Journal of the Marine Biological Association of the United Kingdom, 2010, 90(8), 1693–1699.
doi:10.1017/S0025315410000421

Behavioural strategies in humpback whales, *Megaptera novaeangliae*, in a coastal region of Brazil

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The behavioural patterns of humpback whales are known to vary according to the social function of individuals in a group. To identify behavioural patterns related to specific group compositions, we observed events and behavioural states of humpback whales during research cruises in the Abrolhos Bank, Brazil, in the reproductive seasons from 1992 to 2003. We monitored 3022 groups and found a predominance of competitive groups without calves, when compared to competitive groups with calves. A Bayesian network analysis supplied occurrence probabilities for the behaviours analysed, indicating higher probabilities of occurrence for the behavioural patterns designated travelling and socializing. The model, generated from a binomial logistic regression, was able to predict competitive groups in association with the occurrence of the following aggressive behaviours: head-lunging, trumpet and bubblestreams. This study suggests the existence of behavioural patterns associated with specific group compositions and reinforces the concept that there is a clear-cut relation between competitive groups and the occurrence of aggressive behaviours. The preferential association of males to females with high reproductive potential for the following year (i.e. females without a calf) was also identified.

Keywords: Abrolhos Bank, behaviour, humpback whales, *Megaptera novaeangliae*, reproductive season

Submitted 8 July 2009; accepted 28 January 2010; first published online 2 June 2010

INTRODUCTION

Cetacean social behaviour has important implications for the understanding of reproductive behavioural patterns, spatial distribution, reproductive success and gene flow (Ersts & Rosenbaum, 2003). The social organization of humpback whales (*Megaptera novaeangliae* Borowski, 1781), for instance, is extremely unstable, with typically small groups (Whitehead, 1983; Baker & Herman, 1984; Mobley & Herman, 1985) that behave as a function of group composition during their reproductive periods (Herman & Antinoja, 1977; Baker & Herman, 1984). In this species, where male parental care is absent and reproductive costs are high for females (Clapham & Mayo, 1990), it is reasonable to assume that females exert some mate choice, perhaps based on male body size and competitive ability (Tyack & Whitehead, 1983; Baker & Herman, 1984; Mobley & Herman, 1985). However, one also expects males to apply some criteria in their choice of partners, since females with and without calves or large and smaller females may differ in terms of reproductive potential (Craig *et al.*, 2002; Pack *et al.*, 2009).

The humpback whale is a cosmopolitan species (Dawbin, 1966) usually associated with reef island habitats (Whitehead & Moore, 1982). This species migrates seasonally between high latitude areas near the polar regions and low latitude areas in tropical and subtropical waters (Chittleborough, 1965; Dawbin, 1966). During the migration between high and low latitudes, females at the end of the lactation period are among the first to relocate to the breeding areas, followed by juveniles, male and female adults and, last of all, pregnant females. The return to the feeding areas occurs in reverse order (Dawbin, 1966).

The Abrolhos Bank (Bahia, Brazil) is the main breeding ground for humpback whales in the western South Atlantic (Martins *et al.*, 2001; Morete *et al.*, 2003b; Lunardi *et al.*, 2008), but the species has been recorded from 3°S to 31°S (e.g. Pinedo, 1985; Lodi, 1994; Zerbini *et al.*, 2006; Neto *et al.*, 2007; Rossi-Santos *et al.*, 2008; Meirelles *et al.*, 2009). Population sizes of humpback whales using the north-eastern coast of Brazil were estimated at 628 (CV = 0.335) individuals in 2000 to the north of the breeding concentration (Zerbini *et al.*, 2004) and 6251 (CV = 0.16) in 2005 (Andriolo *et al.*, 2006) along the entire breeding ground on the Brazilian coast.

The main concentration areas for the species on the north-eastern Brazilian coast are the areas around the Abrolhos Archipelago and to the south of the Abrolhos Bank, with a density of 1.6 to 2.3 individuals/nmi^2 (nmi: nautical mile) (Martins, 2004). The distribution of humpback whales according to water depth has been described as a function of social organization, with mothers and their calves occurring more frequently in shallow waters, compared with all other types of groups (Martins *et al.*, 2001; Zerbini *et al.*, 2004). High concentrations of groups with calves are found near the Abrolhos

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Archipelago (Martins *et al.*, 2001; Morete *et al.*, 2003b; Lunardi *et al.*, 2008).

Large groups of humpback whales, characterized by high levels of activity on the surface and, sometimes, intense aggressions among members are called 'competitive groups' (Clapham *et al.*, 1992). These groups typically contain a nuclear animal (usually a female), one escort (usually the alpha male), and one or more subordinate males (Tyack & Whitehead, 1983), and aggressive behaviour is frequently observed during the sparring of the males for access to a fertile female (Tyack & Whitehead, 1983; Baker & Herman, 1984; Herman *et al.*, 2007). Competitive groups with calves have been documented infrequently in the Antilles and Dominican Republic (Clapham *et al.*, 1992), while large groups without calves appear to be common in Hawaii (Craig *et al.*, 2002). These data suggest that the low frequency of calves in competitive groups possibly reflects a preferential association of males for females that are not lactating (Clapham, 1996; Craig *et al.*, 2002).

Humpback whales are known for the frequency with which they engage in aerial and high energy behaviours, some of which have been described in detail (Tyack & Whitehead, 1983; Baker & Herman, 1984; Whitehead, 1985; Corkeron, 1995; Clapham, 2000; Morete *et al.*, 2003a). Many of these displays are exhibited by both sexes and occur in wintering and feeding grounds, but their function remains generally unknown (Clapham, 2000).

The objective of our study was to investigate the correlation of specific behavioural patterns of humpback whales with social contexts. We collected data in research cruises in the Abrolhos Bank, Brazil to test three hypotheses: (1) distinctive behavioural patterns are more frequently associated with specific group compositions; (2) males tend to associate with groups without a calf more than groups with a calf; and (3) there is a relation between competitive groups and the occurrence of aggressive behaviours.

MATERIALS AND METHODS

Study area, terms used and data collection

The study area comprises the Abrolhos Bank (16°40′–19°30′S), an extension of the Brazilian continental shelf located on the eastern coast of Brazil (Figure 1). The area is shallow (approximately 30 m depth), covering approximately 30,000 km^2 (Fainstein & Summerhayes, 1982), with surface water temperatures ranging from 22° to 24°C during the winter (Castro & Miranda, 1998).

Here we define 'group' as one or more individuals that remain together (<100 m between individuals) throughout the observation period, generally moving in the same direction in a coordinated way (Whitehead, 1983; Mobley & Herman, 1985). A 'calf' was defined as an animal next to an adult whale, estimated at less than 50% of the total length of the associated animal (Chittleborough, 1965). An adult is defined as a non-calf of unknown sex.

Behavioural observations were conducted between the months of July and November during research cruises in the Abrolhos Bank from 1992 to 2003. These months correspond to the peak of abundance of humpback whales on Brazil's north-eastern coast (Martins *et al.*, 2001; Morete *et al.*, 2003b). Observations were conducted from 10–16 m wooden boats powered by a 6-cylinder diesel inboard engine. Cruises lasted from one to five days, with an average sampling of 391 ± 141 minutes/day. The search for humpback whales was made with the naked eye or with binoculars (7 × 50). For behavioural observations, we remained with each sighted group of whales for approximately 30 minutes, keeping an average distance of 100 m to the group. All distances were estimated subjectively. Observations were suspended in unfavourable weather or sea conditions (Beaufort sea state greater than 5, winds above 17 knots).

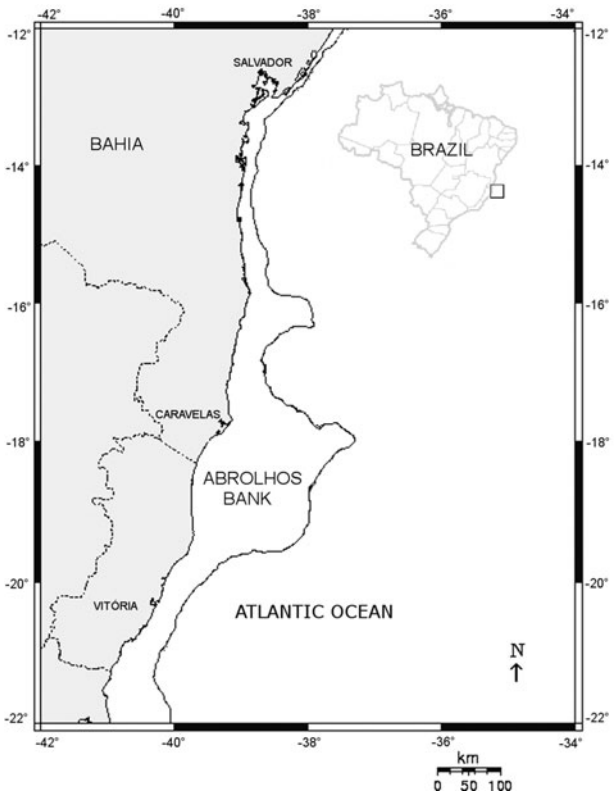

Fig. 1. Localization of study area: Abrolhos Bank.

Based on previous studies (Tyack & Whitehead, 1983; Baker & Herman, 1984; Clapham *et al.*, 1992), social groups were classified according to eight possibilities: (1) mother and calf; (2) mother, calf and escort; (3) mother, calf and two escorts; (4) mother and calf and more than two escorts; (5) adult alone; (6) two adults; (7) three adults; and (8) more than three adults.

In this study a group is called a 'competitive group' if it comprises three or more adults, with or without calves. Behavioural states of focal groups were sampled following Altmann (1974). Behaviour was classified into one or more of five possibilities: (1) travelling: diving or swimming (Corkeron, 1995); (2) resting: motionless at the water surface (Corkeron, 1995); (3) tail-up: at least one group member engaged in tail-up (Morete *et al.*, 2003a); (4) socializing: at least one group member breaching, tail breaching (Clapham, 2000), lobtailing or flippering (Whitehead, 1985); or (5) aggressive: agonistic behaviours, such as head-lunging (Baker & Herman, 1984), trumpet (Corkeron, 1995), bubblestreams and tail slapping (Tyack & Whitehead, 1983). Although aggressive behaviours represent a type of socializing we decided to create a new category named aggressive to provide a greater focus of such behaviours and what they may represent.

https://doi.org/10.1017/S0025315410000421 Published online by Cambridge University Press

Statistical analyses

We used a Bayesian network approach to analyse behaviour in different group compositions. This type of analysis produces a graphical output that can represent a joint distribution of probabilities of a group of variables, considering the relation between them (Charniak, 1991). The analysis was carried out using the program NETICA in its 1.12 version (NETICA, 2004, Vancouver, Canada).

We used a logistic regression model (Wright, 1995) to investigate the relation between competitive groups and the occurrence of specific behaviours, and a Chi-square test (χ^2) to determine differences between competitive groups with and without calves.

RESULTS

Behavioural patterns and group composition

We monitored 3022 groups in 719 days of sampling, totaling 4678 hours of observation. According to the Bayesian network probability analysis, groups of two adults, mother and calf and adult alone had the highest occurrence probabilities, while mother and calf and two escorts and mother and calf and more than two escorts the lowest (Table 1).

Group compositions were inserted in one or more of the five conducts according to observations, and the Bayesian network model was used to determine the behavioural probabilities based upon the possible group compositions. When considering the social arrangement of the individuals in the group, mother and calf and mother and calf and one escort presented the highest probabilities of occurrence for resting conduct (37.7% and 32.8%, respectively), while the group composition adult alone showed the highest probabilities of the tail-up conduct (19.2%). Competitive groups with more than three adults, without calf and with calf presented greater probabilities of the socializing conduct (67.7% and 64%, respectively) and aggressive conduct (68.1% and 76%, respectively) (Table 1).

The behavioural characterizations for the eight group compositions (Table 2) were also identified according to the following sighting criteria: difference between greater and lesser probability values divided by number of categories chosen. We have four categories: Unusual (probabilities less than 7%), Low usual (probabilities between 7% and 12%), Usual (probabilities between 13% and 18%) and Highly usual (probabilities greater than 18%). Groups of up to two adults, with or without calves, were classified as Highly usual or Usual. Only the competitive groups with calves (mother and calf and two escorts and mother and calf and more than two escorts) were identified as Unusual (Table 2). For all group compositions, the most commonly observed conduct was travelling. However, competitive groups, with and without calves, were usually observed in aggressive interactions.

Association of males with females without calves

We analysed the preference of males for females with high reproductive potential by comparing competitive groups with and without calves. Smaller competitive groups (three adults) exhibited a relatively lower occurrence probability of 35.4% of the aggressive conduct, possibly for access to the female, as compared with competitive groups with more than three adults, which exhibited an occurrence probability of twice that much aggressive conduct (68.1%) (Table 1). When comparing the percentage occurrence of competitive groups with and without calves, we found a statistically significant predominance of the latter in both small ($\chi^2 = 74.25$, $P < 0.001$) and large groups ($\chi^2 = 116.51$, $P < 0.001$; Figure 2).

Relation between competitive groups and the occurrence of aggressive behaviours

A binomial logistic regression model was used to predict competitive groups based upon the occurrence of conducts classified as socializing (tail breaching and lobtailing) and aggressive (head-lunging, trumpet, bubblestreams and tail slapping) (Table 3). Despite the impossibility of obtaining a statistically significant model that predicts competitive groups based upon the conduct socializing, the model, using this conduct, predicted 85.7% of competitive groups (variables and parameters in the equation are shown in Table 4). The only behaviour of the aggressive conduct type not included in the model was tail slapping.

DISCUSSION

Our results support the first hypothesis of the study, where we suggest that specific group compositions are associated with distinctive behavioural patterns. The Bayesian network supplied high probabilities of occurrence for conducts of the type travelling and socializing, irrespective of the social arrangement of individuals in the group. Possibly, the high

Table 1. Occurrence probabilities obtained from a Bayesian network of the conducts of humpback whales, in the Abrolhos Bank (1992–2003), as a function of the observed groups: adult whale alone (Alone); two adult whales (Dyad); three adult whales (Trio); more than three adult whales (Trio+); mother and calf (Moca); mother, calf and one escort (Moce); mother and calf and two escorts (Moces); mother and calf and more than two escorts (Moce+). The occurrence probabilities of the behaviours for each type of investigated group differ from 1 because it is possible to observe more than a single behavioural state during sampling. The sum of the occurrence probabilities and of the lack of occurrence probabilities of a determined behaviour equals 1.

Group/conducts	Alone	Dyad	Trio	Trio+	Moca	Moce	Moces	Moce+	Mean ± SD
	19.0	25.9	07.4	07.5	21.5	14.5	02.5	01.6	12.5 ± 09.0
Travelling	94.1	98.1	99.1	99.6	95.1	98.6	98.7	98.0	97.7 ± 02.0
Resting	21.3	22.9	11.5	03.1	37.7	32.8	20.8	20.0	21.3 ± 11.0
Tail-up	19.2	17.4	08.8	03.5	13.2	17.5	09.1	08.0	12.1 ± 05.6
Socializing	–	35.5	58.4	67.7	36.2	39.6	55.8	64.0	51.0 ± 13.6
Aggressive	–	14.0	35.4	68.1	02.8	11.2	36.4	76.0	34.8 ± 28.4

https://doi.org/10.1017/S0025315410000421 Published online by Cambridge University Press

Table 2. Characterization of the behaviour of humpback whales in the Abrolhos Bank (1992–2003) according to the probability of conducts occurrence. The following groups: adult whale alone (Alone), two adult whales (Dyad), three adult whales (Trio), more than three adult whales (Trio+) (Table 2A) and mother and calf (Moca), mother, calf and one escort (Moce), mother and calf and two escorts (Moces), mother and calf and more than two escorts (Moce+) (Table 2B) are classified according to the following occurrence criteria: difference between greater and lesser probability values divided by number of categories chosen. We include four categories: Unusual (probabilities <7%), Low usual (probabilities between 7%–12%), Usual (probabilities between 13%–18%) and Highly usual (probabilities >18%).

Table 2A. Group without calf	**Group occurrence probability**	**Normal behaviour pattern**
Alone	Highly usual	Usually observed in travelling, but also sighted in resting or tail-up
Dyad	Highly usual	Observation of three behavioural patterns: swimming in directional or non-directional manner with varied interactions, behaviours of socialization (flipper slapping and/or breaching) or resting for considerable duration
Trio Trio+	Low usual	Frequently observed in surface travel, with frequent occurrence of breaching and flippering; observed in aggressive interactions like head-lunging or in socializing behaviours such as lobtailing
Table 2B. Group with calf	**Group occurrence probability**	**Normal behaviour pattern**
Moca	Highly usual	Frequently observed in resting for considerable duration. Socialization behaviours are also frequently observed
Moce	Usual	If the female is observed at resting, the escort usually remains underwater; however, if the female is travelling, the escort remains by her side, but also observed occasionally beside the calf. Individuals also observed in socialization or tail-up
Moces	Unusual	The main escort remains next to the female, defending his position with agonistic behaviours directed toward the secondary escort. Socialization behaviours are also frequently observed
Moce +	Unusual	The main escort remains next to the female, defending his position with agonistic behaviours directed toward other escorts. However, head-lunging is frequently used by secondary escorts to dislodge the main escort

occurrence probability of socializing reflects the importance of the use of habitat as a means for social interaction, through behaviours such as breaching and flippering. Due to the context where they usually occurred, these behaviours probably represent a rich repertoire of communication/interaction between individuals. Whitehead (1985), in his study concerning breaching behaviour, pointed out that it occurs more commonly in species that are more social and that tend to segregate in reproductive areas, strengthening, therefore, the interaction scenario.

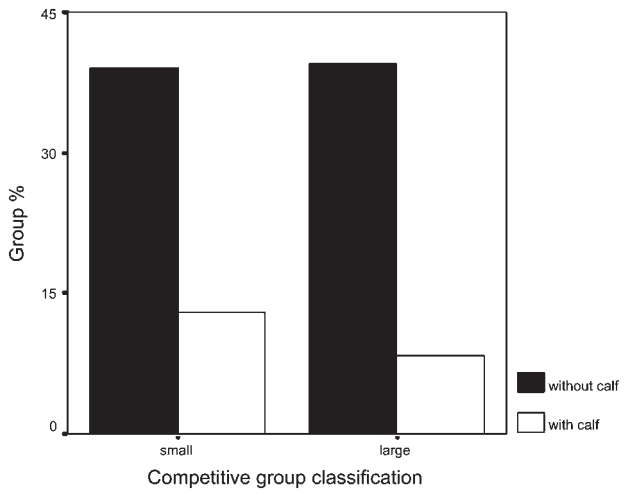

Fig. 2. Percentage of small and large competitive groups of humpback whales in the Abrolhos Bank, Brazil (1992–2003) with respect to the presence or absence of calves. Values statistically significant for small groups ($\chi^2 = 74.25$, $P < 0.001$, $N_{without\ calf} = 224$, $N_{with\ calf} = 75$) and large groups ($\chi^2 = 116.51$, $P < 0.001$, $N_{without\ calf} = 227$, $N_{with\ calf} = 48$).

Competitive groups with more than three adults (four or more whales together and mother and calf and more than two escorts) presented greater occurrence probabilities for socializing and aggressive conducts, suggesting that the high levels of aggressiveness in these groups can involve the conflict of males over access to females. Similar observations in humpback whales and other cetaceans also suggest this (Silverman & Dunbar, 1980; Tyack & Whitehead, 1983; Baker & Herman, 1984; Clapham *et al.*, 1992; Herman *et al.*, 2007). Escorts, in humpback whales, engage in agonistic interactions (aggressive conduct) more frequently in larger competitive groups (four or more whales together and mother and calf and more than two escorts) than in smaller competitive groups (three adult whales together and mother and calf and two escorts).

Table 3. Classification of the binomial logistic regression model based upon the occurrence of aggressive behaviours (head-lunging, bubble-streams and trumpet) in competitive and non-competitive groups of humpback whales in the Abrolhos Bank in the period 1992–2003.

		Predict		
		Competitive group		**Correct percentage**
Observed occurrence		No	Yes	
Competitive group	No	2386	62	97.5
	Yes	370	204	35.5
Total percentage				85.7

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Table 4. Variables and parameters used in the binomial logistic regression equation according to the prediction model of aggressive behaviours (head-lunging, bubblestreams and trumpet) of humpback whales in competitive and non-competitive groups in the Abrolhos Bank in the period from 1992–2003. B, logarithmic variation of the dependent variable as a function of the independent variable; Exp (B), exponential of B, which is the linear variation of the dependent variable as a function of the independent variable.

Effect	B	Standard error	Wald test	df	*P*	Exp (B)
Head-lunging	−3.070	0.461	44.440	1	<0.001	0.046
Trumpet	−1.422	0.138	106.210	1	<0.001	0.241
Bubblestreams	−2.300	0.176	170.251	1	<0.001	0.100
Constant	4.752	0.487	95.031	1	<0.001	115.034

Groups of one and two adults, with or without calves (alone, two adult whales, mother and calf and mother and calf and one escort), were classified according to occurrence criteria adopted in this study as Highly usual or Usual. The predominance of groups of one and two adults without calves was also observed by Martins *et al.* (2001) and Lunardi *et al.* (2008) in the Abrolhos Bank and by Baker & Herman (1984) and Craig *et al.* (2002) in Hawaii. However, the present study had high occurrence probabilities of groups of mothers and calves, classified here as Highly usual. The prevalence of this type of group is probably due to the higher sampling conducted around Abrolhos Archipelago, a typical calving ground of the species (Martins *et al.*, 2001; Morete *et al.*, 2003b).

The second hypothesis we tested was the existence of an association of males with groups without calves as suggested by Craig *et al.* (2002). This hypothesis is based upon the concept of parental investment (*sensu* Trivers, 1972) that suggests that when one of the sexes has a much higher level of parental investment, individuals of the sex investing less will compete among themselves to mate with the high investing members of the opposite sex. Studies with several other taxa have shown that, in the beginning of the courtship, males are frequently aggressive and females shy or reluctant (Cox & LeBoeuf, 1977; Byers *et al.*, 1994; Doutrelant & McGregor, 2000) and it is assumed that one of the functions of courtship is to synchronize sexual receptivity between partners (Liley & Stacey, 1983). However, males of promiscuous species may maximize their fitness by mating with several females, and may be subjected to limitations of their reproductive success through sperm competition, female choice, and costs and risks associated with searching for viable females (Danchin & Cézilly, 2008). As well, males of many species of vertebrates and invertebrates are limited with respect to the number of ejaculations they can produce due to the time necessary to replenish their reduced semen reserves (reviewed in Andersson, 1994), and this may be an additional constraining factor of the reproductive success that can be attained by males. Thus, it is expected that in some species males should be selective about how they distribute mating among females. There is ample evidence that males of some species can and do mate preferentially with some females (Dewsbury, 1982). Examples described in the literature include: rhesus monkeys *Macaca mulatta* (Herbert, 1968), fruit flies *Drosophila melanogaster* (Cook, 1975) and crustaceans *Asellus aquaticus* and *A. meridianus* (Manning, 1975).

Considering the high parental investment performed by humpback whale mothers, low availability of females for reproduction due to the long period of nursing the calves, high cost of producing a calf (Clapham & Mayo, 1990) and long period that a male potentially has to wait to inseminate a female, males would be expected to be biased when choosing a mating partner. The results of this study confirmed this expectation. For the population of humpback whales in Abrolhos Bank, we found a higher number of competitive groups associated with females without calves and decreased probabilities of occurrence of competitive groups with calves (mother and calf and two escorts and mother and calf and more than two escorts). Similar patterns were obtained for other breeding grounds (Clapham *et al.*, 1992; Craig *et al.*, 2002). Pack *et al.* (2009) examined the relation of body size of the female in competitive groups with the number of attending escorts and determined the relation of a female's body size to the size of her calf and concluded that male humpback whales prefer to associate with larger females and that larger females produce larger calves.

Finally, in the last hypothesis we expected a relation between competitive groups and the occurrence of aggressive behaviours. The logistic model, in its totality, predicted the occurrence of approximately 86% of the competitive groups based upon behaviours of the type head-lunging, trumpet and bubblestreams. The only behaviour of the aggressive conduct type not included in the model was tail slapping. Although this behaviour has been described as a clear form of aggression (Tyack & Whitehead, 1983), the lack of its inclusion in the model for predicting competitive groups occurred because the behaviour was observed infrequently, as compared to other aggressive behaviours in the population.

Aggressive behaviour among humpback males has been widely described in several breeding grounds (Tyack & Whitehead, 1983; Baker & Herman, 1984; Clapham *et al.*, 1992; Craig *et al.*, 2002; Herman *et al.*, 2007). For instance, the death of a male in a competitive group due to aggressive attacks by other males was observed by Pack *et al.* (1998). This underscores the potential cost of physical battle during encounters between males for access to females. Many aggressive behaviours are regularly observed within the context of male conflict, where secondary escorts try to displace the primary escort to approach the nuclear female (Tyack & Whitehead, 1983). Competitive groups regularly show periods of aggressive activity on the surface (Clapham *et al.*, 1992). Some of these activities, like the bubblestreams and head-lunging, are more frequently observed in competitive groups without calves, when compared with other types of groups (Tyack & Whitehead, 1983).

In one study, aggressive conduct occurred for all sighted competitive groups, with head-lunging as the most common behaviour (Baker & Herman, 1984). If aggression observed in these groups is primarily a function of competition among males for access to females, then its occurrence should be influenced by seasonal changes in the reproductive status of adult females and males (Baker & Herman, 1984). According to these authors, the lower rates of behaviours of the aggressive type in feeding areas support the argument that aggression varies in relation to reproductive cycles and the hormonal changes involved in both sexes during the reproductive season.

ACKNOWLEDGEMENTS

We are very grateful to the Instituto Baleia Jubarte for the concession of data from 1992 to 2003 and A.N. Zerbini, J.S. Marinho-Filho, P.C. Simões-Lopes, V.F. Saracura and an anonymous referee for revision of the manuscript. We thank

https://doi.org/10.1017/S0025315410000421 Published online by Cambridge University Press

C. Freitas, M. Galiza, C.C.A. Martins, L. Pacheco, L.L. Wedekin, M.R. Rossi-Santos and all the trainees of the Instituto Baleia Jubarte for assistance with the field work. We thank the PETROBRAS (Petróleo Brasileiro SA) for sponsorship of the cruises and the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) for the scholarship to D.G.L (Proc. No. 130062/2003–0) and a research fellowship to R.H.M.

REFERENCES

Altmann J. (1974) Observational study of behaviour: sampling methods. *Behaviour* 49, 227–267.

Andersson M. (1994) *Sexual selection*. Princeton, NJ: Princeton University Press.

Andriolo A., Kinas P.G., Engel M.H. and Martins C.C.A. (2006) *Monitoring humpback whale* (Megaptera novaeangliae) *population in the Brazilian breeding ground, 2002 to 2005*. International Whaling Commission Scientific Committee: SC/58/SH15, 13 pp.

Baker C.S. and Herman L.M. (1984) Aggressive behaviour between humpback whales (*Megaptera novaeangliae*) wintering in Hawaiian waters. *Canadian Journal of Zoology* 62, 1922–1937.

Byers J.A., Moodie J.D. and Hall N. (1994) Pronghorn females choose vigorous mates. *Animal Behaviour* 47, 33–43.

Castro B.M. and Miranda L.B. (1998) Physical oceanography of the western Atlantic continental shelf located between 4°N and 34°S, coastal segment (4, W), v. 11. In Robinson A.R. and Brink K.H. (eds) *The sea*. New York: John Wiley and Sons, pp. 209–251.

Charniak E. (1991) Bayesian networks without tears. *Artificial Intelligence Magazine* 12, 50–63.

Chittleborough R.G. (1965) Dynamics of two populations of the humpback whale, *Megaptera novaeangliae* (Borowski). *Australian Journal of Marine and Freshwater Research* 16, 33–128.

Clapham P.J. (1996) The social and reproductive biology of humpback whales: an ecological perspective. *Mammal Review* 26, 27–49.

Clapham P.J. (2000) The humpback whale: seasonal feeding and breeding in baleen whale. In Mann J., Connor R.C., Tyack P.L. and Whitehead H. (eds) *Cetacean societies—field studies of dolphins and whales*. Chicago: University of Chicago Press, pp. 173–196.

Clapham P.J. and Mayo C.A. (1990) Reproduction of humpback whales (*Megaptera novaeangliae*) observed in the Gulf of Maine. *Reports of the International Whaling Commission* Special Issue 12, 171–175.

Clapham P.J., Palsbøll P.J., Mattila D.K. and Vasquez O. (1992) Composition and dynamics of humpback whale competitive groups in the West Indies. *Behaviour* 122, 182–194.

Cook R. (1975) Courtship of *Drosophila melanogaster*: rejection without extrusion. *Behaviour* 52, 155–171.

Corkeron P.J. (1995) Humpback whales (*Megaptera novaeangliae*) in Hervey Bay, Queensland: behaviour and responses to whale-watching vessels. *Canadian Journal of Zoology* 73, 1290–1299.

Cox C.R. and LeBoeuf B.J. (1977) Female incitation of male competition: a mechanism in sexual selection. *American Naturalist* 111, 317–335.

Craig A.S., Herman L.M. and Pack A.A. (2002) Male-mate choice and male-mate competition coexist in the humpback whale (*Megaptera novaeangliae*). *Canadian Journal of Zoology* 80, 745–755.

Danchin E. and Cézilly F. (2008) Sexual selection: another evolutionary process. In Danchin E., Giraldeau L.-A. and Cézilly F. (eds) *Behavioral ecology*. New York: Oxford University Press, pp. 363–426.

Dawbin W.H. (1966) The seasonal migratory cycle of humpback whales. In Norris K.S. (ed.) *Whales, dolphins and porpoises*. Berkeley and Los Angeles: University of California Press, pp. 145–170.

Dewsbury D.A. (1982) Ejaculate cost and male choice. *American Naturalist* 119, 601–610.

Doutrelant C. and McGregor P.K. (2000) Eavesdropping and mate choice in female fighting fish. *Behaviour* 137, 1655–1669.

Ersts P.J. and Rosenbaum H.C. (2003) Habitat preference reflects social organization of humpback whales (*Megaptera novaeangliae*) on a wintering ground. *Journal of Zoology (London)* 260, 337–345.

Fainstein R. and Summerhayes C.P. (1982) Structure and origin of marginal banks off eastern Brazil. *Marine Geology* 46, 199–215.

Herbert J. (1968) Sexual preference in the rhesus monkey *Macaca mulatta* in the laboratory. *Animal Behaviour* 16, 120–128.

Herman E.Y.K., Herman L.M., Pack A.A., Marshall G., Shepard C.M. and Bakhtiari M. (2007) When whales collide: Crittercam offers insights into the competitive behavior of humpback whales on their Hawaiian wintering grounds. *Marine Technology Society Journal* 41, 35–43.

Herman L.M. and Antinoja R.C. (1977) Humpback whales in the Hawaiian breeding waters: population and pod characteristics. *Scientific Reports of the Whales Research Institute* 29, 59–85.

Liley N.R. and Stacey N.E. (1983) Hormones, pheromones, and reproductive behavior in fish. In Hoar W.S., Randal D.J. and Donaldson E.M. (eds) *Fish physiology*. New York: Academic Press, pp. 1–49.

Lodi L. (1994) Ocorrências de baleias-jubarte, *Megaptera novaeangliae*, no Arquipélago de Fernando de Noronha, incluindo um resumo de registros de capturas no nordeste do Brasil. *Biotemas* 7, 116–123.

Lunardi D.G., Engel M.H. and Macedo R.H.F. (2008) Behavior of humpback whales, *Megaptera novaeangliae* (Cetacea: Balaenopteridae): comparisons between two coastal areas of Brazil. *Revista Brasileira de Zoologia* 25, 159–164.

Manning J.T. (1975) Male discrimination and investment in *Asellus aquaticus* (L.) and *A. meridianus* Racovitsza (Crustacea: Isopoda). *Behaviour* 55, 1–14.

Martins C.C.A. (2004) *O uso do sistema de informações geográficas como ferramenta na identificação de áreas prioritárias para a conservação da população de baleia jubarte*, Megaptera novaeangliae, *em seu sítio reprodutivo na costa leste do Brasil*. Master's thesis. Universidade de Brasília, Distrito Federal, Brazil.

Martins C.C.A., Morete M.E., Engel M.H., Freitas A.C., Secchi E.R. and Kinas P.G. (2001) Aspects of habitat use patterns of humpback whales in the Abrolhos Bank, Brazil, breeding ground. *Memoirs Queensland Museum* 47, 563–570.

Meirelles A.C.O., Monteiro-Neto C., Martins A.M.A., Costa A.F., Barros H.M.D.R. and Alves M.D.O. (2009) Cetacean strandings on the coast of Ceará, north-eastern Brazil (1992–2005). *Journal of the Marine Biological Association of the United Kingdom* 89, 1083–1090.

Mobley J.M. and Herman L.M. (1985) Transience of social affiliations among humpback whales (*Megaptera novaeangliae*) in the Hawaiian wintering grounds. *Canadian Journal of Zoology* 63, 762–772.

Morete M.E., Freitas A., Engel M.H., Pace R.M. III and Clapham P.J. (2003a) A novel behavior observed in humpback whales on wintering grounds at Abrolhos Bank (Brazil). *Marine Mammal Science* 19, 694–707.

Morete M.E., Pace R.M. III, Martins C.C.A., Freitas A.C. and Engel M.H. (2003b) Indexing seasonal abundance of humpback whales around Abrolhos Archipelago, Bahia, Brazil. *Latin American Journal of Aquatic Mammals* 2, 21–28.

Neto E.S., Rossi-Santos M.R., Baracho C.G., Cipolotti S.R., Sampaio C.L.S., Velozo R.S. and Souto L.R.A. (2007) A case study of a lone humpback whale calf (*Megaptera novaeangliae*) inside Baía de Todos os Santos, Bahia State, north-eastern Brazil, with implications for rescue procedures. *Marine Biodiversity Records* 1, e97. doi:10.1017/S1755267207009840.

Pack A.A., Salden D.R., Ferrari M.J., Glockner-Ferrari D.A., Herman L.M., Stubbs H.A. and Straley J.M. (1998) Male humpback whale dies in competitive group. *Marine Mammal Science* 14, 861–872.

Pack A.A., Herman L.M., Spitz S.S., Hakala S., Deakos M.H. and Herman E.Y.K. (2009) Male humpback whales in the Hawaiian breeding grounds preferentially associate with larger females. *Animal Behaviour* 77, 653–662.

Pinedo M.C. (1985) A note on a stranding of the humpback whale on the Southern coast of Brazil. *Scientific Reports of the Whales Research Institute* 36, 165–168.

Rossi-Santos M.R., Neto E.S., Baracho C.G., Cipolotti S.R., Marcovaldi E. and Engel M.H. (2008) Occurrence and distribution of humpback whales (*Megaptera novaeangliae*) on the north coast of the State of Bahia, Brazil, 2000–2006. *ICES Journal of Marine Science* 65, 667–673.

Silverman H.B. and Dunbar M.J. (1980) Aggressive tusk use by the narwhal (*Monodon monoceros* L.). *Nature* 284, 57–58.

Trivers R.L. (1972) Parental investment and sexual selection. In Campbell B. (ed.) *Sexual selection and the descent of man*. Chicago: Aldine Press, pp. 136–175.

Tyack P. and Whitehead H.P. (1983) Male competition in large groups of wintering humpback whales. *Behaviour* 83, 132–154.

Whitehead H.P. (1983) Structure and stability of humpback whale groups off Newfoundland. *Canadian Journal of Zoology* 61, 1391–1397.

Whitehead H.P. (1985) Humpback whale breaching. *Investigations on Cetacea* 17, 117–155.

Whitehead H.P. and Moore M.J. (1982) Distribution and movements of West Indian humpback whales in winter. *Canadian Journal of Zoology* 60, 2203–2011.

Wright R.E. (1995) Logistical regression. In Grimm L.W. and Yarnold P.R. (eds) *Reading and understanding multivariate statistics*. Washington, DC: American Psychological Association, pp. 217–244.

Zerbini A.N., Andriolo A., Rocha J.M., Simões-Lopes P.C., Siciliano S., Pizzorno J.L., Waite J.M., DeMaster D.P. and VanBlaricom G.R. (2004) Winter distribution and abundance of humpback whales (*Megaptera novaeangliae*) off Northeastern Brazil. *Journal of Cetacean Research and Management* 6, 101–107.

and

Zerbini A.N., Andriolo A., Heide-Jørgensen M.P., Pizzorno J.L., Maia Y.G., VanBlaricom G.R., DeMaster D.P., Simões-Lopes P.C., Moreira S. and Bethlem C. (2006) Satellite-monitored movements of humpback whales *Megaptera novaeangliae* in the Southwest Atlantic Ocean. *Marine Ecology Progress Series* 313, 295–304.

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https://doi.org/10.1017/S0025315410000421 Published online by Cambridge University Press