunbar & Bever 1998).

Tschudin (1999) therefore argued that social cognition may not have its beginnings in primates, with its most advanced expression only present in humans (see Tomasello & Call 1997). Rather, the capacity for social intelligence might be more evolutionarily ancient, occurring in dolphins through convergent mental evolution. One way of testing such an hypothesis was to run behavioural tasks examining social cognition in dolphins, with specific reference to theory of mind (ToM) (Tschudin 1999). ToM refers to the capacity of an individual to attribute mental states such as beliefs, desires, and intentions to others (Premack & Woodruff 1978).

At this juncture, Rendell and Whitehead's (R&W's) reservations concerning the experimental method become highly relevant. They argue that research into dolphin culture is not likely to ever occur, owing to the perceived magnitude of the financial and logistical constraints, and that we ought to settle for ethnographic evidence. Yet, to adopt a defeatist position with respect to experimentation would not be optimal, insofar as concerns of the ethnographic method remain unaddressed (see Heyes 1993a). Hence, the question of dolphin culture remains unresolved. Rather, social cognition studies with dolphins (described below) can be used as a reference point to indicate that it is possible to obtain experimental evidence for culture in dolphins.

Prior to investigating ToM in dolphins, we wished to establish whether they display some of the precursors to ToM known as joint attention behaviours, documented in the human developmental literature (Baron-Cohen 1994). Our experimental evidence suggests that dolphins can interpret the referential nature of untrained human signs such as pointing and directed gaze, as well as being able to use a replica of an object to discriminate between different objects (Tschudin et al. 2001; see also Herman et al. 1999). In the light of these findings, we examined whether or not dolphins display ToM by administering a modified nonverbal false belief task (Call & Tomasello 1999) to captive bottlenose dolphins.

The false belief task is regarded as the essential test for a fully developed ToM (Baron-Cohen et al. 1985; Wimmer & Perner 1983). The task requires the naïve participant to select an object at one of two possible locations, based on information provided by a human communicator, who has observed its hiding. On some trials the object's location is switched by another human in the presence (resultant true belief) or absence (resultant false belief) of the communicator (Call & Tomasello 1999; Tschudin et al. 2000). Interesting to note, children do not pass the false belief task prior to age 4 and great apes consistently fail (Call & Tomasello 1999). On test, all of the dolphins pass attribution-of-belief tasks. If their performance cannot be explained by learning or cueing, we suggest that dolphins have the capacity to attribute mental states to others (Tschudin et al. 2000) in a display of second-order intentionality (see Leslie 1987).

If dolphins are capable of attributing mental states, the conservative notion of culture becomes challenged, as ToM in dolphins implies that they have second-order intentionality and possibly even reflexive consciousness (Tschudin 2001). According to Tomasello et al. (1993), the capacity to comprehend "second-order mental states" is the pre-requisite for collaborative learning, the final developmental manifestation of exclusive human cultural learning. If dolphins are capable of collaborative learning, based on experimental evidence of social cognition, cultural learning may prove not to be a uniquely human phenomenon. Future research into animal social learning ought to encompass both ecologically valid experiments and ethnographic methods (see Heyes 1993b). This approach will provide a broader insight into the debate of animal culture and may advance support for the position advocated with respect to cetaceans (R&W) and non-human primates (Whiten et al. 1999).

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Cetacean culture: Humans of the sea?

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Abstract: Rendell and Whitehead adopt a weak definition of culture to allow low standards of evidence for marine mammals, but they do not adequately rule out genetic factors or individual versus social learning. They then use these low standards to argue that some whales have unique cultures only matched by humans. It would have been more helpful to specify data gaps and suggest critical tests.

During the 1960s, John Lilly published several influential books proposing that whales and dolphins had intellectual abilities unique except for humans. John Lilly argued that an animal with the sperm whale's brain must have philosophical abilities that are "truly godlike" (Lilly 1975; p 220). "The sperm whale probably has 'religious' ambitions and successes quite beyond anything we know" (Lilly 1975, p 219). These claims were met with skeptical criticism from most biologists. Now that primatologists have recognized the existence of culture in apes (Whiten et al. 1999), Rendell and Whitehead (R&W) have recognized an opportunity not to claim that whales have gotten religion, but rather that they have gotten culture.

I believe that marine mammals are excellent subjects for studying social learning; they have a fascinating combination of primate-like societies with bird-like abilities of vocal learning. Experimental studies have demonstrated that captive dolphins have highly developed imitative abilities, and the way in which humpback whales track changes in their song can only be explained by vocal imitation. However, R&W argue against a focus on how social learning is used in cultural transmission among cetaceans, saying that those who define culture by imitation or teaching would deny culture to cetaceans. This is puzzling since there is solid evidence that dolphins and humpback whales learn by imitation.

R&W define culture broadly as any behavior or information acquired through social learning. Not only do R&W not bother to discriminate between different forms of social learning, but in their treatment of cetacean, R&W have seldom ruled out individual learning or inheritance of behavioral traits. The treatment of evidence for vertical transmission verges on the comical:

> When mother and offspring have similar, but characteristic, patterns of complex behavior, this suggests vertical cultural transmission through imitation, teaching, or other forms of social learning. However, genetic determination or shared environments leading to parallel individual learning are also potential explanations in some cases.

This reverses the normal standards of evidence, obscuring the weakness of evidence ruling out genetics or individual learning.

The R&W article would stir no heartbeats if it were simply about social learning in animals. The rhetorical trick R&W use to escape their broad definition of culture is to suggest that whales have forms of cultural transmission unparalleled outside of humans. Since social learning is so common among animals, they must find arbitrary distinctions to make cetaceans stand out. R&W describe humpback song as a "unique instance among nonhumans" because whale song is similar over much larger ranges than songs of birds. The large range of whale song occurs because low frequency sound travels far in the ocean. R&W do not explain why this difference in scale is so critical to issues of culture. Similarly R&W argue that killer whale dialects are "unique outside humans," on the basis that the dialects are sympatric and involve more than one call type. This claim arbitrarily minimizes fascinating data on cultural transmission in songbirds with abrupt dialect boundaries of several different syllable types (Catchpole & Slater 1995). R&W finally claim that killer whale cultures "encompass both vocal and physical behaviors; such complex multicultural societies where culture encompasses both the vocal and motor domains are otherwise only known from humans." This overblown claim for cultural superiority simply stems from the lower standard of evidence R&W apply to whales than have been applied by most students of animal culture.

R&W argue that it is impossible experimentally to study imitation in cetaceans, so cetaceans should be subject to looser standards of evidence than are applied to studying culture in most other animal groups. The premise is incorrect: imitation has been demonstrated experimentally in dolphins and in using a careful ethnographic approach for humpback whales. The evidence clearly shows culture in dolphins and humpback whales by more restrictive definitions than adopted by R&W, but the looser standards of evidence are required for most other cetacean species. This problem arises because the definitive studies have not been done, not because they cannot be done. R&W prematurely reject the possibility of experimental study of transmission mechanisms in killer whales. Dozens of killer whales are kept in captivity. Vocal imitation could be demonstrated by training killer whales to imitate man-made sounds as was done for bottlenose dolphins by Richards et al. (1984). Many killer whales are transferred each year from one group to another; spontaneous imitation could be studied when an animal from one dialect group is transferred into a pool with animals from another dialect group, as was parenthetically mentioned by Bain (1986).

There is a broader problem with R&W's attempt to set up cetaceans as culturally unique except for humans. Rather than trying to argue that one's own pet taxon is the closest to humans, we need a broader comparative study of the evolution of culture across the animal kingdom, along with the ecological factors that favor it. Galef's research on social learning of food odors in rats (e.g., Galef & Whiskin 1997) might be used to support an argument using the R&W approach that rats have a gastronomic culture more developed than Anglo-Saxon countries, if not quite on par with France or the Moghul princes of India. This argument is less likely to resonate than R&W's, primarily because our cultural biases elevate whales and treat rats as pests. Yet these cultural biases interfere with appropriate comparative study. For example, it may be particularly illuminating to compare the rat example to honey bees. In both taxa, groups of related individuals share a refuge and forage on rich but unpredictable food resources that may last only hours to days. In both groups, this has led to powerful social learning for food selection, and among honeybees, perhaps the most complex representation of spatial cues in animal communication. Yet when we see complex bee behavior we tend to think what amazing things genes can do, and when we see complex whale behavior R&W argue what amazing cultural institutions. The broader the scope of the taxonomic comparison, the less biased the standards of evidence, and the more diverse the ecological contexts, the better will be our theory of the evolution of culture.

R&W emphasize group cultures of killer and sperm whales, in which "cultural" traits have not been shown to result from social learning, and change so slowly that they correlate highly with genetic differences. I am familiar with killer whale research and have worked on sperm whales, and I believe that much of the focus on group behavior stems from the inability of researchers to follow behavior of individuals. There is much better evidence in dolphins for individualized societies in which individuals recognize one another and interact based upon their history of interaction. This pattern is critical for many models of social complexity. Both humpbacks and dolphins imitate vocal signals and show local foraging specializations suggesting rapid transmission to match local feeding conditions. This behavior matches that envisioned in models on the evolution of social learning (Boyd & Richerson 1988) better than the sperm whale cultures suggested by R&W, in which "cultural" traits may change no more rapidly than genotypes. R&W relate the costs and benefits of culture in a cursory and narrow manner to variability in terrestrial versus marine ecosystems and to costs of transport in marine mammals. A more critical analysis of the evidence for culture and a broader comparative perspective is needed.

If a theory is important but difficult to test, the appropriate scientific stance is to develop creative and original methods, not to accept the inability to test critical assumptions. Many tests of critical theories, such as finding genes or subatomic particles were thought to be impossible before creative science focused on the problem. Marine mammalogists have developed new tags, acoustic localization methods, and playback experiments that could enable better testing of imitation even in wild sperm whales. As has been the case with primates and songbirds, the study of animal culture benefits from synergy between studies of wild animals and more controlled observations and experiments from captive animals. It would have been much more helpful for R&W to highlight the areas needing critical research than to plead a special case for cetaceans because they are smart and the work is difficult.

Imitation and cultural transmission in apes and cetaceans

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Abstract: Recent evidence suggests imitation is more developed in some cetaceans than the authors imply. Apart from apes, only dolphins have so far shown a grasp of what it is to imitate; moreover dolphins ape humans more clearly than do apes. Why have such abilities not been associated with the kind of progressive cultural complexity characteristic of humans?

That there are basically just two major forms of behavioural evolution, occurring through genetic and cultural transmission respectively, must rank amongst the most exciting and fundamental discoveries of biology achieved over the last century and a half. These two processes are materially quite different yet share interesting similarities (Blackmore 1999; Dawkins 1976) and, as Rendell and Whitehead (R&W) note, they may interact and intertwine in their consequences. Yet one – the genetic process – has been the subject of vastly more scientific investment than its cultural counterpart. R&W's analysis is therefore an important step forward. We seem to be living at an exciting time when multiple long-term field studies at last permit the kind of birds' eye view of apparent cultural variation in animals like chimpanzees (Whiten et al. 1999) and cetacean species that was already familiar to us in the human case.

R&W suggest a number of similarities and differences between cultural phenomena in cetaceans, chimpanzees, and humans. Because they define cultural transmission independent of underlying learning mechanisms, they deal relatively minimally with the process of imitation that some other authors have designated a criterion for culture. Whilst (as they note) I share the authors' perspective on this, I suggest that certain aspects of cetacean imitation actually deserve more emphasis. First, apart from the great apes (e.g., Custance et al. 1995), only dolphins have been successfully trained to imitate to order (Harley et al. 1998; Herman in press; Xitco 1988). I have suggested this implies these species are capable of something like a concept of imitation; subjects know their goal is to imitate (Whiten 2000). Knowing when you are imitating may be a critical component of the capacity for conformity that R&W note in the human case (sect. 6); perhaps this is true also in apes and cetaceans.

The second point about dolphin imitation is simply that by contrast with what we have seen in these Do-as-I-do experiments with chimpanzees, where the overall frequency and fidelity of matching can be quite low (Custance et al. 1995), dolphins often present immediately recognisable copies, even when the model is something like a person spinning round outside their tank (Herman in press). From studies to date it looks as if – to put it pithily – dolphins show a greater facility to ape humans than do apes (in this particular context at least). Why might this be? One possibility is suggested by the way in which the dolphins' matching behaviours appear reminiscent of synchronised swimming, where two individuals perform similar acts simultaneously. The latter seems to be a feature of dolphins and other cetaceans (exploited in oceanaria shows, where two performers leap and dive together). This facility for synchrony might have provided an evolutionary foundation for the emergence of imitation proper. This is thus an alternative or additional scenario to the one suggested by R&W, of vocal imitation as the precursor to more comprehensive action imitation.

The results of experimental work can thus importantly complement the ethnographic approach that R&W concentrate on. I was surprised that they equated "experimental approaches" with "captive populations." Experiments conducted in the field represent some of the triumphs of ethology. There seems no reason in principle why the kinds of experiments we have done with primates, in which conspecific models display alternative techniques to deal with artificial analogues of natural foods (e.g., Caldwell et al. 1999), could not be presented in the wild. There are formidable practical obstacles to achieving this, whether with apes or cetaceans, but it may be feasible at least with the smaller species like dolphins at sites the animals repeatedly visit. With both cetaceans and primates, the ethnographic and captive experimental studies now combine to justify the special investment needed to complete such field experiments. As in our own research on primates, I believe the ethnographic approach delivers a vital piece of the scientific jigsaw, yet its conclusions often lack closure (for example, the tentative "unlikely" category occurs in R&Ws Table 3 twice as often as a clear "no," and the clarity of the required "double"-no occurs in only 2 of the 17 phenomena listed, both concerning only vocal learning). Experiments have the power not only to discriminate amongst social learning mechanisms, but to establish whether there is actually a social learning process in operation, rather than an alternative explanation such as genes, ecology, or individual learning.

Juxtaposing the experimental evidence for imitation in cetaceans and primates with the field observations on these taxa seems to present a paradox in relation to the ratchet effect. I think it is still an open question whether small-scale instances of this effect exist in non-human species (Whiten 1998), but the scope of our present human cultural complexity is clearly unmatched by any animal, and it is highly plausible this has been achieved by progressive cultural elaboration. It is a puzzle that this has not occurred in chimpanzees or cetaceans, to the extent that if powers of innovation and imitation exist that have created multiple cultural variations, it is not clear why these processes are insufficient to build progressively on such achievements. Perhaps there are different answers to this puzzle for apes and cetaceans. At least part of an answer for chimpanzees is alluded to by R&W: relative to cetaceans, their habitats may be more stable, less challenging. Their limited cultural repertoire may be all they need. For cetaceans the answer may be quite different: Could it just be the lack of hands? How complex a cultural repertoire could possibly ratchet up, without primate manual dexterity? Evolving hominids, by contrast, had dextrous hands as well as a basic cultural propensity, and survived only by adapting to a drastically novel niche (Potts 1996; Whiten 1999). This unique conjunction of factors may explain the evolution of uniquely complex human culture.

Authors' Response

Cetacean culture: Still afloat after the first naval engagement of the culture wars[1]

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Abstract: Although the majority of commentators implicitly or explicitly accept that field data allow us to ascribe culture to whales, dolphins, and other nonhumans, there is no consensus. While we define culture as information or behaviour shared by a population or subpopulation which is acquired from conspecifics through some form of social learning, some commentators suggest restricting this by requiring imitation/teaching, human analogy, adaptiveness, stability across generations, progressive evolution (ratchetting), or specific functions. Such restrictions fall down because they either preclude the attribution of culture to nonhumans using currently available methods, or exclude parts of human culture. The evidence for cetacean culture is strong in some cases, but weak in others. The commentaries provide important information on the social learning abilities of bottlenose dolphins and some interesting speculation about the evolution of cetacean cultures and differences between the cultures of different taxa. We maintain that some attributes of cetacean culture are currently unknown outside humans. While experimental studies, both in the laboratory and in the wild, have an important role in the study of culture in whales and dolphins (for instance in determining whether dolphins have a Theory-of-Mind), the real treasures will be uncovered by long-term observational studies at sea using new approaches and technologies.

R1. The cultures of the commentaries

"Culture," "whale," and "dolphin" are among the more evocative words (**Boesch**). In the target article, we tried to look objectively at the phenomenon of culture among whales and dolphins. The commentators' assessments as to how we succeeded are very diverse and vigorous, attesting to the power of these words to rouse scientific didacticism. The target article is variously described as "pseudo-science" (**Miller**), "as nuanced and sophisticated as any I have read" (**Rauch**), an "attempt to set up cetaceans as culturally unique except for humans" (**Tyack**), and "careful and objective" (**Fox**). The commentators disagree about the evidence. Dolphins apparently have (**Tschudin**) or do not have (**Dunbar**) a Theory-of-Mind. For **Reader & Lefebvre** the evidence for cetacean culture is perhaps better than that for apes, but **Deputte** considers it so much weaker that, unlike chimpanzee culture, is hardly worth considering. Finally the commentators come to radically different conclusions. For **Barrett-Lennard et al.** our review "dispels notions that culture is an exclusive faculty of humans and higher primates," while **Premack & Hauser** conclude "that cetaceans (and chimpanzees) lack culture."

A consensus in perspectives on non-human culture seems remote. The principal fault lines seem to lie between some experimentalists (e.g., **Galef, Mercado & DeLong**) and observational field scientists (e.g., **Barrett-Lennard et al., Boesch, Connor**), as well as between those who believe that human culture should be the reference (e.g., **Galef, Premack & Hauser, Ripoll & Vauclair**) and others who consider that nonhumans may possess cultures which are biologically significant without reference to humans. Humans are interesting cultural animals, and experimental science has an important role in attempts to understand animal culture, but we are strongly against the human reference and in favour of field observations forming the basis of research into animal culture (the "liberal" camp to use **Tschudin**'s terminology). As we respond to the commentators, we will try to explain the rationale for these perspectives.

However, despite the blocking efforts of the "conservatives," the attribution of culture to nonhumans based purely on observational evidence has become a well-established part of the scientific process. This is most clearly shown in the work of primatologists such as Whiten et al. (1999). Additionally, as the commentary period on our target article ended, two key papers were published describing the evolution of cetacean vocal cultures based on multi-year field recordings. Deecke et al. (2000) looked in detail at the changes over 12–13 years in two calls which form part of the group specific dialects of killer whales. One call showed no change, whereas the other showed significant modification over the study period, and the modifications in this call progressed in parallel within two social groups, suggesting horizontal cultural transmission between the groups in addition to vertical maternal or matrilineal transmission, as well as conformity, within groups. Noad et al.'s (2000) discoveries are even more remarkable. They describe a dramatic transformation in the song of male humpback whales off the east coast of Australia over a two-year period, as the population unanimously adopted a radically new song originally sung by a few "minstrel" (using **Mayer-Kress & Porter**'s term) migrants from the west coast. As Noad et al. (2000) note, a revolution such as this was previously unknown among non-human cultures.

We are particularly pleased by those commentaries which have broadened the treatment into areas as diverse as animal training (**Pryor**), molecular evolution (**Brown**), psychology and neuroanatomy (**Dunbar, Tschudin, Whiten**), human evolution (**Knight**), primatology (**O'Malley**), and philosophy (**Fox**). We found these commentaries fascinating but, having little expertise in such fields, our responses will be few.

The commentaries also introduce important ideas about the mechanisms behind cetacean culture, its relationship to ecology, and its evolution, as well as about how we should make cross-species cultural comparisons. In each of these areas we have a response. A number of commentaries emphasize the potential for experimental studies to address the issue of cetacean culture. While we do not agree with all their arguments (as discussed below), the contributions of these commentators will be important in strengthening the emerging study of cetacean culture and social learning both in the laboratory and field.

The power of culture to affect behaviour is well illustrated by the negative commentaries of **Tyack** and members of his Woods Hole laboratory (**Janik** and **Miller**); the similar points and united opposition of all three probably tells us more about cultural transmission in cetacean research laboratories than cultural transmission in cetaceans. Together with noncetologist critics, they have a number of concerns, some of which we agree with. These fall mainly into two areas: how culture is defined, and the evidence for it in whales and dolphins.

R2. Defining culture

R2.1. Placing the bar?

The definition of "culture" has long been contentious. While many of the commentators accept, explicitly or implicitly, the broad definition of culture used in the target article, others do not. Those who do not like our approach almost universally call for a more restrictive definition, arguing that we place the bar too low (**Mann**).

Some of these commentators suggest that inferring the presence of culture in cetaceans under this definition is "fundamentally empty" (**Mann**), but it is no more empty for cetaceans than it is for birds, apes, or other animals which are studied under the same criterion. **Deputte** and **Tyack** go so far as to accuse us of twisting definitions to allow culture to be granted to cetaceans. This we strongly refute. Not only is our definition drawn from taxon-free theoretical work (Boyd & Richerson 1996), it is also the same approach which has led to such enlightening study of cultural processes in birds (Grant & Grant 1996) and primates (Whiten et al. 1999). This approach allows broad, objective, cross-species comparisons that we believe are essential in exploring the evolution of culture in humans and other animals.

For the anthropologist **Ingold,** the cultural bar is not too low, it is in the wrong universe. He objects to the "impoverished theoretical agenda" within which we place our review, but does not outline a coherent alternative. The evolutionary framework of Boyd, Richerson, and others (e.g., Boyd & Richerson 1985; 1996; Cavalli-Sforza & Feldman 1981; Henrich & Boyd 1998; Laland 1992) provides a logical and usable foundation for viewing both the rather basic cultural elements that are all we can currently extract from whales and dolphins, as well as the more sophisticated products of human ethnography (Bettinger 1991). Ethnography of nonhumans is simple compared with that of humans, largely because, currently, only humans can be interviewed. However, there is more to the ethnography of humans than the interview and the term "ethnography" is now becoming quite standard in studies of nonhumans (e.g., McGrew 1998, as well as many of the commentaries), so that, despite the concerns of anthropologists (**Ingold, O'Malley**), we will retain it.

From the perspective of the "conservatives" who wish to raise the bar, only a subset of the information, or behaviour, which is included in Boyd and Richerson's (1996) definition, and in the target article, should be considered culture. Why a more exclusive definition? They seem to believe that there is a natural break (**Ripoll & Vauclair**) in the range of behaviour patterns transmitted by social learning, with, to use **Galef**'s example, classic French cuisine on one side and the acquisition of foraging information by social learning in guppies (Laland & Williams 1997; not Laland & Reader 1999, which is about innovation) on the other. Yes, there are differences between guppy foraging and French cuisine, but then there are also similarities which need to be acknowledged – guppies solve problems to get food, while French cuisine solves a foraging problem for us: how to make snails edible. It is easy to pick out both extremities of a continuum and say "look how different they are," but if one inserts, say, opening milk bottles by birds (Fisher & Hinde 1949, even though they may not be imitating) and leaf processing by gorillas (Byrne 1999) between these two extremes, then the line becomes harder and harder to draw in a logically convincing fashion. Of course there are differences, but there are between the extremes of any continuum. Where is this natural break some argue for? Here we consider the commentators' suggestions for where the non-culture/culture line should be placed:

R2.2. Imitation or teaching

Restricting culture only to information transmitted by imitation or teaching (as argued by **Deputte, Galef, Premack & Hauser**) has an honourable pedigree, which includes Boyd and Richerson's (1985) seminal book on cultural evolution, and Galef (1992) and Tomasello's (1994) attacks on primate culture. We used this restriction in an early draft of our target article, but found it unsatisfactory, for several reasons. By emphasizing process, this definition values the importance of controlled experiments which investigate transmission mechanisms. But, as explained by **Boesch,** with animals such as primates and especially cetaceans, the results of such experiments are almost impossible to link directly to behaviour observed in the field, leading to unresolvable dichotomies for field workers (McGrew 1998). Second, definitions of teaching and imitation are not universally agreed (McGrew 1998; Whiten 2000). It is also not clear that teaching and imitation are necessarily "more advanced" processes than other types of social learning such as emulation (Whiten 2000), or that what is considered to be "culture" in humans is transmitted by these mechanisms (as noted by **Boesch** and **Dunbar,** contra **Deputte** and **Premack & Hauser**). Finally, cultural evolution is not directly dependent on the transmission mechanism. So, Boyd and Richerson (1996), while continuing to note the importance of transmission mechanisms, removed reference to them in their definition of culture. They were right.

R2.3. Human analogues

Galef reasserts his view (see also Galef 1992) that culture should be reserved for activities that are homologous to human culture, and so have the same phylogenetic origin. The most recent common ancestor of humans and cetaceans was a small mammal which probably shared the Earth with dinosaurs about 95 million years ago (Bromham et al. 1999). We do not know what cultural behaviour it possessed, or shared with the many intermediate organisms joining it to humans and cetaceans, but it is clear that none of the cetacean cultural patterns that we discussed are phylogenetically homologous to those of humans – they are all analogous; here we agree with **Galef,** but we cannot accept that analogy makes these phenomenon irrelevant to the evolution of culture (note that when **Galef** writes "the evolution of culture" he actually means "the evolution of *human* culture"). In fact, analogy is one feature that makes cetacean cultures so interesting (**Reader & Lefebvre**). Whales and dolphins seem to possess some cultural features shared only with humans – to dismiss them because they are not of common descent is extremely counterproductive if we are interested in the evolution of human culture, or the evolutionary effects of culture in humans or other animals. We were disappointed, given the strong opinions he has previously published on this, that **Galef** chose to ignore entirely our discussion of why we think similar processes in other animals should be considered "culture." We can think of no other evolutionary trait whose existence or nonexistence in a given group is decided on homology or analogy with any other group, human, or nonhuman. The probable reason for this is that such an approach is profoundly un-evolutionary (**Poirier & Fitton**).

R2.4. Adaptiveness

From an evolutionary perspective it might make sense, as suggested by **Slater,** to restrict culture to those behavioural patterns that are adaptive, since they may then affect genetic evolution. However, there are fundamental problems with this. It may well be that the dialect adopted by a killer whale group is adaptively unimportant – a group would have the same survival value if its dialect were changed. However, for an individual within a group, the situation is different – it is likely to be highly important that an individual uses the dialect of its group. Similarly, to use **Premack & Hauser**'s example, the side of the road on which a nation drives is arbitrary and of little importance, but the side of the road that an individual drives is closely tied to his or her fitness. Furthermore, as Richerson and Boyd (1998) explain, apparently nonadaptive cultural badges of group membership can drive important trains of cultural group selection (see also **Dunbar**). Therefore, distinguishing between adaptive and nonadaptive culturally transmitted behaviour will be difficult in many cases. In addition, to restrict culture only to adaptive phenomenon in animals would result in a double standard regarding human culture, much of which is nonadaptive.

R2.5. Stability across generations

Freeberg requires stability across generations as a prerequisite for vocal cultures. There is theoretical justification for this, as stability seems to be a necessary, but not sufficient, condition for culture to drive genetic evolution (Laland 1992). As **Freeberg** notes, using the criterion of humpback whale songs, which change progressively over months and years, would not be considered culture, but then neither would human popular culture which changes in a similar manner (will teenagers still be listening to the Backstreet Boys in twenty years?). If this restriction is inserted to a definition of culture, how stable is stable enough? Where in the killer > sperm > humpback rank of stability of vocal pattern for whales, or classical > folk > jazz > pop for humans, do we place the cultural fence? We see no natural break, and, once again, while stability is clearly a very important attribute of a cultural pattern, there is no good reason to use it in a definition of culture.

R2.6. Ratchetting

Some commentators (including **Ripoll & Vauclair**) take almost the reverse position, suggesting that culture is an "accumulative" attribute, evolving and building on itself, or ratchetting. Nonhuman cultures clearly change and evolve (e.g., Deecke et al. 2000), so killer whale dialects and humpback songs could be seen to ratchet in the sense that they change. However, the term ratchetting implies building up, producing something more complex or more efficient than what went before; in evolutionary terms, improving fitness. So from our evolutionary perspective it is an important quality, but as in the cases of transmission mechanisms, adaptiveness and stability, such a restriction to culture possesses two major flaws. It is operationally difficult or impossible to use in the field, and it seems to exclude obvious parts of human culture. As with many aspects of human culture, the adaptiveness of a type of humpback whale song likely depends both on the other songs being sung at that time and the cultural preferences of the females listening to it, both of which change with time. Therefore, the fitness of different song types, or, for instance, human religions, cannot be compared across time. Has the adaptiveness of Christianity or Judaism "improved" over the last 2000 years? Do the Backstreet Boys (or even Benjamin Britten) represent the cumulative ratchetting or improvement of musical culture since Mozart?

R2.7. Definition by function

Ripoll & Vauclair, and as far as we can understand, **Premack & Hauser,** lean toward a definition of culture by function, selecting perceived functions of human culture, and apparently requiring culture in nonhumans to fulfill the same function. First, the attribution of function to human culture is rather arbitrary and unsatisfactory. Some human (e.g., Boyd & Richerson 1985) and nonhuman (e.g., **Slater**) cultural attributes seem to have no function, or even to be maladaptive. We agree that probably the initial function of human culture was to cope with different environments, and one could include social environment along with this (the Machiavellian intelligence theme; Byrne & Whiten 1988). For **Ripoll & Vauclair** to suggest that this role in cetacean culture is "minimal" is strange. Consider the ecological success enjoyed by those species where evidence for culture is strongest: despite a population reduction due to whaling, and the advanced technologies of modern fisheries, sperm whales still rival humans in biomass taken from the ocean (Clarke 1977). Consider the ranges of ocean environments they have colonised: until human settlements on Antarctica, sperm, killer, humpback, and a few other whale species had the greatest latitudinal distributions of any mammals on Earth. Consider the range of foraging specialisations in killer whales, bottlenose dolphins, and humpback whales (sperm whales we cannot see foraging), and consider their social complexity (bottlenose dolphins form second order alliances, Connor et al. 1992, and killer whales maintain highly stable groups within a labile pattern of inter-group interactions, Bigg et al. 1990, as do sperm whales, Whitehead et al. 1991). These attributes correlate with the evidence for culture, and while correlation is not the same as causation, is it really reasonable to state that cetacean culture plays a "minimal" role in their relationship with their environment? Claiming that social regulation and spiritual agencies (**Ripoll & Vauclair**) or clarifying "what people value" (**Premack & Hauser**) are "functions" of human culture moves onto very obscure ground largely free of empirical material. Regardless, the principal problem of this approach is the inherent anthropocentrism which defines culture using features which can *only* be examined in human culture. At least **Premack & Hauser** acknowledge that culture must not be defined in such a way that it is by definition uniquely human – unfortunately their subsequent discussion of culture as shared values directly contradicts this, as shared values cannot currently be examined in nonhumans, and drags their commentary into an intellectual tangle from which it never escapes – but **Ripoll & Vauclair** seem not even to recognise this.

R2.8. Drawbacks of narrow definitions

The commentators have suggested a number of ways of restricting our broad definition of culture. These potential definitions are sometimes mutually antagonistic. For instance, whereas **Galef** considers classic French cuisine culture to be culture and guppies passing on information about food sources not culture, under **Slater**'s adaptiveness criterion the guppies may have culture but not French chefs.

Those who oppose the idea of cetacean, or more generally nonhuman, culture fall down because they cannot produce a definition or concept of culture which both matches their ideas (i.e., nonhumans do not have culture) and at the same time: (1) at least allows for the potential for nonhuman culture; and (2) does not exclude much of what we call cultural in humans. Definitions such as the presence of "shared values" (**Ripoll & Vauclair**) cannot be tested in nonhumans as yet, and so are inadmissable by criterion 1, whereas those which insist on imitation or teaching (**Galef**), or stability (**Freeberg**), or ratchetting (**Ripoll & Vauclair**) fall down on criterion 2. Instead, there are some very weak ideas regarding a "theory of culture" (**Premack & Hauser**), which seems to rely heavily on arbitrary categories such as "trivial" versus "non-trivial." A rigorous, mathematically formulated theory of culture already exists (Boyd & Richerson 1985; Cavalli-Sforza & Feldman 1981). This and its developments, such as those suggested by **Mayer-Kress & Porter,** should form the basis of our explorations of human and nonhuman cultures.

Why is so much effort put into defining culture? Why did our use of a broad definition, a definition already well imbedded in the literature, provoke so much commentary? A few of the commentators are clearly making rather futile attempts to maintain a Cartesian dichotomy between humans and other animals in the area of culture. For example, the primary rationale that **Mann** gives for not using the word "culture" is simply that culture is too "loaded and complex" a term. While specific forms of cultural transmission could be accurately described as "vocal imitation" for example, this is not an argument as to why they are not also culture. Calling essentially the same process "tradition" in nonhumans and "culture" in humans is unacceptably Cartesian to us. **Mann**'s argument is basically a semantic one reflecting an irrational unwillingness to use the term "culture" in nonhumans.

Other commentators seem to wish to assert a primacy of experimental science over natural observation by using a definition which depends on the results of experimental studies of transmission processes. For us, the what and why of animal behaviour in the wild are primary (de Waal 1999). The how is important, but secondary.

In summary, there are logical or operational problems with all of the alternative, more restrictive, definitions of culture put forward by the commentators. We continue to believe that a broad evolutionarily-based definition will most advance the field.

R2.9. A revised definition

Having said this, some commentators do make some more substantive criticisms of our definition, sharing a viewpoint best expressed by **Mann** ("it is entirely unclear what then, the term 'culture' *adds* to the concept of 'social learning'"), but also raised by **Blute, Herman & Pack, Poirier & Fitton.** These points are justified, and lead to us altering, and we think, improving, our definition of culture. It is undoubtedly true that social learning does not necessarily give rise to culture. For culture to arise, social learning must produce behavioural conformity (which can include avoided behaviour, **Rauch**) within a population or some part of it, and usually, although not necessarily, behavioural variation within a species (**Blute, Boesch, Poirier & Fitton, Premack & Hauser**). Thus we arrive at a slightly different definition:

> Culture is information or behaviour – shared by a population or subpopulation – which is acquired from conspecifics through some form of social learning.

This differs from our original definition and that of Boyd and Richerson (1996) in that it specifies that social learning alone is not culture, because it does not necessarily give rise to conformity in behaviour, or the potential for it. An enlightening example is bottlenose dolphin vocal learning, which, as **Slater** points out, was not much considered in the target article. Here is sophisticated social learning (vocal imitation has been well demonstrated in this species), which as far as we know, does not give rise to systematic population or subpopulation level behavioural variation. It is interesting to ask why this is so (see sect. R3.3).

So, by our definition, culture is indeed widespread in the animal kingdom. This does not mean that all cultures are equal; we think that variation in cultural processes between species is best understood and studied as variation in the form of culture (c.f., **Dunbar**'s "levels of culturalness"), under a broad definition of culture itself (**Kako**). We strongly support **Slater**'s call for a rigorous consideration of the variation among the cultures covered by this definition, and perhaps a taxonomy of culture, and thus reject **Mitchell**'s perspective that comparisons should only be made between what is called culture, and what is not called culture. There are many different forms of culture, which will lead to different ethnographic patterns resulting from different types of cultural behaviour (vocal, material, social), different transmission processes, and hence varying levels of copying fidelity, stability and ratchetability, adaptive significance (and hence potential for co-evolutionary effects), strength of the conformity drive (and hence, again, stability and potential for co-evolutionary effects and rate of innovation), and the nature of the cultural grouping (e.g., geographical area, population, social group within area). Such an approach acknowledges the similarities that exist and makes it easier to focus on the *true* differences between the cultures of various species, which is really what everyone is concerned about.

R3. The evidence for cetacean culture

R3.1. Pseudoscience?

The commentators' reactions to the evidence we present are as varied as their definitions of culture. In keeping with our target article we will discuss the reactions to the evidence for cultural variation in the field and social learning mechanisms separately.

Before this though, we want to refute the accusations that we are any less rigorous in considering evidence for cetaceans than in other species (**Deputte** and **Tyack**). We have been no more or less rigorous in considering the evidence than have, say, students of primate culture (a number of primatologist commentators appear to consider our evidence convincing, e.g., **Dunbar, Whiten**). Enough commentators took our approach and evidence seriously to give the lie to these accusations of loose standards. **Deputte** thinks we have "put the cart before the horse," but is unclear on what he considers the cart and what the horse in his definition of culture. The order of presentation seems to agree with what we actually did: we identified behavioural variation and considered using available evidence in the likelihood that each pattern can be attributed to social learning. Similarly, **Tyack**'s claim that we make a special case for cetaceans so grossly misrepresents our position that we wonder whether **Tyack** really considered our arguments with anything approaching an open mind. His suggestion that we argue for weaker standards of evidence cannot draw on any quotation from our target article because we simply do not do this. **Miller**'s labeling our work as "pseudo-science" misunderstands both our and Popper's ideas. The hypothesis of cetacean culture is falsifiable by observations which shows the patterns we suggest are cultural are in fact the result of genetic variation, or ecology plus individual learning.

Some commentators are perplexed that we both reject a process-centered definition, but then go on to consider evidence for imitation and teaching in cetaceans (e.g., **Day et al.**). However, we explicitly set out our intention to consider evidence from both the process and product perspectives and attempt a synthesis. In contrast, **Tyack** is puzzled by our de-emphasis of transmission mechanisms in defining culture, given the impressive evidence for imitation in dolphins. This is only puzzling if, as **Tyack** obviously believes, we sought to show culture by any means necessary; the puzzlement reveals the prejudice.

R3.2. Observed behavioural variation

By its nature, much of the observational evidence we describe "lacks closure" (**Whiten**). For various cases of behavioural variation among cetaceans, it is impossible, currently, to conclusively rule out individual learning in different ecological regimes (contra **Janik,** this potential explanation was included in Table 3 under "ecology," but, we acknowledge, not clearly explained) or genetic transmission, and many commentators pick up on this. Given that we acknowledge these weaknesses explicitly in our target article, we see no reason to dispute these comments, and leave the readers to judge the evidence for themselves. However, we would like to respond to the more erroneous criticisms.

Humpback whales provide both the strongest and perhaps some of the weakest evidence of culture from their observed behaviour. The strongest is surely humpback song; the patterns observed by Noad et al. (2000) and previous work (e.g., Payne 1999) can only be explained by cultural transmission of vocal patterns; even **Tyack,** our most vociferous critic, admits this. **Kuczaj** correctly points out how weakly we had explained the evidence available, given that learners must have models, but hopefully the useful discussion of **Herman & Pack** on where transmission may take place clarifies this. The only major objectors to the attribution of culture in this instance are **Freeberg** and **Ripoll & Vauclair. Freeberg**'s reservations are based mostly on ignorance: there clearly are systematic differences in song between breeding populations (Payne & Guinee 1983), and while the actual songs do change, the differences between these populations are usually maintained over long time scales (but see Noad et al. 2000); the group versus individual sampling issue is nonexistent because singers are always recorded individually. **Ripoll & Vauclair**'s objection that variation "could simply reflect the play of random processes associated to the plasticity of learning mechanisms" is about as desperate as they come; we see no reason why much human culture could not be described the same way!

The attribution of culture to the spread of lobtail feeding in humpback whales is much weaker. We accept **Day et al.** and **Galef**'s points about variation in learning latencies leading to sigmoidal rates of spread, which we had not considered. Individual learning in changing ecological conditions cannot be ruled out in this case, as stated in the target article. Contrary to **Day et al.**'s assertion that much of our evidence involves increasing incidence of a behaviour, this is in fact the *only* evidence we submit concerning such a phenomenon. **Galef**'s discussion of this particular pattern reveals how easily underlying biases can become entrenched. Consider his assertion that bubble-feeding is not socially learned in humpbacks. Now, while there is some inconclusive evidence that lobtail feeding *is* socially learned, there is not a single piece of evidence that bubble-feeding is *not* – we do not know, but then neither does **Galef.**

The case for killer whale dialects being culturally transmitted has been made even stronger during the commentary period for this article due to the work of Barrett-Lennard (2000), who found that mating is common between different groups which share no calls but rare within groups (the evidence is particularly strong for the "northern resident" community in British Columbia, where paternities were tested using microsatellite loci), and Deeke et al. (2000) who showed how some discrete calls change over time while others do not. This evidence really removes any necessity for experimental demonstration of vocal learning abilities, since it eliminates the possibility of calls being genetically determined: the only way dialects can be maintained and evolve if mating is between pods is by cultural transmission. In the future, the ongoing study of this killer whale population may make a Grant and Grant (1996) type study, as suggested by **Miller**, possible. However, the Woods Hole group (**Janik**, **Miller**, and **Tyack**) still do not accept the case. **Tyack** believes that apparent dialects could simply be the result of sampling groups over individuals (a concern shared by **Freeberg**), despite **Miller** (a member of his own research laboratory) finding that group recordings appear to be representative of individual repertoires; within-laboratory cultural transmission obviously has its limits! **Miller**'s own refrain about the killer whale evidence self-destructs when he cites Barrett-Lennard's (2000) genetic evidence at the end of his argument, and his opinion that our article devalues the work of those currently studying killer whale dialects is, judging from their commentary, not shared by **Barrett-Lennard et al.**, who are actually doing the work.

While discussing apparently highly stable cultures like those of the killer whale, it is worth correcting a misreading by **Day et al.** At no point in our target article is the stability of cetacean cultures considered "evidence of imitation and high cognitive ability," so their subsequent discussion is baseless. We never at any point judge a phenomenon to be cultural or not based on whether it is transmitted by teaching or imitation rather than any other transmission process. When we do look at transmission processes, the discussion is largely limited to imitation and teaching because, to our knowledge, no one has experimentally or otherwise studied other forms of social learning in cetaceans.

Moving on to sperm whales, **Freeberg** wonders how we can argue that sperm whale groups can be bearers of culture given that they may only last for a number of days. While sperm whale groups with about 20 members are often made up of more than one social unit (with about 12 members), these constituent units are orders of magnitude more stable than the day-to-day groups (Whitehead & Weilgart 2000). A few transfers between units have been recorded, but many unit members remain together for a decade or more (Christal et al. 1998). **Mesnick** point out that while some unit members are matrilineal relatives, others are not, and are surprised that we use the word "matrilineal" in this context. However, by "matrilineal" we mean that most females remain grouped with their mothers while their mothers are alive, and we believe that the genetic evidence from sperm whales is consistent with this, although **Mesnick et al.** are right to highlight the emerging complexity of sperm whale social structure. Differences in the vocal repertoires of groups likely then reflect differences in repertoires of the underlying units. Furthermore, the observed correlation between mtDNA haplotype and repertoire is perhaps most convincingly explained by stable cultural transmission, although, as noted in the target article and by **Mesnick**, this explanation needs elaboration to deal with the genetic and social complexities of sperm whale society. **Freeberg** and **Tyack** are right that we also need to know more about how individual repertoire relates to unit and group repertoire. **Tyack** (who accuses us of "reversing normal standards of evidence") complains that slow-changing group-specific cultures such as we suggest for sperm whales do not match Boyd and Richerson's (1988) model very well. However, evidence should not be denied because it does not necessarily fit a theory and, in fact, Boyd, Richerson, and their colleagues have considered group-specific cultures (e.g., Henrich & Boyd 1998; Richerson & Boyd 1998). **Janik** questions the cultural transmission of sperm whale coda dialects. We thank him for identifying our confusing reference to Ohsumi – we miscited this reference. We meant Ohsumi (1971) which, contra **Janik,** does imply that mating occurs outside matrilineal groups. For instance: "Most of bulls are considered to live solitary. Bulls struggle with one another for joining a nursery school in the breeding season. " (1971, p. 17). However, as with the killer whales, the strongest evidence is genetic. Lyrholm et al. (1999) found much greater variability and much less geographic structure in nuclear microsatellites than in mtDNA among sperm whales, and attributed this to male dispersal and female philopatry. This study indicates that male sperm whales often disperse between oceans, and the results are not consistent in any way with within-group mating. **Janik,** however, in his determination to dismiss the cultural transmission of coda dialects, then starts stretching even harder. We agree that related animals within sperm whale groups share mtDNA, and mitochondria affect energy budgets, and so potentially some forms of behaviour. But he goes on to suggest that this convoluted process might account for similar patterning of clicks within codas (e.g., "Click-pause-Click-pause-Click-pause-Click" vs. "Click-pause-Click-pause-Click-double pause-Click"), which are almost entirely made at the surface (Watkins & Schevill 1977) where energetic factors would have a minimum influence, within a species whose mtDNA is remarkably homogeneous (Lyrholm & Gyllensten 1998). The alternative is that they learned the patterns from their mothers. **Janik**'s argument would, we suspect, horrify his admired William of Occam.

Finally, there is some confusion among the commentators regarding whether individual learning under different ecological conditions could account for foraging specialisations in bottlenose dolphins. While **Janik** asserts that we cannot dismiss this as a potential cause for behavioural variation, **Mann** considers that ecological explanations cannot account for sponge carrying since non-sponging animals also forage in the same areas as sponging animals. However, **Mann** goes on to state that ecological factors "are not irrelevant" (see also **Connor**). **Janik** and **Mann** also question whether individual learning could account for cooperative fishing with humans. As these fishing cooperatives are group activities, a young animal joining them is not learning the behaviour individually (see Simöes-Lopes et al. 1998 for more information on the development of this behaviour). Some form of social learning is taking place. It could be imitation, local enhancement, exposure, or some other form, but all of these can lead to culture (Whiten & Ham 1992).

R3.3. Social learning mechanisms

Much commentary was devoted to the experimental study of social learning mechanisms and cognitive abilities in bottlenose dolphins. Surprisingly, given the supposed unambiguity of experimental results, opinion here is as diverse as on any other aspect of our article. Evidence for motor imitation in this species is described as "weak" by **Premack & Hauser** and **Deputte** considers that social learning remains to be demonstrated in cetaceans, while **Mitchell** asserts that "performance is generally poor in comparison with humans and apes." In contrast, **Bauer & Harley** describe a "sophisticated, flexible ability to imitate," **Herman & Pack** "a broad concept of imitation," **Tyack** considers the evidence "solid," and **Whiten** concludes that dolphins are better imitators of humans than any nonhuman primate. Although **Bauer & Harley** think us "overly cautious" in our interpretations of the available evidence, given the diversity of the commentaries perhaps we were justified in being cautious. However, **Bauer & Harley, Herman & Pack,** and **Whiten,** with the better referenced commentaries, have stronger arguments: bottlenose dolphins are undoubtedly capable of social learning (contra **Deputte**), and almost certainly the more sophisticated forms such as imitation. Such knowledge strengthens our interpretation of behavioural variation in wild bottlenose dolphins as cultural. Particularly significant are **Pryor**'s observations on apparently imitative behaviour in a wide range of cetaceans, emphasising the need for research, at least in captivity, to move away from the bottlenose dolphin bias (see also **Herman & Pack**). The "fads" that **Pryor** describes suggest another way culture could be studied in captivity. The fact that dolphins are more easily trained with socially oriented rewards than food oriented ones (**Lynn & Pepperburg**) further highlights the complexities of experimenting with these animals, and also suggests that wild dolphins may learn more easily in a social rather than individual context.

Similarly the interesting commentaries on dolphin Theory-of-Mind have differing conclusions. **Tschudin** is of the opinion that bottlenose dolphins are capable of second order intentionality, whereas one of the co-authors of the cited paper, **Dunbar,** thinks it likely that they are not. Presumably, we must await further tests controlling for the factors like cueing mentioned by both authors. Such work is of obvious importance in exploring the differences and similarities between human and cetacean culture (**Dunbar,** see below).

According to **Galef,** we imply that the presence of "vocal traditions" means that cetaceans can learn other motor acts by imitation. There is no such statement or implication in the target article, although an evolutionary route from vocal to motor imitation is discussed (sect. 5).

Little attention (**Slater**) was given to bottlenose dolphin vocal learning in the target article since variation in signature whistles is primarily at the individual level and so does not give rise to easily recognised group level variation; hence we did not include this as culture (see R2.9). Still, in this species, there do appear to be community-level cultures in foraging – sponging, beaching, provisioning, and cooperative fishing – so maybe we just have not looked in the right place for vocal culture. Some work does point to community level variation in bottlenose dolphin vocalisations (Ding et al. 1995).

The description of killer whale beaching behaviour and interpretation of teaching attracts much criticism. We are and were aware of the weakness of the available data, but nothing we have read changes our opinion, shared by **Herman & Pack,** that the evidence is compelling. Some of the criticism however goes too far and falls off the edge of its own zeal. For example, **Maestripieri & Whitham** complain that "no evidence was provided to support the notion that the strandings were intentional." It is very hard to imagine that killer whales hurling their bodies (weighing several tons) up onto beaches could somehow be accidental! **Galef** cites Hoezel (1991) for the hunting success of a female accompanied by one juvenile (3 out of 3 occasions), but chooses not to mention the result in the same paper that the same female had significantly reduced hunting success when accompanied by two juveniles (31% of 11 occasions, vs. 82% of 14 occasions when alone). Similarly, adults do not "only" engage in behaviour to return stranded calves (**Galef**) to the water, they also push them onto the beach in the first place, and push them towards prey (Guinet & Bouvier 1995) and throw prey "towards" calves (not "around" them as stated by **Galef;** Lopez & Lopez 1985) – observations which **Galef** ignored. **Mitchell** states that in Guinet

& Bouvier's (1995) study both mothers self-stranded with their calves, and that this is not compatible with our interpretation; now, while A4's mother did indeed strand with A4, she was observed doing so twice (out of 35 strandings by A4), dramatically less than A5's mother, who *always* stranded with A5 (53 of 53 strandings; see Table 2 of target article). While the teaching data are weak on other points, they are clear here.

R4. Culture and ecology

The relationship between culture and ecology is complex. Many of the most interesting aspects of human culture are ecologically based. Our houses, food, clothes, religion, and even music (alpenhorns and yodeling in the Alps) are based upon, or incorporate, the surrounding environment. Many characteristics of human populations result from the social learning of behaviour which relates to the environment. As **Boesch** notes, such behaviour is accepted as cultural in humans (which makes **Ripoll & Vauclair**'s dismissal of cetacean culture as responses to environmental constraints nonsensical).

But not with nonhumans. The foraging specializations of bottlenose dolphins described by **Connor** likely result from just such interactions between ecology and social leaning, but the conservatives will point out, correctly, that individual learning has not been formally ruled out, and so deny culture. McGrew et al. (1997) felt that they had to falsify nine competing hypotheses for patterns of nut cracking in chimpanzees before they could conclude that it was cultural. In the population which did not crack nuts, they examined the following hypotheses: "(1) nuts are absent; (2) nuts are few; (3) nuts are unsuitable; (4) hammers are absent; (5) hammers are unsuitable; (6) anvils are absent; (7) anvils are unsuitable; (8) nuts are displaced by better food items; (9) intelligence is insufficient." All were refuted. But supposing nuts were fewer at the site without nut-cracking, then culture would have been denied, although, given the cultural diversity of chimpanzees in similar attributes (Whiten et al. 1999), it would still have been a plausible, and probably the most plausible, explanation. Thus we are likely missing a large part of nonhuman culture if we restrict to those cases in which there are no ecological differences between populations (**Boesch, Day et al.**).

Is there any way around this? Perhaps, as noted by **Connor,** we should focus on individual and social learning. A crucial aspect of individual learning is independence. If one set of dolphins has double the access to sponges compared with another, and proportions of animals using sponges in the two populations were 0.2 and 0.1, then we might reasonably infer individual learning, but if they were 0.9 and 0.1 then independent origins of the trait might be rejected and social learning would be indicated. Following the suggestions of **Day et al.**, this could be formalized in some cases by using the Akaike Information Criterion, or something similar, to choose the most mathematically parsimonious model, without designating either individual or social learning as "null."

R5. The evolution of cetacean culture

The commentators provide some interesting perspectives on our speculations as to how and why cultures arose among the whales and dolphins, as well as to possible evolutionary consequences of such cultures.

Lynn & Pepperburg suggest that culture did not arise independently with cetaceans, but may have existed in their terrestrial ancestors (ungulate-like creatures). Given our broad definition of culture, we would agree that this is possible, and note that in the target article we state that cetaceans "*perhaps* represent an independent evolution of social learning and cultural transmission" [emphasis added]. However, if terrestrial conditions at the time promoted the evolution of culture in cetacean ancestors, then why did it not do the same in the mammalian lines which did not return to the sea: we would expect culture to be much more widespread in terrestrial mammals than it currently seems to be. Hence, we strongly suspect that many of the most prominent characteristics of some cetacean cultures, such as the stability and sympatric multiculturalism of sperm and killer whale dialects, originated independently within the cetacean line, and maybe multiple times: sperm and killer whales are as distantly related phylogenetically as is possible within the odontocetes (Rice 1998), many of which do not seem to have social systems which could form the foundation for such cultures (Whitehead 1998). It is notable that some of the most remarkable characteristics of odontocete and mysticete cultures are antitheses: the apparent stability of some odontocete cultures (especially killer, but perhaps also sperm, whales) is unusual, whereas it is the evolutionary, and sometimes revolutionary (Noad et al. 2000), character of humpback whale vocal and foraging cultures that make them so interesting. These contrasts must have arisen after pre-cetaceans left the land.

So why did cetacean cultures arise? **Slater** makes the important point that culture does not need to be adaptive (with respect to individual or inclusive fitness) to persist, emphasizing results from the early models of Boyd and Richerson (1985). However, their later models suggest that there may be substantial costs of developing the cognitive infrastructure needed for stable cultures (Boyd & Richerson 1996). Therefore, at least in the case of such stable cultures as seem to be possessed by killer and sperm whales, it is reasonable to look for an adaptive explanation for their evolution.

Reader & Lefebvre provide interesting evidence for, at the best, only weak links between sociality and social learning capacity in birds, and group size and social learning frequency in primates. These relationships may also hold in cetaceans. However, this does not necessarily imply that sociality and culture are also weakly linked. The evolution of culture depends both on social learning ability and on how it is used. More social species may have more frequent opportunities to learn from each other (although this is not indicated in the primate data presented by **Reader & Lefebvre**), and the information that animals gather may be of greater significance, particularly if it is used to structure the social interactions themselves (Richerson & Boyd 1998). In cetaceans, there is an additional problem in that it is far from clear that group size, however defined, is an appropriate measure of sociality (Connor et al. 1998a).

Thomas believes that we misrepresent Steele's (1985; 1991) and Boyd and Richerson's (1988; 1996) work when comparing variability in marine and terrestrial ecosystems and how such variability may favour or disfavour the evolution of culture. We were not entirely clear in this area of the target article, but neither is **Thomas.** Steele's argument runs roughly as follows: temporal variability in the *physical* marine environment is similar to that of terrestrial systems at large temporal scales, but very low at small scales. This means that small short-lived marine organisms can expect to live in highly stable physical conditions throughout their lives. However, for such organisms, conditions may change radically in any place over a few generations. Thus, these short-lived plankton at and near the base of the oceanic food web have generally adopted "specialist plus dispersal" life-history strategies. Together with the greater variability over larger temporal scales, the result is that the *biological* variability of the ocean, the variability that is of most significance for large homeotherms such as cetaceans, is substantial over moderate to large scales, in fact, in Steele's argument, greater than that on land.

As **Thomas** and **Tyack** note, we were not very specific in relating Boyd and Richerson's (1988; 1996) models to the relationship between environmental variability and the evolution of social learning. There were good reasons for this. In their original model, Boyd and Richerson (1985) found a U-shaped relationship between the advantages of social learning and environmental variability, with social learning being more adaptive in intermediate environments but individual learning being favoured in highly variable environments, and genetic determinism in highly stable ones. Later models (Boyd & Richerson 1988; 1996; Henrich & Boyd 1998; Laland et al. 1996) explored parts of this relationship in more detail, and in different ways. It is not reasonable to map Steele's largely verbal description of the different patterns of variability in marine and terrestrial environments onto Boyd and Richerson's analytical models. We could not align the time scales in a convincing fashion, and so contented ourselves with simply noting that the adaptive advantage of social learning is strongly related to environmental variability. However, using some of the commentators' ideas, we will try and be a little more specific here as to the circumstances in which culture might be adaptive in a variable environment:

(1) Unpredictable, low-frequency variation. Characteristic of such phenomena are the "super El Niños" which dramatically alter the oceanography of the eastern tropical Pacific and surrounding areas (Arntz 1986). These may occur once or twice in the lifetime of a long-lived cetacean. For sperm whales, we know that these phenomena can dramatically decrease their feeding success (Whitehead 1996), may affect reproductive rates (Whitehead 1997), and that the animals respond to them by moving (Ramirez & Urquizo 1985). Optimizing such movements may be key to fitness, and social direction of movement could greatly improve their efficiency (Whitehead 1996). In such situations the presence of older individuals, who have experienced such circumstances before, and lived through them, may be especially important (as suggested by **Barrett-Lennard et al.** and **Poirier & Fitton**). Although there is evidence for food sharing, and even provisioning, in killer whales (Baird 2000), we think it more likely that information rather than food (see **Knight**) is an older female's most important endowment to her descendants (see Diamond 1998, pp. 103–25, for this argument applied to humans, and Whitehead & Mann 2000 for the more detailed consideration of menopause in cetaceans requested by **Mann**). In this situation, the models of Boyd and Richerson are not directly relevant as they consider cases in which, after an environmental change, previously learned behaviour has no value. Here, we are interested in the situation in which, after an environment change, previously learned behaviour at some time, perhaps a long time, before (when the environment was similar) is useful.

(2) Unpredictable, medium-frequency variation. **Barrett-Lennard et al.** make the interesting suggestion that it is the high variation of prey availability in the ocean over medium spatial (kms.) and temporal (hours to days) scales that may have driven the evolution of cetacean culture. Once again Boyd and Richerson's models do not apply to this situation, as it is communal behaviour and communal memory across such variation that is of value.

(3) Exploitation of new opportunities. As pointed out by **Poirier & Fitton,** social learning may aid animals in exploiting new types of resources, especially if there is biased transmission (in which individuals can recognize and adopt more favourable behaviour, Boyd & Richerson 1985). In our target article we noted several new foraging opportunities which cetaceans seem to have learned of socially, including killer whales taking prey from long-lines and bottlenose dolphins fishing cooperatively with humans.

(4) Consequences of mobility. **Day et al.** draw attention to Laland et al.'s (2000) important idea of niche construction. If cetaceans dampen environmental variability at medium and large scales using movements, which may be at least partially culturally determined (ideas 1 and 2 above), then parents and offspring may experience more similar environments than randomly chosen members of the population, mediating vertical cultural transmission. This also relates to **Connor**'s point that mobility potentially renders foraging specializations more affordable. It is particularly interesting that birds and bats also show such strong evidence of culture, given that flight gives these groups better potential mobility in relation to most terrestrial animals; it would interesting to look more closely at birds to see how culture relates to movement across species.

Bauer & Harley and **Whiten** identify another characteristic of the aquatic environment which may have facilitated the evolution of social learning and thus culture: the potential for synchronized behaviour. Dolphins are notable for their synchronized behaviour both in captivity (**Bauer & Harley**) and in the wild (Connor et al. 2000; Fig. R1). Three-dimensional movements are much more controllable in an environment which provides resistance in all directions, and in which the effects of gravity are nearly eliminated. Therefore synchronized movement is less constrained for aquatic animals. Synchronicity among nearby

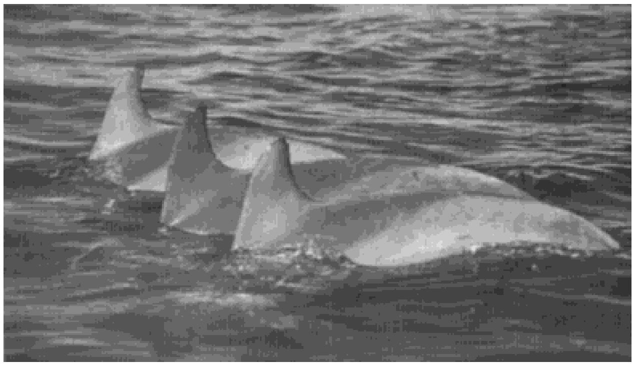

Figure R1.

animals may be adaptive when feeding or confusing predators (Norris & Schilt 1988), and among dolphins is an important marker of social relationships (Connor et al. 2000; Fig. 1). Thus, perhaps, as suggested by **Bauer & Harley** and **Whiten,** synchronization has served as a foundation for more general imitative abilities.

Brown, Janik, and **Mesnick** comment on the "cultural hitchhiking" hypothesis, the suggestion that, in the societies of the matrilineal whale species – killer sperm and the two species of pilot whale – which have remarkably reduced mtDNA diversity, given their population sizes, cultural selection might have reduced mtDNA diversity (Whitehead 1998). **Janik** proposes increased selection on the mtDNA of diving mammals as an alternative explanation. This would only apply if the matrilineal whale species were especially affected by this process. However, while sperm whales are very deep divers (e.g., Watkins et al. 1993) and so fit with **Janik**'s suggestion, killer whales do not dive particularly deep or long by cetacean standards (Baird 2000). There is less information on pilot whales, but their diving seems intermediate between that of killer and sperm whales (Mate 1989). **Mesnick** (see also Mesnick et al. 1999) and Deecke et al. (2000) consider that their evidence for non-matrilineality in sperm whales, and cultural evolution in killer whales, argue against the cultural hitchhiking hypothesis, as, in its original formation of a single advantageous cultural innovation, cultural hitchhiking only reduces mtDNA diversity if cultures are both highly stable and transmitted almost entirely matrilineally (Whitehead 1998). However, new models show that cultural hitchhiking can reduce genetic diversity if cultures evolve over time and there is moderate non-matrilineal transmission. Whether this actually happened in the case of the matrilineal whales remains open.

R6. Comparing cultures across species

Our approach to studying culture has the distinct advantage of permitting the comparison of forms of culture across species, concentrating on the important questions "how are they different" and "why are they different," not "do they have culture or not." We agree strongly with **Boesch**'s concept of culture as a dynamic process reaching different complexities, and **Slater**'s call for a taxonomy of cultures. To this end, in the target article, we sought to compare culture in cetaceans with available evidence for other taxa under a broad definition of culture (which makes **Tyack**'s call for a broad-based approach incomprehensible, since this is exactly what we tried to do), and we were pleased with the debate this produced in the commentaries.

Many of the commentators favour their own study species. For instance, **Lynn & Pepperburg** consider that we underestimated the imitative abilities of parrots compared with cetaceans in our target article while **Herman & Pack** believe dolphins were downplayed in the same section. However, the commentators' contrasts of cetacean and primate cultures (e.g., **O'Malley, Poirier & Fitton, Whiten**) are useful and even-handed, and we have nothing to add, except to agree with **Mitchell** that calling chimpanzee and some cetacean cultures "closely parallel" was not appropriate. The comparison between cetacean and human cultures in a number of commentaries raises a number of interesting issues to which we will respond, before considering other nonhuman cultures in general, and birds in particular.

R6.1. Cetaceans and humans

Notwithstanding our process-free definition of culture, it is undoubtedly true that imitation is particularly important among social learning processes as it allows innovations to accumulate so that cultures "ratchet" (Boyd & Richerson 1996). Given cetaceans' ability to imitate, why have cetacean cultures not ratcheted more than they seem to have, and human cultures clearly have (**Ripoll & Vauclair, Whiten**)? Why are the elements of human "hyperculture" (**Barkow**) seemingly absent? Tool use, as **Whiten** notes, is probably important – most of the more ratcheted human cultural elements depend on tool use (agriculture, architecture, transport, and technology in general). **Whiten**'s comments on the differences between human and cetacean culture perhaps relating simply to the presence or absence of hands might be coupled with the fact that much human culture is material. Now, material culture is simply much harder to achieve and maintain in water, whether because in the deep ocean there simply are no rigid materials (just water) or because in the coastal zone materials are so flimsy compared to the forces of waves and tide (make a block of mud in the desert and it dries into something you can build a house with, make one in 5 m. of water and it soon dissipates). Thus, cetacean culture may be akin to the information economy: more mental than material. We tentatively conclude that, as **Whiten** suggests, the primary qualitative differences between cetacean and human cultures may principally relate to a lack of manual dexterity in cetaceans and difficulties with material processing beneath the ocean.

However, it is also relevant to note that, while there is good evidence that Stone Age hominids did imitate one another, their material cultures did not seem to ratchet much or at all (Mithven 1999). Thus, some additional faculty, probably cognitive and perhaps a Theory-of-Mind and/or language (**Dunbar**), may have evolved which allowed modern human culture to develop in new and very exciting ways that were not characteristic of its predecessors (Mithven 1999). Cetacean culture may have a bearing on this question (see **Barkow, Dunbar**). If further research shows that cetacean and other nonhuman cultures do not ratchet to any substantial degree, then this indicates that only modern humans have this faculty, while if cetacean cultures do turn out to evolve routinely, then we should look for some quality shared by modern humans and cetaceans but absent in other hominids.

Some complex aspects of human cultures, although using material tools, do not depend crucially on them: language, music, and religion for example. Although there is little current evidence for language including syntax among wild cetaceans (Tyack 1999), we are excited by **Kako**'s promise of a more broad-based study of language capabilities. Much research on non-human language has been concerned with trying to teach animals human-like language, which seems to us a conceptually impoverished approach. In the same way that social learning demonstrated in captivity does not necessarily map directly onto cultural variation in the wild, so trained human-language-like behaviour in captivity does not necessarily relate directly to either the nature or complexity of communication these animals actually use in the wild, and so continued study of cetacean communication in the field will be an essential part of this process. Given that language abilities, like cultural faculties, are likely an evolutionary response to ecological and social conditions, there is no more reason why research on language should be tied to the human example than for research on culture. The important questions here concern communication in the wild. There are some tantalising observations of cetacean cooperative foraging techniques (e.g., rocking seals off ice floes; Smith et al. 1981), which require high degrees of coordination, showing that cetaceans may have sophisticated communication abilities in the wild. While the conceptual and practical challenges involved in studying communication in such contexts are formidable, new techniques for localising calls hold much promise (e.g., Janik et al. 2000; Miller & Tyack 1998). The prospect **Blute** holds up of a similar consideration of language to the one we give to culture is exciting and not impossible, but we think it will take more than a decade to achieve.

Barkow asks four interesting questions following his consideration of "hyperculture" in humans, and possibly cetaceans. Some very preliminary answers:

(1) "What is the relationship, if any, between socially transmitted information and sexual selection, among cetaceans?" At least in the case of humpback whale song, the relationship is probably strong: culturally transmitted songs may be the objects of female choice (Payne 1999).

(2) "Is there any evidence of a predation or self-predation process affecting cultural capacity?" There is little evidence for or against this, because predation on cetaceans is so rarely observed. However, in the target article we speculated on whether alternative communal defensive strategies of sperm whales were culturally determined; they may have different survival values.

(3) "Is there any socially transmitted information that has to do with 'moral behavior,' that is, behavior having to do with how individuals in a group treat one another, rather than simply how they transmit vocalizations or foraging strategies?" The "greeting ceremonies" of killer whales (Osborne 1986) might fall into this category, but we know of no other good examples.

(4) "If aquatic environments are conducive to the evolution of normal culture, could it be that they may provide novel ways for normal culture to become hyperculture?" Perhaps the greater potential for synchronous behaviour under water, leading to greater imitative abilities, (sect. R5) might be such a way.

R6.2. Unique outside humans?

Several commentators (including **Janik, Mitchell, Tyack**) challenge our description of some forms of cetacean culture as unique outside humans. We agree with the often made point that this may simply reflect a lack of research effort, and that other taxa (e.g., bats, birds, elephants, otters) may, as **Boesch** points out, upon closer inspection also show evidence of culture paralleling or exceeding cetaceans. **Janik** is right that further research on greater spear-nosed bats may reveal interesting cultural variation in other call types since this species makes a wider range of calls than the one that has currently been examined (J. Boughman, personal communication). Hence, our argument should more correctly describe cetacean culture as unique outside humans *according to current knowledge.* As to **Tyack**'s attack on our article as an attempt to set up cetaceans as unique, let us make our attitude quite clear: if future work reveals comparable cultural systems in other species, then our understanding of the evolution of culture will only increase. To this end, we would whole-heartedly welcome such work, and hope that our consideration of cetacean culture will stimulate such a research effort. However, we stand by our original argument that to date, such evidence has not been found.

R6.3. Cetaceans and birds

Most controversy is raised by our comparisons with the cultures of birds, and specifically our arguments that killer whale dialects, humpback song, and the combined vocal and behavioural cultures of killer whales are all unique outside humans (see **Day et al.**, **Janik, Lynn & Pepperburg, Mitchell, Slater, Tyack**). Some of this arises from a confusion between product and process. Both **Day et al.** and **Slater** seem to think that we argue for superior underlying social transmission processes in killer whales, and are right in pointing out that there is no evidence for such cognitive processes being superior in comparison to birds. However, we do not argue this, we simply highlight that the *product* is unique. According to **Janik, Mitchell,** and **Tyack,** we ignore evidence for sharp dialect boundaries in birds; we do not. **Slater** (whom both **Janik** and **Tyack** cite in support of their criticisms) has a deeper understanding of vocal culture in birds, and he, like us, sees the difference between dialects which are tied to geographic location, no matter how sharp the boundaries, and dialects maintained in a fully sympatric situation such as a community of interacting killer whale pods. The underlying cognition may well be the same as in birds, but the product is different. While **Slater** correctly points out this may be due to differences in when and from whom individuals learn, we do not agree with his opinion that such differences are trivial, since when and from whom one acquires ones culture will have profound effects on the resultant form of culture (Cavalli-Sforza et al. 1982). Neither are we inconsistent in our consideration of humpback song as **Mitchell** and **Tyack** claim; the geographic range of humpback song homogeneity is not critical to the issue of culture, it is simply a fascinating feature of this phenomenon, which makes it stand out from other examples of vocal culture. Even **Janik,** otherwise a harsh critic, agrees this pattern may be unique. While the large geographic range may simply be due to the long migrations the animals make, which links to the discussion of mobility (sect. R.5), this neither alters the large geographic scales concerned nor the fact that these songs are culture. To maintain such a pattern over such a large a dispersed population suggests interesting features in the way social learning becomes culture.

Lynn & Pepperburg sketch some of the remarkable variety and complexity of the social structures and cultures of bird species. However, having read most of the references they cite, we can find nothing directly comparable to the societies of the matrilineal, nonterritorial, sympatric killer whales, nor to their stable multi-faceted cultures. Perhaps the evidence for culture in birds would benefit from a similar review, to clarify these issues.

R7. Studying culture in cetaceans and other animals

The discussion of how culture can be studied in cetaceans and in other animals in the commentaries is particularly stimulating. It breaks down into two main areas: the relative merits of observational and experimental data, and the methods available for the future study of culture in cetaceans.

R7.1. Experimental and observational data

Many commentators (including **Fox, Janik, Mercado & DeLong, Tyack**) seem to have misunderstood our position with regard to experimental evidence. We do not suggest that laboratory study is an unproductive approach, only that it is unproductive to define culture in a way that it can only be identified using laboratory studies. The worst misunderstanding is **Tyack**'s fictional account of us claiming the study of imitation to be impossible, which we simply do not do. We agree with **Bauer & Harley**'s statement that controlled studies will contribute strongly to the understanding of cetacean culture, and believe that research on culture will be most productive when it integrates both laboratory and field evidence, and a full understanding demands both. We are puzzled as to how many commentators seem not to have registered this, given clear statements in sections 1 and 3 of our target article: "Both [approaches] make important contributions to our understanding of culture"; "We strongly believe that research on cultural processes is best served by an approach which integrates the sometimes opposing process and product oriented perspectives, as well as the laboratory and field approaches, taking good data from each"; "we do think that understanding process (cultural transmission) is crucial to our understanding of the product (culture)." An honest acknowledgment of the strengths and weaknesses of both approaches is needed, and **Kuczaj, Tschudin,** and **Whiten** provide this in their commentaries.

Some commentators, though, go so far in promoting the experimental approach that they leave the facts behind. To redress the balance, it is worth considering the evidence we currently have from both approaches. The two strongest examples of cetacean culture, humpback songs, which even **Tyack** admits are culture, and killer whale dialects, draw solely on observational data, coupled in the case of killer whales with molecular genetic analyses. Thus **Deputte**'s assertion that culture cannot be studied using observational methods alone is simply wrong (see also **Maestripieri & Whitham**). Experimental data is not required here to attribute culture. Careful observational study is in some cases (but not all) perfectly capable of distinguishing between social learning, individual learning, and genetic determination. However, experimental study *is* necessary for a complete understanding of the social learning processes underlying these examples. Some commentators (**Bauer & Harley, Kuczaj, Premack & Hauser**) note the unambiguity of experimental data, but the diversity of opinion on the results of experiments on imitation and Theory-of-Mind in bottlenose dolphins suggests that this is not really the case – there is as much controversy in these cases, and imitation in parrots, as there is over the observational data we present, and some (**Deputte, Premack & Hauser**) still believe the evidence does not prove that bottlenose dolphins can imitate nonvocally. Field biologists should not and will not sit around and wait for experimentalists to sort these arguments out before going out and collecting ethnographic data which are perfectly capable of investigating culture.

Bauer & Harley are mistaken in claiming that most evidence for cetacean culture has come from the laboratory: observational data has provided rich empirical material for at least four species, while experimental data is almost confined to just one. We make this point not to assert the superiority of one methodology over the other, only to promote a more objective consideration of the practical and theoretical strengths and weaknesses of each approach, which we now attempt.

Whiten is right about the dissatisfying lack of closure sometimes inherent in the ethnographic approach, its principal weakness. In some cases, in particular where culture may be closely linked with ecology, discounting individual learning will be difficult, requiring long-term study of known individuals, and here experimental demonstration of social learning has an important role to play. **Mercado & DeLong**'s criticism that observational studies in the wild record behaviour that has been affected by the observers presence is literally true and needs to be considered, but the problem is minor compared with the effects of captivity itself.

Contra **Mercado & DeLong,** we do not suggest that experimental results are not representative of natural abilities, but it is true that experimental results should be considered alongside both the socio-ecological validity of the experimental environment and the reward system used (R3.3). **Mercado & DeLong**'s ideas on the stress-free captive environment are rather strange, for two reasons; first since they are based on the idea that human cultural sophistication is a result of our artificial environment – we would argue that it is our cultural sophistication that has allowed us to create artificial environments; and second because choosing to live in a house is very different from being forced to live in captivity.

Experimental evidence does strengthen the social learning hypothesis (**Herman & Pack**), but cannot be directly used to assume all variation observed in that species in the wild is due to the process demonstrated (**Ripoll & Vauclair**). Careful ethnographic study is required to show that behaviour in the wild is socially learned, then laboratory evidence of what mechanisms that species is capable of can be related to the ethnographic evidence, and ideally also to experiments in the field, to give the fullest understanding of culture in that species. Currently the taxonomic bias towards bottlenose dolphins in experimental work (**Herman & Pack**) is a problem, and while it could be corrected for some of the smaller species which are available in captivity, we simply cannot see laboratory experiments on social learning in large whales ever being feasible. **Janik** is right that single sperm and grey whale *calves* have been kept in captivity temporarily, but this is a long way from the socio-ecologically valid setting necessary to test for social learning among multiple subjects.

R7.2. Broadening the study of culture

A number of commentators rightly point out that we have presented an unnecessarily narrow range of options for studying culture in whales and dolphins, and suggest a number of useful routes forward.

First, there is the potential for actually doing experiments at sea, as noted by **Maestripieri & Whitham, Mercado & DeLong** and **Whiten.** Field experiments have provided very useful information on terrestrial cultures, as exemplified by the work of Matsuzawa (1994) on chimpanzees. However, while the oceanic environment can be manipulated (e.g., by fishing), it is notoriously difficult to do so in a controlled fashion that is meaningful to cetaceans. Currently, the most controllable aspect of the ocean is the sound field. Playback experiments have been used, with varying success, to examine the functions of cetacean vocalisations (e.g., Tyack 1983), as well as to look at the behavioural effects of sounds of predators (Cummings & Thompson 1971) and anthropogenic noise (Richardson et al. 1995). We have tried to study cetacean imitation using playbacks in the wild (Jones & Rendell 2000), but found it difficult. Others will be more ingenious, and hopefully more successful (**Mercado & DeLong** provide some interesting ideas as to how to proceed).

In contrast, the passive recording of cetacean sounds is quite simple. We agree with **Barrett-Lennard et al.** that vocal traits are most easily studied in cetaceans and currently provide the best evidence for cetacean culture. Methodology for recording and analysing cetacean sounds is improving (e.g., Deecke et al. 2000; Janik et al. 2000; Miller & Tyack 1998). Perhaps even more important, acoustic records of the vocalizations of cetaceans are growing longer (e.g., Deecke et al. 2000), covering larger spatial areas (e.g., Weilgart & Whitehead 1997), and being linked to genetic, morphological, and other behavioural data (e.g., Whitehead et al. 1998).

New methodology should make it easier to study other cetacean behavioural patterns (Read 1998; Whitehead et al. 2000). Movements are a promising area. Individuals can be tracked using satellite, VHF, or data-logging tags (Goodyear 1993; Mate 1989), or photoidentifications (Whitehead, in press), compiling large data sets on who was where when. These can be processed using methods such as those described by Turchin (1998). Movement measures can then be compared between individuals and groups (see Whitehead 1999 for an attempt at this). However, movement patterns are particularly likely to be related to ecological conditions, so these need to be carefully controlled or considered (see sect. R4). New methods of analysing field data mentioned by **Day et al.** may be important in such situations.

R7.3. Anecdotes

We strongly disagree with the de-valuing of anecdotal evidence by **Maestripieri & Whitham.** While cases built upon it are nowhere near as strong as those based on quantitative data, to suggest that because something is so rare that it is not regularly observed says absolutely nothing about its importance to the animal in question. Rare observations of important events such as birth, predation, innovation, and teaching can be vitally important in directing research toward potentially important areas. They also show minimum capabilities for at least some members of the population. To reject anecdotal evidence is to make dogma more important than progress.

R7.4. Ethographic techniques

Ingold, in pointing out the differences between human ethnography and what is practised on nonhumans, calls for a "true" ethnographic study of cetaceans. While we agree that it would indeed be wonderful to be able to use the full range of human ethnographic techniques, if our understanding of cetaceans had progressed to the point where we were able both to live with, and interview them, our article would be entirely obsolete. Currently, it is not.

R7.5. Individuals and groups

Tyack, perhaps influenced by his own remarkable work on dolphin signature whistles (Sayigh et al. 1990; Tyack 1986), devalues the group-specific studies on sperm whales and killer whales. He seems to believe that by focusing on the group, the important issues that are taking place at the level of the individual are missed. However, in sperm whales we are able to study social relationships at the level of the individual, and find a remarkable homogeneity among relationships between members of long-term social units (Christal & Whitehead, in press). In contrast, killer whale "pods" show quite clear substructure, although much of their behaviour, including their dialects, are organized at the level of the pod (Bigg et al. 1990). **Tyack** is wrong when he implies that the social structure attributed to a population is the product of the shortcomings of our methods. For instance, Gowans et al. (in press) studied the social structure of the northern bottlenose whale (*Hyperoodon ampullatus*) using the same methods which uncovered the long-term social units and within-unit homogeneity of female sperm whales, but found an individually-based fission-fusion social structure quite similar to that of bottlenose dolphins and dissimilar to that of the sperm whales. Thus the methods that we use to study social structure based on individual identifications (described by Whitehead & Dufault 1999), combined with sufficient effort, can uncover the principal elements of whatever social structure exists. To study the societies and cultures of cetaceans we need work at both the level of the individual, and, where such entities exist, the long-term group.

R8. The future of cetacean culture

The commentators, once again, have diverse opinions as to how studies of culture in whales and dolphins should progress. At one extreme are **Premack & Hauser** and **Deputte** who question the worth of the whole enterprise and suggest that studies of culture should be restricted to more experimentally tractable animals. However, as **Boesch** and **Fox** point out so clearly, many of the most interesting aspects of the universe are immune to experiments. While experiments with cetaceans in tanks have much to inform us about cetacean culture, particularly in resolving issues such as whether dolphins possess a Theory-of-Mind (**Dunbar, Tschudin**), we believe that the real treasures are out at sea.

Perhaps the most exciting prospect for studies of cetacean culture is the possibility of comparative work both among species of whales and dolphins, and with animals of other taxa (**Reader & Lefebvre**). Evidence for culture in cetaceans is, so far, strongly correlated to research effort at the species level, but as the data aggregate, with more evidence as to which species may or may not show cultural faculties and/or social learning abilities, we might hope to be able to relate this to variation in the evolutionary and social ecology of these species, and perhaps even their neuroanatomy. Such comparisons could potentially lead to powerful insights into the forces which have shaped the evolution of culture.

One hopeful aspect for cetacean studies is that research with other aims, especially population monitoring and social structure, are necessarily long term, in fact very long term in comparison with many other species (Connor et al. 1998b). This often gives a conducive background of data for the study of culture in these same populations. Cetologists have risen admirably to the considerable challenge of studying social structure in cetaceans (Whitehead et al. 2000), and we are confident that they are equally capable of rising to the challenges of studying cetacean ethnography. In addition to suggesting new ethnographic and experimental approaches, the commentators have identified important issues that need to be considered. These include genomic imprinting (**Brown**), ecology (**Connor**), and variation in individual learning abilities (**Day et al.**, **Galef**), all of which can theoretically lead to ethnographic data in which individual and social learning processes are hard to distinguish.

The examination of culture in whales and dolphins is not self-contained. As the commentators have so clearly shown, it is linked to many other fields of science. There are also, as **Fox** reminds us, links to areas of human culture outside science. How we view and treat these animals and their habitat will determine whether they survive as subjects of study, as well as cultural beings "in their own right" (**Fox**). The results of these studies should inform humans when allocating rights to whales and dolphins in the face of the mounting threat that they and their habitats face from ratchetting human culture.

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NOTE

1. This title was inspired by a talk given by W.C. McGrew at the Animal Social Complexity and Intelligence conference, Chicago, August 2000, entitled "Dispatches from the chimpanzee culture wars."

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Letters "a" and "r" appearing before authors' initials refer to target article and response, respectively.

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