4 · *Hunting Optimally*

4.1 Introduction

Like other animals, humans engage in foraging tasks that involve the acquisition of multiple 'targets', in this case foods, from their environment. Different foods, whether they are berries or animal prey, are often distributed in fairly discrete 'patches' in space and time. Thus, humans and other animals face decisions on which items to harvest, when to quit searching and when to move on to the next patch.

Theories of optimality involve mathematical models of cost and benefit analysis that can give quantitative predictions about an animal's behaviour. Such proximate decision models, such as those jointly classified under the umbrella of optimal foraging theory (OFT) have been used to understand and to predict foraging behaviour in animals as well as humans. Optimal foraging theory allows researchers to develop a large set of fundamental hypotheses that predict which food resources foragers will pursue when encountered during a search, or where foragers will travel to search for resources and how long they will stay in these places before moving to other areas. The optimal strategy for each individual is to leave a patch when the instantaneous rate of return of food from the current patch falls below the mean return rate from the environment when following the optimal strategy. When a forager first enters a rich patch, gains from exploiting it are high, because the resources are initially plentiful and easy to find. As time passes, however, the forager depletes non-renewing resources, and it takes longer and longer to find the next item.

Optimal foraging theory models were first developed by ecologists to understand non-human foraging behaviour. Since the publication of seminal papers in the mid-1960s on the topic, the annual number of publications considering foraging theory has grown exponentially (Perry & Pianka 1997; Pyke 2010). The key hypothesis is that foragers make choices on the trade-off between the highest possible rate of return and the foraging effort. These decisions lead to the maximization of the net

rates of energy intake while foraging (energy gained from foraging minus the pre-encounter energy spent for the search minus the post-encounter energy spent for pursuit, killing and handling). The assumption is that choices made by a forager, to maximize net energy intake, is evolutionarily selected and will impact the individual's fitness. In essence then, OFT models consist of: (1) a goal, normally the maximization of foraging efficiency such as food gathered over some period of time; (2) a currency, most often the calories inherent in the food collected and the energy spent for the collection; (3) a set of constraints, such as the maximum amount of time available for foraging, information available, technology available, and the distribution, density and nutritional content of the available resources and (4) a set of options such as the potential food resources to pursue and to harvest. These basic elements are applicable to human hunters particularly since optimal foraging decisions will lead to a good diet (and then increase the individuals' survival and fertility) and by managing the time dedicated to foraging, other activities can be incorporated that benefit the hunter groups (Alvard 1998).

4.2 Optimal Foraging Theory Models

The success of the exploitation of prey species by humans is clearly influenced by the different techniques used for hunting, a topic even discussed in relation to the emergence of more efficient technologies amongst ancient hominins (Dusseldorp 2012; Hill 1982). Because prey species vary in terms of the energy they provide, and in the time a human predator uses in searching and handling them, some species are more profitable than others. Higher prey profitability is often linked to greater size, greater abundance, greater accessibility, less danger or cost of acquisition or even better nutritional qualities. In standard OFT models, however, profitability is measured as the return divided by the handling costs, usually calories divided by time, after encounter. Abundance and accessibility are not factored in OFT models. The issue of hunting technology is also not directly addressed by standard OFT, but only indirectly in the set of constraints.

Recent applications of OFT models to human foraging are based on the assumption, as for any animal, that short-term decisions are made to maximize yields from prey; this optimization is quantified in the form of energy or calories (Alvard 1993). Each prey species has a singular value as determined by its particular size and is distributed heterogeneously, often patchily in time and space, with a density that is not constant. Prey

abundance is limited and there is a cost associated with locating it, pursuing it, hunting it down and processing it before being consumed. According to OFT predictions, species are chosen in order to maximize return rates and avoided regardless of their density and their size (Stephens & Krebs 1986). Three basic variables are central to OFT models. Prey species can then be classified according to their: (1) search time, (2) handling time (pursuit + capture + processing + transportation) and (3) average net energy they provides (calories / hour of manipulation) (Fig. 4.1a). Derived from the basic tenets in the original Stephens and Krebs (1986) OFT model, a number of more specific models have been developed. These models, which focus on prey and patch choices, residence time and central place foraging, are applicable to human foragers:

> **The diet–breadth model**, **also called prey–choice model,** predicts whether a forager will utilize a resource upon encounter by defining the optimal diet combination by stepwise addition of diets which have been ranked by their pursuit and handling profitability. It predicts whether a diet should be narrow, i.e. focused on a small number of food resources, or broad (Charnov & Orians 1973; Emlen 1966; MacArthur & Pianka 1966).

> **The patch–choice model**, similar to the diet-breadth model, suggests that the forager has a choice of an array of patches that differ in the energy they contain; patches are ranked according to the net rate of energy intake per unit of total foraging time rather than energy per unit handling time as for the diet-breadth model (MacArthur & Pianka 1966). An example of this is given in Box 4.1.

> **Patch residence time: marginal value theorem, MVT.** When food is patchily distributed, the MVT predicts when to best leave the currently utilized patch and move to a new one. It is an optimality model describing the feeding strategy that maximizes gain per time when resource availability decreases with time spent in the patch. Specifically, 'the predator should leave the patch it is presently in when the marginal capture rate in the patch drops to the average capture rate for the habitat' (Fig. 4.1b; Charnov 1976).

> **Central place foraging.** Choices about prey and patches are contingent not only on the energy content of each prey relative to handling time but also relative to travelling time and transport cost to a home base (Fig. 4.1c; Cannon 2000; Orians & Pearson 1979).

Due to its simplicity and versatility, the diet-breadth model is the most widely applied in ethnology (e.g. Hames & Vickers 1982; Hawkes *et al.*
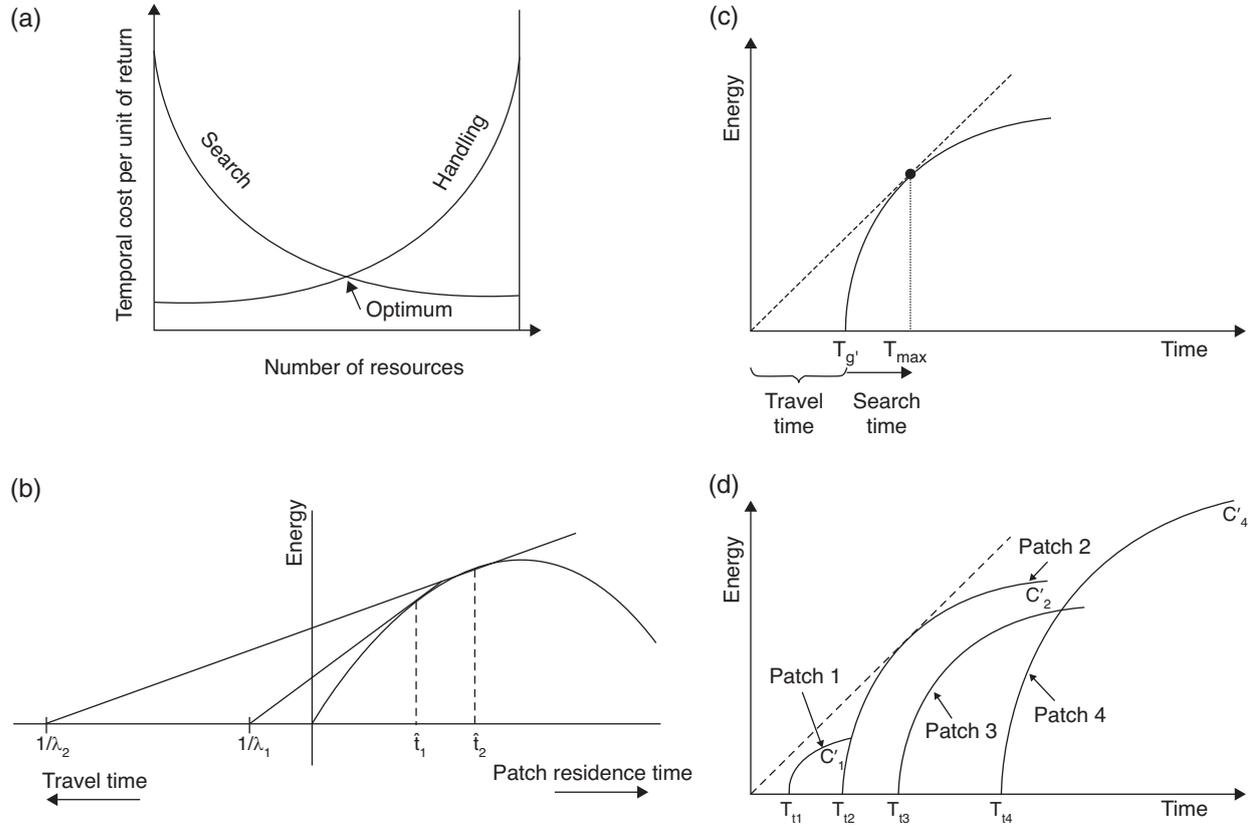
(a) Temporal cost per unit of return — Search, Handling, Optimum — Number of resources

(c) Energy — $T_{g'}$, T_{max} — Time — Travel time, Search time

(b) Energy — $1/\lambda_2$, $1/\lambda_1$, $\hat{t}_1$, $\hat{t}_2$ — Travel time, Patch residence time

(d) Energy — Patch 1, Patch 2, Patch 3, Patch 4, C'_1, C'_2, C'_4 — T_{t1}, T_{t2}, T_{t3}, T_{t4} — Time

Figure 4.1 (a) Graphic representation of OFT. The two curves indicate cost differences in the time of search and manipulation of food, as well as the optimal diet corresponding to the cut-off point of both functions (from Stephens and Krebs 1986; adapted with permission from Princeton University Press); (b) The marginal-value theorem in the one-patch-type case. Two quantities are plotted on the abscissa: travel

1982; Hawkes & O'Connell 1985; Hill *et al.* 1987; Hill & Hawkes 1983; Smith *et al.* 1983; Winterhalder 1986a, 1986b) and archaeology (e.g. Bird & O'Connell 2006; Broughton 1999; Lupo 2007). This model has been used to successfully predict hunter-gatherer diets in different ecological settings, such as boreal forest (Winterhalder 1981), Amazonian forest (Hames & Vickers 1982), Southeast Asian forest (Kuchikura 1988), savanna (Hawkes *et al.* 1991), Australian desert (O'Connell & Hawkes 1984) and in the Arctic (Smith 1991). The two *crucial parameters* are (1) how long it takes to find each food resource (*search costs*) and (2) how long it takes to harvest and process each food source once it is found (*handling costs*). These costs, and the resulting diet-breadth model, are demonstrated by one of the early classic OFT studies (Box 4.1). There are two important consequences of the diet-breadth model. First, lower ranked resources are not part of the optimal diet irrespective of their abundance. Second, all those in the optimal diet, i.e., the higher ranked resources, are always taken even when they are rare.

The MVT has been tested for humans only in one study, namely for Nahua mushroom foragers in Mexico (Pacheco-Cobos *et al.* 2019). The study analysed intrapatch and interpatch search behaviour, in particular the time for a transition to interpatch search after the last encounter with

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Figure 4.1 (cont.) time increases and patch residence time. The optimal residence time is found by constructing a line tangent to the gain function that begins at the point $1/\lambda$ on the travel time axis. The slope of this line is the long-term average rate of energy intake, as $1/\lambda$ is the average time required to travel between patches. When travel time is long $(1/\lambda_2)$, the rate-maximizing residence time $(\hat{t}_2)$ is long. When travel time is short $(1/\lambda_1)$, then rate-maximizing residence time $(\hat{t}_1)$ is shorter (from Stephens and Krebs 1986; adapted with permission from Princeton University Press); (c) The patch choice model for central place foragers (after Orians and Pearson 1979). (d) For any patch i, T_{ti} is the round-trip travel time to the patch and $C'i$ is the gain function of the patch, which describes the expected energetic return from that patch per unit search time. Search time begins once the patch is entered. Gain functions are assumed to be negatively accelerated, which is to say that marginal energetic return diminishes as search time increases. Energetic return per total time (travel time plus search time) is maximized for any patch by foraging in that patch until time T_{maxi}, which is given by a line tangential to the gain function beginning at the origin of the graph. Patches with higher densities of high-return resources will, as a generalization, have 'taller' gain functions, or higher maximum profitabilities. The patch that provides the highest overall rate of energy delivery to the central place is the one that produces the steepest line between the origin and a point tangential to its gain function. Patch 2 is the delivery rate-maximizing patch for this hypothetical set of four patches. (From Cannon 2000; Adapted with permission from Elsevier.)

Box 4.1 *Optimal foraging by the Aché of eastern Paraguay*

The Indigenous Aché have lived as hunter-gatherers in the forests of eastern Paraguay since before the arrival of the Spanish. According to a study by Hawkes *et al.* (1982), Aché diet consisted of a large number of mammals (33+ species), reptiles and amphibians (at least 10 species), birds, fish (more than 15 species) and at least 5 adult insects and 10 types of larvae. Also, more than 14 kinds of honey and the edible products of 40 or more plant species were consumed. Researchers gathered data during seven foraging trips (lasting between 4 and 15 days), focussing on Aché groups consisting of 5–27 men, 4–15 women, 1–14 children and 2–8 infants. The most frequently hunted mammals were collared and white-lipped peccaries, red brocket deer and capuchin monkeys. Hunters used bows and arrows or shotguns for pursuing large mammals and birds. However, armadillos were dug from their burrows often by solitary hunters, and pacas were captured by groups of hunters in their dens. Most food processing was undertaken in overnight camp. Over the study period, average intake from foraging was about 3,600 calories per day per capita, 80% of which were from animals. OFT ranks resources according to the ratio of returns they provide (calories) *versus* the cost (handling time) of acquiring and processing the resources once they have been encountered, E_i/h_i (Fig. 4.2). Therefore, Aché should not take any resource with a post encounter return rate of less than 870 calories per hour, i.e., rank 13 or lower. It is important to note that the resource rankings say nothing about the quantitative importance of a resource to optimal foragers. In other words, however frequently a resource is below the critical return rate of 870 calories per hour, they should not harvest it. Indeed, the Aché were not observed to have harvested any resources ranked 13 or lower. However, palm fruit, which was just inside the optimal set on rank 12 were ignored on several occasions, whilst this never happened for oranges, ranked 4. By and large, however, the observed foraging patterns by the Aché is consistent with predictions derived from the optimal diet model. The authors also analysed the same data with the patch choice model and observed that the foraging pattern was also consistent with that model.
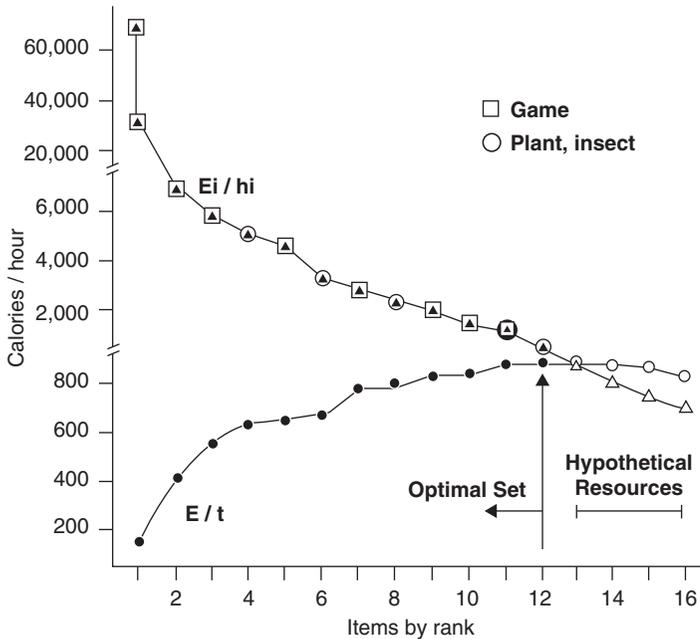
Figure 4.2 Example of the diet-breadth model. The figure shows the ratio of calories returned to handling time (Ei/hi) for each of the resources ordered by rank and the average returns for foraging in general (E/t) that result from the addition of each of these resources. From foraging data for Indigenous Aché in Paraguay the model predicts the optimal set that will be utilized. (From Hawkes *et al*. 1982; adapted with permission from the American Ethnological Society.)

a harvested mushroom within a patch. The empirically estimated 'giving-up times', i.e., the intrapatch search duration, was accurately predicted for the giving-up times as predicted by the MVT. For non-human organisms, Nonacs (2001) surveyed 26 studies that applied the MVT which is the dominant paradigm in predicting patch use. Whilst many studies have shown 'good qualitative support for MVT predictions', quantitative observations differed from the predicted MVT optima in 23 of 26 studies, whereby foragers consistently stayed too long in patches. Simulating state-dependent behaviour, Nonacs (2001) observed consistently longer patch residence times than predicted by the MVT, which were consistent with the observed deviations from the MVT. The suggested modifications for future predictive models of patch use are to consider: (1) the type of predator behaviour, e.g. sit-and-wait *versus*

actively foraging; (2) activities that can occur simultaneously to foraging such as parental care; and (3) the nutritional states of the foraging animals. Cases of human hunting behaviour where observed deviations from the prediction of the OFT occur can be used to refine the models by incorporating the ecological settings. Case studies of historic resource depression (Box 4.2) and the question of hunting large-bodied species not for nutritional value but for social prestige are good examples (Section 3.4).

Overall, OFT has been tested in several settings. In a high percentage of studied cases, its predictions are consistent with what has been

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Box 4.2 *Prehistoric prey resource depression*

Optimal foraging theory, particularly Charnov's (1976) MVT and Orians and Pearson's (1979) patch-choice model, predict that: (1) overhunting of 'high-return' species either leads to the decline in relative abundances, and changes in mean age of the overhunted species, if no alternative, high-productive patches occur, or (2) increases in both high-ranked prey abundances and mean age take place if alternative, high-productive patches exist. Both predictions are fulfilled in the archaeological late Holocene Emeryville Shellmound faunal sequences in California. Excavations of different horizons of the Shellmound demonstrate that the abundance of large-sized prey, such as the North American elk, white sturgeon and geese species declined through time relative to the smaller prey types that occurred in their respective patches (Fig. 4.3a). These large species were confined to the immediate vicinity of Emeryville, thus providing compelling evidence for the first prediction for resource depression. In contrast, the abundance of black-tailed deer, the second largest prey type from the terrestrial mammals' patch, first declined in the oldest strata but then increased across the younger strata (Fig. 4.3b). In contrast to the very localized red deer habitat, black-tailed deer habitat was not locally confined but extended uninterrupted far to the east, thus providing many productive patches. The result was an increased deer index after the first signature of local depletion. That the deer from the younger strata were hunted in more distant patches is supported from patterns in skeletal part representation indicating long-distance transport of high-value parts of carcasses to the central habitation at the Shellmound (Broughton 1999, 2002).
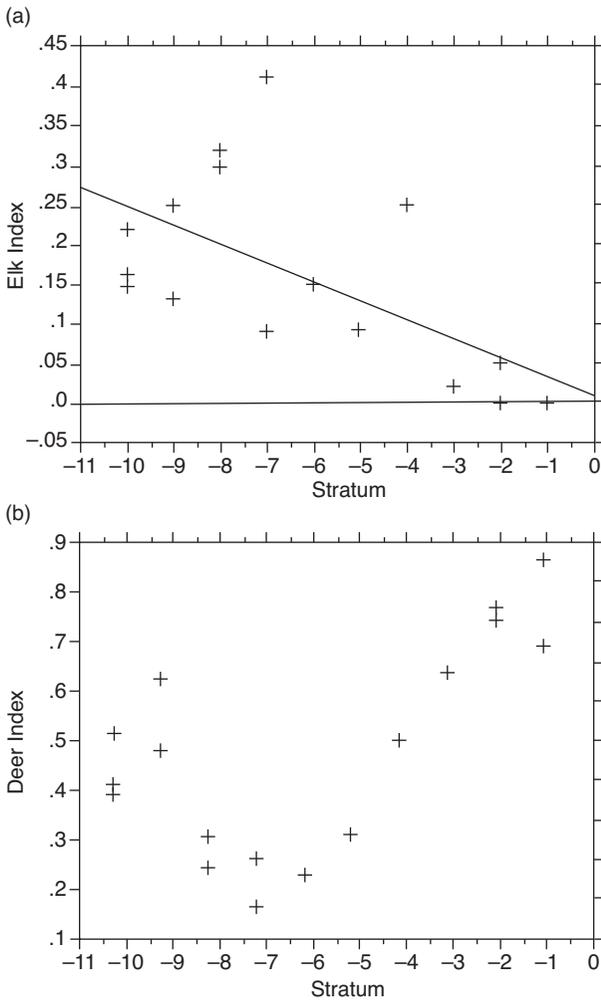
Figure 4.3 The distribution of (a) elk and (b) black-tailed deer abundance indices over archaeological strata at the Emeryville Shellmound, California, USA (from Broughton 2002; adapted with permission from Taylor & Francis).

observed in different hunter–gatherer societies (see the review by Alvard 1998, for example). This means that many Indigenous hunters maximize their short-term catch returns. A clear example of this is Alvard's (1995a) study of Piro hunters of Amazonian Peru. Alvard showed that these hunters do not select a particular age or sex class of prey, but act according to OFT. This is interesting since the alternative hypothesis,

namely that hunters select certain age classes to minimize their impact on species or populations may not apply always (see Sections 4.3.1 and 4.8). Piro hunters therefore pursue larger animals, those weighing more than 4–5 kg, because species within this body mass are the commonest (see Chapter 2). However, hunters do not selectively target old, reproductively unimportant males, but would pursue any adult of reproductive age. For species whose immature animals are relatively small, hunters focus on adults but they are more likely to pursue immatures of large species. The result is that hunters choose an optimal set of species where according to the diet-breadth model, high value prey will always be hunted whenever encountered.

Prey body size is often assumed to be a proxy for profitability. However, different prey characteristics such as predator defence mechanisms and physical characteristics can impact handling costs. Lupo and Schmitt (2016), for example, showed that African forest elephants are ranked lower and are less efficient to hunt by Aka Pygmies, than many relatively smaller-sized animals. When measured by conventional currencies, elephants are relatively uneconomical to hunt, regardless of their encounter rates, and despite the fact that they are the largest terrestrial animal in the African forests. Congo Basin forest foragers normally do not hunt elephants when encountered but they are deliberately pursued by specialist hunters for whom hunting of very costly prey is worthwhile because they can gain social recognition (Section 3.4; Bahuchet 1990; Putnam 1948).

4.3 Cultural Settings and the Optimal Foraging Theory

Superimposed on optimal foraging behaviour, shaped by biological evolution, are cultural behaviours, shaped by social evolution. Hunters regularly sidestep profitable prey types despite their being part of the optimal diet set because of anthropological phenomena, such as taboos and religious belief, meat taste and costly signalling (see Section 3.4). In other cases, species in the optimal diet set are particularly valued and hunted because of add-on effects. For example, woolly monkeys are of large size with good returns of meat, but are particularly sought after by Amazonian Kichwa People in Ecuador as centrepieces for festivals and weddings (Sirén 2012). Good hunters earn high prestige that is unmatched by other occupations including fishing despite fish being a more important food source than wild meat (Sirén & Machoa 2008).

There is a large diversity of individual and communal hunting behaviour within the same habitats. Contrasting outcomes of the prey profile

of colonist and Indigenous communities have been reported. In a comparison of 31 tribal and nontribal settlements in Neotropical forests, the prey species profiles obtained by hunters were influenced by the local availability of wildlife species rather than cultural aspects (Jerozolimski & Peres 2003). Similarly, the ethnic background of hunters (i.e., Indigenous vs mixed communities) had no detectable effect on how different primate populations were exploited in French Guiana (Thoisy *et al.* 2009). In contrast, 19 studies carried out between 1960 and 1980 in the Neotropics demonstrated differences in the number of prey species between Indigenous and colonist communities based on cultural factors such as hunting tools/methods, taboos/prohibitions, and or 'agreed upon' hunting rules within the community. Francesconi *et al.* (2018) observed hunting rate disparities in a study in Peru suggesting there are different types of hunters (specialized vs opportunistic) and that prey composition differs between Indigenous and colonist communities. Indigenous communities displayed higher take–off values and diversity of species than colonists. Specialized *versus* opportunistic hunting strategies have been observed in several studies including Van Vliet *et al.* (2015c) who observed that specialized hunters may spend more time in the forest and use more bullets compared to diversified hunters leading to a higher average game offtake. Individual foraging and hunting skills and their development with individual age also show cross-cultural variation across a vast spectrum of 23,000 hunting records generated by more than 1,800 individuals at 40 locations (Koster *et al.* 2019).

Stafford *et al.*'s (2017b) large cross–site analysis of neotropical hunting profiles confirmed the offtake for some species that appear to deviate from the predictions of OFT. In particular, woolly monkeys were more often targeted than would be predicted by their body size whereas capybaras were avoided despite their relatively large body size, possibly protected by the bad taste of their meat. Moreover, hunting profiles change substantially over short distances, but it remains unknown whether the observed dissimilarities are driven by differences in forest productivity over very small scales, rapidly diverging cultural preferences or both. Sympatric Panoan and Arawakan speaking Indigenous groups and non–indigenous communities in Southwestern Amazonia demonstrated that ethnolinguistic group identity significantly affected the taxa comprising the hunted assemblages, while the other predictors of country, ecoregion and watershed had no influence (de Araujo Lima Constantino *et al.* 2021). This reflects the pronounced cultural diversity and plasticity of hunting practices of overlapping communities living in

the same environments, irrespective of OFT. Non-indigenous hunters targeted medium-sized rodents, and Indigenous hunters showed a preference for large species whereby the Pano typically hunted peccaries, and the Arawak preferentially consumed large primates and birds.

The observation that hunters regularly bypass profitable prey types or focus on prey more than their energetic value predicts, may be interpreted as contradicting the OFT. However, these deviations do not negate the heuristic value of the OFT as all the cited studies show that hunters pursue prey in the optimal diet set and that deviations are omissions from, not additions to the optimal diet set in some but not all hunter communities and in some but not all circumstances. Because of the plasticity of cultural factors impacting individual and communal hunting behaviour, conservation programmes need to tailor interventions closely to each community whereby even sympatric or close-by communities may require different wildlife management and conservation approaches.

4.4 Optimal Foraging Theory Applied to Human Foraging and Its Critics

Optimal foraging theory has advanced our understanding of subsistence patterns for individual human societies, helping us explain variability in the foraging behaviour between individuals and groups (Alvard 1995a; Begossi 1992; Belovsky 1987; Hawkes & O'Connell 1985; Hill 1988; Hill *et al*. 1987; Kelly 2013). The application of OFT models to human foraging has not been without its critics (e.g. Mithen 1989; Pierce & Ollason 1987; Pyke 1984). Criticism of optimization models in general and OFT in particular has ranged from the polemic – arguing that they are naïve, tautological and wrong (Ghiselin 1983; Gould & Lewontin 1979; Pierce & Ollason 1987) – to the more constructive deliberations that highlight problems and cases where deviations from the predictions of the OFT have been observed (Martin 1983; Nonacs 2001; Pyke 1984; Stephens & Krebs 1986). Critiques include:

• **Lack of 'true' testability**: If the predictions of an OFT model are not supported by observations, model parameters – which are notoriously difficult to estimate – are sometimes modified *a posteriori* until predictions and observations fit. This modification of models is standard scientific procedure to improve model outcomes, for example, it led to Chang and Drohan's (2018) optimal stopping diet choice model (see Section 4.5.4). However, some interpret such approaches as too

bendable, 'tautological' or 'not scientific'. These critics question the usefulness of models because they can be modified whenever they do not fit the data (e.g. Ghiselin 1983; Gould & Lewontin 1979; Pyke 1984; Stephens & Krebs 1986). The argument is that OFT is then not truly testable (Gray 1987).

- **Optimality assumption is questionable**: Another line of criticism addresses the OFT's optimality assumption that the most economically advantageous resource is selected through evolutionary processes. Mithen (1989) argues that 'fitness is defined by doing better than other individuals, not by achieving some optimum'. Therefore, the concept of 'meliorizing' might be more adequate that the concept of 'optimizing' (Mithen 1989). Detractors indicate that deviations from the optimization assumptions are found in many culturally transmitted traits, where maladaptation is common. For example, Hallpike (1986) gives examples where there has been the 'survival of mediocre', such as stone axes and horse harnesses which have persisted despite being suboptimal or even maladaptive. In another study, Joseph (2000) discusses the Canadian Inuit as an example of the survival of the mediocre because different models predict that foraging is less profitable than alternative sources of livelihood, but foraging still endures (Smith 1991). But, as highlighted by Stephens and Krebs (1986), 'these criticisms amount to reasons why optimization models might be wrong but not why they are bound to be wrong'.

- **Contrasting conclusions**: Different researchers come to contrasting conclusions for the same ecological systems and evolutionary processes. For example, the transition from hunter–gathering to the first domestication of animals and plants has been explained with the OFT and the niche construction theory (NCT). The NCT's core principle is the deliberate engineered modification or enhancement of ecosystems, which provide organisms with a selective advantage. Smith (2015, 2016) argues that both theories constitute 'antithetical explanatory frameworks for initial domestication'. Discussing the archaeological and paleoenvironmental evidence for the Neotropics, he concludes that OFT does not predict the circumstances around which initial domestication occurred as well as NCT. Also for the Neotropics, Piperno *et al.* (2017) reject these conclusions and demonstrate that the available empirical evidence is fully in accord with hypotheses and predictions generated from OFT. Moreover, they reject the assumption that both theories are antithetical, but argue that they can be complementary, informing and explaining different aspects of human foraging behaviour.

- **Lack of formal testing**: Many studies do not explicitly or formally test the predictions derived from OFT but 'use the general ideas of foraging to organize data and ideas' (Stephens & Krebs 1986). Foraging by the Aché (Box 4.1) is by-and-large consistent with the predictions of the diet-breadth model (Hawkes *et al.* 1982) and is often cited as a prime example in favour of the OFT. Kelly (2013) also concludes that the diet-breath model 'predicts the Aché's choice of food items while on foraging treks'. However, the model did not explain why palm fruit, which is part of the optimal diet, albeit its lowest ranked item, is sometimes not utilized. The model explicitly does not include state-dependent behaviour, such as physiological or nutritional state, travel cost or opportunity costs, which might influence the Aché's decision to harvest palm fruit. Here, a refinement of the model that incorporates state–dependency, as suggested by Nonacs (2001), might explain why palm fruit is sometimes not taken.

For applied scientists and policy makers dealing with wild meat use, the critique of the OFT and, indeed the OFT framework itself, may appear rather academic and without direct applicability. Notwithstanding potential problems, OFT models have been successfully applied to human foraging behaviour of contemporary populations, archaeological settings and to other human behaviours such as how we visually search our environment (e.g. Cain *et al.* 2012; Dusseldorp 2012; Hawkes & O'Connell 1992; Martin 1983; Rode *et al.* 1999; Smith *et al.* 1983). An important conclusion from OFT is that hunters will pursue species whether they are abundant or rare. Thus, even when a species has been hunted to a low density, hunters will kill animals whenever encountered and not grant it temporary reprieve, which would allow it to recover. Moreover, as Alvard (1995a) has demonstrated for Piro people, hunters do not select species or specific age or sex class of prey to proactively conserve prey animals, but follow the predictions of the OFT (see Section 4.11).

4.5 Alternatives to the Optimal Foraging Theory Models

4.5.1 Theory of the Prudent Predator or Intelligent Predator

According to the prudent predator theory, the main objective of hunters is not the immediate maximization of hunting yields (as predicted by the OFT) but the sustainability of resources in the medium and long term

(Slobodkin 1974). This implies that a species will stop being hunted even if it is in the optimal diet when the population density falls below a certain risk threshold. Such behaviour would guarantee the sustainability of the prey species and implies the prioritization of catches towards other more abundant species. This can bring about a change away from the habitual hunting territory towards others with more abundant prey. This hypothesis is related to the concept of the 'ecologically noble savage' as defined by Redford (1991). This concept suggests that groups of hunter-gatherers live in harmony with nature and behave (as prudent predators) guided by their deep knowledge of the environment, which they culturally transmit from generation to generation (Alvard 1993; Hames 2007). Up until about the 1990s, the view of many anthropologists, academics and conservationists was that native people are knowledgeable stewards of natural resources (Alvard 1998; Hames 2007). It was Redford's (1991) book *The Ecologically Noble Savage* which firmly declared this view a myth. Since then, there have been many empirical studies rejecting the hypothesis (Sections 3.6 and 4.11).

4.5.2 Theory of Passive Selection of Prey

This little-known theory, due to Blondel (1967), was originally applied to explain prey selection by birds of prey (Falconiformes and Strigiformes), and proposes that prey species must meet three main requirements for the predator: (1) adequate size, (2) accessibility and (3) abundance. According to this hypothesis, there is no order of preference in how prey meet these three conditions, but rather prey items are selected opportunistically in relation to their space–time availability. Blondel (1967) argues that under these conditions, the energy spent by the raptor to capture its prey must be at least compensated for by the energy it derives from eating it. Unlike predictions of the OFT, the abundance or easy access to a prey can compensate for its suboptimal size and be captured, instead of refusing it in favour of searching other more energetically profitable prey. On the other hand, the passive selection of prey is not conditioned or directed by criteria of conservation of the prey species that are part of the diet, but by mere opportunism. However, the theory has found no empirical support and the OFT − notwithstanding its limitations − has in numerous studies shown, as outlined in the section above, that prey is taken non-randomly and not opportunistically as Blondel's (1967) theory assumes.

4.5.3 Robust–Satisficing Model

The concept of satisficing was suggested as an alternative to the OFT (Simon 1955; Ward 1992, 1993). According to Simon (1955), satisficing individuals, first, satisfy a minimum requirement and, second, will choose among a subset of behaviours when information–processing or time constraints limit their ability to make an optimal decision (Simon 1955). Ward (1992, 1993) introduced the idea that satisficing might constitute an alternative hypothesis to the OFT, but the concept lacked a testable mathematical model until Carmel and Ben–Haim (2005) formalized it by incorporating information gap decision theory. The latter is a non–probabilistic method for prioritizing alternatives and making choices and decisions under severe uncertainty; the 'information gap' is the disparity between what *is known* and what *needs to be known* for a responsible decision (Ben–Haim 2001, 2019). The predictions of the quantitative robust–satisficing model were compared with the predictions from the OFT's MVT, for 26 studies for a diverse range of taxa, including 24 in Nonacs' (2001) study (Carmel & Ben–Haim 2005). Nineteen studies reported significantly longer patch residence times than predicted by MVT but which were predicted by the robust–satisficing model. This contradiction of the prediction of OFT's MVT confirms Nonacs' (2001) review although he suggests that a refinement of the MVT was required rather than the rejection of the OFT.

4.5.4 Optimal Stopping Diet Choice Model

This model, due to (Chang & Drohan 2018), originates in economics and identifies a minimum threshold for a target trait such as body size, denoted by economists as a 'reservation value', that can define the cut–off for species to be included in the diet set. The stopping model requires less field data than the OFT, specifically the distribution of the trait under investigation and the opportunity cost for time spent hunting. In an application to hunter catch by sports hunters in Southwest China, the reservation values predicted by the optimal stopping model corresponded to catch data better than the diet threshold yielded by the OFT. Moreover, the optimal stopping model suggested that hunters should be less selective in their prey choice when they experience a larger opportunity cost for their time. Why the OFT performed worse remains unclear. The mismatch between the estimated and real handling times, important parameters for the tested OFT model, could be explained by

the fact that handling times were simulated because they could not be collected in the field. Nevertheless, these results indicate that the optimal stopping diet choice model could be considered as an additional model to the OFT. Whilst Chang and Drohan (2018) regard the model as an alternative to the OFT, it can also be viewed as an extension to the OFT that incorporates opportunity cost.

4.6 Prey Selection

According to OFT, hunters will select, among all possible prey, those that minimize the cost of search and handling, while maximizing the amount of energy they provide. This implies the existence of one or several species in the optimal diet that will be searched for and captured, depending on their availability, size and handling ease (Dusseldorp 2012). However, when the density of the most desirable species decreases then the diet broadens leading to the consumption of other, lower ranked species (Madsen & Schmitt 1998). This may imply a change in the priority of the species within the optimal set but also include the incorporation of new prey species (Marín Arroyo 2009). This change is governed by the availability of preferred species, which will always be pursued by hunters even when the encounter rate is low and is reversible if population densities of these recover. This points to a dynamic and flexible foraging strategy. In general, specialization lengthens search time for prey but reduces handling time, in contrast to what happens when the diet is broadened. In the latter case, it is more efficient to improve the techniques of post-mortem manipulation (processing) than those of search, pursuit and capture (Hawkes & O'Connell 1992). Specialization can also be facilitated other than by OFT, such as through the accumulation of technical knowledge of search pursuit and kill, as well as improving the social structure that facilitates the cooperation required to kill a species that otherwise no one could kill alone (see Section 4.8; Alvard & Gillespie 2004).

As predicted by OFT, individual animals will be subject to intraspecific selection. Thus, although in most case males and females will be captured relative to their abundance, in sexually dimorphic species it becomes more profitable to target one or the other sex. Likewise, because adults have a greater intrinsic value than young animals, except when the size of the immature is comparable to that of adults as for large species, such as tapirs and capybaras (Alvard 1995a).

Prey selection is heavily impacted by the type of weapons used. Projectile weapons, in particular firearms, radically change the distance at which prey can be killed and its pursuit time, as well as the size of targeted animals. For example, a study of two Indian communities in southeastern Peru, one of which hunted with guns, the other with traditional weapons, showed that shotgun hunters averaged 1.3 shots per kill whereas bow hunters averaged 30 shots (Alvard & Kaplan 1991). Pursuits by shotgun hunters were also significantly shorter than bow hunter pursuits. Shotguns also bring into killing range animals that are difficult to target by arrows, such as arboreal primates. When a less efficient hunting technology is used, OFT predicts a broader prey profile compared to a more efficient hunting technology such as firearms. Indeed, the prey profile of Aché bow hunters is broad and includes smaller, less profitable species typically not targeted by hunters using guns (Alvard 1993b). Shotgun hunters primarily focus on large prey (Alvard 1993a; Kümpel 2006). Chapter 3 gives more details on hunters and technology.

4.7 Selection of the Foraging Space

Available food is not distributed uniformly throughout a landscape, and its abundance changes during the annual cycle. Therefore, according to OFT predictions, foragers must decide which area is more profitable in terms of distance, annual period and abundance of prey, and for how long to stay within it. As a result, as shown by Murdock (1967) for a sample of 168 societies, human hunter-gatherers can be divided into four distinct groups according to their mobility patterns of behaviour:

- Fully migratory or nomadic bands (75% in equatorial zones, 64% in semitropical zones, 42% in boreal zones, 10% in temperate zones and 8% in temperate–cold zones).
- Semi-nomadic communities, whose movements are interrupted by periods of permanence in stable camps.
- Semi-sedentary communities, where the tendency to remain tied to a camp takes precedence over mobile phases.
- Sedentary communities. Those that live fixed to a territory throughout the year.

Two dominant strategies can be distinguished: one that implies the displacement of consumers in search of resources (foragers) and one based on the total or partial transport of these resources to consumers

(collectors) (Binford 1980). Generally, most forager groups are small, quite mobile, especially in temperate climates, and according to Marlowe (2005) undertake on average around seven trips every year. This also implies a cyclical and predictable use of different resources throughout the year. In favourable habitats, where food is more abundant and therefore can sustain a higher population density, local group size tends to remain fairly constant, around 30 individuals according to Marlowe (2005).

The collector model assumes a fixed camp from where hunters leave and to which they return. This strategy is followed, for example, by the !Kung (Binford 1980). In some cases, hunting parties use mobile camps for several days. In both situations, hunting effort tends to concentrate around the inhabited nucleus (Ohl-Schacherer *et al.* 2007; Smith 2008) causing an impoverishment of the peripheral area. The size of these depleted areas around settlements, termed an 'extinction envelope' (Levi *et al.* 2011b), is inversely proportional to the distance travelled by the hunters (Alvard 1994, 1998; Muchaal & Ngandjui 1999). Factors involved in this impoverishment are directly related to the size of the human population and its spatial distribution, types of weapons used and the average number of annual catches per hunter (Levi *et al.* 2011b). The existence of roads and rivers favours motorized transport, which allow travel of greater distances in less time than walking and thus causing resource depletion within a wider geographical area (De Souza-Mazurek *et al.* 2000).

The mobility and the size of areas used by human groups are positively related to how much hunting contributes to the total diet (Fig. 4.4). In temperate climates, mobility in hunter-gatherer populations differs from 14 km per day for men to 9.5 km per day for women (Marlowe 2005). Mobility is not necessarily related to food abundance or scarcity, although the number of trips varies according to the abundance of food in the environment. By contrast, sedentarism can result from local resource abundance in the context of regional scarcity, thus promoting territorial defence of resources and domestication (Alvard & Kuznar 2001). Hence, large home ranges and increased mobility are needed if hunting is the priority activity while fishing is associated with more sedentary lifestyles (Marlowe 2005). However, in some situations, by increasing resource productivity through environmental management, agriculture and livestock rearing, reducing mobility and even birth control, it is possible not to exceed the carrying capacity of a group's natural setting (Zeder 2012).
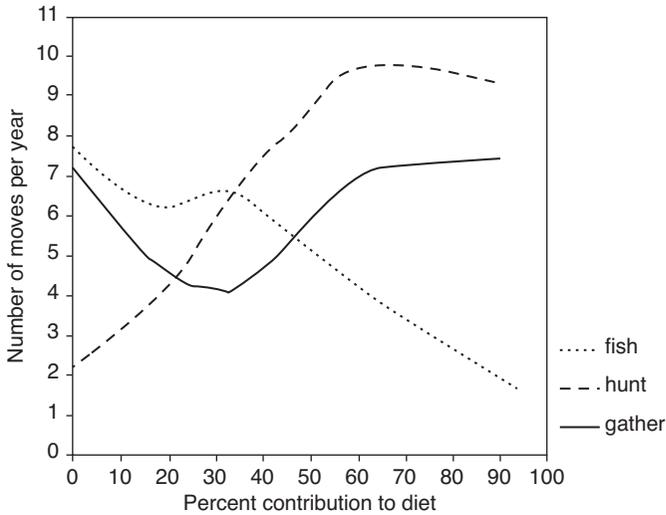
Figure 4.4 Number of residential moves per year by the percent contribution to the diet from hunting, gathering, and fishing (*n* = 340 forager samples); fitted lines are Lowess smoothed (from Marlowe 2005; adapted with permission from John Wiley & Sons).

Both foragers and collectors must make decisions on the choice of hunting range. According to OFT, this choice is conditioned by the availability of prey in the optimal diet set. The richest patches are used first, but are abandoned when benefits fall below the average of those obtained in other patches (Alvard 1995a). As a consequence, there is an inverse relationship between the number of trips made by foragers throughout the year and the average distance between the patches they visit. Therefore, distance between patches plays a very important role. Alvard (1994) found that the hunting pressure by the Piro (hunter horticulturists) was greater in the vicinity of their settlements. As a result, the average rate of return was 0.98 kg/h at a distance of no more than 4 km from settlements and 3.2 kg/h between 4–8 km. Greater distances are not covered, even when there are optimal hunting zones, since the energy cost of the displacements and transport of the prey does not compensate for the hunting yields obtained.

4.8 Group Hunting *versus* Individual Hunting

Group hunting allows the taking of more and larger prey and, in general, increases hunting success (Janssen & Hill 2014). In addition, it reduces the

risk of confrontation with dangerous animals, makes it possible to ambush flocks and facilitates the isolation of gregarious individuals. Cooperative hunting is usually practiced by hunter-gatherers as different as !Kung, Mbuti Pygmies and Inujjuamiut, for example (Alvard 1999b). Packer and Ruttan (1988) argue that cooperative hunting occurs when it favours the probability of encountering or capturing optimal prey and compensates for having to distribute them, which is part of the predictions of OFT. In fact, an inverse relationship between the hunting success rate and the size of the prey has been observed. Among the Aché and Hadza, the success rate against prey weighing or exceeding 40 kg is 10 times lower than that obtained for prey less than 10 kg, and 5 times lower than the !Kung (Hawkes *et al.* 2001). Benefits provided by collective hunting have been quantified for the Lamalera whale hunters, who obtain 3 kg of meat / person / hour of collective hunting compared to 0.39 kg fishing alone of smaller species (Alvard 1999b).

Technological improvements brought about by the development of poison, bow and arrow, and firearms (Chapter 3) has favoured individual hunting or at least, the possibility of smaller hunting groups, as in the case of the Hadza. As a corollary, the probability of cooperation declines when the capture of the prey does not require the necessary participation of third parties (Scheel & Packer 1991). Vice versa, net hunting (see Chapter 3; Carpaneto & Germi 1989, 1992; Ichikawa 1983; Terashima 1983) or the technology required for whale hunting (Alvard & Gillespie 2004) requires larger groups.

4.9 Sexual Division of Hunting Roles

Hunting appears an eminently male activity although exceptions exist. Sexual division of labour is selected for where significant danger of injury, such as hunting mobile prey, exists and can expose infants to substantial risks when human mothers engage in this type of hunting. Differential costs of hunting for the two sexes has led to the sexual division of labour with subsequent sharing of resources and biparental investment within families (Hooper *et al.* 2015; Hurtado *et al.* 1985, 1992). Complementary strategies between both sexes seem to prevail, in which men and women pursue activities of a different nature (Hawkes *et al.* 1993; Hurtado & Hill 1992). In certain circumstances, men focus on hunting difficult-to-acquire prey, which often increases their social status and the dependence of other non-active members, while women concentrate on the collection of products that involve less effort but ensure a

daily and sometimes constant supply of food (tubers in many cases: Speth 2010) for her, her offspring and other group members (Hawkes *et al.* 1997). Members of a group will perform different activities at different intensities according to their age, sex and reproductive status, and this in turn affects the size of the group. Ultimately, the way in which resources are distributed in the environment and their abundance has also a direct effect.

Foraging group size and composition is also impacted by the sexual division of labour, intergenerational division of labour and the economies of scale in production (Hooper *et al.* 2015). When groups are very small, generally fewer than 10 people, men and women are more equal in finding and obtaining resources increases (Binford 1980). This homogenization of tasks could have been favoured, in addition, by the use of tools that reduce the risk (net, traps) and the exclusive use of force to capture certain types of prey. This is the case, for example, of the Aka Pygmies (Hewlett 1993).

4.10 Handling and Distribution Strategies of Catches

The strategies which hunters employ for pursuing and handling prey depend on the technology used, as well as on the habits and customs of the group (Bright *et al.* 2002). Such strategies affect the amount of energy that can be made available to the hunters as well as to the rest of the group. For example, when multiple individuals cooperate to hunt the same prey, they can both increase the probability of successful prey capture and reduce the individual costs associated with hunting. Cooperative hunting provides mutualistic benefits only when the per capita intake rate increases with group size. Sharing of benefits resulting from cooperative hunting is common though not exclusive among hunter–gatherers who do not store food (Binford 1980); food storage occurs generally in environments where the effective temperature is below 15°C although meat can also be preserved at higher temperature by drying, marinating or curing (e.g. whale jerky by Lamalera whale hunters; Alvard & Gillespie 2004). Cooperative hunting is linked to the pursuit and capture of large prey species that are generally inaccessible to a lone hunter. Examples of cooperative hunting and sharing of meat are abundant (Hawkes 1990), and have been well studied in the !Kung, Mbuti Pygmies, Aché, Hadza and Nunamiut, for instance (e.g. Carpaneto & Germi 1992; Hawkes *et al.* 1991; Hawkes & O'Connell 1985; Hill & Hawkes 1983; Hurtado *et al.* 1992; Ichikawa 1983; Terashima 1983) or the technology required for

whale hunting (Alvard & Gillespie 2004). Small catches are usually owned by the hunter and are not shared, although there are exceptions as in the Hadza (Hawkes *et al.* 2001).

The distribution of food within a social group reduces the risk of shortfall, since hunting is associated with a large variance in returns, and thus the risk of malnutrition and mortality amongst its members (Kaplan *et al.* 2000). There can either be an egalitarian sharing amongst hunters and other group members, but also situations in which certain group members gain a greater share (benefit) over others according to previously agreed rules (Barnes & Barnes 1996; Wiessner *et al.* 1996). Egalitarian sharing of meat, for example, is typical of hunter-gatherers groups in tropical forest environments, in which the hunters themselves do not control how a large prey animal is divided amongst their group, since this is considered a common good accessible to even those who have not participated in its capture (see Hawkes 2001).

4.11 Conservation and Sustainability

Many studied hunter-gatherer societies exploit their food sources in a sustainable manner but conservation is not their main *modus vivendi* (Section 3.5; Alvard 1995b). The active conservation of exploited resources by humans is a rational survival-linked decision that has a short-term cost for those who implement it, so as to maintain the long-term sustainability of resources (Alvard 1993). Therefore, this implies the deliberate manipulation of the environment to favour the production of resources (Balée & Erickson 2006), such as by restricting hunting activity of declining prey and impoverished territories. To achieve the expected results, actions must be intentional. The reality is that in a large number of societies, natural resources are considered inexhaustible since they are thought to depend on the generosity of supernatural forces. When resources become limited, mystical forces seem to have ceased their generosity, in which case it is necessary to implement magical expiatory rituals to appease the wrath of the spirits (Hames 2007; Krech 1999). Many of these societies do indeed adapt their behaviour to ensure that hunting continues in their territories, but often do not take direct actions that regulate prey extraction, even though they may be aware that overexploitation is harmful. Moreover, taboos cannot be interpreted as a primitive form of protection because, with some exceptions (Ross *et al.* 1978), their origin is usually not directly related to the conservation of overexploited species or places, but rather to cultural myths (Alvard 1998).

Living in harmony with nature does not necessarily reflect a 'conservationist' attitude (Alvard 1998), as many anthropologists argued between the 1960s and 1980s (FitzGibbon 1998). Many hunter–gatherer populations are in balance with their prey. But often this is not a fixed aim of these communities set in advance but a consequence of other factors (Alvard 1995b), an effect that has been named by Hunn (1982) as a 'conservationist epiphenomenon'. The balance with the environment can arise from low human population density, limited technology and high mobility. Indeed, human population size was significantly linked with mammalian extinctions over the past 126,000 years (Section 6.1; Andermann *et al.* 2020). In particular, low human population density results in the 'inability to overexploit' (Alvard 1995b). Therefore, it is not inconsistent to find a positive correlation between the presence of native peoples, often at low population densities, and areas of high diversity (Borgerhoff Mulder & Coppolillo 2005; Fa *et al.* 2020; Garnett *et al.* 2018).

Sustainability (Chapter 5) is possible in the absence of clear conservationist attitudes among users of a resource when the extraction rate does not exceed the intrinsic rate of growth of the target populations. The vulnerability of the species, the number of catches and the size of the population of consumers are factors to be taken into account (Alvard *et al.* 1997). Hence, in practice, sustainability depends on the behaviour of the hunter and the prey species, since they determine the number and type of animals collected (FitzGibbon 1998). Therefore, OFT and sustainability are compatible when overexploitation is spurious.

Currently, the idea prevails that many traditional societies have overexploited their prey and deteriorated the habitat (Alvard 1998; Diamond 1988). According to Krech (1999), there is little evidence of conservation among Native Americans prior to contact with Europeans and none during that period. Similarly, conservation among contemporary hunters is rare and occurs only when prey species are valuable and scarce: they constitute private goods (abundant and predictable resources) and are worth defending both in the short and long term (Alvard & Kuznar 2001). On the other hand, a study by Hames (1987) on various Amazonian peoples does not find support for the conservation hypothesis: the more decimated the target species are, the more time they invest in hunting them (Siona-Secoya and Yanomami hunters, among others). The Piro, for example, do not avoid hunting vulnerable species in fallow zones if they find them (Alvard 1995a). This does not obviate the existence of evidence in favour of proactive conservation by different hunter–gatherer societies (Ohl-Schacherer *et al.* 2007). For example, the

transition of animal husbandry from hunting is a special case of resource conservation (see below). But these tests are scarce and those that point in the opposite direction are very abundant (Smith & Wishnie 2000). A recent review on the ecologically noble savage debate (Hames 2007) highlights the lack of empirical arguments in support of a generalized conservationism, concluding that the idea of 'proactive conservation' attributed to the hunter–gatherer communities is a myth. There is no doubt that Indigenous Peoples have extensive knowledge of the environment, but it is not clear whether they use it to maintain a balance with nature or to be more efficient hunters (Hames 1987). The causes of non-conservation are attributed to the fact that prey species are freely acquired (Hames 1991; Smith *et al.* 1983) or to the low impact caused by hunting on the biodiversity of the territory, which does not exclude the possibility that some species are overexploited (Alvard 1995b).

A very special case of conservation is the transition of animal husbandry from hunting. Alvard and Kuznar (2001) suggest that animal husbandry is prey conservation where the husbanded animals are prey that are not pursued upon encounter. At first, this appears to be in contrast to the diet-breadth model which predicts that foragers always pursue prey that are in the optimal diet set. The initiation of animal husbandry, however, does not involve immediate pursuit and killing of prey species and the benefits are deferred to the future by slaughtering the husbanded animals or their offspring. Alvard and Kuznar (2001) show that under certain, feasible conditions, OFT can explain the emergence of husbandry. The conditions are: (1) private ownership or territorial defence of animals, (2) sufficient value of animals to justify defence and (3) low opportunity cost of restraint of animals. Archaeological evidence for Neolithic transition in the Middle East indicates that these conditions were met. Alvard and Kuznar's (2001) OFT model predicts that animals below 40 kg should be husbanded under these conditions whilst larger animals should be hunted. The archaeological record indicates that the first domesticated animals, such as goat and sheep, fall within the range below 40 kg, whilst heavier animals such as cattle and pigs were only later domesticated (Alvard & Kuznar 2001).

One important conclusion from the emergence of animal husbandry is the crucial importance of property rights for conservation. Wild meat is typically extracted legally where ownership of animals does not exist or illegally where any ownership is ignored. Lack of ownership is the typical setting for the 'tragedy of the commons', where modern hunters and traditional hunter-gatherers have no incentive to limit their own

harvesting when others can unilaterally maximize their own returns (e.g. Beckerman & Valentine 1996). Thus, property rights can contribute to successful conservation of prey species (see Chapter 8).

It is appropriate to remember that the conclusion that traditional hunter–gatherers generally follow the predictions of OFT and are not conserving prey species has a strictly academic value and does not justify inappropriate moral judgments. Because it is not about resurrecting the hunting–conservation dilemma, but to turn it into a conservation strategy where we are all part of the problem and together, we must contribute to its solution. According to Peres (1994), simply considering Indigenous peoples as ecologically noble is insufficient if other complementary measures are not adopted, without impositions and prior consensus.

Optimal foraging theory allows us to understand how those who depend on hunting for subsistence behave. Continuing to maintain the myth of the ecologically noble savage (Section 3.6) is as fallacious as it is dangerous and partly derives from confusing sustainability and conservation. Perhaps defending the view that they are the best guarantors of the rational use of resources is not condemning subsistence hunters involuntarily to remain in a cultural stasis that prevents population growth, technological modernization and the acquisition of consumer goods in exchange for raw materials alter the balance, whether circumstantially or voluntarily enter into this dynamic?