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Deconstructing Hunting Returns: Can We Reconstruct and Predict Payoffs from Pursuing Prey?

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Abstract

Explaining variation in hunter-gatherer livelihoods hinges on our ability to predict the tradeoffs and opportunities of pursuing different kinds of prey. Central to this problem is the commonly held assumption that larger animals provide higher returns upon encounter than smaller ones. However, to test this assumption, actualistic observations of hunting payoffs must be comparable across different social, technological, and ecological contexts. In this meta-analysis, we revisit published and unpublished estimates of prey return rates ($n = 217$ from 181 prey types) to assess, first, whether they are methodologically comparable, and second, whether they correlate with body size. We find systematic inter-study differences in how carcass yield, energetic content, and foraging returns are calculated. We correct for these inconsistencies first by calculating new estimates of energetic yield (kcals per kg live weight) and processing costs for over 300 species of terrestrial and avian game. We then recalculate on-encounter returns using a standardized formula. We find that body size is a poor predictor of on-encounter return rate, while prey characteristics and behavior, mode of procurement, and hunting technology are better predictors. Although prey body size correlates well with processing costs and edibility, relationships with pursuit time and energetic value per kilogram are relatively weak.

Keywords Human behavioral ecology · Foraging theory · Hunting · Foraging · Hunters-gatherers · Diet

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Introduction

Hunting is thought to be pivotal in the evolution of human social organization and life history. It has been argued that the pursuit of animals with high social (Bliege Bird et al., 2018; Bliege Bird & Smith, 2005; Hawkes, 2016; Hawkes et al., 2018; Speth, 2010) or nutritional (Domínguez-Rodrigo et al., 2014; Hill, 1982; Isaac, 1984; Kaplan et al., 2000, 2001; Speth, 1989; Washburn & Lancaster, 1968) payoffs may have played a role in our characteristic extended juvenile periods, central place foraging, food sharing, large social groups, cooperative subsistence, and expansive social coordination. But which animals or types of animals were important? In archaeology, long-standing assumptions about prey rankings have suggested that larger animals were more important than smaller ones with respect to energy acquisition because they are thought to provide larger packages of food per unit time (*e.g.*, Ben-Dor et al., 2011; Ben-Dor & Barkai, 2020; Yessner, 1981). Yet, ethnographic observations indicate that larger animals may not always provide higher caloric returns if the *per capita* costs of pursuit and processing, along with the failure rate, are taken into account (Winterhalder, 1981; Hawkes et al., 1991; Smith, 1991; Bird et al., 2009; Lupo and Schmitt, 2016). By ignoring these costs, we run the risk of misconstruing the role of large game hunting in our models of the evolutionary contexts of human sociality and economic variability (Hawkes et al., 1991; O'Connell et al., 2002). To understand what sorts of animals provide high energy payoffs per encounter we require comparable estimates of the net benefits of acquiring one type of prey over another, knowledge that is critical for inferences about social organization and cooperation, resource intensification, and the emergence of broad-spectrum economies, among other topics.

Researchers working on these topics commonly draw on theory from behavioral ecology, particularly the encounter-contingent prey choice model (PCM), which originated with the work of MacArthur and Pianka (1966), Schoener (1974), and others (review in Pyke et al., 1977; historical account in Schoener, 1987). Early anthropological applications of the PCM in the 1970s were initiated by archaeologists such as Beaton (1973) and Bayham (1977) and the archaeologists and ethnographers in Winterhalder and Smith (1981). Ethnographic studies of hunting decisions found general support for model predictions with some critical departures, the latter generally centered on variability in the goals, currencies, and constraints of acquiring resources (*e.g.*, Alvard, 1993a; Bird et al., 2009, 2013; Hames, 1979; Hawkes et al., 1982; Hill, 1988; Hill et al., 1987; Hill & Hawkes, 1983; Koster, 2008; Kuchikura, 1987; Lupo & Schmitt, 2005, 2016; O'Connell & Hawkes, 1984; Smith, 1991; Winterhalder, 1983).

Parameterizing aspects of prey choice such as energetic yield, pursuit time, encounter rates, and processing costs requires long-term behavioral observations, a task particularly difficult for those attempting to reconstruct the past. In these cases, cross-site comparisons of prey rankings and their correlates are critical for generating values for different components of the PCM (Bird et al., 2009; Broughton et al., 2011; Lupo & Schmitt, 2016; Morin et al., 2020; Simms, 1987; Smith & Winterhalder, 1992; Ugan, 2005). The use of standardized models such as the PCM should, in theory, facilitate *a priori* definitions of model components, and allow us to estimate returns using observable characteristics of prey such as body size, evasion strategy, and context of encounter—from different ecological, technical, and social contexts. The problem is that published applications of the PCM in anthropology sometimes vary in how they measure certain parameters of the model, complicating meta-analyses across sites.

To fully explore the reliability and generality of expectations about prey choice in different contexts we first assess the replicability and methodological comparability of hunting returns across a diverse, global dataset of 217 distinct post-encounter return rates for 181 terrestrial and avian prey types. Because our focus is on terrestrial hunting, and given that most marine mammals, fish, and shellfish have evolved very different antipredatory mechanisms in comparison to terrestrial prey, resources acquired through non-terrestrial hunting are not considered here. We then provide methodological recommendations for a more standardized derivation of hunting return rates focused on consistent calculations of prey edible fraction and energetic value. Equipped with these methodological tools we recalculate and standardize ethnographic, historical, and experimental return rates for different prey types, and using these new standardized values, we explore how energetic returns are influenced by differences in the costs of pursuit, capture, and processing relative to the size, energy value, proportion of adipose tissue and behavioral properties of the prey. The accumulated empirical data from hunter-gatherer studies now affords us a more refined approach to archaeofaunal analyses based in foraging theory than the earlier assumption that mostly focuses on prey size as an approximation for energetic value.

Fundamentals of the PCM

The PCM begins by assuming that the forager's goal is to maximize the overall return for time spent foraging in a given type of patch or activity, which consists of total energy (E_f) captured per unit time (T) spent in a bout of foraging, where a foraging bout consists of time spent searching (s) and handling (h) all items. Handling includes all post-encounter time (*e.g.*, pursuit, capture, and processing). The overall return rate (R) is thus expressed as:

$$R = \frac{E_f}{T_s + T_h} \tag{1}$$

The model assumes that search time is shared across all prey types in the patch/activity, that encounters with prey items during a type of foraging activity are sequential, and that searching and handling are mutually exclusive. These assumptions set the basic algorithm from which the model's predictions are derived (Stephens & Krebs, 1986:22), whereby a forager is expected to add prey types to the set handled on encounter in order of decreasing profitability rank (where $e_1/h_1 > e_2/h_2 > \ldots e_n/h_n$) until:

$$\frac{\sum_{i=1}^{j} \lambda_i e_i}{1 + \sum_{i=1}^{j} \lambda_i h_i} > \frac{e_{j+1}}{h_{j+1}} \tag{2}$$

where λ_i is the rate at which a forager expects to encounter items of type i while searching, e_i is the expected energy gained from an individual prey item of type i, and h_i is the expected handling time spent with an individual prey item of type i on encounter. In the equation above, the highest j that satisfies the expression is the lowest ranking prey type expected to be handled on encounter.

If the model's assumptions hold, it follows that the decision to handle (pursue, capture, and process) an encountered item of a specific prey type depends not on the abundance of the encountered prey type, but instead on the opportunity costs set by the expected rate of encounter of higher-ranked prey types. Thus, diet breadth expands; prey types are added to the "optimal diet" in order of their profitability (*e/h*) if encounters with higher-ranked resources diminish. Conversely, prey types are dropped from the optimal diet in reverse order as encounter rates with higher-ranked resources increase. A forager is predicted to always pursue the highest-ranked resource on encounter, regardless of its abundance, as no opportunity can be lost by handling an item of the highest possible rank.

Operationalizing the PCM

For economy of presentation, and because the PCM and all of its underlying assumptions are well described in other sources, both biological (Stephens & Krebs, 1986) and anthropological (Smith, 1991:197–243; Kaplan & Hill, 1992), here we narrow our focus to explore comparisons of resource type ranking vis-a-vis measures of post-encounter profitability (*e/h*). Estimating this parameter is the initial step in the algorithm for determining the set and order of prey types predicted to be pursued on-encounter (Sih, 1979).

According to Winterhalder (1977) and Smith (1980), the *net acquisition rate* is the potential energetic yield of a prey type less the energy expended in its pursuit, capture, and processing, divided by the time invested in those activities. Perhaps because estimating energetic expenditure adds to already daunting demands for data, and because human expenditures while foraging seem to show limited variation between hunt types (*e.g.*, Smith, 1980)—with some important exceptions (persistence hunting, Liebenberg, 2006)—many anthropological studies have used a simpler measure of return rate: *gross energy gains* (without subtracting energetic expenditure) relative to pursuit and processing time (*e.g.*, Alvard, 1993b; Bird et al., 2009; Hawkes et al., 1982; Hill & Hawkes, 1983; Koster, 2008; Kuchikura, 1987; Simms, 1987; Smith, 1991).

For simplicity, unless otherwise indicated, here we use "return rate" to refer to *gross post-encounter return rate* (e/h, or R_{prey}). Likewise, we use "overall return rate" to refer to energy gained from searching and handling ($R_{overall}$). The key PCM distinction is this: search time is included in the calculation of $R_{overall}$, but not in the calculation of R_{prey}. The distinction is important because R_{prey} is concerned with determining post-encounter profitability of a *given prey type*, so that it may be compared to the hunting efficiency of higher-ranked types. Importantly, in the PCM costs and gains are calculated *per capita* regardless of whether the forager is hunting alone or in group.

In the PCM, a prey type is a set of potential resources that is immediately recognizable and is associated with a unique, constant post-encounter return rate. As with other model simplifications, the constant element in this definition is a useful fiction; we use averages in analysis while recognizing that practice is often highly variable. Handling costs vary across foragers (by age or motivation, for example; see Bird & Bliege Bird, 2005) and prey types may be characterized by substantial variation in either or both terms of the equation, e/h. Energetic yield of game may vary by sex, age, and season. The cost of pursuit to the hunter will fluctuate between foraging bouts and depends on the context of the encounter, the amount and type of vegetation cover, whether or not a steady breeze creates a reliable down-wind advantage, or the type of weapons used, among other factors.

In an ideal application prey type distinctions would recognize a subset of individuals with unvarying characteristics (*e.g.*, prime adult female moose [*Alces alces*]) in fall condition, when they are considerably fatter than in the late spring) and a specific context of procurement. For similar reasons, a wolf-killed moose discovered by a hunter has a very different return rate than one that must be actively pursued and killed. Likewise, Alvard (1993b) notes dramatic variation in post-encounter return rate if agoutis (*Dasyprocta punctata*) are inattentive or wary and poised to flee a pursuit. The contexts of encounter may also dramatically change foraging returns. As pointed out for the European rabbit and passenger pigeon, social animals at high density likely yield higher returns than encounters with few individuals (Morin et al., 2020). Despite such variation, to make the most of small sample sizes, PCM analyses frequently equate prey type with a biological species, with finer distinctions, if they are made, based on seasonal (fall *vs.* winter moose; Winterhalder, 1983), behavioral (animal encountered in den or on the surface; Bliege Bird & Bird, 2005), or technological grounds (shot with projectile *vs.* netted). Below we discuss parameters that are key to the derivation of R_{prey} values and provide information about how we estimated them in the present analysis.

Materials and Methods

The full details of our methodology are in the Supplemental Online Material (SOM 1–4); here we highlight key points about critical parameters of R_{prey}.

Edible Portion

Published estimates of the edible fraction of prey whole body weight derive from heterogeneous assumptions and methods in which guesstimates and Western standards of edibility play no small part. Seeking a more consistent approach, we recalculated edible fractions for all of the taxa present in the dataset that we assembled. In these new calculations we adopt, for reasons provided below, the convention that species smaller than 35 kg likely were transported to living sites whole and we consider all tissues except bones edible. Larger species are frequently field processed to lessen transport difficulties or increase efficiency. To account for this trend, we identify a list of "inedible" (*i.e.*, non-transported) tissues we assume will be left behind or given to dogs—brain, skin, tendons, cartilage, stomach, intestinal tract, and tail—which we apply uniformly across taxa >35 kg. Although based on a survey of the ethnographic literature, we are aware that this selection is partly arbitrary and is likely to vary locally. We note that altering this list would have a greater impact on the intercept than the slope or the form of the edibility/body size relationship. Whether all soft tissue actually is consumed rather than used for other purposes is an issue that we address below. We also note that adopting a lower threshold value for transport (*e.g.*, 25 kg) has only a limited impact on our results given that very few of the collated return rates concern species that fall within the 25–35 kg range (9/217 or 4.1%).

In order to derive edible portion/body size relationships, we located detailed body composition data for 40 small and 7 large species, ranging from 0.2 kg (common tree shrew, *Tupaia glis*) to 32.9 kg (Japanese serow, *Capricornis crispus*), and from 63 kg (mule deer, *Odocoileus hemionus*) to 5386 kg (African elephant, *Loxodonta africana*), respectively. Edible fractions for these 47 species are presented in SOM 1.1.

Processing Costs

Few well controlled observations assess variation in processing costs across species and those that are available range widely in their estimates. To shed further light on these issues, Lupo and Schmitt (2016) collected data on African prey types to examine how processing costs relate to body mass. The data compiled in SOM 1.2 expand on Lupo and Schmitt's findings by drawing on a larger sample of species from different continents.

Processing of small game raises a related issue. It is not always clear whether small game processing should be included in the calculations of prey ranking. Here, we have excluded these costs because hunters who acquire small animals usually do not field process them; thus, processing imposes no delay, no opportunity cost, on the time being allocated to the hunt. With the capture, hunters are able to quickly resume searching for additional prey (see also Smith, 1991:234; Alvard, 1993b:370). In contrast, larger prey generally require field processing at the kill site, delaying the resumption of search. For the sake of consistency, we apply no processing cost to prey types under 15 kg; between 15 and 35 kg, we increment processing cost 5%/kg up to 100% of our derived value for 35-kg prey. Further details on how we charged these costs are provided in SOM 1.2.

Handling Costs During Cooperative Large-Game Hunts

Cooperative hunts targeting large game may involve a division of labor. Participating non-hunters or hunters not engaged in searching may assume some part of the handling or processing costs. Again, the micro-economic, opportunity-cost logic of the PCM model suggests that only those handling costs incurred by foragers actively involved in searching should be included in calculating R_{prey}. Processing also may be delayed until conditions are not propitious for hunting. Cree hunters, for instance, will often bury a winter moose carcass in the snow; the hunters—or others—returning later to retrieve it. We have calculated two sets of return rates for prey types collected by multiple individuals: one set includes handling time for all individuals present at any point in the hunt, whereas the second set assumes that 80% of handling time should be subtracted as they relate to those who did not participate in any other element of the hunt, such as searching. We arrived at the 80% estimate informed by instances documented in six ethnographic studies (SOM 1.3).

Hunting strategies can also depend on labor-expensive construction of nets, fences, corrals and other forms of trap or enclosure, all of which are relevant to pursuit and handling. Simms (1987) estimates that 250 h were spent building an antelope drive corral, costs that he treated as pursuit time. However, not all of that labor may have represented a foraging opportunity cost and, because these structures may have been reused over extended periods of time, their construction and maintenance should be amortized. That antelope corrals were repaired (Egan, 1917) and owned by particular individuals (Fowler, 1989) provides support for their repeated use. To account for reuse, we assume that antelope corrals served 10 times, as some of these enclosures were still standing many decades after their last known episode of use (Frison, 2004; Jensen, 2007).

Energy (E)

Our review of the literature suggests that estimates of wild game energetic value are inconsistent and typically lower than they should be, often because they are exclusively based on muscle meat, a lean tissue in many wild animals. Yet, depending on how and where animals store their body fat, applying an *E* value derived from meat (*e.g.*, duck breast) to the entire body overlooks the important source of fat stored near the viscera, organs, and/or skin, among other tissue. This is critical because body fat is a substantial and highly variable component of animal energetic value. The adipose tissue contribution to total energy ranges from 3 to 75% for the species in our energy sample (SOM 2). Intra-species variation can be equally impressive, as illustrated by the seasonal variation in body fat among mule deer (*Odocoileus hemionus*), which ranges from 3.7 to 10.8% (representing 46,130 to 57,813 kcal in an animal providing 40.8 kg, edible fraction)—a 20% change in energetic yield.

To address these issues, we obtained records of body fat percentage from dissection reports or *in vivo* ultrasound, and then extrapolated trends in adipose tissue depots across major taxonomic groups (SOM 1.4) to better predict the composition of prey types for which such information is unavailable. We then use these data to calculate new energy values (kcal/edible kg) for a wide range of taxa, including all species for which return rates were recalculated (SOM 1.5 and SOM 2).

Statistical Methods

Our statistical analyses consist of two principal approaches: (i) We use simple univariate statistics and least squares regression to assess the potential interactive effects of various parameters (*e.g.*, body size, taxonomy, evasion strategy, mode of locomotion, method of procurement) on edibility, fat content, handling costs, and energy to determine which of these parameters best predicts return rates and, (ii) we evaluate a set of multivariate candidate models using a model AICc comparison approach (Burnham & Anderson, 2003). Additional information about statistical methods is provided in SOM 1.6. Our analysis compares original or published return rates with our standardized, recalculated return rates, and assesses the predictive value of our statistical models (predicted returns) against our recalculated returns.

Readers with a knowledge of hunting, perhaps gained through participant observation, will no doubt have thought of a dozen exceptions to the standardizing choices we have just described. Those who have carefully considered, observed, or calculated all elements of a post-encounter return rate in the field might object to our standardized reformulation as introducing more local error in the service of global comparability. These are concerns we ourselves share. Nonetheless, our goal is not to impose analytical uniformity on reality but to ensure clarity of a reasonable analytical baseline such that the inevitable exceptions that are justified are easily identified and explained, and their implications better appreciated. Sounder comparative analysis is the objective.

Results: Assessments of Reproducibility and Methodological Comparability of Published Estimates

Prior to standardizing methods, we first attempted to replicate return rates as reported in the original publications (Table 1). Excluding cases where the necessary information was unavailable ($n = 13$) and the Martu data, which we recalculated separately ($n = 8$, SOM 1.7), our results are encouraging. Of the remaining 196 cases, 185 (94.4%) were within 10% of published values, and 87.8% within 5% of the original value. Suspected sources of divergence include typos, unclear or incomplete information, and, probably more importantly, incaution with rounding errors, which can have a disproportionate effect when small fractions are rounded too liberally (*e.g.*, hrs/kg). Actual calculation errors appear to be very rare in the literature represented in the dataset.

On a less positive note, methodological inconsistencies are common. Return rates and thus prey rankings were calculated using no less than seven different equations (Table 2). This is a conservative count, as differences in processing time calculations were not considered due to the difficulty of determining from the original publications how this variable was handled. A first contrast in the formulations of Table 2 is between the values produced by Winterhalder (1977, 1983)—all are *net* return rates (equation A in Table 2)—and those published by the other authors who consider time but not energy expenditure in their calculations of R_{prey}. Smith (1980, 1991) subtracted energy costs from energy gains in his derivation of $R_{overall}$ but omitted these costs when deriving R_{prey}.

A second contrast in Table 2 arises from analysis of data from Martu hunters in Western Australia (Bird et al., 2009, 2013; also see SOM 1.7). In the Martu literature, average R_{prey} values are calculated as a mean of the post-encounter return rates across individual bouts (where n is the number of foraging bouts during which a given prey type was handled), see equation F in Table 2:

$$\frac{\sum_{1}^{n}\left(\frac{e_i}{h_i}\right)}{n} \tag{3}$$

Other studies sum all energy gained over all hunting bouts in the prey type sample and divide by the summed time devoted to those bouts, see equations B–E in Table 2:

$$\frac{\sum_{1}^{n}(e_i)}{\sum_{1}^{n}(h_i)} \tag{4}$$

The bout averaging approach (used in Bird et al., 2009, 2013; Eq. 3 above, and equation F in Table 2) allows for analysis of inter-bout (and inter-hunter) variance (Bliege Bird & Bird, 2008) which, from a risk-sensitive perspective, can reduce the

Table 1 Data used to rederive published return rates presented by continent and author

Species/prey type	Live weight (item kg)	Live weight (total kg)	Edible fraction	Edible weight (kg)	Calories (kcal/kg)	Total kcal	Pursuit (in min)	Processing (in min)	Published *e*/*h*	Rederived *e*/*h*	Source
North America											
1. Moose (*Alces alces*) and caribou (*R. t.*) winter[a] gun	*600.0*	*710.0*	0.5	355.0	Several species	*722,118*	*5499*		8220	*7879*	W77:334, 342, 496, 607; W83:212
2. Moose (*Alces alces*) early spring gun	*600.0*	*1200.0*	0.5	600.0	*2417*	*1,432,300*	*3259*		25,140	*26,368*	W77:336, 342, 496, 607; W83:212
3. Moose (*Alces alces*) summer and fall gun	*600.0*	*1200.0*	0.5	600.0	*2417*	*1,446,584*	*945*		95,600	*91,847*	W77:338, 342, 496, 607; W83:212
4. Snowshoe hare (*Lepus am.*) fall snare I	*1.1*	*20.9*	0.7	14.6	*1627*	*23,136*	*173*		8260	*8024*	W83:210–2, 214
5. Snowshoe hare (*Lepus am.*) fall snare II	*1.1*	*110.0*	0.7	77.0	*1623*	*124,181*	*483*		15,220	*15,426*	W83:210–2, 215
6. Muskrat (*Ondatra zibeth.*) spring trap. I	*0.9*	*2.7*	0.7	1.9	*1521*	*2470*	*124*		1280	*1199**	W77:419, 421, 607; W83:212
7. Muskrat (*Ondatra zibeth.*) spring trap. II	*0.9*	*16.1*	0.7	11.3	*1540*	*16,974*	*171*		6230	*5968*	W77:421–2, 607; W83:212
8. Muskrat (*Ondatra zib.*) fall hunt. I gun	0.9	*23.4*	0.7	16.4	*1530*	*24,098*	*244*		4740	*5916***	W77:423, 425, 607; W83:212
9. Beaver (*Castor can.* and other sp.) winter trap.	20.5?	*28.0*	0.7	19.6	Several species	*40,884*	*403*		5690	*6090**	W77:211, 449, 496, 607; W83:212
10. Beaver (*Castor can.* and other sp.) winter trap. est.	20.5?	*110.0*	0.7		Several species		*403*		23,620		W77:211, 449, 450, 496, 607; W83:212
11. Waterfowl (several species) pre-breakup			0.7	28.4	Several species	*63,685*	*1405*		3000	*2720**	W77:465, 496, 607; W83:212
12. Grouse (*Bonasa umbellus/Falcip. can.*) gun	0.6?	*7.8?*	0.7				*240*		1220		W77:233, 399–400, 607; W83:212
13. Caribou (*Rangifer tar.*) winter gun	102.5	*3792.5*	*0.53*	*2009.1*	*2732*	5,489,690	7260		45,370	*45,369*	S91:181, 221
14. Caribou (*Rangifer tar.*) summer gun	102.5	*102.5*	*0.53*	*54.3*	*2732*	*148,370*	346		25,370	*25,729*	S91:234
15. Snow goose (*Anser caerul.*) jig/goose gun	2.7	*8.1*	*0.59*	*4.8*	*1756*	8430	19		26,620	*26,621*	S91:181, 223
16. Eider (*Somateria mollis.*) summer gun	2.6	*70.2*	*0.42*	*29.7*	*1300*	38,600	99	*270*	6280–23400[b]	*6276–23,394*	S91:215, 233–4
17. Eider (*Somateria mollissima*) fall gun	2.6	*65.0*	*0.42*	*27.5*	*1300*	35,370	166	0–*250*	5160–12,920	*5101–12,784*	S91:181, 216, 234
18. Goose (*Branta canad.*) summer gun	3.5	*31.5*	*0.63*	*19.8*	*1632*	32,300	38	0–*279*	6120–51,020	*6114–51,000*	S91:181, 215, 233–234
19. Goose (*Branta canadensis*) spring gun	3.5	*241.5*	*0.63*	*151.8*	*1632*	247,710	1954	0–*2139*	3460–7800	*3631–7606*	S91:181, 222, 234
20. Goose (*Branta can.*) jig/goose gun	3.5	*45.5*	*0.63*	*28.6*	*1632*	46,670	1225	0–*403*	1720–2290	*1720–2286*	S91:181, 223, 234
21. Merganser (*Mergus serr.*) summer gun						1440	12	0–*20*	2700–7200	*2700–7200*	S91:215, 233

Table 1 (continued)

Species/prey type	Live weight (item kg)	Live weight (total kg)	Edible fraction	Edible weight (kg)	Calories (kcal/kg)	Total kcal	Pursuit (in min)	Processing (in min)	Published *e*/*h*	Rederived *e*/*h*	Source
22. Ptarmigan (*Lagopus l./muta*) jig gun	0.7	*3.5*	*0.57*	*2.0*	*1225*	2450	18		8170	*8167*	S91:181, 227
23. Ptarmigan (*Lagop. l./muta*) canoe gun	0.7	*37.1*	*0.57*	*21.2*	*1225*	25,970	266	0–*265*	3020–5860	*2934–5858*	S91:181, 220, 234
24. Ptarmigan (*Lagop. l./muta*) winter gun	0.7	*8.4*	*0.57*	*4.8*	*1225*	5880	90		3920	*3920*	S91:181, 221
25. Ptarmigan (*Lagop. l./muta*) spring gun	0.7	*4.2*	*0.57*	*2.4*	*1225*	*2940*[c]	49		3600	*3600*	S91:181, 222
26. Ptarmigan (*Lag. l./muta*) jig/goose gun	0.7	*4.9*	*0.57*	*2.8*	*1225*	3430	74		2780	*2781*	S91:181, 223
27. Arctic fox (*Vulpes lagopus*) trap.	2.5	*10.0*	*0.20*[d]	*2.0*	*2240*	4480	420	0–*240*	410–640	*407–640*	S91:181, 221, 234
28. Mountain sheep (*Ovis canadensis*)	57.0	57.0	0.60	34.0	1258	42,900	1–60	90	17,971–31,450	17,160–28,286**	S87:43–6, 64
29. Mule deer (*Odocoileus hemionus*)	56.8	56.8	0.60	34.0	1258	42,900	1–60	90	17,971–31,450	17,160–28,286**	S87:43–6, 60–1
30. Antelope (*Antilocapra americana*)	40.0	40.0	0.60	24.0	1258	30,888	1–60	60	15,725–31,450	*15,444–30,382*	S87:43–6, 65
31. Jackrabbit (*Lepus californicus*)	*2.0*[d]	*2.0*	0.50	1.0	1078	1103	1–2	3	13,475–15,400	13,236–16,545*	S87:43–6, 68, W53:398
32. Gophers (*Thomomys* sp.)	0.5	0.5	0.85	0.43	1078	464	1–2	1	8983–10,780	9280–13,920**	S87:43–6, 71
33. Cottontail rabbit (*Sylvilagus* sp.)	*1.2*	*1.2*	0.50	0.6	1078	637	1–2	2	8983–9800	9555*–12740**	S87:43–6, 68; W53:398
34. Large gr. squirrels (*Urocitellus*?)				0.29	1078	309	1–2	2	5390–6341	4635**–6180	S87:43–6, 69
35. Ground squirrel (*Ictidomys tridecem.*)	*0.143*	*0.143*	0.91	0.13	1078	140	1–2	1	2837–3593	2800–4200**	S87:43–6, 70
36. Ducks (*Anas* sp.)	*0.9*	*0.9*	0.70	0.63	948	630	1–6	12	1975–2709	2100*–2908*	S87:43–6, 72; W53:398
37. Jackrabbit (*Lepus c.*) hypot. snare low	2.0[e]	2.0	0.50	1.0	1140	*1140*	*20.75–40.75*	5	1495–2656	*1495–2656*	U05:78
38. Snowshoe hare (*Lepus americ.*) trap. low	*1.5*	*7.5*	*0.67*	5.0	1250	*6250*	*238.75*	*25*	1422	*1422*	H80, U05:78
39. Snowshoe hare (*Lepus am.*) trap. high	*1.5*	*15.0*	*0.67*	10.0	1250	*12,500*	*257.5*	*50*	2439	*2439*	H80, U05:78
40. Deer mouse (*Peromyscus* sp.) trap.				*0.36*[f]	1300	*468*	*60*		468	*468*	U05:78
41. Rodents (chipmunk/woodrat size) trap. hypot.				*1.8*[f]	1300	*2340*	*60*		2340	*2340*	U05:78
42. Pocket gopher (*Thomomys*) trap. est.	0.5	*4.0*	0.85	3.4	1078	*3665*	*128*		1718	*1718*	S87:71, U05:78
43. Jackrabbit (*Lepus c.*) hypot. drive low	2.0	*1.2*	0.50	*0.6*	1078	*647*	60	*2*	628	*628*	S87; U05:80–1
44. Jackrabbit (*Lepus calif.*) hypot. drive high	2.0	*9.8*	0.50	*4.9*	1078	*5282*	60	*15*	4243	*4243*	S87; U05:80–1
45. Jackrabbit (*Lepus californ.*) drive	2.0	*50.0*	0.50	*25.0*	1140	*28,500*	*480*[g]		3563	*3563*	U05:80–1

Table 1 (continued)

Species/prey type	Live weight (item kg)	Live weight (total kg)	Edible fraction	Edible weight (kg)	Calories (kcal/kg)	Total kcal	Pursuit (in min)	Processing (in min)	Published *e*/*h*	Rederived *e*/*h*	Source
46. Antelope (*Antilocapra amer.*) drive	40.0	*1000*	0.60	*600.0*	1258	*754,800*	*22,500–37,500*	*1500*	1161–1887	*1161–1887*	S87; U05:80–1
47. “Rabbits” (*Lepus*?)[h] drive low	2.0	*90.0*	0.50	*45.0*	1140	*51,300*	*3600*	*225*	805	*805*	S50; U05:80–1
48. “Rabbits” (*Lepus*?)[h] drive high	2.0	*120.0*	0.50	*60.0*	1140	*68,400*	*2700*	*300*	1368	*1368*	S50; U05:80–1,
49. Ducks (Anatidae) drive (molt) low	*0.9*	*1.0*	0.70	0.73	948	*692*	60	*13*	561	*568*	S87:45; U05:80–1
50. Ducks (Anatidae) drive (molt) high	*0.9*	*3.6*	0.70	2.5	948	*2370*	60	*45*	1317	*1354*	S87:45; U05:80–1
51. Jackrabbit (*Lepus calif.*) drive low	2.0		0.50		1140				415		U05:80–1; P96
52. Jackrabbit (*Lepus calif.*) drive high	2.0		0.50		1140				805		U05:80–1; P96
53. Jackrabbit (*Lepus calif.*) drive low	2.0	*60.0*[i]	0.50	*30.0*	1140	*34,200*	*4800*	*150*	415	*415*	L24:196–7; U05:80–1
54. Jackrabbit (*Lepus calif.*) drive high	2.0	*80.0*[i]	0.50	*40.0*	1140	*45,600*	*3600*	*200*	720	*720*	L24:196–7; U05:80–1
55. Jackrabbit (*Lepus calif.*) drive low	2.0	*800.0*[j]	0.50	*400.0*	1140	*456,000*	*48,000*	*2000*	547	*547*	L39:327; U05:80–1
56. Jackrabbit (*Lepus calif.*) drive high	2.0	*1000.0*[j]	0.50	*500.0*	1140	*570,000*	*48,000*	*2500*	720	*677**	L39:327; U05:80–1
57. Black bear (*Ursus americanus*)	115.0	115.0	0.5	58.0	1610	93,380	1–60	90	37,352–61,434	*37,352–61,569*	T08:148
58. White-t. deer (*Odocoileus virginianus*)	42.0	42.0	0.6	25.2	1200	30,240	1–60	90	12,096–19,895	*12,096–19,938*	”
59. Softsh. and snap. turtle (*Apalone*, *Chelyd.*)	10.25	10.25	0.2	2.1	1300	2730	5–10	15	6547–8273	*6552–8190*	”
60. Raccoon (*Procyon lotor*)	6.0	6.0	0.7	4.2	1680	7056	1–15	30	9408–13,569	*9408–13,657*	”
61. Turkey (*Meleagris gallopavo*)	5.2	5.2	0.7	3.64	1600	5824	1–15	30	7765–11,200	*7765–11,272*	”
62. Virginia opossum (*Didelphis virg.*)	3.2	3.2	0.7	2.24	1460	3270	1–15	15	6540–12,111	*6540–12,263*	”
63. Goose (*Branta canadensis*)	3.0	3.0	0.7	2.1	1610	3381	1–15	15	6762–12,522	*6762–12,679*	”
64. Swamp rabbit (*Sylvilagus aquaticus*)	1.84	1.84	0.7	1.29	1140	1471	1–15	15	2942–5248	*2942–5516**	”
65. Small turtles (*Kinosternon* and others)	3.5	3.5	0.2	0.7	1300	910	5–10	15	2182–2758	*2184–2730*	”
66. Marsh rabbit (*Sylvilagus palustris*)	1.28	1.28	0.7	0.896	1140	1021	1–15	15	2042–3781	*2042–3829*	”
67. Duck (sp.?)	0.72	0.72	0.7	0.5	1230	615	1–15	15	1230–2278	*1230–2306*	”
68. Terrapin (*Malaclemys terrapin*)	0.5	0.5	0.2	0.1	1300	130	1	5	1304	*1300*	”
69. Squirrel (*Sciurus carolinensis*)	0.4	0.4	0.7	0.28	1200	336	1–15	15	672–1244	*672–1260*	”
70. Bison (*Bison bison*) Ogden gun	*590.0*	*120,950.0*	0.6	*72,570*	1450	*105,226,500*	67,200	49,200	54,105	*54,240*	H04:909–10
71. Bison (*Bison bison*) Russell gun	*590.0*	*32,450.0*	0.6	*19,470*	1450	*28,231,500*	13,440	13,200	63,606	*63,584*	”
72. Bison (*Bison bison*) Townsend gun	*590.0*	*9440.0*	0.6	*5664*	1450	*8,212,800*	14,400	3840	44,480	*27016***	”

Table 1 (continued)

Species/prey type	Live weight (item kg)	Live weight (total kg)	Edible fraction	Edible weight (kg)	Calories (kcal/kg)	Total kcal	Pursuit (in min)	Processing (in min)	Published *e*/*h*	Rederived *e*/*h*	Source
73. Bison (*Bison bison*) long gun	591.0	*9456.0*	0.6	*5674*	1220	*6,921,792*	9120	2880	22,976	*34609***	N11:21–22
74. Bison (*Bison bison*) Dodge gun	591.0	*44,325.0*	0.6	*26,595*	1220	*32,445,900*	21,000	13,500	56,221	*56,428*	”
75. Elk (*Cervus canadensis*) Pike gun	318.0	*636.0*	0.6	*382*	1110	*423,576*	840	240	23,567	*23,532*	”
76. Elk (*Cervus canadensis*) Glenn gun	318.0	*1590.0*	0.6	*954*	1110	*1,058,940*	1740	600	27,206	*27,152*	”
77. Mule deer (*Odocoileus hem.*) long gun	95.0	*1995.0*	0.6	*1197*	1200	*1,436,400*	14,940	1260	5319	*5320*	”
78. Mule deer (*Odocoil. hem.*) Glenn gun	95.0	*665.0*	0.6	*399*	1200	*478,800*	2580	420	9577	*9576*	”
79. Antelope (*Antiloc. amer.*) long gun	58.0	*580.0*	0.6	*348*	1140	*396,720*	8880	600	2525	*2511*	”
80. Antelope (*Antiloc. amer.*) Pike gun	58.0	*116.0*	0.6	*69.6*	1140	*79,344*	1140	120	3846	*3778*	”
81. Turkey (*Meleagris gallop.*) Glenn gun	6.0	*48.0*	0.79	*37.9*	1570	*59,534*	2460	480	1282	*1215**	”
82. Turkey (*Meleagris gallopavo*) gun	6.0	*6.0*	0.79	*4.7*	1570	*7442*	300	60	1308	*1240**	”
South America											
83. Collared peccary (*Pecari tajacu*) bow	20.0	77.0	1.00	77.0	1950 (3000)	*150,150*	*277*	*92*	24,375	*24,375*	H83:158, 167; H82:382
84. Collared peccary (*Pecari taj.*) shotgun	20.0	163.8	1.00	163.8	1950 (3000)	*319,410*	*98*	*197*	65,000	*65,000*	”,”
85. Brocket deer (*Mazama americ.*) bow	30.0	71.5	1.00	71.5	819 (1250)	*58,559*	*257*	*86*	10,237	*10,238*	”,”
86. Brocket deer (*Mazama amer.*) shotgun	30.0	270.0	1.00	270.0	819 (1250)	*221,130*	*162*	*324*	27,300	*27,300*	”,”
87. Paca (*Cuniculus paca*)	7.5	327.9	1.00	327.9	1950 (3000)	*639,405*	*4722*	*787*	6964	*6964*	”,”
88. Coati (*Nasua nasua*)	3.5	279.0	1.00	279.0	1950 (3000)	*544,050*	*3683*	*1004*	6964	*6964*	”,”
89. Armadillo (*Dasypus novemcinctus*)	4.3	379.8	1.00	379.8	1950 (3000)	*740,610*	*6153*	*1367*	5909	*5909*	”,”
90. Snake (sp.?)	1.4	8.3	1.00	8.3	1000 (1500)	*8300*	*5*	*80*	5882	*5882*	”,”
91. Bird (sp.?)	1.4	24.6	1.00	24.6	1240 (1900)	*30,504*	*148*	*369*	3542	*3543*	”,”
92. Wh.-l. peccary (*Tayassu pecari*) bow	30.0	307.1	1.00	307.1	1950 (3000)	*598,845*	*10,134*	*369*	3421	*3421*	”,”
93. Wh.-l. peccary (*Tayassu pecari*) shotgun	30.0	212.1	1.00	212.1	1950 (3000)	*413,595*	*6490*	*255*	3679	*3679*	”,”
94. Capuchin monkey (*Cebus apella*)	2.5	492.0	1.00	492.0	1300 (2000)	*639,600*	*28,634*	*2952*	1215	*1215*	”,”
95. Anteater (*Myrm. tridactyla*) dog	30.0	30.0	0.65	*19.5*	1950 (3000)	38,025.0	4.5	7.5	190,125	*190,125*	K07:83, K08:940
96. Agouti (*Dasyprocta punct.*) river dog	4.6	4.6	0.65	*3.0*	1950 (3000)	5830.5	*3.5*		99,289.5	*98,822*	K07:77, 92
97. Tamandua (*Tamandua mexicana*) dog	5.5	5.5	0.65	*3.6*	1950 (3000)	6971.3	0.5	7.5	52,284.4	*52,285*	K07:83, K08:940
98. Collared peccary (*Pecari tajacu*) dog	19.7	19.7	0.65	*12.8*	1950 (3000)	24,927.5	*33.3*	7.5	36,643.3	*36,658*	K07:77, 83, 92

Table 1 (continued)

Species/prey type	Live weight (item kg)	Live weight (total kg)	Edible fraction	Edible weight (kg)	Calories (kcal/kg)	Total kcal	Pursuit (in min)	Processing (in min)	Published *e*/*h*	Rederived *e*/*h*	Source
99. Iguana (sp.?) dog	1.4	1.4	0.65	*0.9*	1000 (1500)	910.0	*2.5*		22,038.3	*22,195*	”
100. Armadillo (*Dasypus novemcinctus*) dog	3.8	3.8	0.65	*2.5*	1950 (3000)	4832.3	*26.6*		10,871.5	*10,884*	”
101. Paca (*Cuniculus paca*) earth dog	3.2	3.2	0.65	*2.1*	1950 (3000)	4085.3	*29.5*		8312.6	*8320*	”
102. Paca (*Cuniculus paca*) trunk dog	2.5	2.5	0.65	*1.6*	1950 (3000)	3137.1	*23.5*		8020.5	*8023*	”
103. Agouti (*Dasyprocta punc.*) trunk dog	2.3	2.3	0.65	*1.5*	1950 (3000)	2865.2	*26.5*		6503.2	*6497*	”
104. Paca (*Cuniculus paca*) river dog	3.3	3.3	0.65	*2.1*	1950 (3000)	4140.5	*44.0*		5640.9	*5641*	”
105. Paca (*Cuniculus paca*) stream dog	2.9	2.9	0.65	*1.9*	1950 (3000)	3675.8	*56.5*		3907.9	*3906*	”
106. Agouti (*Dasyprocta punctata*) earth dog	1.6	1.6	0.65	*1.1*	1950 (3000)	2074.1	*35.0*		3560.1	*3558*	”
107. Baird’s tapir (*Tapirus bairdii*) gun	180.0	180.0	0.65	*117.0*	1950 (3000)	*228,150.0*	300		45,630	*45,630*	K07:76, 77
108. Collared peccary (*Pecari tajacu*) gun	*20.8*	519.4	1.00	519.4	1950 (3000)	1,012,830	690		88,072	*88,072*	A93:371, A91:88
109. Agouti (*Dasyprocta punctata*) gun	*3.0*	5.9	1.00	5.9	1950 (3000)	11,505	24		28,762	*28,763*	”,”
110. Spider monkey (*Ateles paniscus*) gun	*10.3*	82.5	1.00	82.5	1300 (2000)	107,250	282		22,819	*22,819*	”,”
111. Howler monkey (*Alouatta seniculus*) gun	*7.3*	65.4	1.00	65.4	1300 (2000)	85,020	228		22,383	*22,374*	”,”
112. Deer (*Mazama* spp.) gun	*30.0*	30.0	1.00	30.0	819 (1250)	24,570	96		15,356	*15,356*	”,”
113. Game birds (sp.?) gun	*1.5*	36.7	1.00	36.7	1240 (1900)	45,508	258		10,583	*10,583*	”,”
114. Capuchin monkey (*Cebus* spp.) gun	*3.6*	28.6	1.00	28.6	1300 (2000)	37,180	450		4966	*4957*	”,”
115. Brazilian tapir (*Tapirus terrestris*) gun	*145.0*	*145.0*	1.00	*145.0*	1950 (3000)	282,750	60		282,750	*282,750*	A93:372, A91:88
116. Capybara (*Hydroch. hydroch.*) gun	*31.5*	*31.5*	1.00	*31.5*	1950 (3000)	61,425	60		61,425	*61,425*	”,”
117. Squirrel monkey (*Saimiri* sp.) gun	0.8	0.8	1.00	0.8	1200	*960*	56		1075	*1029*	”,”
Africa											
118. Elephant (*Loxodonta africana*) gun	4104.0	4104.0	0.42	*1723.7*	1300	*2,240,784*	2282	5175	3615.3	*3606*[k]	L16:191–2
119. Giraffe (*Giraffa camelopardalis*)	983.0	983.0	*0.60*	*589.8*	1230	*725,454*	4800	770	1563.4	*1563*[k]	”
120. Buffalo (*Syncerus caffer*)	533.0	533.0	0.60	*319.8*	*1300*	*415,740*	180	481	18,880.5	*18869*[k]	”
121. Eland (*Taurotragus oryx*)	337.0	337.0	0.65	*219.1*	1250	*273,813*	1893	540	2700.4	*2701*[k]	”
122. Zebra (*Equus quagga*)	239.0	239.0	0.55	*131.5*	*1350*	*177,458*	60	302	14,767.9	*14706*[k]	”
123. Wildebeest (*Connochaetes taurinus*)	227.0	227.0	0.50	*113.5*	1290	*146,415*	544	44	7503.1	*7470*[k]	”
124. Kudu (*Tragelaphus strepsiceros*)	215.0	215.0	0.50	*107.5*	1320	*141,900*	40	481	6567.1	*6537*[k]	”

Table 1 (continued)

Species/prey type	Live weight (item kg)	Live weight (total kg)	Edible fraction	Edible weight (kg)	Calories (kcal/kg)	Total kcal	Pursuit (in min)	Processing (in min)	Published *e*/*h*	Rederived *e*/*h*	Source
125. Gemsbok (*Oryx gazella*)	215.0	215.0	0.50	*107.5*	1320	*141,900*	474	481	2687	*2675*[k]	”
126. Hartebeest (*Alcelaphus buselaphus*)	130.0	130.0	0.50	*65*	*1170*	*76,050*	544	44	3880.1	*3880*[k]	”
127. Warthog (*Phacochoerus africanus*)	70.0	70.0	0.65	*45.5*	1320	*60,060*	600	30	2891.4	*2860*[k]	”
128. Impala (*Aepyceros melampus*)	51.0	51.0	0.65	*33.2*	1020	*33,813*	150	26	5737.5	*5764*[k]	”
129. Bush duiker (*Sylvicapra grimmia*)	18.5	18.5	0.80	*14.8*	1320	*19,536*	13	49	15,329.0	*15125*[k]	”
130. Steenbok (*Raphicerus campestris*)	11.5	11.5	0.80	*9.2*	1050	*9660*	18	23	10,178.3	*10178*[k]	”
131. Bat-eared Fox (*Otocyon megalotis*) dog	3.6	3.6	0.80	*2.9*	1590	*4579*	16	12	8177.1	*7850*[k]	”
132. Springhare (*Pedetes capensis*)	3.5	3.5	0.80	*2.8*	1590	*4452*	10	12	10,407.3	*9713*[k]*	”
133. Steenbok/duiker (*Raphic./Cephal.*) trap. low				0.28[l]	1200	*336*	60		336	*336*	W88, U05:78
134. Steenbok/duiker (*Raphic./Cephal.*) trap. high				0.97[l]	1200	*1164*	60		1164	*1164*	W88, U05:78
135. Duikers (mostly *Cephalophus*) net	*6.5*	*2.2*	0.60	1.3378	1200	*1605*	*180–360*[m]		268–535	*268–535*	N97:76, 79, 81; U05:80–1
136. Duikers (mostly *Cephalophus*) net low		63.0	0.67	*42.2*	1200	*50,652*	*5712–11,424*		263–525	*266–532*	T76:126; U05:80–1
137. Duikers (mostly *Ceph.*) net high				0.32	1200	*384*	60		384	*384*	L02; U05:80–1
138. Duikers (mostly *Cephal.*) net	*6.5*	*0.9*	*0.60*	0.55	1200	*660*	*180–360*		110–220	*110–220*	N97:79, 81; U05:80–1
139. Duikers (mostly *Cephalophus*) net		0.18		0.18	1200	*216*	60		216	*216*	W91; U05:80–1
140. Small duikers (sp.?) net	*6.3*								106		L05:341
141. Small duikers (sp.?) net	*6.3*								215		”
142. Duikers (*C. dorsalis*/*C. callipygus*)	*19.5*								6769		”
143. Blue duiker (*Philantomba monticola*)	*6.3*								3044		”
144. Brush-t. porcupine (*Atherurus africanus*)	*2.3*								2152		
145. Various duikers (sp.?)									4909		”
146. Giant pouched rat (*Cricetomys emini*)	*1.2*								561		”
147. Brush-t. porcupine (*Atherurus afr.*) trap.	*2.8*								1037		”
148. Murid rats and mice (sp.?) trap.	*0.045*								10		”

Table 1 (continued)

Species/prey type	Live weight (item kg)	Live weight (total kg)	Edible fraction	Edible weight (kg)	Calories (kcal/kg)	Total kcal	Pursuit (in min)	Processing (in min)	Published *e*/*h*	Rederived *e*/*h*	Source
Southeast Asia											
149. Monitors (*Varanus* sp.)	*3.2*	35.4	1.00	35.4	680 (1130)	*24,072*	168		8500	*8597*	K87:150, 165, 176
150. Python (*Malayopython reticulatus*)	*10.8*	21.6	1.00	21.6	560 (940)	*12,096*	90		8000	*8064*	”
151. Brown tortoise (*Manouria emys*)	*8.9*	337.3	1.00	337.3	400 (820)	*134,920*	1212		6670	*6679*	”
152. Water tortoise (*Cyclemys dentata*)	1.7	396.4	1.00	396.4	430 (820)	*170,452*	2142		4780	*4775*	K87:41, 165, 176
153. Spiny hill tortoise (*Heosemys spinosa*)	*1.3*	22.4	1.00	22.4	430 (820)	*9632*	120		4780	*4816*	K87:150, 165, 176
154. Malayan pangolin (*Manis javanica*)	*6.5*	19.4	1.00	19.4	760 (1170)	*14,744*	300		2920	*2949*	”
155. Mud turtle (*Amyda cartilaginea*)	9.7	310.2	1.00	310.2	500 (820)	*155,100*	4656		2000	*1999*	K87:41, 165, 176
156. Giant frog (*Limnonectes blythii*)	0.54	42.4	1.00	42.4	530 (880)	*22,472*	690		1960	*1954*	K87:165, 176; K96:151
157. Dusky leaf monkey (*Trachypithecus obscurus*)	*6.4*	869.3	1.00	869.3	760 (1170)	*660,668*	*20,342*	*4173*	1620	*1617*	K87:140, 165, 175; K88:301
158. B. leaf monkey (*Presbytis melalophos*)	*5.6*	168.3	1.00	168.3	760 (1170)	*127,908*	*4140*	*808*	1550	*1551*	K87:140, 165, 175
159. White-handed gibbon (*Hylobates lar*)	*5.4*	43.4	1.00	43.4	760 (1170)	*32,984*	*1094*	*234*	1490	*1490*	”
160. Musangs and civets (*Viverra* and *Arctictis bint.*)	*8.9*	17.8	1.00	17.8	760 (1170)	*13,528*	*545*	*85*	1290	*1288*	K87:140, 165, 175; K88:301
161. Bamboo rat (*Rhizomys sumatrensis*)	*1.1*	9.0	1.00	9.0	760 (1170)	*6840*	354		1080	*1159**	K87:150, 165, 176
162. Giant squirrels (*Ratufa bicolor* and *R. aff.*)	*1.5*	4.5	1.00	4.5	760 (1170)	*3420*	*151*	*43*	1060	*1056*	K87:140, 165, 175
163. Macaques (*Macaca fasc./M. nemestr.*)	*7.7*	38.5	1.00	38.5	760 (1170)	*29,260*	*2033*	*231*	780	*776*	K87:140, 165, 175; K88:301
164. Medium squirrels (*Callosciurus* spp.)	0.5	0.5	1.00	0.5	760 (1170)	*380*	*48*		480	*478*	K87:165, 175, 176
165. Small squirrels (*Sundasciurus* spp.)	0.1	0.1	1.00	0.1	760 (1170)	*76*	*14*		330	*328*	”
166. Small birds (passerine birds <100 g)	0.1	0.1	1.00	0.1	460 (?)	*46*	*12*		230	*230*	”
Australia											
167. Sand monitor (*Varanus gouldii*)	0.5^{n}	*0.5*	*1.00*	*0.5*	1050	*525*	*7.5*		4200	*4200*	O81:119, 123–124
168. Red kangaroo (*Macropus rufus*)				20.3	1175	*23,853*	1–60	20	17,910–68,275	*17,889–68,150*	O89, U05:77
169. Finch and pigeon (Fring./Columb.) net	0.5	*50.0*	0.85	*42.5*	1400	*59,500*	*360*	*200*	6375	*6375*^{o}	Sa87; U05:80–1

Table 1 (continued)

Species/prey type	Live weight (item kg)	Live weight (total kg)	Edible fraction	Edible weight (kg)	Calories (kcal/kg)	Total kcal	Pursuit (in min)	Processing (in min)	Published *e*/*h*	Rederived *e*/*h*	Source
170. Pigeon (Columbidae) net	0.3	*365.4*	0.85	*310.6*	1400	*434,826*	*1440–1680*[p]	*2436*	6339–6783	*6339–6731*[o]	Sa87; U05:80–1
171. Wallaby (Macropodidae) net	20.0	*400.0*	0.80	*320.0*	1200	*384,000*	*12,000*	*300*	1873	*1873*	Sa87; U05:80–1
172. Ducks (sp.?) net low	*0.9*	*18.3*	0.70	*12.8*	948	*12,134*	*1440*	*40*	492	*492*	Sa87; S87:45; U05:80–1
173. Ducks (sp.?) net high	*0.9*	*27.4*	0.70	*19.2*	948	*18,202*	*1200*	*60*	867	*867*	Sa87; S87:45; U05:80–1
174. Sand monitor (*Varanus gouldii*)	0.461	*109.7*	*0.90*	*98.7*	*2100*	*207,268*	*3873*		4931	*3211*	B09:11; this study
175. Bustard (*Ardeotis australis*) gun	5.491	*267.4*	*0.74*	*197.9*	*1830*	*362,110*	*2836*	*548*	10,261	*6420*	”
176. Kangaroo (*Macropus robustus*) gun	21.970	*269.3*	*0.65*	*175.0*	*1670*	*292,277*	*3972*	*229*	3844	*4174*	”
177. Perentie (*Varanus giganteus*)	2.304	*16.5*	*0.90*	*14.9*	*2100*	*31,185*	*626*		3455	*2989*	”
178. Feral cat (*Felis silvestris*)	2.536	*17.9*	*0.64*	*11.5*	*1460*	*16,768*	*856*	*130*	5179	*1020*	”
179. Skink (*Tiliqua scincoides*)	0.301	*8.8*	*0.90*	*7.9*	*2100*	*16,660*	*71*		20,403	*14,079*	”
180. Python (*Aspidites ramsayi*)	0.703	*7.9*	*0.75*	*5.9*	*1090*	*6434*	*287*		1491	*1345*	”
181. Arabian camel (*Camelus dromedarius*) gun	*332.47*	*5653.5*	*0.45*	*2544.1*	*1600*	*4,070,534*	*2526*	*2435*	122,944	*49,230*	B13:160; this study

Values in italics are those that we derived or rederived using the published information. Return rates are for encounter hunts, unless specified otherwise. Other methods of procurement are identified as “trap.” (trapping), “snare” (snaring), “net” (net hunting), or “drive” (drive hunting). Return rates that are based on different catch sizes are presented on distinct rows, whereas those that only vary with respect to handling time estimates are presented as ranges on the same row. “Low” means low returns, whereas “high” means the opposite. Rederived return rates that differ by more than 5% from the published return rates are identified by an asterisk, those that are more than 10% different are identified by two asterisks

A91 Alvard & Kaplan, 1991, *A93* Alvard, 1993a, b, *B09* Bird et al., 2009, *B13* Bird et al., 2013, *H04* Henrikson, 2004, *H80* Hara, 1980, *H82* Hawkes et al., 1982, *H83* Hill & Hawkes, 1983, *K87* Kuchikura, 1987, *K07* Koster, 2007, *K08* Koster, 2008, *K88* Kuchikura, 1988, Kuchikura, 1996, *L02* Lupo & Schmitt, 2002, *L05* Lupo & Schmitt, 2005, *L16* Lupo & Schmitt, 2016, *L24* Lowie, 1924, *L39* Lowie, 1939, *N11* Newton, 2011, *N97* Noss, 1997, *O84* O’Connell & Hawkes, 1984, *O89* O’Connell & Marshall, 1989, *P96* Palmer, 1896, *S50* Speck & Schaeffer, 1950, *S87* Simms, 1987, *S91* Smith, 1991, *Sa87* Satterthwait, 1987, *T08* Thomas, 2008, *T76* Tanno, 1976, *U05* Ugan, 2005, *W53* White, 1953, *W77* Winterhalder, 1977, *W83* Winterhalder, 1983, *W88* Wilmsen & Durham, 1988, *W91* Wilkie & Curran, 1991

[a] The “total calories” values for the Winterhalder return rates correspond to the output energy value listed in his “input-output” analyses (*e.g.*, p. 342) minus the input energy value listed in the same analyses, the latter weighed by the energy proportion for pursuit time provided on p. 496 (*e.g.*, for winter caribou: 755000 kcal - [40,100 kcal × 0.82]). Values for handling time were calculated using the “time” in Winterhalder’s “input-output” analyses multiplied by the “pursuit” proportion listed on p. 496 (*e.g.*, winter caribou: 8460 min × 0.65). For hares, we used the raw handling data provided in Winterhalder (1983:210, Table 1)

[b] There appears to be some confusion in Smith's (1991) "Total time" column on p. 234. Some of the values (*e.g.*, Canada goose, eider) for "Summer resources" correspond to "Overall rate" values on p. 233, whereas other values (*i.e.*, ringed seal) correspond to "Handling rate" values on the same page. When there was ambiguity, we used the value that is closest to the ones we rederived

[c] The value reported by Smith seems to be a typo. The corrected value is shown here

[d] Smith (1991) assumed a 0.20 "edible" fraction for fox because only the fur was used

[e] These values assume that Ugan used live weight and edible fraction as in Simms (1987)

[f] Value derived using this equation: weight (0.02 or .1 kg) × 150 trap/h × 0.12 (success rate)

[g] 1 day = 8 h

[h] Low: 45 rabbits, 20 people, 3 h; high: 60 rabbits, 15 people, 3 h

[i] Low: 30 rabbits, 20 people, 4 h; high: 40 rabbits, 15 people, 4 h

[j] Low: 400 rabbits, 200 people, 4 h; high: 500 rabbits, 200 people, 4 h

[k] Following Lupo and Schmitt's (2016) approach, the values were multiplied by the species' success rate to account for failure. The butchering value (in min) for elephant is here corrected using the data in Lupo and Schmitt's Appendix A

[l] Although the original text is unclear, these values appear to be edible weights

[m] Information corrected by Ugan (pers. comm., 2019): low: 3 h, high: 6 h. Both values assume 1200 cal/kg

[n] The original text suggests that this value corresponds to live weight

[o] Return rates are inverted in the original publication

[p] 1 morning = 4 h

Table 2 Equations used by various authors to derive post-encounter return rates for prey types

	Studies	Equation
A	Winterhalder (1977)	$R_{prey} = \frac{\sum W_{edible} \times \left(e_{prey} - e_{costs}\right)}{\sum h_{h-hr}}$
B	Simms (1987), Smith (1991), Ugan (2005), Lupo and Schmitt (2005, 2016), Thomas (2008)	$R_{prey} = \frac{\sum w_{edible} \times e_{prey}}{\sum h_{h-hr}}$
C	Hawkes et al. (1982), Hill and Hawkes (1983)	$R_{prey} = \frac{\sum w_{total} \times e_{edible}}{\sum h_{h-hr}}$
D	Alvard (1993), Kuchikura (1987, 1988)	$R_{prey} = \frac{\sum w_{total} \times e_{edible}}{\sum h_{p-hr}}$
E	Koster (2007, 2008)	$R_{prey} = \frac{\sum w_{edible} \times \sum e_{edible}}{\sum h_{p-hr}}$
F	Bird et al. (2009), Bird et al. (2013)	$R_{prey} = \frac{\sum R_{bout}}{N_{bouts}}$ where R_{bout} is calculated as in Eq. B
G	Henrikson (2004), Newton (2011)	$R_{prey} = \frac{\sum w_{edible} \times e_{prey}}{\sum (s_{h-hr} + h_{h-hr})}$

R_{prey} is the post-encounter return rate for the prey type; W_{total} is the total live weight of the prey type in kilograms summed over all observations of h, where h is time spent handling; W_{edible} is total live weight of the prey type converted into edible weight (in kg) summed over all observations; e_{prey} is the average energy provided by the prey type in calories/kilogram; e_{costs} is the energy expended in the pursuit, capture, and processing of R_{prey}, in units of kcal/kg; e_{edible} is the average energy provided by the prey type converted into edible calories per kilogram, $h_{h\text{-}hr}$ is total hunter-hours spent in handling, where handling includes pursuits summed over all observations; $h_{p\text{-}hr}$ is total pursuit-hours summed over all observations regardless of the number of hunters; and $s_{h\text{-}hr}$ is hunter-hours spent searching prey summed over all observations. Equations B and C are mathematically equivalent, and not equivalent with Equation F, which focuses on comparing R_{prey} mean and variance between bouts. In Equation F, R_{bout} is the post-encounter return rate for a given prey type calculated as per Equation B on a single bout of foraging, where a bout includes the summed time that a focal individual forager spent handing a given prey type during a bout of foraging and the kilocalories from that prey type acquired by that forager, and N_{bouts} is the number of bouts. In Equation G, R_{prey} corresponds to the overall return rate for a patch, R_{patch}, which contravenes the PCM assumption of mutually exclusive search and handling

expected utility of prey types when variance is high (Jones et al., 2013). The summed average approach used in studies adopting versions of Eq. 4 (*e.g.*, equations B–E of Table 2) facilitates evaluation of changes in foraging efficiency ($R_{overall}$) as prey types are added to or dropped from those selected for pursuit. However, Eq. 4 provides no information about the distribution of R_{prey} values for a prey type. To make the Martu data comparable with most other studies, in Table 1, we recalculate the Martu data using the method of summed averaging described in Eq. 4 above and equation B in Table 2. It is important to keep in mind that averaging a rate (Eq. 3 above) which contains both a numerator and denominator across bouts is not mathematically equivalent to summing energy and time separately for all bouts and then dividing the former by the latter (*e.g.*, Eq. 4 above) to obtain a summed average rate.

Other methodological inconsistencies affecting calculations represented in Table 2 revolve around three key parameters: (i) handling time and the associated issue of pursuit failure, (ii) edible fraction, and (iii) energy value of an animal (per unit live weight). We examine problems with each of these parameters successively.

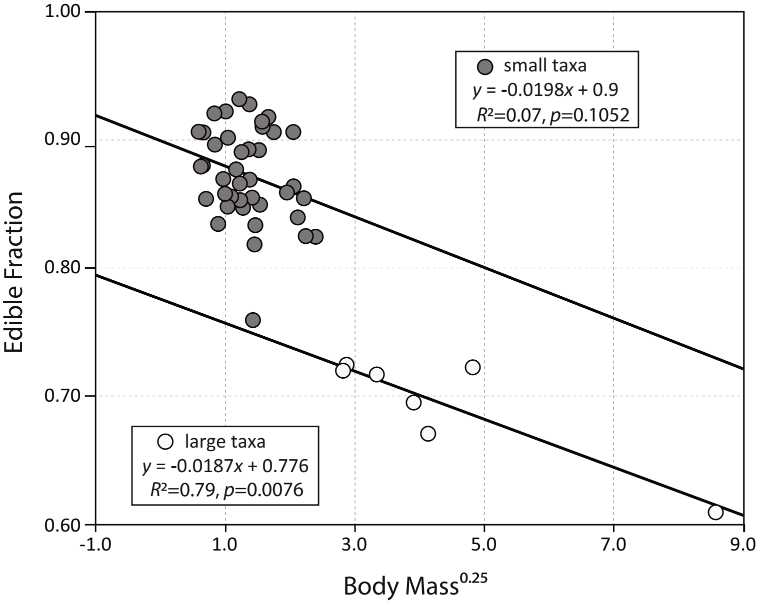

Fig. 1 Relationship between the edible fraction and body mass$^{0.25}$ for small (<35 kg) *versus* large (>35 kg) taxa. In the equation, x is the body mass$^{0.25}$, whereas y is the edible fraction. Data from SOM 1.1

Assessment of Handling Time Calculations

Return rates based on ethnographic field observations all distinguish between the search and handling phases of foraging based on direct evidence, although they do not always agree on how to classify activities such as tracking (*e.g.*, Ugan & Simms, 2012; Bird et al., 2012; see SOM 1.8). In the absence of ethnographic data, return rates must be estimated indirectly, most often by use of ethnohistorical accounts or actualistic experiments that typically lack information on foraging time allocation. Moreover, ethnohistorical accounts are likely biased toward successful, and especially highly successful, hunts, with failures being underreported. These problems of indirect data and reporting biases affect the accuracy and comparability of estimated return rates. For example, return rates for hunting in the Great Plains in the early nineteenth century (#70–82 in Table 1), derived by Henrikson (2004) and Newton (2011) from fur trappers' and explorers' journals, use 5-h "hunter days" as an approximation of handling time, a value they derived from cross-cultural comparisons. However, this estimate is best described as total foraging time because it includes search time. Calculations made in this manner are likely to significantly underestimate R_{prey}; they are more consistent with overall return rates of hunting for a single prey type.

A critical inconsistency in the calculation of handling cost arises from differences in accounting for the often substantial risk of pursuit failure. Summed averages can make it difficult to assess the effects of pursuit failures, in some cases minimizing the impact of large prey pursuit failures on success rates, in others by reversing prey rankings, and this regardless of whether the data are derived from ethnohistorical or ethnographic observations (Bird et al., 2009; Lupo & Schmitt, 2016). To account for un- or underreported pursuit failures, analysts have proposed multiplying R_{prey} by an independent measure of success rate (Ugan & Simms, 2012:182). For instance, using historical records, Lupo and Schmitt (2016) estimate that 20% of elephant hunts are successful. Applying this value to their result from equation B (Table 2), Lupo and Schmitt (2016:192) multiply R_{prey} for elephants (18,077 kcal/h-hr) by 0.20 arriving at an adjusted post-encounter return rate of 3615 kcal/h-hr. However, for game in which processing costs comprise a substantial proportion of handling, and the post-encounter rate of failure is uncertain, charging a low pursuit success rate to both pursuit and processing may overestimate handling costs (see SOM 1.7 for a Martu illustration of this problem). We recommend multiplying only pursuit time by a measure of success rate, and have recalculated the post-encounter efficiency of African taxa following this approach (in our sample, this problem only applies to prey from this region). Sih and Christensen (2001, eq. (1), pp. 385–387) provide a flexible multivariate equation for calculating prey value in a manner consistent with the PCM model and rates of pursuit failure.

Another point of methodological divergence concerns handling costs. Earlier studies frequently merged field butchering time with pursuit time (*e.g.*, Smith, 1980, 1991; Winterhalder, 1977). In contrast, more recent analyses generally report field butchering time *separately* from pursuit time (*e.g.*, Kuchikura, 1988; Lupo & Schmitt, 2016; Newton, 2011; Simms, 1987; Ugan, 2005). In other cases, values are provided only for total handling time, field butchering included (*e.g.*, Alvard, 1993b; Koster, 2007). Although the calculation of R_{prey} is unaffected, neglecting to report processing time separately from other components of handling poses problems for attempts to estimate the impact of pursuit failure. On a more encouraging note, our literature review suggests that most authors are in agreement in excluding cooking and in-camp processing from foraging calculations, on the basis that they likely entail few foraging opportunity costs.

Costs in the PCM, including handling time, are calculated *per capita*. However, as indicated by equations D and E in Table 2, our review finds that the handling times for #95–117 and 149–166 are calculated as pursuit duration independently of the number of hunters participating. By failing to convert handling time into forager-hours, this approach inflates return rates, a practice inconsistent with theory and how most other studies have treated cooperative hunting, which involves summing the time commitments of all hunters actively searching for and pursuing prey. We correct for this problem below. Moreover, we note significant variation in how "hunters" are defined, a problem especially salient in cooperatively acquired prey types where the number of "hunters" is not equal to the number of individuals involved in pursuit and/or processing (see SOM 1.8 for further discussion). As a first attempt to acknowledge these ambiguities, we calculate return rates for cooperatively acquired prey as ranges, the upper bound excluding "supernumerary" participants and the lower range including them (see the "Material and Methods" section).

Consistency of Edible Fraction Estimates Across Studies

When preparing animal prey for consumption hunters may discard tissues not considered edible or worth exploiting. This "inedible" fraction often consists of bones (*sensu stricto*) but may, depending on the context and size and type of species, include other tissues such as the intestines, viscera, brain, and skin. The edible fractions given in publications represented in Table 1 vary widely, even for the same or closely related species. For instance, Smith (1991:181) used an edible fraction of 0.42 for the common eider (*Somateria mollissima*, #16–17), while Simms (1987) favored a fraction of 0.70 for "ducks" (*Anas* spp., #36), a closely related taxon. This difference attributes an energy yield to ducks that is 67% greater than that of the common eider. Even small percentage differences in edible fraction can have a significant impact on return rate calculations. Unfortunately, few studies detail precisely how measures of edibility were derived, making comparisons across cases difficult.

Allometric scaling adds a further dimension to the comparative problem. In vertebrates, mass increases to the cube of changes in the linear dimension while strength, which depends on the cross-sectional area of muscles, only increases to the square (Schmidt-Nielsen, 1984). Consequently, skeletal architecture mass must increase at a faster rate than the associated muscle tissues if individuals are to support their own weight (Prange et al., 1979; West & Brown, 2005). This principle implies that the inedible bone tissue fraction in animal prey will increase faster than body size. Allometric considerations seem implicit in certain calculations of edible fractions (*e.g.*, Lupo & Schmitt, 2016; Simms, 1987), whereas other studies have used a single value for multiple taxa of different sizes, presumably due to a lack of data (*e.g.*, Alvard, 1993a; Hill & Hawkes, 1983; Koster, 2008). Use of a constant adds simplicity and transparency to calculations but in cases in which species differ widely in size, allometric scaling may be more appropriate. Below, we correct for this problem using a standardized allometric formula for calculating edibility.

Several edible fractions in Table 1 were derived directly or indirectly from livestock industry "carcass yields" (*e.g.*, Ledger, 1968). This approach privileges meat to the near exclusion of tissues and fluids routinely consumed by human foragers (ethnographic documentation in SOM 1.9). Although there are exceptions (*e.g.*, pigs), estimates based on carcass yield may markedly underestimate the energetic value of wild game to foragers.

Comparability of Methods for Calculating Energetic Yield

In our sample, caloric values reported for specific prey types sometimes differ between studies, likely due to the difficulty of locating relevant data for poorly documented wild game species (*e.g.*, Hawkes et al., 1982; Hill et al., 1984). Differences in energetic values also occur among authors in our dataset. For instance, Simms (1987) uses an energy value of 948 kcal/kg for ducks (*Anas* sp., #36), which is very low relative to the value (1240 kcal/kg edible portion, #91) found in Hill and Hawkes (1983) for unspecified low-latitude, presumably lean, birds. Obviously, this methodological variation has undesirable effects on comparisons of return rates.

Our investigation also highlights potentially confusing disparities in energy yield computations. A majority of authors in our dataset have calculated energetic yield by first multiplying live weight by the edible fraction (equations B, F–G, Table 2), then the result by energetic value. However, other authors have instead multiplied the *caloric value* by the edible fraction (equations #C–D, Table 2). The latter procedure is less intuitive and, although the two approaches are mathematically identical, they are difficult to distinguish in practice. For instance, Koster (2007, 2008) applied the edible fraction to *both* live weight and caloric value, possibly not realizing that the caloric values borrowed from other authors working in South America were already converted

Table 3 Recalculated return rates presented by continent and study

Species/prey type	Live weight (item kg)	Live weight (total kg)	Edible fraction	Edible weight (kg)	Calories (kcal/kg)	Total kcal	Pursuit (in min)	Processing (in min)	Published *e*/*h*	Rederived *e*/*h*
North America										
1. Moose (*Alces alces*)/ winter gun	600.0	710.0	0.683	485.2	1573.8	763,675.1	5499		8220	8333
2. Moose (*Alces alces*) early spring gun	600.0	1200.0	0.683	820.1	1573.8	1,290,718.4	3259		25,140	23,761
3. Moose (*Alces alces*) summer/fall gun	600.0	1200.0	0.683	820.1	1573.8	1,290,718.4	945		95,600	81,950
4. Snowshoe hare (*Lepus americanus)* fall snare I	1.1	20.9	0.880	18.3	1311.0	24,055.1	173		8260	8343
5. Snowshoe hare (*Lepus americanus*) fall snare II	1.1	110.0	0.880	96.8	1311.0	126,865.9	483		15,220	15,760
6. Muskrat (*Ondatra zibethicus*) spring trap. I	0.9	2.7	0.881	2.4	1540.3	3682.1	124		1280	1787
7. Muskrat (*Ondatra zibethicus*) spring trap. II	0.9	16.1	0.881	14.2	1540.3	21,899.6	171		6230	7700
8. Muskrat (*Ondatra zibethicus*) fall hunt. I gun	0.9	23.4	0.881	20.6	1540.3	31,782.4	244		4740	7803
9. Beaver (*Castor can.* and other sp.) winter trap.	20.5[a]	28.0[b]	0.858	24.0	3164.1	76,001.7	403		5690	11,321
12. Grouse (*Bonasa umbellus/Falcip. can.*) gun	0.7[a]	7.8	0.882	6.9	1927.2	13,259.4	240		1220	3315
13. Caribou (*Rangifer tarandus*) winter gun	102.5	3792.5	0.716	2717.3	2024.7	5,501,896.6	7260		45,370	45,470
14. Caribou (*Rangifer tarandus*) summer gun	102.5	102.5	0.716	73.4	2024.7	148,699.9	346		25,370	25,786
15. Snow goose (*Anser caerulescens*) jig/goose gun	2.7	8.1	0.875	7.1	2371.4	16,800.1	19		26,620	53,053
16. Eider (*Somateria mollissima*) summer gun	2.6	70.2	0.875	61.4	1841.7	113,109.5	99		23400[c]	68,551
17. Eider (*Somateria mollissima*) fall gun	2.6	65.0	0.875	56.9	1841.7	104,731.0	166		12920[c]	37,855
18. Goose (*Branta canadensis*) summer gun	3.5	31.5	0.873	27.5	2587.9	71,159.2	38		51020[c]	112,357
19. Goose (*Branta canadensis*) spring gun	3.5	241.5	0.873	210.8	2587.9	545,553.8	1954		7800[c]	16,752
20. Goose (*Branta canadensis*) jig/goose gun	3.5	45.5	0.873	39.7	2587.9	102,785.5	1225		2290[c]	5034
21. Merganser (*Mergus serrator*) summer gun	1.1[a]	2.2	0.880	1.9	1417.6	2681.7	12		7200[c]	13,408

Table 3 (continued)

Species/prey type	Live weight (item kg)	Live weight (total kg)	Edible fraction	Edible weight (kg)	Calories (kcal/kg)	Total kcal	Pursuit (in min)	Processing (in min)	Published *e*/*h*	Rederived *e*/*h*
22. Ptarmigan (*Lagopus lagopus*/*muta*) jig gun	0.7	3.5	0.882	3.1	1580.3	4877.9	18		8170[c]	16,260
23. Ptarmigan (*Lagopus lagopus*/*muta*) canoe gun	0.7	37.1	0.882	32.7	1580.3	51,705.4	266		5860[c]	11,663
24. Ptarmigan (*Lagopus lagopus*/*muta*) winter gun	0.7	8.4	0.882	7.4	1580.3	11,706.9	90		3920	7805
25. Ptarmigan (*Lagopus lagopus*/*muta*) spring gun	0.7	4.2	0.882	3.7	1580.3	5853.4	49		3600	7167
26. Ptarmigan (*Lagopus lagop.*/*muta*) jig/goose gun	0.7	4.9	0.882	4.3	1580.3	6829.0	74		2780	5537
27. Arctic fox (*Vulpes lagopus*) trap.	2.5	10.0	0.875	8.8	2241.1	19,612.1	420		640[c]	2802
40. Deer mouse (*Peromyscus* sp.) trap.	0.02	0.36	0.893	0.3	1883.8	605.3	60		468	605
45. Jackrabbit (*Lepus californ.*) drive	2.0	50.0	0.876	43.8	1404.7	61,559.5	480		3563	7695
46. Antelope (*Antilocapra americana*) drive	40.0	1000.0	0.729	729.0	1061.3	773,640.5	4800–24000[d]	361.3	1161	1824–8994
47–48. Rabbits (*Sylvilagus florid.*)[e] drive	1.205[a]	63.3[f]	0.879	55.6	1422.1	79,103.0	3150[f]		1086.5[f]	1507
49–50. Ducks (Anatidae) drive (molt)	0.9	2.3[f]	0.881	2.0	1908.6	3878.2	60		939[f]	3878
53–54. Jackrabbit (*Lepus calif.*) drive	2.0	70.0[f]	0.876	61.4	1404.7	86,183.3	4200[f]		567.5[f]	1231
55–56. Jackrabbit (*Lepus calif.*) drive	2.0	900.0[f]	0.876	788.8	1404.7	1,108,071.1	48,000		612[f]	1385
South America										
83. Collared peccary (*Pecari tajacu*) bow	20.0	77.0	0.858	66.1	1437.4	94,979.0	683.6	9.6	24,375	8221
84. Collared peccary (*Pecari tajacu*) shotgun	20.0	163.8	0.858	140.6	1437.4	202,046.3	548.6	9.6	65,000	21,720
85. Brocket deer (*Mazama americana*) bow	30.0	71.5	0.854	61.0	1320.1	80,571.7	635.9	36.6	10,237	7189
86. Brocket deer (*Mazama americana*) shotgun	30.0	270.0	0.854	230.5	1320.1	304,256.7	893.9	36.6	27,300	19,619
87. Paca (*Cuniculus paca*)	7.5	327.9	0.867	284.4	2009.7	571,494.5	9969.1		6964	3440
88. Coati (*Nasua nasua*)	3.5	279.0	0.873	243.5	2370.0	577,189.5	8484.7		6964	4082
89. Armadillo (*Dasypus novemcinctus*)	4.3	379.8	0.871	331.0	2173.7	719,459.0	13,603.2		5909	3173
90. Snake (sp.?)	1.4	8.3	0.878	7.3	1527.1[g]	11,134.4	168.8		5882	3958

Table 3 (continued)

Species/prey type	Live weight (item kg)	Live weight (total kg)	Edible fraction	Edible weight (kg)	Calories (kcal/kg)	Total kcal	Pursuit (in min)	Processing (in min)	Published *e*/*h*	Rederived *e*/*h*
91. Bird (sp.?)	1.4	24.6	0.878	21.6	1652.2[h]	35,704.4	949.2		3542	2257
92. White-lipped peccary (*Tayassu pecari*) bow	30.0	307.1	0.854	262.2	1433.7	375,849.7	18,992.5	36.6	3421	1185
93. White-lipped peccary (*Tayassu pecari*) shotgun	30.0	212.1	0.854	181.1	1433.7	259,582.3	12,202.4	36.6	3679	1273
94. Capuchin monkey (*Cebus apella*)	2.5	492.0	0.875	430.6	1432.7	616,851.1	57,086.7		1215	648
95. Anteater (*Myrm. tridactyla*) dog	30.0	30.0	0.854	25.6	2223.4	56,939.6	37.5[i]		190,125	91,080
96. Agouti (*Dasyprocta punctata*) river dog	4.6	4.6	0.871	4.0	1843.1	7384.6	6.4[i]		99,289.5	69,272
97. Tamandua (*Tamandua mexicana*) dog	5.5	5.5	0.870	4.8	2250.9	10,766.6	22[i]		52,284.4	29,306
98. Collared peccary (*Pecari tajacu*) dog	19.7	19.7	0.858	16.9	1331.3	22,476.8	81.6[i]		36,643.3	16,521
99. Iguana (sp.?) dog	1.4	1.4	0.878	1.2	1309.3	1610.2	4.4[i]		22,038.3	21,736
100. Armadillo (*Dasypus novemcinctus*) dog	3.8	3.8	0.872	3.3	2173.7	7224.4	56[i]		10,871.5	7734
101. Paca (*Cuniculus paca*) earth dog	3.2	3.2	0.873	2.8	2009.7	5652.5	61.6[i]		8312.6	5508
102. Paca (*Cuniculus paca*) trunk dog	2.5	2.5	0.875	2.2	2009.7	4361.8	57[i]		8020.5	4590
103. Agouti (*Dasyprocta punctata*) trunk dog	2.3	2.3	0.876	2.0	1843.1	3647.7	61.8[i]		6503.2	3542
104. Paca (*Cuniculus paca*) river dog	3.3	3.3	0.873	2.9	2009.7	5739.6	95.3[i]		5640.9	3614
105. Paca (*Cuniculus paca*) stream dog	2.9	2.9	0.874	2.5	2009.7	5094.8	120.2[i]		3907.9	2543
106. Agouti (*Dasyprocta punctata*) earth dog	1.6	1.6	0.878	1.4	1843.1	2652.7	73.4[i]		3560.1	2169
107. Baird's tapir (*Tapirus bairdii*) gun	180.0	180.0	0.708	127.4	1178.6	150,100.2	556.9[j]		45,630	16,173
108. Collared peccary (*Pecari tajacu*) gun	20.8	519.4	0.858	445.5	1331.3	593,118.8	896.1[j]		88,072	39,713
109. Agouti (*Dasyprocta punctata*) gun	3.0	5.9	0.874	5.2	1843.1	9504.7	31.2[j]		28,762	18,296
110. Spider monkey (*Ateles paniscus*) gun	10.3	82.5	0.865	71.3	1578.5	112,582.0	366.2[j]		22,819	18,444
111. Howler monkey (*Alouatta seniculus*) gun	7.3	65.4	0.867	56.7	1582.3	89,772.8	296.1[j]		22,383	18,191
112. Deer (*Mazama* spp.) gun	30.0	30.0	0.854	25.6	1169.4	29,949.3	124.7[j]		15,356	14,413

Table 3 (continued)

Species/prey type	Live weight (item kg)	Live weight (total kg)	Edible fraction	Edible weight (kg)	Calories (kcal/kg)	Total kcal	Pursuit (in min)	Processing (in min)	Published *e*/*h*	Rederived *e*/*h*
113. Game birds (sp.?) gun	1.5	36.7	0.878	32.2	1652.2[h]	53,250.7	335.1[j]		10,583	9536
114. Capuchin monkey (*Cebus* spp.) gun	3.6	28.6	0.873	25.0	1432.7	35,762.2	584.4[j]		4966	3672
115. Brazilian tapir (*Tapirus terrestris*) gun	145.0	145.0	0.711	103.1	1178.9	121,556.9	77.9[j]		282,750	93,599
116. Capybara (*Hydroch. hydrochaeris*) gun	31.5	31.5	0.853	26.9	1725.3	46,362.6	77.9[j]		61,425	35,699
117. Squirrel monkey (*Saimiri* sp.) gun	0.8	0.8	0.881	0.7	2142.5	1510.5	72.7[j]		1075	1246
Africa										
118. Elephant (*Loxodonta africana*) gun	4104.0	4104.0	0.626	2570.4	891.4	2,291,357.2	11410[k]	901.2	3615.3	11,167
119. Giraffe (*Giraffa camelopardalis*)	983.0	983.0	0.671	659.9	901.2	594,663.5	24000[k]	386.1	1563.4	1463
120. Buffalo (*Syncerus caffer*)	533.0	533.0	0.686	365.7	1122.2	410,423.2	360[k]	268.6	18,880.5	39,178
121. Eland (*Taurotragus oryx*)	337.0	337.0	0.696	234.5	1100.1	257,984.7	4732.5[k]	204.6	2700.4	3135
122. Zebra (*Equus quagga*)	239.0	239.0	0.702	167.9	949.5	159,414.6	120[k]	166.9	14,767.9	33,339
123. Wildebeest (*Connochaetes taurinus*)	227.0	227.0	0.703	159.7	1433.7	228,930.3	1088[k]	161.9	7503.1	10,990
124. Kudu (*Tragelaphus strepsiceros*)	215.0	215.0	0.704	151.4	892.5	135,165.5	100[k]	156.7	6567.1	31,588
125. Gemsbok (*Oryx gazella*)	215.0	215.0	0.704	151.4	1059.4	160,436.0	1580[k]	156.7	2687	5543
126. Hartebeest (*Alcelaphus buselaphus*)	130.0	130.0	0.713	92.7	1064.3	98,629.2	1088[k]	116.3	3880.1	4914
127. Warthog (*Phacochoerus africanus*)	70.0	70.0	0.722	50.5	1026.4	51,865.8	1200[k]	80.6	2891.4	2430
128. Impala (*Aepyceros melampus*)	51.0	51.0	0.726	37.0	1007.7	37,312.2	300[k]	66.8	5737.5	6104
129. Bush duiker (*Sylvicapra grimmia*)	18.5	18.5	0.859	15.9	882.2	14,019.0	16.25[k]	7.3	15,329.0	35,690
130. Steenbok (*Raphicerus campestris*)	11.5	11.5	0.864	9.9	1039.3	10,321.1	25[k]		10,178.3	24,771
131. Bat-eared Fox (*Otocyon megalotis*) dog	3.6	3.6	0.873	3.1	1872.0	5881.4	20[k]		8177.1	17,644
132. Springhare (*Pedetes capensis*)	3.5	3.5	0.873	3.1	1927.1	5887.7	12.5[k]		10,407.3	28,261
135. Duikers (mostly *Cephalophus*) net	6.5	2.2	0.868	1.9	901.0	1744.3	180		268	291

Table 3 (continued)

Species/prey type	Live weight (item kg)	Live weight (total kg)	Edible fraction	Edible weight (kg)	Calories (kcal/kg)	Total kcal	Pursuit (in min)	Processing (in min)	Published *e*/*h*	Rederived *e*/*h*
136. Duikers (mostly *Cephalophus*) net low	6.5^{l}	63.0	0.868	54.7	901.0	49,294.7	5712		263	259
138. Duikers (mostly *Cephalophus*) net	6.5	0.9	0.868	0.8	901.0	717.3	180		110	120
139. Duikers (mostly *Cephalophus*) net	6.5^{l}	0.2	0.868	0.2	901.0	140.8	60		216	141
Southeast Asia										
149. Monitors (*Varanus* sp.)	3.2	35.4	0.873	30.9	1921.5^{m}	59,416.3	223^{n}		8500	16,022
150. Python (*Malayopython reticulatus*)	10.8	21.6	0.864	18.7	1509.8	28,180.8	119^{n}		8000	14,185
151. Burmese brown tortoise (*Manouria emys*)	8.9	337.3	0.866	292.0	1971.6	575,784.7	1605^{n}		6670	21,521
152. Water tortoise (*Cyclemys dentata*)	1.7	396.4	0.877	347.8	1984.5	690,206.4	2837^{n}		4780	14,597
153. Spiny hill tortoise (*Heosemys spinosa*)	1.3	22.4	0.879	19.7	1985.3	39,080.5	159^{n}		4780	14,753
154. Malayan pangolin (*Manis javanica*)	6.5	19.4	0.868	16.8	1922.4	32,387.2	397^{n}		2920	4891
155. Malayan mud turtle (*Amyda cartilaginea*)	9.7	310.2	0.865	268.3	1970.8	528,845.1	6167^{n}		2000	5145
156. Giant frog (*Limnonectes blythii*)	0.54	42.4	0.883	37.4	983.5	36,822.8	914^{n}		1960	2418
157. Dusky leaf monkey (*Trachypithecus obscurus*)	6.4	869.3	0.869	755.0	1583.7	1,195,729.4	32468^{n}		1620	2210
158. Banded leaf monkey (*Presbytis melalophos*)	5.6	168.3	0.870	146.3	1585.1	231,966.4	6553^{n}		1550	2124
159. White-handed gibbon (*Hylobates lar*)	5.4	43.4	0.870	37.7	1585.5	59,849.1	1759^{n}		1490	2042
160. Musangs and civets (*Viverra* and *Arctictis bint.*)	8.9	17.8	0.866	15.4	2084.5	32,124.3	835^{n}		1290	2310
161. Bamboo rat (*Rhizomys sumatrensis*)	1.1	9.0	0.880	7.9	1742.4	13,794.0	469^{n}		1080	1765
162. Giant squirrels (*Ratufa bicolor* and *R. aff.*)	1.5	4.5	0.878	4.0	1402.8	5542.9	257^{n}		1060	1292
163. Macaques (*Macaca fascicularis*/*M. nemestr.*)	7.7	38.5	0.867	33.4	1581.8	52,799.8	2998^{n}		780	1057
164. Middle-sized squirrels (*Callosciurus* spp.)	0.5	0.5	0.883	0.4	1409.0	622.3	63^{n}		480	591
165. Small-sized squirrels (*Sundasciurus* spp.)	0.1	0.1	0.889	0.1	1415.5	125.8	18^{n}		330	409

Table 3 (continued)

Species/prey type	Live weight (item kg)	Live weight (total kg)	Edible fraction	Edible weight (kg)	Calories (kcal/kg)	Total kcal	Pursuit (in min)	Processing (in min)	Published *e*/*h*	Rederived *e*/*h*
166. Small-sized birds (passerine birds <100 g)	0.1	0.1	0.889	0.1	1338.4	119.0	16[n]		230	449
Australia										
167. Sand monitor (*Varanus gouldii*)	0.5	0.5	0.883	0.4	1805.1	797.3	8		4200	6378
169. Finch and pigeon (Fringill. and Columb.) net	0.5	50.0	0.883	44.2	2070.4	91,442.5	360		6375	15,240
170. Pigeon (Columbidae) net	0.3	365.4	0.885	323.5	2070.4	669,772.1	1440		6339	23,920
171. Wallaby (Macropodidae) net	20.0	400.0	0.858	343.3	1275.3	437,759.8	12,000	191.6	1873	2154
172–173. Ducks (sp.?) net low	0.9	22.9[f]	0.881	20.1	1908.6	38,418.5	1320[f]		679.5[f]	1746
174. Sand monitor (*Varanus gouldii*)	0.461	109.7	0.884	96.9	1805.1	174,932.7	3873		4931	2710
175. Bustard (*Ardeotis australis*) gun	5.491	267.4	0.870	232.6	1517.8	352,968.6	2836		10,261	7468
176. Hill kangaroo (*Macropus robustus*) gun	21.970	269.3	0.857	230.8	1153.9	266,298.0	3972	170.2	3844	3857
177. Perentie (*Varanus giganteus*)	2.304	16.5	0.876	14.4	1926.6	27,834.8	626		3455	2668
178. Feral cat (*Felis silvestris*)	2.536	17.9	0.875	15.7	2095.2	32,900.1	856		5179	2306
179. Skink (*Tiliqua scincoides*)	0.301	8.8	0.885	7.8	1098.4	8572.1	71		20,403	7244
180. Python (*Aspidites ramsayi*)	0.703	7.9	0.882	6.9	1529.1	10,613.6	287		1491	2219
181. Arabian camel (*Camelus dromedarius*) gun	332.47	5653.5	0.696	3935.7	1872.6	7,370,029.7	2526	3450.8	122,944	73,987

Row numbers as in Table 1. Our recalculated values omit those cases: (a) in which pursuit time was derived from recreational hunters (#28–36, 57–69); (b) that are incompletely documented or hypothetical (#10–11, 37–39, 41–44, 51–52, 133–134, 140–148, 168); (c) in which return rates have been replaced by newer estimates (#137); and (d) those that include search time (#70–82). Because new measures of pursuit have been published for Aché prey types (Janssen & Hill, 2014) building on 30 years of fieldwork subsequent to values published in the 1980s by Hill and Hawkes (1983) (#83–94 in Table 1), we recalculate return rates for the Aché prey types using both the 1983 and new pursuit estimates. Values for columns 2–3 and 8 are taken from Table 1, unless specified otherwise. The edible fraction was calculated using the equations in Fig. 1, whereas the calorie values are taken from Supplemental Online Material 2. When relevant, processing time was calculated using the equation in Fig. 2. Return rates for #47–48, 49–50, 53–54, 55–56, and 172–173 are averages derived from the corresponding rows in Table 1

[a] Live weight taken from Supplemental Online Material 2

[b] Total weight include other species

[c] In-camp processing costs excluded

[d] Construction time divided by 10 to account for reuse of the corral. The low value assumes that only 0.20 of people present are hunters (see text) whereas the high value includes them all. Calculation method for the low value: 25 people × 0.20 (proportion of "hunters") × 15 h of pursuit +1 h of construction (10 h divided by 10 to account for reuse) × 60 (to obtain minutes)

[e] Note that Ugan (2005) pointed out that it was unclear whether the drive focused on hares or rabbits. Discussions with several biologists working in the area strongly suggest that the species was the cottontail rabbit

[f] Average for the corresponding rows in Table 1 (note the change in live weight for #47–48)

[g] Average for snakes (see Table 4)

[h] Average for tropical birds (see Table 4)

[i] Converted into hunter-hrs using data from Koster (2007:74–75, 159 hunters in 88 trips for an average of 1.81 hunters/trip). Dog catching up time (Koster, 2008:940, Table 2) is included in pursuit time. Example of calculation method for the nine-banded armadillo: .444 h of pursuit + .073 h of dog catching up × 60 (to obtain minutes) × 1.81 (hunter-hrs)

[j] Converted into hunter-hours using data from Alvard (1993a:135–137, 100 hunters in 77 trips for an average of 1.30 hunters/trip)

[k] Pursuit time multiplied by success rate (see text)

[l] Assuming that live weight was as in #135

[m] Value for *Varanus olivaceus* (see Supplemental Online Material 2)

[n] Converted into hunter-hours using data from Kuchikura (1987:37, 249 hunters in 188 hunts for an average of 1.32 hunters/trip)

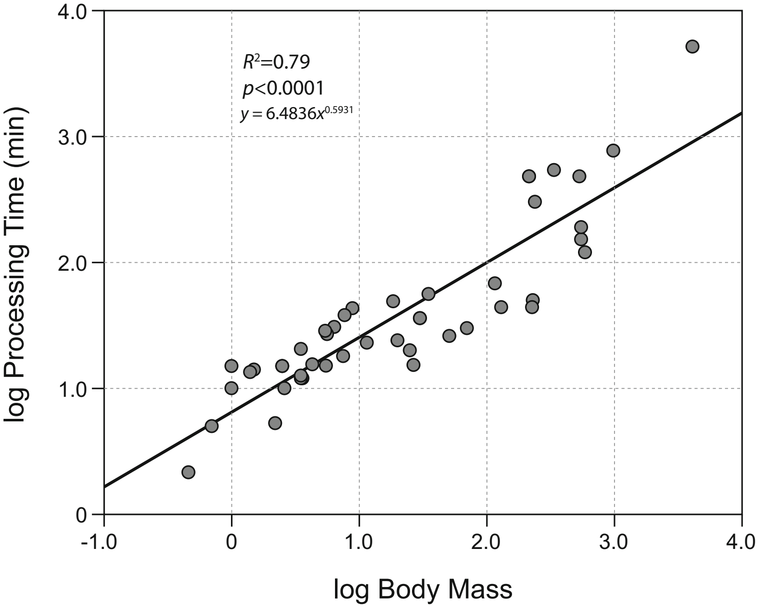

Fig. 2 Relationship between processing costs (min) and body mass (in kg) after log transformation. For simplicity, the equation is for data that have not been log-transformed; x is edible weight (in kg) and y is the predicted processing costs (in min). To determine the trendline, we use a simple linear model with a forced intercept of 0 to prevent negative values at small body masses. Data are taken from SOM 1.2

into "edible" energy. We initially made the same error when replicating the South American data. The oversight does not compromise the analysis of prey ranking in Koster's study—the error is consistent across all of the calculated values—but it does mean that in comparison to the other values in the dataset used here, Koster's published energetic yield estimates are depressed by 35% if not corrected.

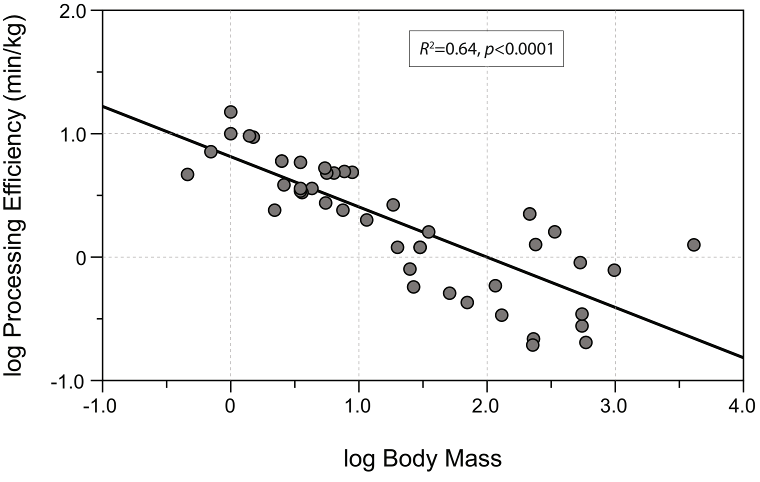

Fig. 3 Relationship between the processing efficiency (min/kg) and body mass (in kg) after log transformation. Data are taken from SOM 1.2

Results: Recalculated R_{prey} Estimates

Predicting Edibility Using Body Mass

SOM 1.1 lists 47 species representing mostly glires—rodents and lagomorphs—primates, carnivores and ungulates for which detailed gross tissue composition data were found. In agreement with West and Brown's (2005) observation that scaling of physiological mammalian properties with body mass frequently coincides with

Table 4 Energy classes. Data from Supplemental Online Material 2

Metabolizable class	*n*	Kcal/kg	Metabolizable class	*n*	Kcal/kg
Ungulates			**Birds**		
Bovids: mid/high latitudes	4	1841.6	Waterfowl	16	1955.8
Bovids: low latitudes	23	1015.0	Galliformes: mid/high latitudes	8	2238.3
Antilocapridae	1	1061.3	Galliformes: low latitudes	3	2227.8
Cervids: mid/high latitudes	8	1559.1	Charadriiformes	11	1833.6
Cervids: low latitudes	1	1169.4	Passeriformes	3	1341.6
Giraffidae	1	901.2	Columbiformes	5	2073.7
Camels	1	1872.6	Bustards	1	1517.8
Suinae: mid/high latitudes	1	1861.4	Raptors	4	1376.3
Suinae: low latitudes	5	1114.6	Gruiformes	2	1467.6
Equids: mid/high latitudes	1	1624.1	Ratites (ostriches and emu)	2	1723.4
Equids: low latitudes	1	949.5	Cormorants	1	1715.0
Tapirs	2	1178.8	Tropical birds	3	1652.2
Hippopotami	1	930.2	**Carnivores**		
Elephants	1	891.4	Carnivores (non-hibernating)	20	1874.6
Glires			Carnivores (hibernating)	5	2537.2
Hystricomorphs	11	1967.3	**Marsupials**		
Muroids and like	21	1732.9	Kangaroos	4	1243.7
Marmots, ground squirrels and dormice	13	2569.7	Opossums	2	1663.0
Beavers and gophers	4	2022.4	**Other taxa**		
Hedgehogs, shrews and moles	6	1859.9	Anteaters	3	2246.3
Tree squirrels	7	1412.6	Armadillos	4	2238.3
Lagomorphs	11	1384.3	Hyraxes	1	1640.5
Scaly-tailed squirrels and springhares	1	1927.1	Primates	14	1575.9
Reptiles and amphibians			Pangolins	1	1922.4
Lizards	9	1370.3	Bats	13	2130.0
Skinks	3	1095.9	Monotremes	1	2212.5
Snakes	9	1527.1			
Crocodilians	4	1288.4			
Turtles	15	1981.1			
Varanids	9	1800.2			
Frogs	7	1001.4			

increments of one fourth, we obtain linear relationships with nearly identical slopes for small and large taxa when scaling edible fraction to body mass$^{0.25}$ (Fig. 1). Although the coefficient of determination is low for small species ($R^2 = 0.07$, $p = 0.1052$)—those that are likely to be transported with minimal or no processing—the group as a whole shows little variation in the edible fraction (mean: 0.87±.04), presumably due to a narrow range of body masses (out of 40, 36 have a mass < 20 kg). In contrast, the coefficient of determination is high for large taxa ($R^2 = 0.79$, $p = 0.0076$), likely due to a wider distribution of body masses. The overall results suggest that the edible fraction varies predictably as a function of body mass, allowing that some of the variation probably reflects differences in carcass conditions and dissection protocols. We use the regression formulas represented in Fig. 1 to recalculate edible fractions (Table 3, column 4) of the taxa listed in Table 1. The recalculated values reduce idiosyncratic variation in return rates through use of a consistent method that better conforms to ethnographic observations (see SOM 1.9) and current knowledge on allometric scaling.

Predicting Processing Costs Using Body Mass

Lupo and Schmitt's (2016:190) evaluation of the relationship between processing costs and body mass in an African sample shows a strong linear trend, with body mass accounting for much of the variance in processing costs ($R^2 = 0.55$, $p < 0.05$). We find a yet stronger relationship using an expanded global sample (SOM 1.2), in which log-transformed body mass accounts for most ($R^2 = 0.79$, $p < 0.0001$) of the variance in (log) processing costs among taxa (Fig. 2). On the strength of this regression, we have recalculated processing costs for the prey types listed in Table 1 (see Table 3, column "processing (in min)"). For several handling estimates, the approach could not be applied because field butchering costs were not listed separately from pursuit costs (*e.g.*, Alvard, 1993b; Koster, 2007; Smith, 1991; Winterhalder, 1977); consequently, no processing time was added to handling time in these cases to avoid cost duplication.

The recalculated processing data also shed light on processing costs and efficiency. With processing costs converted into minutes/kilogram live weight (see table in SOM 1.2) and log transformed, there is a linear trend for smaller species to take proportionately more time to process than larger ones (Fig. 3) ($R^2 = 0.64$, $p < 0.0001$). Moreover, the ratio of the five smallest to five largest species is 0.6:9.3, suggesting that small species can take up to 15 times longer to process per kilogram. This economy of scale implies that pursuit is likely to account for a larger fraction of handling time in larger prey. As noted above, the decision to incorporate processing time into pursuit and handling for purposes of prey ranking depends on case-specific assessments of the foraging opportunity costs it entails.

New Standardized Estimates of R_{prey} Energetic Yield

In SOM 2, we address comparability issues with previous assessments of energetic yield by systematically considering the energy content of body fat and muscle tissue and by using more accurate estimates of the edible fraction. The results are more in line with the equations Hill et al. (1984) use to derive estimates for South American species: the fattest animals have ~3000 kcal/kg live weight (mostly hibernating rodents, carnivores, and bats) or higher (woodchuck *Marmota monax*, 3320 kcal/kg; edible dormouse *Glis glis*, 4221 kcal/kg), and the leanest ones (*e.g.*, frogs, the giraffe, several

Table 5 Percent change between the published (Table 1) and recalculated return rates (Table 3) by group and/or region

Prey type	Percent change	Prey type	Percent change	Prey type	Percent change
North America (M. Dam Cree)		90. Snake (sp.?)	−32.7	130. Steenbok	143.4
1. Moose/caribou (winter)	1.4	91. Bird (sp.?)	−36.3	131. Bat-eared fox	115.8
2. Moose (spring)	−5.5	92. W.-l. peccary bow	−67.9	132. Springhare	171.6
3. Moose summer/fall	−14.3	93. W.-l. pec. shotgun	−68.0	135. Duikers	8.6[c]
4. Snowshoe hare snare I	1.0	94. Capuchin monkey	−46.6	136. Duikers	−1.4[c]
5. Snowshoe hare snare II	3.5	**South America (Miskito)**		138. Duikers	8.7
6. Muskrat spring trap. I	39.6	95. Giant anteater	−52.1	139. Duikers	−34.8
7. Muskrat spring trap. II	23.6	96. Agouti (river)	−30.2	**Southeast Asia (Semaq Beri)**	
8. Muskrat fall hunt. I	64.6	97. Tamandua	−43.9	149. Monitors	88.5
9. Beaver winter trap.	99.0	98. Collared peccary	−54.9	150. Reticulated python	77.3
12. Ruffed/spruce grouse	171.7	99. Iguana	−1.4	151. Burmese br. tortoise	222.7
North America (Inujjuamiut)		100. 9-B. armadillo	−28.9	152. Water tortoise	205.4
13. Caribou winter	0.2	102. Paca (trunk)	−33.7	153. Spiny hill tortoise	208.6
14. Caribou summer	1.6	103. Agouti (trunk)	−42.8	154. Malayan pangolin	67.5
15. Snow goose jig/goose	99.3	104. Paca (river)	−45.5	155. Malayan mud turtle	157.3
16. C. eider summer	193.0	105. Paca (stream)	−35.9	156. Giant frog	23.3
17. Common eider fall	193.0	101. Paca (earth)	−34.9	157. Dusky leaf monkey	36.4
18. Canada goose summer	120.2	106. Agouti (earth)	−39.1	158. Band. leaf monkey	37.0
19. Canada goose spring	114.8	107. Baird's tapir	−64.6	159. White-h. gibbon	37.0
20. Can. goose jig/goose	119.8	**South America (Piro)**		160. Musangs or civets	79.0
21. Merganser summer	86.2	108. Collared peccary	−54.9	161. Bamboo rat	63.4
22. Ptarmigan jig	99.0	109. Agouti	−36.4	162. Giant squirrels	21.9
23. Ptarmigan canoe	99.0	110. Spider monkey	−19.2	163. Macaque	35.5
24. Ptarmigan winter	99.1	111. Howler monkey	−18.7	164. Middle-s. squirrels	23.1
25. Ptarmigan spring	99.1	112. Deer	−6.1	165. Small-s. squirrels	24.1
26. Ptarmigan jig/goose	99.2	113. Game birds	−9.9	166. Small-sized birds	95.3
27. Arctic fox[a]	337.8	114. Capu. monkey	−26.1	**Australia (various groups)**	
South. N. Amer. (various groups)		115. Brazilian tapir	−66.9	167. Sand monitor	51.9
40. Deer mouse	29.3	116. Capybara	−41.9	169. Finch/pigeon (net)	139.1
45. Black-t. jackrabbit	116.0	117. Squirrel monkey	15.9	170. Pigeon (net)	295.0[c]
46. Antelope (drive)	376.6[b]	**Africa (various groups)**		171. Wallaby	15.0
47–48. Rabbits	38.1	118. Elephant	208.9	172–173. Ducks	157.0
49–50. Ducks	313.0	119. Giraffe	−6.4	**Australia (Martu)**	
53–54. Black-t. jackrabbit	116.9	120. Buffalo	107.5	174. Sand monitor	−45.0
55–56. Black-t. jackrabbit	126.3	121. Eland	16.1	175. Bustard	−27.2
South America (Aché)		122. Zebra	125.8	176. Hill kangaroo	0.3
83. Collared peccary bow	−68.8	123. Wildebeest	46.5	177. Perentie	−22.8
84. Collared pec. shotgun	−69.1	124. Kudu	381.0	178. Feral cat	−55.5
85. Brocket deer bow	−37.8	125. Gemsbok	106.3	179. Skink	−64.5
86. Brocket deer shotgun	−36.3	126. Hartebeest	26.6	180. Python	48.8

Table 5 (continued)

Prey type	Percent change	Prey type	Percent change	Prey type	Percent change
87. Paca	−50.6	127. Warthog	−16.0	181. Arabian camel	−39.8
88. Coati	−41.4	128. Impala	6.4		
89. Armadillo	−46.3	129. Bush duiker	132.8		

[a] Smith (1991) considered that only half of the carcass was used because this species is only exploited for fur. For this reason, the percent change shown here is inflated

[b] The percent change is 79.4 if construction costs are not amortized

[c] Average for low and high value

African bovids) are just under 1000 kcal/kg. These new values are used below to examine trends in prey profitability. A list of proxy energy values was also produced for species that are *not* present in our dataset (Table 4; methods in SOM 1.4, 1.5, and 2), made up of 52 classes of taxa that should be applicable in a wide range of foraging contexts. Although they trade off precision for substantial gains in terms of robustness, these classes should be less affected by sampling error. However, sample sizes remain small for some classes (*e.g.*, Antilocapridae, elephants, hyraxes).

Comparison of Published and Recalculated R_{prey} Return Rates

Table 5 shows the percent change observed between the previously published and our recalculated R_{prey} estimates. The difference is greater than ±50% for nearly half of the prey types (56/117 or 47.9%). This means that the corrections potentially can reorder prey rankings and alter inter-study foraging efficiency comparisons. A majority of the R_{prey} estimates increase (71/117 or 60.7%), while others (46/117 or 39.3%) decrease. The changes are not random with respect to study and region. Accounting for amortization in construction costs of drive fencing and excluding non-habitual large game hunters in the calculation of handling time has a dramatic impact on the efficiency of antelope drives (#46: +377%). In North America, the adoption of more realistic edible fractions and caloric values increases the profitability of several prey types, particularly those of small size (Fig. 4a). In the South American sample, the substitution of pursuit-hrs by hunter-hrs decreases the returns in most instances (Fig. 4b). In the African sample, charging failure to pursuit time instead of total handling time produces a dramatic increase in profitability for several large taxa (*e.g.*, buffalo: +108%; zebra: +126%; elephant: +209%; kudu: +381%, Fig. 4c). This last observation has significant implications for our understanding of megafaunal procurement (Lupo & Schmitt, 2016). In Australia, recalculating the Martu estimates with a summed average rather than averaging rates tends to lower values (Fig. 4d). Finally, the use of more appropriate caloric values in Malaysia increases profitability for many of the Semaq Beri prey types (Table 5). Note that in an attempt to increase standardization in future analyses, we created a spreadsheet template (SOM 3) that can be used to automatically calculate new return rates.

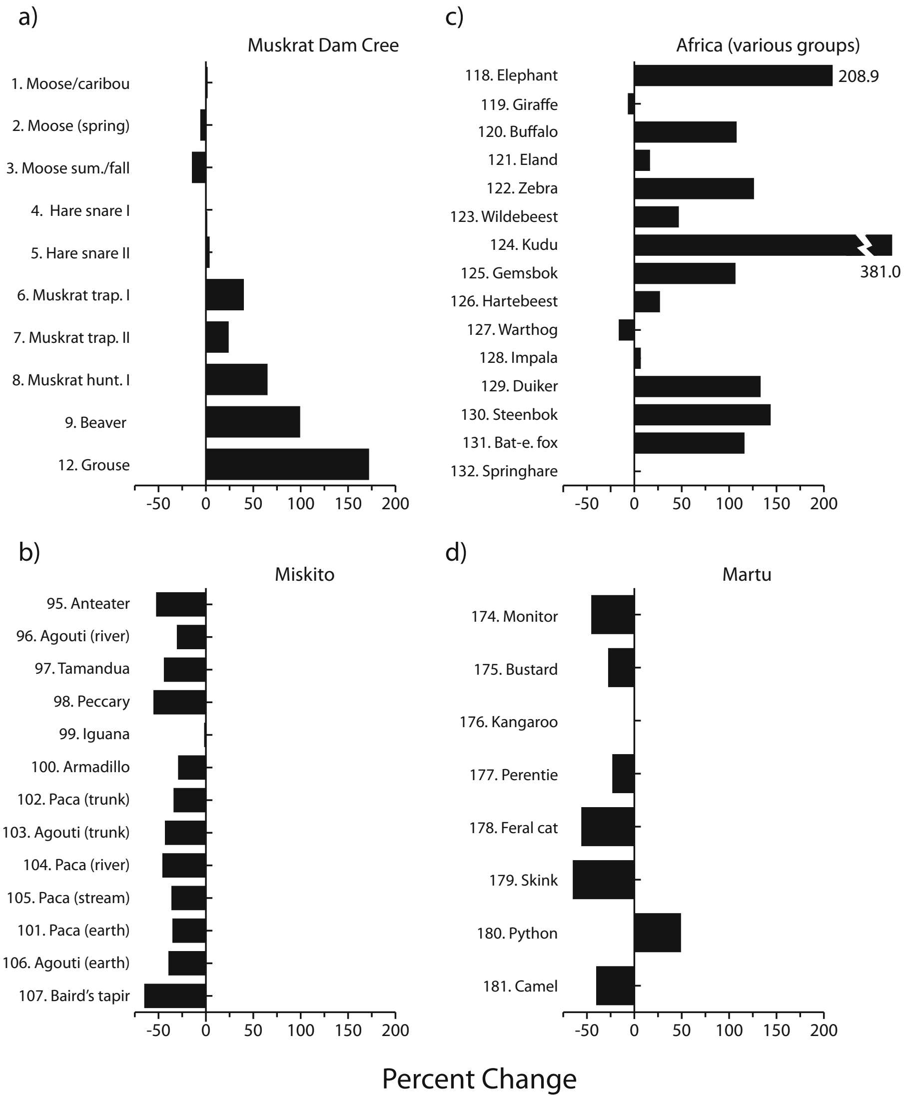

Fig. 4 Percent change between the original (published) and recalculated return rates for four groups or geographical areas: **a** Muskrat Dam Cree, Canada (Winterhalder, 1983); **b** Miskito, Nicaragua (Koster, 2008); **c** Africa (Lupo & Schmitt, 2016); and **d** Martu, Australia (this study). Data from Table 5

Results: Determinants of Prey Type Profitability

Phylogeny and Method of Procurement

We find substantial overlap in return rates among most taxonomic groups (Fig. 5), one factor that has been argued to predict variation in profitability estimates (*e.g.*, Bird et al., 2009; Madsen & Schmitt, 1998; Morin, 2012; Stiner et al., 1999; Ugan, 2005).

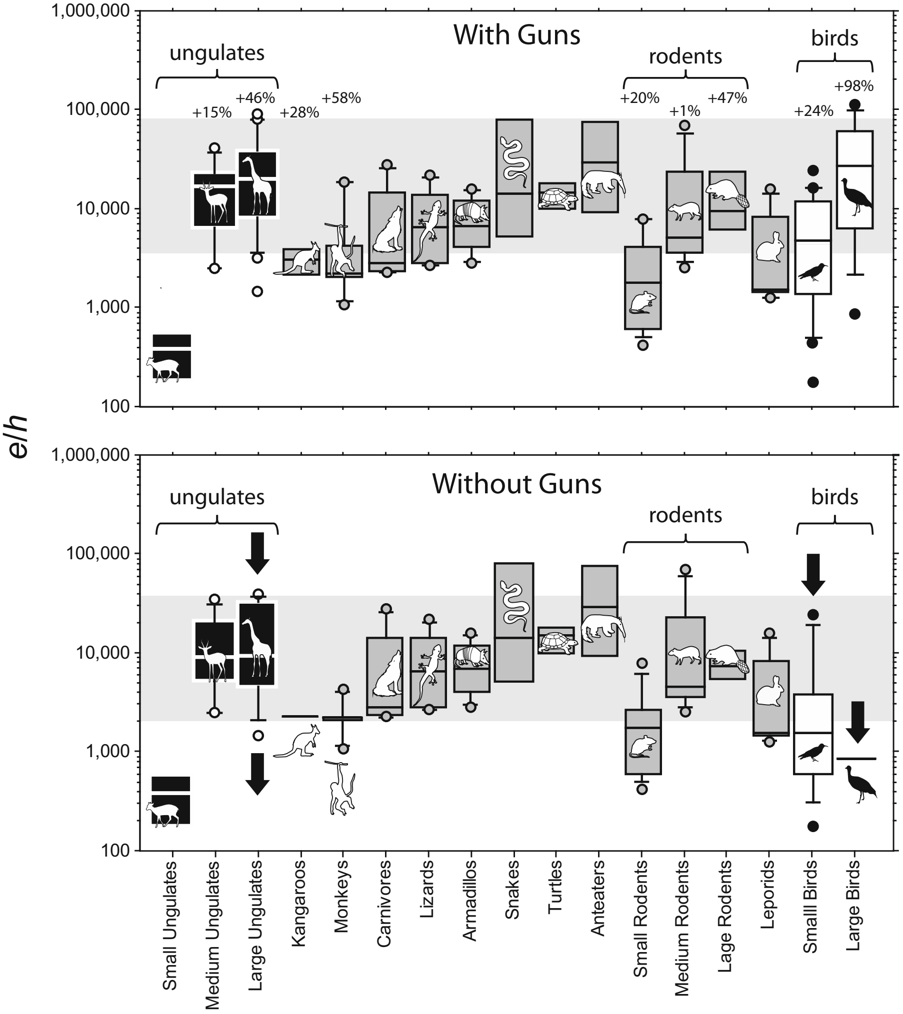

Fig. 5 The recalculated return rates presented by taxonomic group for all procurement methods (upper, "With Guns") and for all methods excluding firearms (lower, "Without Guns"). The shaded area corresponds to the range of values for large ungulates. Percent change in the average return rate for cases with firearms is shown above the taxonomic group (an absence of value means that there are no data for firearms). Data from Tables 3 and 6. The coding for the procurement methods is provided in SOM 4

Return rates for small and large birds are particularly variable, despite a small range of body sizes (0.1–6.0 kg). For prey types obtained with firearms, large birds appear to provide higher returns than smaller ones. Large ungulates (taxa>100 kg, giraffe symbol) have relatively high return rates, but this too is influenced by the use of firearms. Other high-return taxa may be those that have evolved relatively slow escape strategies, including snakes, turtles, anteaters, large birds (>2 kg) and, to a lesser extent, large (>5 kg) rodents (see Morin, 2012).

The use of firearms compared to muscle-powered weapons limits the comparability of returns. Firearms tend, at the global scale, to increase return rates (see "percent change" in Fig. 5), a result consistent with ethnographic observations comparing

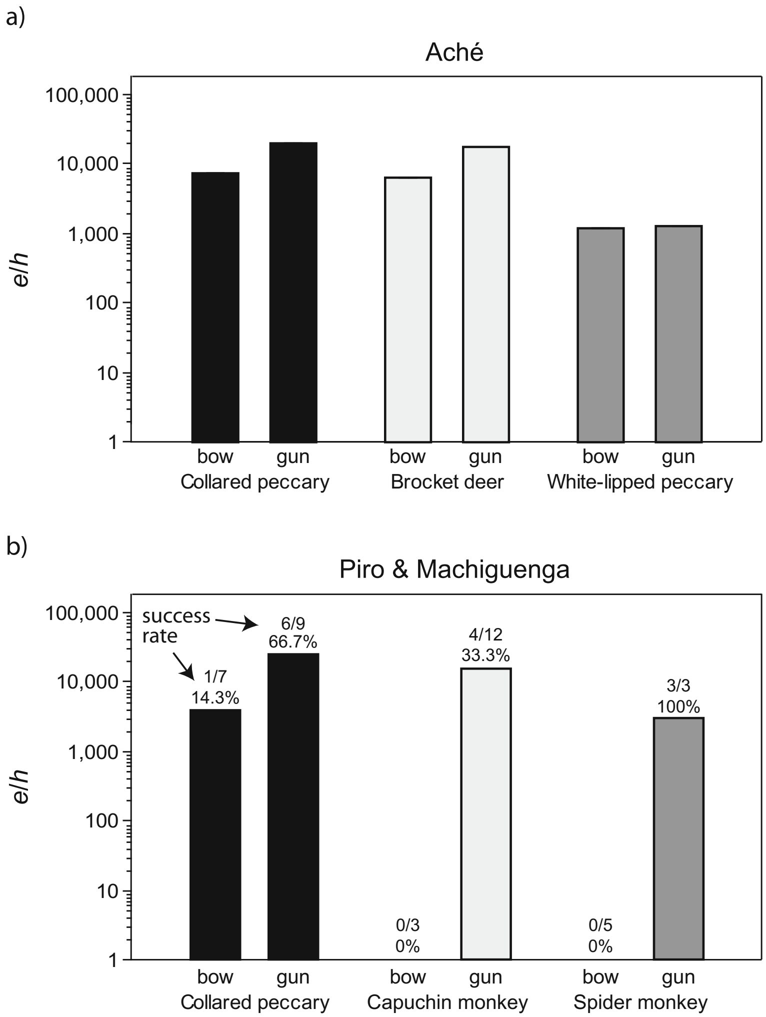

Fig. 6 Comparison of return rates between firearms and the bow and arrow for the Aché of Paraguay **a**) and the Piro and Machiguenga of Peru **b**). In this and the following figures, the data are from Tables 3 and 6, unless specified otherwise. The success rates were calculated using data in Alvard and Kaplan (1991:89–92)

firearms to traditional weapons such as the spear, bow and arrow, and the blowgun (Alvard, 1995; Alvard & Kaplan, 1991; Hames, 1979; Hill & Hawkes, 1983; Levi et al., 2009; Shaffer et al., 2017; Yost & Kelly, 1983). The recalculated values for various Aché prey (#83–94) corroborate Hill and Hawkes' (1983) argument that the prey types represented are more efficiently harvested using shotguns than the bow (Fig. 6a). Return rates calculated for prey types acquired by the Piro and Machiguenga (Table 6, #247–252)—two neighboring groups from South America occupying similar habitats but hunting with different weapons—also confirm the pattern (Fig. 6b), the use of firearms increasing success rates as well for the three prey types (collared peccary:

Table 6 New return rates for Aché (#221–246) and Piro prey types (#247–252)

Species/prey type	Live weight (item kg)	Live weight (total kg)	Edible fraction	Edible weight (kg)	Calories/kg	Total calories	Pursuit (in min)	Processing (in min)	*e*/*h*
221. Guan (*Penelope superciliaris*)	0.8	0.8	0.881	0.7	2229.4	1571.8	80		1179
222. Capuchin monkey (*Cebus apella*)	2.3	2.3	0.876	2.0	1432.7	2885.3	79		2203
223. 9-B Armadillo nest (*Dasypus nov.*)	3.8	3.8	0.872	3.3	2173.7	7205.5	36		11,932
224. 9-B Armadillo burrow (*Dasypus nov.*)	3.8	3.8	0.872	3.3	2173.7	7205.5	76		5707
225. 9-B Armadillo tracks (*Dasypus nov.*)	3.8	3.8	0.872	3.3	2173.7	7205.5	156		2767
226. Brocket deer (*Mazama americana*)	25.8	25.8	0.855	22.1	1169.4	25,808.1	56	24.5	19,339
227. Coatimundi (*Nasua nasua*) mass collected	3.5	3.5	0.873	3.1	2370.0	7240.7	16		27,935
228. Collared peccary (*Pecari tajacu*)	16.3	16.3	0.860	14.0	1331.3	18,667.5	154	1.7	7201
229. Tegu lizard (*Tupinambis teguixin*)	2.3	2.3	0.876	2.0	1268.8	2555.3	49		3117
230. Paca (*Cuniculus paca*)	6.7	6.7	0.868	5.8	2009.7	11,689.6	94		7435
231. Tapir (*Tapirus terrestris*)	177.0	177.0	0.708	125.3	1178.9	147,691.1	800	139.7	9430
232. White-lipped peccary (*Tayassu pecari*)	24.9	24.9	0.856	21.3	1327.6	28,289.2	625	21.8	2624
233. King vulture (*Sarcoramphus papa*)	2.4	2.4	0.875	2.1	1369.5	2877.1	200		863
234. Piping Guan (*Pipile yakutinga*)	1.78	1.78	0.877	1.6	2224.4	3472.9	80		2605
235. Howler monkey (*Alouatta caraya*)	4.0	4.0	0.872	3.5	1588.3	5540.1	79		4231
236. Naked-tail armadillo (*Cabassous tat.*)	4.87	4.87	0.871	4.2	2252.5	9549.9	36		15,815
237. Agouti (*Dasyprocta azarae*)	1.8	1.8	0.877	1.6	1848.8	2918.7	43		4086
238. Tinamou (*Crypturellus obsoletus*)	1.1	1.1	0.880	1.0	1849.2	1789.5	80		1342
239. Tayra (*Eira barbara*)	3.2	3.2	0.874	2.8	1606.5	4490.5	120		2245
240. Rabbit (*Sylvilagus brasiliensis*)	1.0	1.0	0.880	0.9	1423.3	1252.8	50		1503
241. *Boa constrictor* (*Boa constrictor*)	8.0	8.0	0.867	6.9	1512.7	10,488.2	6		100,686
242. Crab eating fox (*Cerdocyon thous*)	4.8	4.8	0.871	4.2	2038.5	8519.6	100		5112
243. Collared anteater (*Tamandua tetrad.*)	1.6	1.6	0.878	1.4	2264.8	3180.5	79		2429

Table 6 (continued)

Species/prey type	Live weight (item kg)	Live weight (total kg)	Edible fraction	Edible weight (kg)	Calories/kg	Total calories	Pursuit (in min)	Processing (in min)	*e*/*h*
244. 7-B armadillo (*Dasypus septemcinctus*)	1.28	1.28	0.879	1.1	2185.0	2458.2	36		4071
245. Black vulture (*Coragyps atratus*)	1.6	1.6	0.878	1.4	1372.9	1928.0	200		578
246. Red-br. toucan (*Ramphastos dicolorus*)	0.4	0.4	0.884	0.4	1382.1	488.9	167		176
247. Collared peccary (*Pecari tajacu*) bow	20.8	20.8	0.858	17.8	1331.3	23,724.8	348	11.8	3957
248. Collared peccary (*Pecari tajacu*) gun	20.8	124.7	0.858	106.9	1331.3	142,348.5	324.6	11.8	25,392
249. Spider monkey (*Ateles paniscus*) bow	10.3	0.0	0.865	0.0	1578.5	0.0	502.2		0
250. Spider monkey (*Ateles paniscus*) gun	10.3	30.9	0.865	26.7	1578.5	42,218.3	166.8		15,186
251. Capuchin monkey (*Cebus* spp.) bow	3.6	0.0	0.873	0.0	1432.7[a]	0.0	25.2		0
252. Capuchin monkey (*Cebus* spp.) gun	3.6	14.3	0.873	12.5	1432.7[a]	17,881.1	351		3057

Values for columns 2–3 are taken from Janssen and Hill (2014:827, Table 1) and Table 1. For the Aché, values in column 8 correspond to pursuit time multiplied by the reciprocal of the success rate (probability), as provided by Hill and Janssen (*e.g.*, guan, 5 min × (1/0.0625) = 80 min) in the same table. Note that Janssen and Hill's pursuit time are rounded to the nearest 5 min. For the Piro, the values in Column 8 are taken from Alvard and Kaplan (1991:89–92) and correspond to the sum of hunter-hours (*e.g.*, Capuchin monkey bow, 0.24 + 0.10 + 0.08 = 0.42 h or 25.2 min). The edible fraction was calculated using the equations in Fig. 1, whereas the calorie values are taken from Supplemental Online Material 2. When relevant, processing time was calculated using the equation in Fig. 2. Note that all of the prey types listed in this table are treated here as being procured with traditional means of procurement. However, the description provided by Hill and Hawkes (1983:150) suggest that the coati (#227) is probably best described as a mass collected prey

[a] Value for *Cebus apella*

Table 7 Relationship between $\log_{10}$ body mass and $\log_{10}$ *e*/*h* presented by taxonomic group and procurement method, as calculated using the recalculated data. Significant results are highlighted in bold

	r	*p* value	R^2
All prey types (*n*=131)	**0.39**	**<0.0001**	**0.15**
Firearms excluded (*n*=97)	**0.35**	**0.0004**	**0.12**
Firearms only (*n*=34)	**0.40**	**0.0194**	**0.16**
Spear/bow/blowpipe/trapping (*n*=69)	**0.48**	**<0.0001**	**0.23**
Dog (*n*=13)	**0.62**	**0.0243**	**0.38**
Mass collected (*n*=15)	−0.37	0.1758	0.14
Escape strategy (birds and monkeys excluded)			
Run (cursorial, *n*=68)	**0.32**	**0.0071**	**0.10**
Run (cursorial, *n*=55, firearms excluded)	0.17	0.2155	0.03
Hide (*n*=27)	**0.68**	**<0.0001**	**0.47**
Hide (*n*=25, firearms excluded)	**0.71**	**<0.0001**	**0.50**
Mode of locomotion			
Aquatic (*n*=10)	0.36	0.3006	0.13
Arboreal (*n*=17)	**0.55**	**0.0230**	**0.30**
Cursorial (*n*=63)	**0.35**	**0.0052**	**0.12**
Fossorial (*n*=17)	**0.69**	**0.0020**	**0.48**
Volant (*n*=24)	0.36	0.0866	0.13
Ungulates (*n*=33)	**0.44**	**0.0096**	**0.20**
Firearms excluded (*n*=22)	**0.44**	**0.0416**	**0.19**
Firearms only (*n*=11)	−0.22	0.5126	0.05
Spear/bow/blowpipe/trapping (*n*=16)	−0.18	0.5097	0.03
Birds (*n*=26)	**0.41**	**0.0379**	**0.17**
Firearms excluded (*n*=11)	−0.04	0.9094	0.00
Firearms only (*n*=15)	0.47	0.0768	0.22
Spear/bow/blowpipe/trapping (*n*=7)	0.56	0.1887	0.32
Glires (*n*=28)	**0.67**	**<0.0001**	**0.45**
Firearms excluded (*n*=25)	**0.63**	**0.0007**	**0.40**
Spear/bow/blowpipe/trapping (*n*=14)	**0.71**	**0.0046**	**0.50**
Dog (*n*=7)	**0.77**	**0.0411**	**0.60**
Reptiles (*n*=14)	0.48	0.0835	0.23
Firearms excluded (*n*=14)	0.48	0.0835	0.23
Spear/bow/blowpipe/trapping (*n*=13)	0.52	0.0715	0.27
Monkeys (*n*=10)	0.48	0.1568	0.23
Carnivores (*n*=7)	−0.06	0.8969	0.00

Data from Tables 3 and 6 (the high estimate was used in the case of #46). When body mass was 1 kg, we converted the value to 1.00001 kg to avoid values equal to zero in the log-transformed dataset. Also note that the 1983 Aché data (#83–94) are excluded to avoid duplication with the new values calculated here for the same group (Table 6). "Hide" species: #6–9, 40, 96, 100–106, 109–111, 114, 117, 132, 149, 151–159, 161–165, 167, 174, 177, 222–224, 229, 233–235, 237–239, 245–246 (see Tables 3 and 6 for corresponding species). All other numbers are considered "run" species

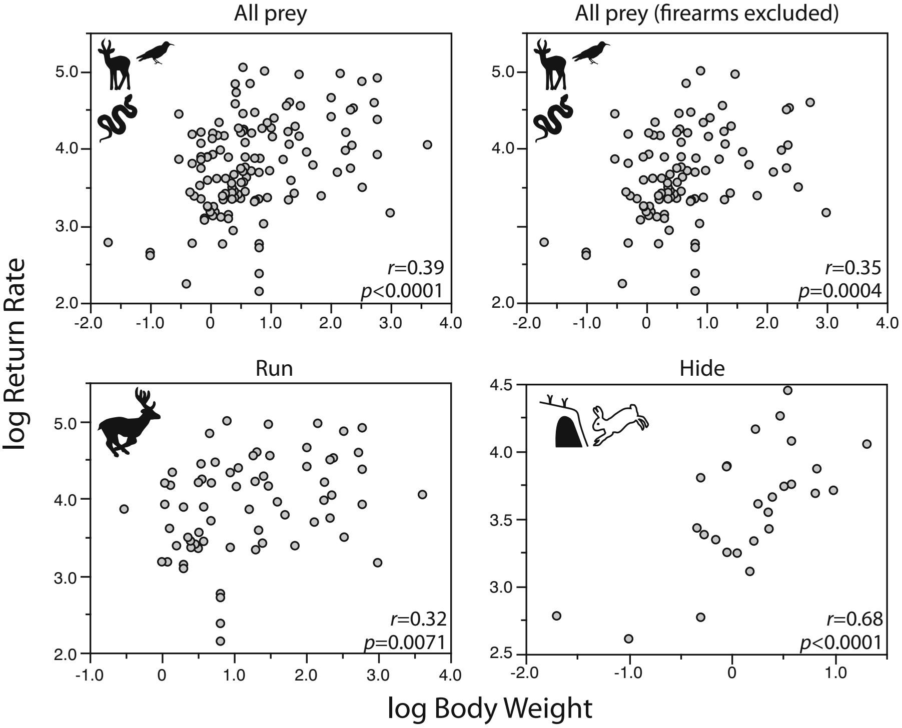

Fig. 7 Relationships between log body size and log R_{prey} for all prey (with and without firearms) and according to whether the species uses a cursorial or hide strategy. In this and the following figures, #83–94 are excluded to avoid duplication with the data in Table 6

$t_s = 2.25$, $p = 0.0244$; capuchin monkey: $t_s = 1.91$, $p = 0.0561$; spider monkey: $t_s = 4.30$, $p < 0.0001$).

Prey Size and R_{prey}

Having examined the effect of taxonomy on return rates, we here explore relationships with body size (Table 7, Fig. 7). Considering the entire set of prey types, the correlation between log body mass and log R_{prey} is moderate (Fig. 7) but only a small fraction of the variance is explained by body size ($R^2 = 0.15$) and excluding firearms actually *decreases* the fit. A contrasting pattern emerges if prey types are classified by evasion strategy (using a simple dichotomy: run/hide): returns increase with size for hiding prey but not running prey. Correlations are weak for aquatic and volant taxa, but moderately strong in fossorial species. Dividing the dataset into taxonomic groups reveals that correlations with body size are relatively strong only for glires (rodents and leporids, $R^2 = 0.67$, Fig. 8); in this group excluding firearms has little effect. Stratifying the dataset by procurement method also produces fairly low correlations with body size ($R^2 = 0.12$–0.38, Figs. 9 and 10). Overall, prey size is a relatively poor predictor of R_{prey}, with the exception of fossorial species. These weak relationships are not surprising, given that R_{prey} values for species under 10 kg range from 141 to over 110,000 kcal/h and mostly overlap those for species >10 kg (from 1463 to slightly

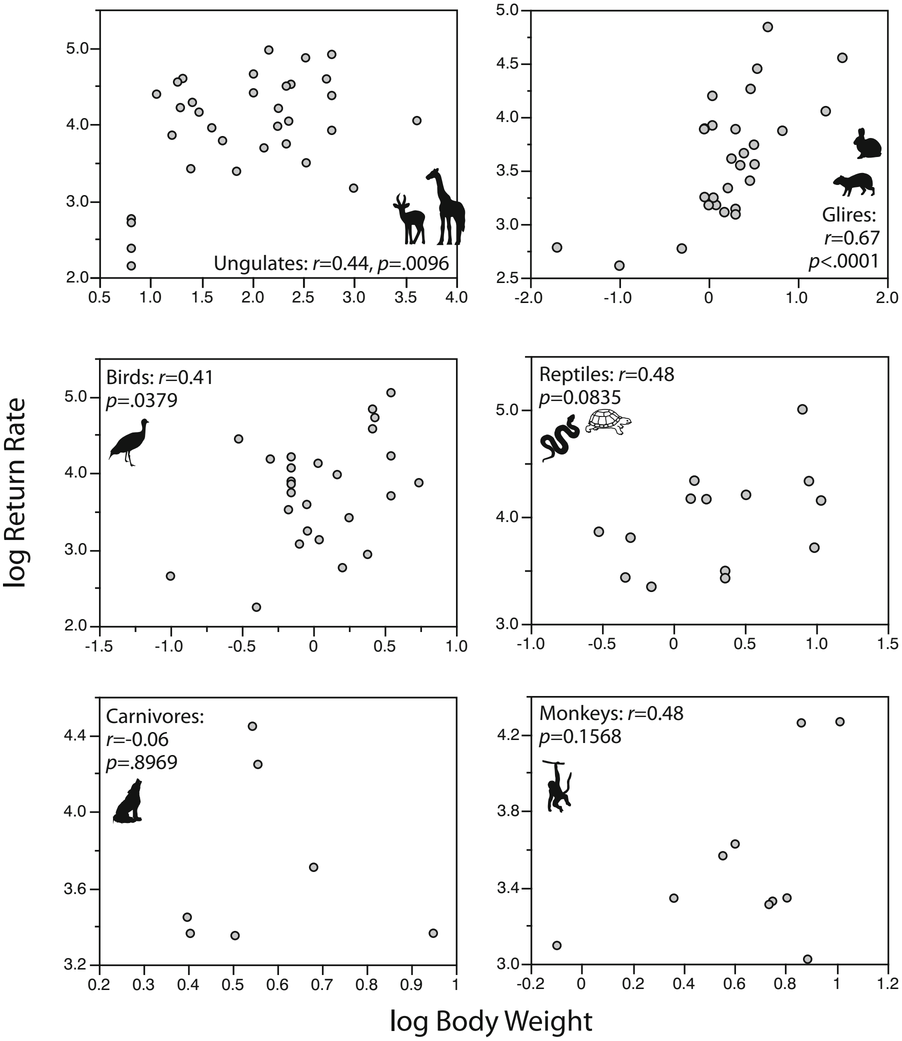

Fig. 8 Relationships between log body size and log R_{prey} according to major taxonomic groups

under 100,000 kcal/h, Tables 3 and 6). The highest R_{prey} estimate in our dataset (112,357 kcal/h) is derived from the 3.5-kg Canada goose. In contrast, marked differences between several taxonomic groups mean that antipredator mechanisms, in large part mediated by phylogeny, have a much stronger impact on profitability.

Deconstructing R_{prey}: Body Mass, Energetic Yield, and Pursuit Costs

Statistical comparisons yield no overall pattern to the relationship between body mass and prey profitability. Nonetheless, other factors affecting R_{prey} may hold clues pointing toward reliable predictions of prey profitability. We start with fat content, a factor known to fluctuate widely within and among species (Pond, 1992). SOM 2 lists 308 species, 165 with observed body fat values. There is a very weak correlation between

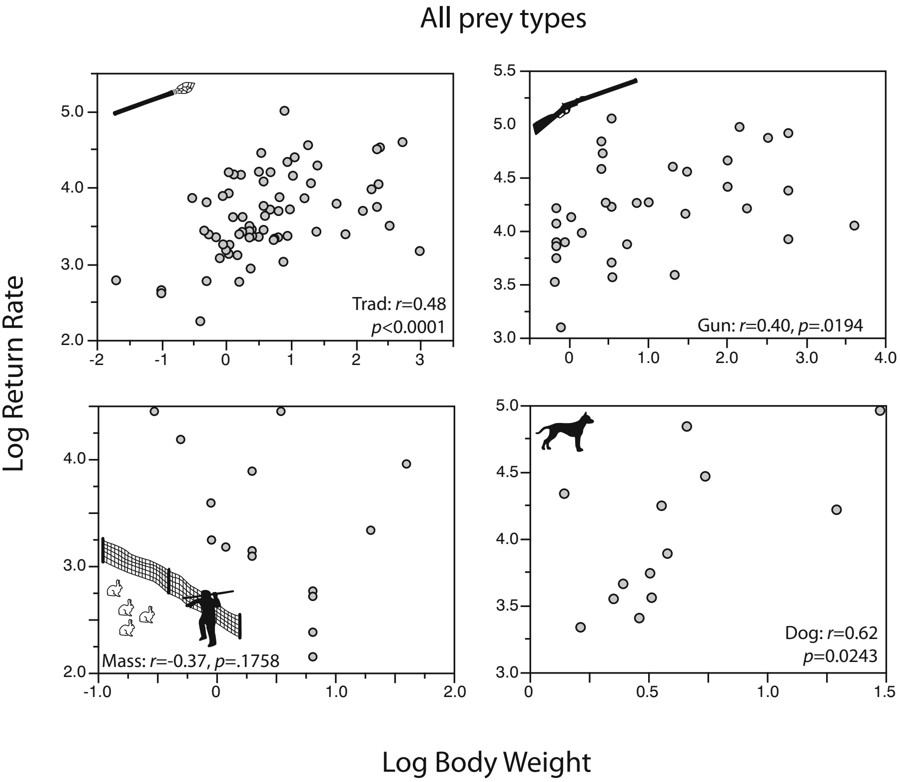

Fig. 9 Relationships between log body size and log R_{prey} as a function of method of procurement

(log) body mass and (log) fat in this sample (Table 8). The relationship is slightly stronger in glires, birds, and even more so in carnivores, but extremely weak in ungulates. It improves slightly by excluding megafauna—hippopotamus, giraffe, and elephant—likely because, we suspect, excessive fat storage might have been selected against as a result of scaling effects on the body architecture of very large animals. It is low for African ungulates, possibly due to the metabolic costs of heat dissipation and/or tradeoffs with maintaining high predator escape velocities. Overall, fat composition has weak to moderate effects on R_{prey}, mediated perhaps by latitudinal effects. High latitude terrestrial species tend to be larger and fatter than their equatorial counterparts, possibly due to the evolution of fasting endurance in highly seasonal habitats (Lindstedt & Boyce, 1985). If we focus on total energetic yield (in kcal/kg) including both fat and muscle tissues, the relationship with body mass disappears for all but ungulates (excluding megafauna). Including all 308 species yields a negative and significant relationship with body mass, but explains very little (6%) of the variance in the sample. None of the other correlations are significant, except for those involving ungulates and carnivores. Overall, energetic yield on a per-kilogram basis correlates poorly with prey size.

Pursuit costs (Table 9) constitute another key parameter affecting R_{prey}. The dataset assembled by Lupo and Schmitt (2016) indicates that log pursuit time is significantly correlated with log body mass ($r = 0.40$, $p < 0.05$, $R^2 = 0.16$). Our larger sample

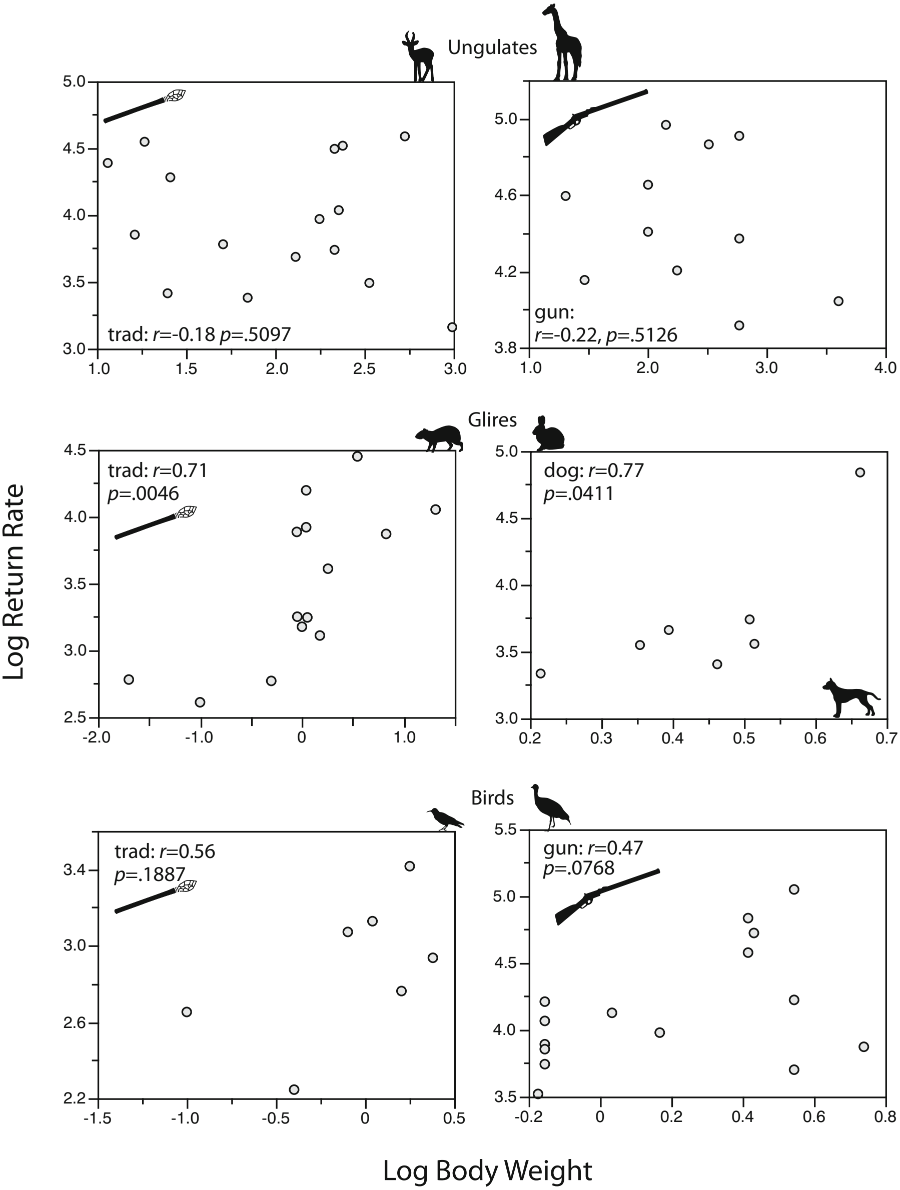

Fig. 10 Relationships between log body size and log R_{prey} according to taxonomic group and method of procurement

analysis is consistent with their result ($r = -0.50$, $p < 0.0001$, $R^2 = 0.25$, Table 9), the "r" value here being negative because we are analyzing hours/kilogram rather than pursuit time. Partitioning our sample according to escape strategy yields a moderate relationship for cursorial species and a more robust one for hiding taxa. Variation is limited among taxonomic groups, weakest in birds and reptiles, and strongest in glires (Fig. 11). Excluding prey types obtained with firearms has a limited impact on the pattern, except in birds where the relationship becomes virtually non-existent. The

Table 8 Relationship between $\log_{10}$ body mass and $\log_{10}$ fat or $\log_{10}$ energy in the dataset. Significant results are highlighted in bold

	r	*p* value	R^2
Fat (observed only)			
All animals (*n*=165)	**0.17**	**0.0278**	**0.03**
Ungulates (*n*=22)	0.15	0.5143	0.02
All ungulates minus megafauna (*n*=19)	**0.57**	**0.0111**	**0.32**
African ungulates (*n*=13)	0.14	0.6506	0.02
African ungulates minus megafauna (*n*=10)	0.49	0.1502	0.24
Bats (12)	0.55	0.0637	0.30
Birds (*n*=28)	**0.41**	**0.0287**	**0.17**
Glires (*n*=43)	**0.38**	**0.0128**	**0.14**
Reptiles (*n*=22)	0.27	0.2158	0.08
Carnivores (*n*=16)	**0.74**	**0.0010**	**0.55**
Energy (observed fat only)			
All animals (*n*=165)	−0.14	0.0724	0.02
Ungulates (*n*=22)	0.02	0.9403	0.00
All ungulates minus megafauna (*n*=19)	**0.49**	**0.0332**	**0.24**
African ungulates (*n*=13)	−0.22	0.4623	0.05
African ungulates minus megafauna (*n*=10)	0.33	0.3541	0.11
Bats (12)	0.41	0.1848	0.17
Birds (*n*=28)	0.25	0.2009	0.06
Glires (*n*=43)	0.23	0.1386	0.05
Reptiles (*n*=22)	0.08	0.7106	0.01
Carnivores (*n*=16)	**0.71**	**0.0019**	**0.51**
Energy (estimated fat included)			
All animals (*n*=308)	**−0.24**	**<0.0001**	**0.06**
Ungulates (*n*=51)	0.15	0.2824	0.02
All ungulates minus megafauna (*n*=48)	**0.35**	**0.0136**	**0.13**
African ungulates (*n*=30)	−0.01	0.9433	0.00
African ungulates minus megafauna (*n*=27)	0.22	0.2619	0.05
Bats (13)	0.28	0.3566	0.08
Birds (*n*=59)	0.12	0.3659	0.01
Glires (*n*=68)	0.11	0.3642	0.01
Reptiles (*n*=45)	0.23	0.1271	0.05
Carnivores (*n*=25)	**0.63**	**0.0007**	**0.40**

Data from Supplemental Online Material 2. When a value was equal to "1," we converted it to 1.00001 to avoid zeros in the log-transformed dataset. Megafaunal species include the giraffe, hippopotamus, and elephant

majority of these correlations are moderate and negative, implying an economy of scale in pursuit costs. Larger species tend to have lower pursuit costs than smaller taxa. The

Table 9 Relationship between $\log_{10}$ body mass and $\log_{10}$ pursuit (hr/kg) by taxonomic group. Significant results are highlighted in bold

	r	*p* value	R^2
All animals (*n*=131)	**−0.50**	**<0.0001**	**0.25**
Firearms excluded (*n*=97)	**−0.48**	**<0.0001**	**0.23**
Firearms only (*n*=34)	**−0.51**	**0.0022**	**0.26**
Spear/bow/blowpipe/trapping (*n*=69)	**−0.58**	**<0.0001**	**0.34**
Dog (*n*=13)	−0.59	0.0320	0.35
Mass collected (*n*=15)	0.25	0.3630	0.06
Escape strategy (birds and monkeys excluded)			
Run (cursorial, *n*=68)	**−0.45**	**0.0001**	**0.20**
Run (cursorial, *n*=55, firearms excluded)	**−0.34**	**0.0105**	**0.12**
Hide (*n*=27)	**−0.62**	**0.0005**	**0.39**
Hide (*n*=25, firearms excluded)	**−0.66**	**0.0004**	**0.43**
Mode of locomotion			
Aquatic (*n*=10)	−0.13	0.7148	0.02
Arboreal (*n*=17)	**−0.53**	**0.0296**	**0.28**
Cursorial (*n*=63)	**−0.47**	**0.0001**	**0.22**
Fossorial (*n*=17)	**−0.68**	**0.0027**	**0.46**
Volant (*n*=24)	−0.33	0.1186	0.11
Ungulates (*n*=33)	**−0.44**	**0.0098**	**0.20**
Firearms excluded (*n*=22)	**−0.46**	**0.0332**	**0.21**
Firearms only (*n*=11)	0.10	0.7627	0.01
Spear/bow/blowpipe/trapping (*n*=16)	0.06	0.8113	0.00
Birds (*n*=26)	−0.38	0.0568	0.14
Firearms excluded (*n*=11)	0.07	0.8484	0.00
Firearms only (*n*=15)	−0.37	0.1764	0.14
Spear/bow/blowpipe/trapping (*n*=7)	−0.59	0.1643	0.35
Glires (*n*=28)	**−0.62**	**0.0004**	**0.39**
Firearms excluded (*n*=25)	**−0.58**	**0.0025**	**0.33**
Spear/bow/blowpipe/trapping (*n*=14)	**−0.65**	**0.0117**	**0.42**
Dog (*n*=7)	**−0.75**	**0.0498**	**0.57**
Reptiles (*n*=14)	−0.42	0.1370	0.17
Firearms excluded (*n*=14)	−0.42	0.1370	0.17
Spear/bow/blowpipe/trapping (*n*=13)	−0.47	0.1087	0.22
Monkeys (*n*=10)	−0.53	0.1150	0.28
Carnivores (*n*=7)	0.06	0.8929	0.00

Data from Tables 3 and 6. Hour/kilograms were obtained by dividing pursuit time by edible weight. When body mass was 1 kg, we converted the value to 1.00001 kg to avoid values equal to zero in the log-transformed dataset

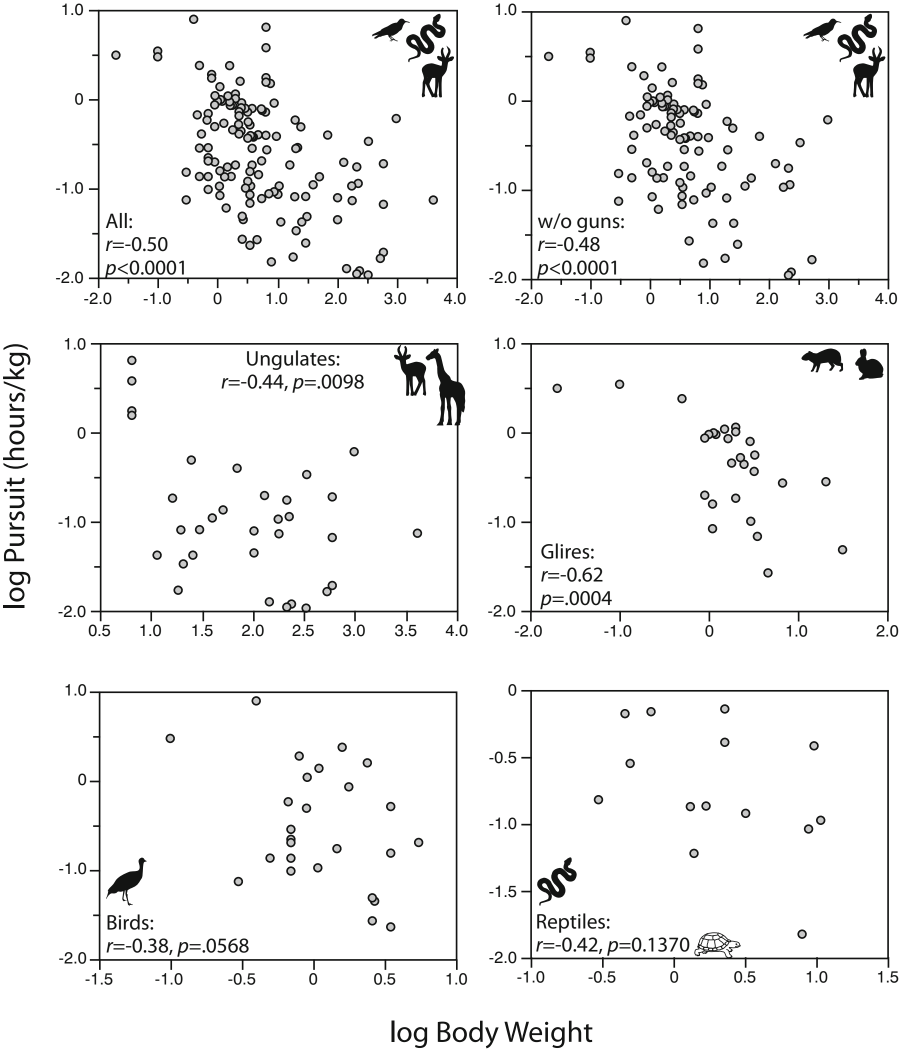

Fig. 11 Relationships between log body size and log pursuit hours/kilogram (low estimates) according to major taxonomic groups. Pursuit hours/kilogram estimates were obtained by dividing pursuit time (converted into hours) by edible weight. For example, Merganser (#21): 12 min (0.2 h)/1.892 kg = 0.1057

explanatory power of pursuit time, however, is limited, accounting for only 25% of the total, full sample variance.

A Multivariate Model Fitting Analysis

For a more synthetic analysis of the factors that predict $R_{prey,}$ one that controls for potential confounding variables, we employed a multivariate model selection approach (Burnham & Anderson, 2003). Our model (full details in SOM 4) separately predicts

Table 10 Multimodel inference and model selection for predictors of pursuit cost and energetic value

Set 1. Model comparison: pursuit hours/kg (<10 kg)	AIC$_c$	AIC$_c$	$e^{-.5\Delta AICc}$	w$_i$	R^2
LogKG, Taxon, Tech, Lat, LogKG x Tech, LogKG x Lat	20.327	0	1	0.697	0.731
LogKG, Taxon, Tech, Lat, LogKG x Tech	22.019	1.692	0.429	0.299	0.716
LogKG, Taxon, Tech, Lat	31.275	10.948	0.004	0.002	0.635
LogKG, Taxon, Tech	35.913	15.586	0	0	0.605
Taxon, LogKG, Lat	49.043	28.716	0	0	0.494
Tech, LogKG, Lat	58.858	38.531	0	0	0.466
Taxon, Tech, Lat	59.049	38.722	0	0	0.493
Taxon, Tech	61.854	41.527	0	0	0.463
Tech, LogKG	62.724	42.397	0	0	0.429
Tech, Lat	69.17	85.662	0	0	0.387
Tech	71.868	51.541	0	0	0.353
Taxon, LogKG	75.499	55.172	0	0	0.31
Taxon, Lat	76.473	56.146	0	0	0.303
LogKG, Lat	80.651	60.324	0	0	0.235
Taxon	90.914	70.587	0	0	0.165
Lat	92.873	72.546	0	0	0.107
LogKG	94.86	74.533	0	0	0.087

Set 2. Model comparison: pursuit hours/kg (>10 kg)	AIC$_c$	AIC$_c$	$e^{-.5\Delta AICc}$	w$_i$	R^2
Tech	−16.492	0	1	0.513	0.173
Tech, LogKG	−13.899	2.593	0.273	0.140	0.176
Tech, Lat	−13.78	2.712	0.257	0.132	0.174
LogKG	−12.37	4.122	0.127	0.065	0.005
Lat	−12.26	4.232	0.120	0.061	0.003
Tech, LogKG, Lat	−11.001	5.491	0.064	0.032	0.176
LogKG, Lat	−9.872	6.62	0.036	0.018	0.007
Taxon	−9.06	7.432	0.024	0.012	0.058
Taxon, Tech	−8.587	7.905	0.019	0.009	0.192
Taxon, Lat	−6.304	10.188	0.006	0.003	0.061
Taxon, LogKG	−6.165	10.327	0.005	0.002	0.058
LogKG, Taxon, Tech	−5.839	10.653	0.004	0.002	0.205
Taxon, Tech, Lat	−5.306	11.186	0.003	0.001	0.193
Taxon, LogKG, Lat	−3.218	13.274	0.001	0	0.062
LogKG, Taxon, Tech, Lat	−2.261	14.231	0	0	0.205
LogKG, Taxon, Tech, Lat, LogKG x Tech, LogKG x Lat	0.67	17.162	0	0	0.282
LogKG, Taxon, Tech, Lat, LogKG x Tech	3.17	19.662	0	0	0.261

Set 3. Model comparison: kcal/kg	AIC$_c$	AIC$_c$	$e^{-.5\Delta AICc}$	w$_i$	R^2
%Fat, logKG, Taxon, Anteater, Lat, Velo, %Fat x Velo, %Fat x Lat	1513.723	0	1	0.888	0.969
%Fat, logKG, Taxon, Anteater, Lat, Velo, %Fat x Velo	1518.002	4.279	0.117	0.104	0.968
%Fat, Taxon, Lat, Velo, logKG, Anteater	1523.574	9.851	0.007	0.006	0.965
%Fat, Taxon, Lat, Velo	1651.246	137.523	0	0	0.904

Table 10 (continued)

%Fat, Taxon, Lat, Velo, logKG	1652.957	139.234	0	0	0.904
%Fat, Taxon, Lat	1661.337	147.614	0	0	0.893
%Fat, Taxon	1665.511	151.788	0	0	0.888
%Fat, Anteater	1685.999	172.276	0	0	0.865
%Fat, logKG	1702.548	188.825	0	0	0.846
%Fat, Lat, fat x Lat	1734.934	221.211	0	0	0.806
%Fat, Lat	1735.502	221.779	0	0	0.802
%Fat, Velo	1741.033	227.31	0	0	0.793
%Fat, Velo, fat x Velo	1742.652	228.929	0	0	0.794
$\%Fat_c$	1746.559	232.836	0	0	0.78
%Fat, Evasion	1748.561	234.838	0	0	0.78
Taxon	1890.25	376.527	0	0	0.352
Anteater	1925.359	411.636	0	0	0.121
logKG	1927.329	413.606	0	0	0.107
Lat_c	1927.724	414.001	0	0	0.104
Evasion	1936.551	422.828	0	0	0.042
$Velo_c$	1937.002	423.279	0	0	0.037

Multimodel inference (Symonds & Moussali, 2011) compares combinations of possible predictors using the Akaike Information Criterion for small samples (AICc), a measure of how informative the predictor is relative to the outcome variable. Models within 20 points of the top model are likely to be within the candidate set of possible models. Akaike weights (w_i) give the probability that each model is the top model. In model set 1, pursuit hours/kilograms were square root transformed to improve measures of normality. The R^2 gives the proportion of variance explained by each model

the numerator *(e)* and denominator (*h*) of R_{prey} on the premise that factors predicting caloric value may differ from those predicting pursuit and processing time. As we have already predicted processing time ($\hat{b}_{kg}$) with body size (Table 9, SOM 4 Col AA), here, we attempt to separately predict the energy value of prey (e_{kg} in units of gross energy per kilogram whole body weight, see SOM 4 Col X) and the pursuit cost component of handling time (p_{kg}) (see SOM 4 Col Z). Following the model selection phase in which we generated AICc values for each predictor, combination of covariates, and interactions in a linear model, we used the top model to generate predicted per kg values of *e* *(*$\hat{e}_{kg}$*)* and *p (*$\hat{p}_{kg}$*)*, added $\hat{b}_{kg}$ *to* $\hat{p}_{kg}$ to produce total predicted handling time $\hat{h}_{kg}$, and then used these predicted values to calculate *e*/*h* ($\widehat{R}_{prey}$) for all prey types in Table 3. We then compare the predictive power of the modeled $\widehat{R}_{prey}$(SOM 4, col. AG) against our recalculated estimates of R_{prey} (SOM 4, col. AD, Table 3).

The top model predicting the energy value of prey, e_{kg}, is well separated from the next-ranked choice; it explains 96.9% of the variation in e_{kg} and, with an Akaike weight of 0.889, was 89% more likely to be the top model than the next ranked model (Table 10). Percent body fat was the single most important predictor of e_{kg}, alone explaining 78% of the variability. Additional fit-improving predictors included

Table 11 Model estimates for the top models predicting per kilogram pursuit time and energetic value

Pursuit time, hours/kg: under 10 kg	Estimate	Std error	t Ratio	P>|t|	95% CI	Std beta	Marginal mean	Std error	95% CI
Intercept	0.657	0.088	7.42	<0.0001	0.480, 0.832				
Taxonomy: amphibian/reptile	−0.258	0.104	−2.49	0.0148	−0.464, −0.051	−0.260	0.156	0.098	0.039, 0.349
Taxonomy: arboreal mammal/bird	0.217	0.107	2.03	0.0461	0.004, 0.431	0.289	0.757	0.076	0.515, 1.046
Taxonomy: other terrestrial mammal	0.001	0.075	0.02	0.9844	−0.148, 0.152	0.002	0.428	0.051	0.305, 0.572
Taxonomy: ungulate	0.039	0.222	0.18	0.8606	−0.405, 0.483	0.053	0.479	0.284	0.016, 1.580
Log live weight (kg)	−0.006	0.066	−0.09	0.9248	−0.137, 0.1251	−0.016			
Latitude: >40 (northern)	−0.198	0.066	−3.03	0.0033	−0.329, −0.068	−0.401	0.206	0.106	0.059, 0.442
Latitude: < 40 (southern)	0.199	0.066	3.03	0.0033	0.068, 0.329	0.401	0.725	0.089	0.456, 1.057
Log weight x northern latitudes	0.121	0.061	2.00	0.0489	0.0005, 0.242	0.333			
Log weight x southern latitudes	−0.121	0.061	−2.00	0.0489	−0.242, −0.000	−0.333			
Technology: bow or spear	0.199	0.085	2.36	0.0209	0.031, 0.368	0.255	0.726	0.117	0.384, 1.176
Technology: dog	0.110	0.183	0.60	0.5496	−0.254, 0.474	0.114	0.582	0.207	0.122, 1.382
Technology: gun	−0.209	0.107	−1.95	0.0546	−0.421, 0.004	−0.263	0.197	0.125	0.038, 0.481
Technology: hand capture	−0.043	0.096	−0.45	0.6554	−0.234, 0.148	−0.055	0.372	0.112	0.149, 0.694
Technology: mass collection	−0.188	0.088	−2.14	0.0358	−0.362, −0.013	−0.195	0.216	0.108	0.063, 0.461
Technology: trapping	0.130	0.125	1.04	0.3014	−0.11, 0.379	0.135	0.613	0.140	0.255, 1.127
Log weight x Tech[bow/spear]	−0.084	0.055	−1.52	0.1336	−0.193, 0.026	−0.157			
Log weight x Tech[dog]	−0.235	0.156	−1.51	0.1364	−0.546, 0.076	−0.317			
Log weight x Tech[gun]	−0.190	0.097	−1.96	0.0535	−0.382, 0.003	−0.279			
Log weight x Tech[hand]	0.017	0.060	0.28	0.7810	−0.102, 0.136	0.029			
Log weight x Tech[mass]	0.552	0.120	4.61	<0.0001	0.313, 0.791	0.760			
Log weight x Tech[trap]	−0.060	0.073	−0.82	0.4132	−0.205, 0.085	0.085			

Table 11 (continued)

Pursuit time, hours/kg: over 10 kg	Estimate	Std error	t Ratio	P > |t|	95% CI	Std beta	Marginal mean	Std error	95% CI
Intercept	0.382	0.040	9.61	<.0001	0.301, 0.463				
Technology: bow/spear/dog	−0.032	0.046	−0.70	0.4864	−0.126, 0.061	−0.112	0.162	0.034	0.093, 0.232
Technology: gun	−0.125	0.048	−2.61	0.0136	−0.224, −0.027	−0.416	0.079	0.040	−0.002, 0.160
Technology: mass/trap	0.135	0.060	2.27	0.0301	0.013, 0.257	0.53	0.324	0.086	0.149, 0.499
Energetic value, kcal/kg									
Intercept	1257.01	23.319	53.90	<0.0001	1210.834, 1303.190				
%Fat	75.71	1.902	39.81	<0.0001	71.948, 79.479	0.784			
Log(Kg/liveweight)	−18.97	5.858	−3.24	0.0016	−30.573, −7.374	−0.090			
Latitude	2.37	0.414	5.73	<0.0001	1.551, 3.189	0.104			
Velocity	−0.55	0.368	−1.52	0.1314	−1.28, 0.169	−0.030			
%Fat x latitude	0.20	0.082	2.51	0.0134	0.043, 0.367	0.047			
%Fat x velocity	−0.20	0.069	−3.02	0.0031	−0.343, −0.071	−0.051			
Anteater/armadillo	239.11	15.743	15.19	<0.0001	270.285, 207.934	0.277			
Not Anteater or armadillo	−239.11	15.743	−15.19	<0.0001	−270.285, −207.934	−0.277			
Taxonomy: amphibian/reptile	−42.87	20.503	−2.09	0.0386	−83.479, −2.276	−0.057	1793.761	29.898	1734.556, 1852.967
Taxonomy: arboreal mammal/bird	142.10	14.504	9.80	<0.0001	113.385, 170.827	0.237	1978.745	21.139	1936.885, 2020.606
Taxonomy: other terrestrial mammal	32.88	14.160	2.32	0.0219	4.847, 60.928	0.057	1869.527	16.536	1836.780, 1902.274
Taxonomy: ungulate	−180.48	17.716	−10.19	<0.0001	−215.562, −145.399	−0.315	1704.523	29.842	1645.427, 1763.619

Pursuit time has a square root transform in the <10 kg model, thus all predictions calculated from this model should be squared

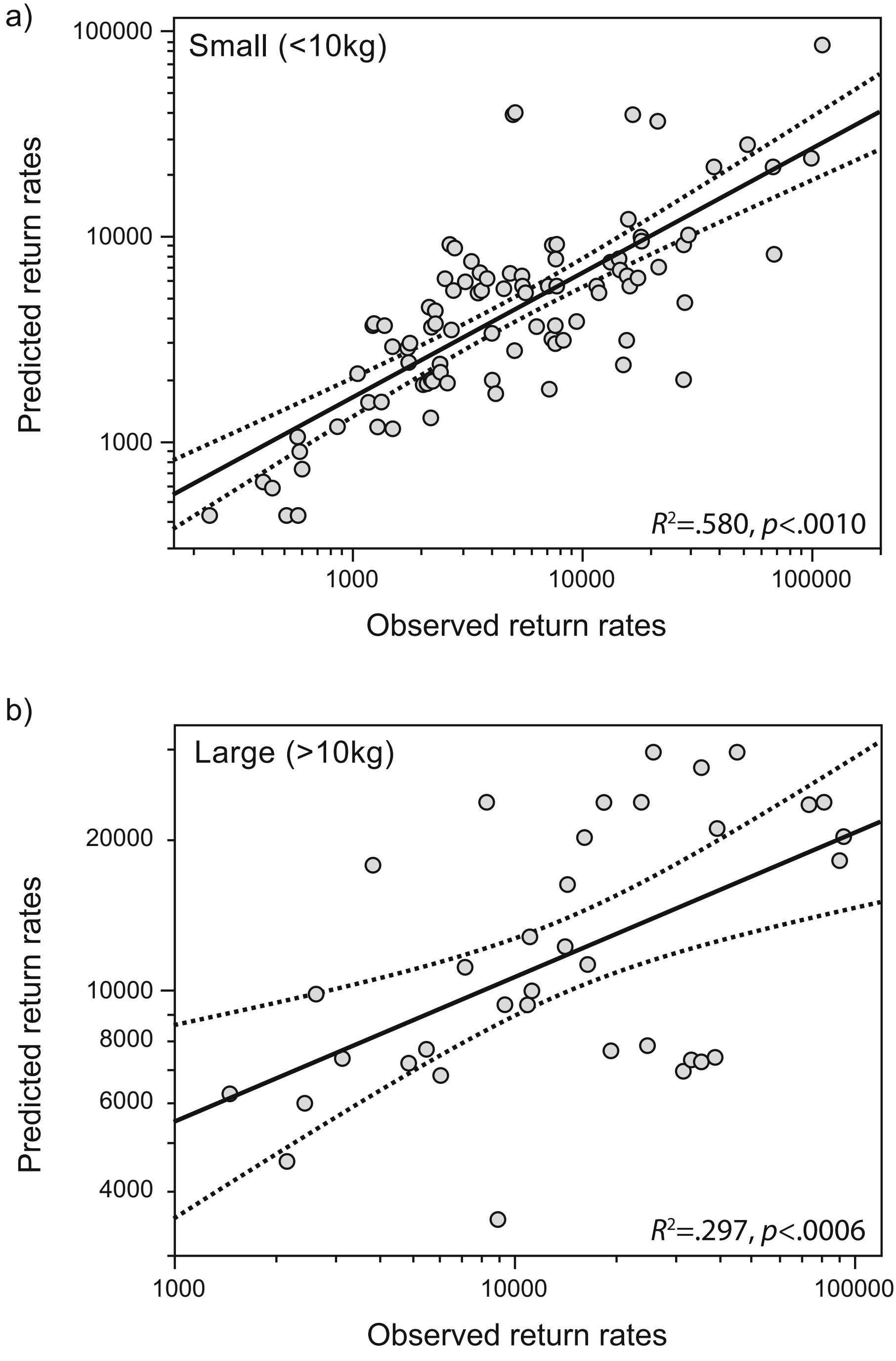

Fig. 12 Actual R_{prey} by predicted $\widehat{R}_{prey}$ values separately derived from the top multivariate models for energetic value (e), pursuit costs (p), and processing time (b) ($\frac{e_{kg}}{p_{kg}+b_{kg}}$). While returns for small prey are fairly accurately predicted using separate models for each R_{prey} component, those for large prey are not well predicted

taxonomic categories (amphibian/reptile, arboreal mammal/bird, other terrestrial mammal, ungulate), the continuous variables log body weight, latitude, escape velocity (in km/h), and two interaction terms: %fat × velocity, and %fat × latitude. Larger, low-latitude, and faster animals tend to have lower e_{kg}, along with amphibians/reptiles and ungulates. Birds/arboreal mammals and terrestrial mammals have higher e_{kg}. Some of these patterns likely are due to the interaction between fat and both velocity and latitude: northern animals tend to be fatter and faster animals tend to be leaner.

The pursuit component of handling, p_{kg}, was more difficult to predict (Table 11). It was necessary to separately estimate models for animals under ($n = 93$) and over ($n = 36$) 10 kg, as beyond this point the relationship with pursuit became decidedly nonlinear. The top model for small animals predicts 73.1% of the variation in p_{kg}, and includes log body weight, taxonomic group, technology (spear/bow, firearms, dog/hand capture, mass collection), latitude (as a dichotomous variable split at 40°N), and two interactions: weight × technology, and weight × latitude. Amphibians/reptile pursuit costs tend to be lower and those of arboreal mammals/birds higher than other taxonomic groups. Lower pursuit costs characterize animals in northern latitudes compared to tropical or temperate regions, possibly because all were hunted with firearms. Hunting with firearms and mass collecting significantly lower pursuit costs. The overall model found no relationship between body size and pursuit costs, except for mass collecting, where pursuit costs rise with body size in the small prey subsample. For the subsample over 10 kg, only a single variable, technology, predicted pursuit cost, and it explained only 17.3% of the variation.

The modeled $\widehat{R}_{prey}$ calculated from the top model's predicted values for small animals correlates moderately well with observed values of R_{prey}, explaining 58% of the variation (Fig. 12a). However, $\widehat{R}_{prey}$ for larger animals explains only 29.7% of the observed R_{prey} variability (Fig. 12b). Multivariate analysis offers these conclusions: first, the e in the R_{prey} formula is well-estimated with knowledge about an organism's taxonomy and ecology, and the processing component is tied to body size as we described earlier. However, the pursuit time component of handling is subject to extensive (unpredictable) variation. When pursuit comprises a larger fraction of total handling costs, as it often does with larger prey, it becomes difficult to predict returns with any degree of accuracy.

Discussion

The Relative Importance of the Factors Determining R_{prey}

The degree to which prey body size provides a reliable proxy for post-encounter prey profitability, R_{prey}, has been debated extensively (*e.g.*, Ben-Dor et al., 2011; Ben-Dor & Barkai, 2020; Bird et al., 2009, 2012; Broughton et al., 2011; Codding et al., 2010; Jones, 2006; Lupo et al., 2020; Lupo & Schmitt, 2016; Madsen & Schmitt, 1998; Morin, 2012; Ugan, 2005; Ugan & Simms, 2012). Our bivariate, full sample analyses show that the overall relationship is relatively weak, accounting for only 15% of total variance. Stratifying the sample by taxonomic groups or evasion strategy yields only marginally improved correlations, except in hiding taxa for which the relationships are stronger regardless of procurement method. However, even in the hiding taxa, all but one of which are <10 kg, body size only explains approximately 50% of the variance. Similarly, our multivariate analysis of the components of R_{prey} reveals body size to be a poor predictor of both energetic value and pursuit costs, even for smaller animals.

For these reasons, caution is advised in the use of body size as a proxy for the relative costs and benefits of acquiring different prey types. It can be a good predictor of per kilogram processing costs, but it is not a strong predictor of either energetic value or pursuit cost, at least for animals captured singly. Body fat percentage, taxonomic groupings, latitude, and technology are better. A more reliable approach will consider each of the components of prey profitability—energy, pursuit (including failure rate), and processing—using species-specific information and with a focus on contextual, ecological, and technological dimensions. More robust predictions are possible when close attention is paid to taxonomic category, prey behavior, and hunting technologies, but only for small (<10 kg) animals. With care, it should be possible to devise empirically accurate abundance indices—a ratio measure routinely used in archaeology to examine the changing representation of low- and high-ranked prey in faunal samples (*e.g.*, Bayham, 1979; Broughton, 1994)—but these will not necessarily involve contrasting specimen counts for small *vs.* large prey. Depending on the species that are compared, the widely used procedure of comparing small to large species can be problematic and earlier studies made on that basis may merit reanalysis for confirmation. Likewise, the practice of combining species of similar body size into single prey categories (*e.g.*, medium-sized ungulates) may overlook important disparities in prey profitability when the species differ noticeably in terms of herding behavior, escape strategies, or any other parameter that noticeably influences handling. For this reason, archaeologists must improve the methodologies that they use for estimating post-encounter rates, for instance, by paying greater attention to the behavioral properties of the prey, the season of acquisition, the nature of the reconstructed environment, and the age profiles associated with distinct methods of procurement. Simply assuming that body size is a robust proxy of profitability does not do proper justice to the broad range of procurement methods and contexts of encounter historically documented for most prey species.

One limitation with the sample of published return rates is that it only includes a single instance of large game communal hunting (antelope drive, Table 1, #46). For instance, no R_{prey} estimates are currently available for bison surrounds, caribou drives, and other similar cooperative hunts that are known to have been seasonally important in several ethnographic contexts. To address this limitation, we recently began collecting relevant data from various ethnohistorical sources. Our preliminary analysis of these semi-quantitative data suggests a stronger relationship between prey size and profitability for animals obtained in cooperative hunts relative to those obtained one at a time. Although they remain to be fully analyzed, these results are consistent with previous arguments noting that single species may encompass a wide range of prey types (*e.g.*, Koster, 2008; Morin et al., 2020; Smith, 1991).

Leaving the point about communal hunts aside, the analyses that we have presented here emphasize the importance of using accurate estimates of handling costs. Our modelling indicates that pursuit time is the most variable, and hence the most critical, component of handling. In contrast, processing costs scale moderately well with body size. Ethnographers report that a single species may sometimes exhibit dramatic differences in pursuit time costs (*e.g.*, Alvard, 1993b; Koster, 2008; Morin et al., 2020; Smith, 1991; Winterhalder, 1977). In the field, context often determines these intra-specific differences. For instance, in the fall rut encounter with signs of a male moose portends a quick kill, the animal's defenses being sabotaged by its hormones; in winter, the same animal is cunningly evasive and pursuit tactics must adjust. Unfortunately, this type of variation has rarely been documented. We note that evaluating the probability distribution of return rates for a given species may provide clues for detecting the presence of more than one prey type.

Evasion strategy also is a critical factor in the distribution of pursuit costs. Our data shows that body size is a stronger predictor of R_{prey} in hiding or burrowing species than in cursorial ones. The authors' field experience suggests that capture of burrowing prey is less costly and more reliable than capture of fleeing prey, especially those superior in velocity or endurance (Bird et al., 2009). Moreover, hiding species tend to be smaller and slower than cursorial taxa, behavioral characteristics that may decrease variation in pursuit costs.

In our comparisons, the relationship between prey size and profitability was particularly weak in birds. A small range of body weights, 0.5 and 3.5 kg in our sample, may be a factor, although we suggest that flocking may be more important. Birds that are mostly solitary (*e.g.*, guan *Penelope superciliaris*, 1179 kcal/h) yield markedly lower return rates than the more social ones (*e.g.*, eider *Somateria mollissima*, 37,855–68,551 kcal/h). Future body size-profitability analyses probably would benefit from separating solitary from highly social birds and treating the latter as encounters with a patch rather than with individual animals. Our data suggest that, all else equal, payoffs from social birds benefit from an economy of scale in pursuit costs. The context of encounters with flocks also seems also to be important. Smith (1991:223) emphasizes how this factor influences the profitability of the Canada goose (*Branta canadensis*), a semi-colonial breeder hunted by the Inujjuamiut of Québec:

> "When geese first arrive in the Inujjuaq area, scarcity of open water (ponds, lakes, streams) forces them to concentrate in relatively few favorable spots. Within a few weeks [...] increased melting allows the geese to disperse widely [...] This dispersal seriously constrains Inujjuamiut goose-hunting efficiency [...] This effect can be seen in the more than 3-fold decline in handling efficiency for Canada geese [between the two contexts of encounter]"

Morin et al. (2020) make a similar argument about the effect of flock size on the capture of the now extinct passenger pigeon (*Ectopistes migratorius*), a species once commonly hunted in North America. These examples show the marked advantage of technological innovations that take advantage of the patchiness of highly social species. Finally, technological variability is a key determinant of pursuit time. Our results show that firearms strengthen the relationship between prey size and R_{prey}, probably because this technology is more effective at reducing pursuit costs for large than small prey.

Comparability and Reproducibility

Science is grappling with a replication crisis (Baker, 2016) and anthropology has an opportunity to benefit from comparable introspection. In this study, what began as a straightforward task—replicating and comparing documented estimates of prey rankings based on observations of post-encounter return rates for different resources—

proved challenging. Although the majority of the published estimates that we examined could, sometimes with difficulty and lingering uncertainty, be reproduced, this was not the case for all of them. Despite this, our attempts to compare estimates of prey rankings across studies revealed important insights.

Our study highlights six main issues in comparing published post-encounter return rates (R_{prey}) across studies: (i) we identified several different equations used in R_{prey} calculations, complicating direct comparisons; (ii) the effects of variability in pursuit costs on search and handling decisions are often not assessed, with few estimates of R_{prey} reported as statistical means with variance across a distribution of foraging bouts; (iii) in cases where the effects of unsuccessful pursuits are not known, and where processing represents a significant proportion of handling time, studies that multiply energy gained for *total* handling time by a failure rate likely substantially underestimate R_{prey}; (iv) reported edible fractions, particularly those based on "carcass yield" measures, sometimes markedly underestimate the proportion of an animal that is normally consumed by foragers; (v) the scaling relationship between skeletal architecture and body mass has been ignored in many analyses, which lead at times to unrealistic measures of the edible fraction in small versus large prey; and (vi) visceral or subcutaneous fat—the main determinant of the energetic value of a prey—often is not included in the calculation of energy.

The present study tackles these problems by providing supplementary documents with expanded methodological discussions and datasets. We recommend and attempt to demonstrate standardization in definition of variables and parameters and in analytical methods and formulas, in part to demonstrate the benefits for comparative study. In the accompanying documents (SOM 1–4), we elaborate on examples taking up the PCM distinction between search and pursuit, the analysis of pursuit failures, presentation of summed averages and statistical means, calculation of edible portion and energy yield, the importance of adipose tissue, and sample limitations affecting our statistics. Because it automatically calculates return rates using the methods presented here, the spreadsheet provided in SOM 3 should contribute to increased standardization in future analyses of prey profitability.

General Implications

Failures of the PCM to predict foraging decisions may often arise when we assume that prey types and species are synonymous. It probably is *uncommon for a species to coincide with only one prey type*. In fact, several of the published R_{prey} estimates that we examined would probably benefit from being reevaluated and broken down into two or more prey types. Experienced foragers are well aware of context-specific prey type return rate patterns. Indeed, when questioned about seemingly "odd" decisions, their answers often make it clear that the encountered animal has been misclassified by the Western analyst tempted to think of it as a Linnean species. A species typically low-ranked and therefore predicted to be outside of the diet may nonetheless show up in faunal assemblages in frequencies representing its rarer, high-ranked variants. Such an argument has recently been put forward to account for the presence of rabbits (*Oryctolagus cuniculus*) in some Middle Paleolithic contexts of the Northwestern Mediterranean (Morin et al., 2020). Contexts in which one or more species are associated with both low- and high-return prey types are critical because they can confound the study of resource intensification and the emergence of broad-spectrum economies. In the European rabbit case, assuming that this prey is always lower ranked than artiodactyls may lead to a mistaken interpretation that an increase in its representation relative to artiodactyls is evidence of diet breadth expansion caused by large-prey resource depression. However, as we showed, a reversal of prey ranking for small game may occur when foragers decide to mass collect rabbits in areas of high rabbit densities.

Our analysis suggests that if food acquisition and provisioning shape foraging goals, certain prey types, regardless of taxonomic classification, should always be pursued upon encounter. Encountered animals that are debilitated or were recently killed should be "pursued" because they have low opportunity costs. This includes the displacement of carnivores from kill sites ("power scavenging," O'Connell et al., 1988; Bunn, 2007), assuming that the prey is relatively large, the hunters/carnivores ratio favorable, and that the competing predator(s) have comparatively low resource holding potential (Blurton Jones, 1984). For similar reasons, animals encountered in the open that use their "armor" as a defense mechanism (*e.g.*, tortoises, porcupines, pangolins, echidnas) should always be pursued because they tend to be slow and, consequently, have low pursuit costs (*e.g.*, Silberbauer, 1981). Conversely, very small (<1 kg) solitary animals hiding in burrows or in trees are typically associated with low returns. Finally, as noted above, animals that are encountered in patches—bird colonies in particular—can be very high-ranked with the right mass collection technology. Given the potential for high impact on profitability, social animals were probably the focus of early technological innovation. Mass collection tends to reduce pursuit costs compared to other methods, but it interacts with body size to produce greater costs for moderate-sized animals (albeit only up to 10 kg in size).

All of the preceding assumes that hunters' decisions are guided primarily by goals involving food procurement in the form of energy rate maximization. Of course, other goals and currencies are also important, including the minimization of time or risk (relative to a nutritional threshold), the maximization of non-energy currencies such as status or monetary value (Bliege Bird & Bird, 2008; Jones et al., 2013), and the extent to which sharing or signaling goals motivate foraging time allocation and prey choice (Bliege Bird et al., 2001; Hawkes, 1991). Moreover, animals or their parts are also often valued for use as medicine, tools, or ornaments (pangolin scales for instance, D'Cruze et al., 2018), and social perceptions concerning edibility are also often at play (Koster, 2008), with sometimes interesting archaeological implications (see Morin & Laroulandie, 2012 for a Middle Paleolithic case). This is not necessarily a bad thing: better estimates of prey rankings will generate greater certainty about whether or not the models assumptions have been violated, and if so, in what ways. And, by facilitating comparative analysis, we will be better able to highlight the contexts in which these and other factors shape variability in hunting decisions.

Our analysis also assumes a high level of carcass utilization, but kills are not always fully utilized: partial consumption (Sih, 1980) and field processing models (Bettinger et al., 1997; Bird & Bliege Bird, 1997; Metcalfe & Barlow, 1992) predict the contexts in which low utility parts will be left behind. Although full consumption is common, especially of small carcasses (see SOM 1.9), ethnographic and historical observations make it clear that sometimes large animals are selectively consumed for their fat or, in some seasons, only exploited for their skin (Speth, 2020). Fat may pre-empt energy as the relevant currency (Morin, 2012), confirmed by the many reports of lean animals being ignored or fatless carcasses left untouched, including armadillos (Hill et al., 1984:126) and zebras (Bunn et al., 1988:444) at low latitudes, and hares and ptarmigans (Birket-Smith, 1928:127), and reindeer/caribou (Nordenskiöld, 1882: 408) at high latitudes. Such issues are salient because the PCM framework helps to identify social, ecological, and archaeological contexts in which the model's energy assumptions are unlikely to be valid (*e.g.*, Bird et al., 2013; Hawkes, 2016).

Conclusions

Debates about hunting and human evolution, the origins of broad-spectrum economies, and the factors that drive intensification have relied extensively on ethnographic observations of the relative rankings of different prey types, coupled with the assumption that larger species typically will be higher ranked than smaller ones, especially when the latter involve fast prey. Increases in the relative proportion of small-bodied animals have typically been interpreted as a reduction in overall return rates driven by declines in the density of large-bodied species. Although this may be correct in some ecological contexts, our data indicate that, at a global scale, species with high fat content and low pursuit costs are more consistently higher-ranked, regardless of body size. Shifts in prey assemblages to incorporate a higher proportion of small animals could thus indicate not an increase in diet breadth, or resource depression of larger animals, but long-term shifts in precipitation trends. For example, increased precipitation can drive shifts from grassland to woodland in savannas; communal driving of large game is difficult to conduct in the former but can be highly productive in more wooded habitats. It could also reflect increased seasonality: cooler environments host many gregarious (smaller-bodied) species of birds and ungulates, which also favors mass collecting, among other possibilities, and more seasonal climates may promote fat accumulation in small animals. If environments simultaneously become drier and more seasonal, shifts in behavior and relative abundance of different prey types could easily produce a reversal in prey ranking by body size. Our results thus throw into question most models of intensification that rely extensively on the assumption of a strong relationship between body size and profitability.

Finally, our analysis underscores the continued utility of the prey choice model for understanding subsistence shifts, including the emergence of large game hunting. It is clear that well-supported inferences about prey choice require robust models whose assumptions are systematically evaluated in light of contemporary ethnographic observations of foraging behavior and/or well-contextualized ethnohistoric or actualistic experimentation. However, because our sample is largely dominated by prey types obtained singly, what remains to be better documented is how communal hunting affects payoffs and what were its potential feedback effects on human sociality (and *vice versa*). We strongly encourage efforts to expand fieldwork to include understudied regions, societies, and resource types. While the present analysis has focused on terrestrial prey, similar comparative analyses of plant collecting, marine hunting, shellfishing, and fishing are sorely needed. Analyses of prey type rankings remain too few for certain regions, especially Asia and Africa, a problem that may be addressed with more concerted efforts to undertake actualistic experiments aimed at better estimating prey rankings for a broad set of resources. Carefully implemented research designs—like those of Simms (1987) and Thomas (2008) and colleagues, in the Great Basin and coastal Georgia, respectively—provide exemplary illustrations of the potentialities of this approach. Likewise, surveys of the ethnohistoric literature can provide insights on capture methods poorly documented ethnographically, mass collection, and the use of traps, pitfalls, and snares being examples. Human behavioral ecologists have studied only a small portion of the prey types that hunters routinely encounter and the techniques they have employed to efficiently secure them. For this reason, much remains to be learned about the factors that condition prey selection.

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