Luck in Food-finding Affects Individual Performance and Population Trajectories


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Highlights

● There is extreme variation in the probability of food-finding across vertebrate species
● Decreasing probability results in increasing inter-individual variation in the time taken to acquire food
● This variability can result in individual ruin (starvation) or breeding ruin (progeny starvation)
● Apex predators and scavengers are most likely to suffer such ruin under changing environmental conditions

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SUMMARY

Energy harvesting by animals is important because it provides the power needed for all metabolic processes. Beyond this, efficient food-finding enhances individual fitness [1] and population viability [2], although rates of energy accumulation are affected by environmental- [3] and individual stochasticity [4]. Typically, differences between individuals in the rate of food acquisition are attributed to varying competencies [5] even though food encounter rates are known to be probabilistic [6, 7]. We used animal-attached technology to quantify food intake in four disparate free-living vertebrates (condors, cheetahs, penguins and sheep) and found that inter-individual variability depended critically on the probability of food encounter. We modelled this to reveal that animals taking rarer food, such as apex predators and scavengers, are particularly susceptible to breeding failure because this variability results in larger proportions of the population failing to accrue the necessary resources for their young before they starve, and because even small changes in food abundance can affect this variability disproportionately. A test of our model on wild animals indicated why Magellanic penguins have a stable population while the congeneric African penguin population has declined for decades. We suggest that such models predicting probabilistic ruin can help predict the fortunes of species operating under globally changing conditions.

RESULTS AND DISCUSSION

Consumer resource theory recognizes the importance of food-finding and deals with broad issues ranging from optimal diet models [8] through behavioural strategies [9] to population dynamics and food web structure [10]. However, although some work recognizes the importance of variation in rates of energy accumulation [11] and how animal condition depends on foraging decisions [12], many models ignore such
variation and so cannot build appropriate risks of breeding failure or starvation into their outputs. In fact, resources are generally considered to be distributed probabilistically [4, 7], which does not necessarily equate with linear rates of food procurement across a population [6]. Indeed, probabilistic food encounter makes foraging animals more analogous to serial gamblers who may, or may not, be successful at any given moment, and whose fortunes may vary considerably over time depending on whether they are ‘lucky’ or ‘unlucky’ [6]. In animal terms, such gambling specifically relates to the probability of finding food, the energetic value of that food, and the energetic costs of foraging (with the balance between these factors being couched within a risk-reward framework [13]). A serial gambler incurs ‘ruin’ if money to bet runs out. By analogy, a foraging animal experiences ruin if its energy reserves (e.g. those needed for survival ['individual ruin'] or breeding ['reproductive ruin']) become exhausted. Indeed, this simple gambit often underlies state-dependent models of foraging. Since the time course of such ‘luck’ in foraging animals relates to energy gain, with consequences for species reproductive success, it is surprising that rates of food intake have only rarely been determined for wild animals.

Food ingestion rates and the implications of probabilistic feeding

Our field work using animal-attached technology to determine the details of animal feeding revealed very different patterns of food accumulation (defined as food actually ingested, with the time between food ingestion events being defined by the time spent searching for, and attempting to secure, food – see Star- Methods) between the four species examined. The domestic sheep *Ovis aries* (grazing herbivores that feed virtually continuously on low reward plants and which ingest the smallest food items - corresponding to single bites of vegetation), were monitored for 24 h each and had the shortest period between food ingestion events (typically less than 5 s (Fig. 1) although a tail of longer inter-bite intervals occurred). They had an approximately linear cumulative intake of food over hours of foraging, and the least inter-individual variation (Figure 1). They were followed by the Magellanic penguins *Spheniscus magellanicus* (high power, pursuit piscivores that typically ingest dozens of prey items per trip [14]). All penguins
were monitored over one full foraging trip (the mean deployment period of the devices was 18 h at sea) and also showed an approximately linear increase in cumulative food items ingested over hours of foraging, although inter-individual variation was substantially greater than in the sheep. This was presumably due, in part, to patchiness in the prey distribution and/or differences in foraging ability between individuals. The cheetahs *Acinonyx jubatus* (high power, pursuit carnivores, that usually capture a single food item per foraging trip [15]) and the Andean condors *Vultur gryphus* (low power, scavenging carnivores that also, at best, encounter a single, high quality, food item per foraging trip [16, 17]) both had step functions in food-finding events over periods of hours of foraging (Figure 1). Individuals from both species were monitored for several days (means; cheetahs = 5.01 days, condors 7.8 days) and showed the most inter-individual variability in the time taken to find food, with search times varying between 8,561 and 62,259 s and 1,560 s to 128,100 s, for the cheetahs and the condors, respectively (Fig. 1).
Figure 1. Feeding patterns of disparate vertebrates.

Coloured line graphs show the accumulation of food over time spent foraging by four different vertebrates; domestic sheep in two localities (yellow traces are from Argentine Patagonia; green from Northern Ireland), while Magellanic penguins, cheetahs and Andean condors have different colours showing different individuals. The grey histograms show frequency plots of the time between food items for each species showing the major modes for sheep and penguins (the sheep, in particular, had a number of much longer intervals between bites which were assumed due to processes other than foraging).
Such data can be modelled to determine the effects of food-finding on overall animal energy reserves by breaking down the activities into ‘foraging’ and ‘all other activities’ and considering the probability of food-finding (Supplemental data, Figure S1). A simple mathematical model using a binomial process (Supplemental data 1) can represent foraging periods as a sequence of discrete time steps of equal length, in which we can record; (i) the number of food items accumulated by the animal (cf. Figure 1), (ii) the corresponding energy accumulated by the animal, (iii) and the energy reserves of the animal. This approach translated our animal feeding data (Figure 1) into a probability of success, $P_s$, of; 0.00004, 0.00004, 0.03 and 0.05/s for the cheetah, condor, Magellanic penguin and sheep, respectively (Supplemental data 2). Using these three distinct $P_s$ values as a basis to simulate the number of food items accumulated for three hypothetical species (Supplemental Figure S2A – cf. Fig. 1), we observed that, as the probability of success decreased, both the search time for a success and the variability in overall search times increased non-linearly (Supplemental data 1 & Supplemental Figure S2B).

Critically, we noted that $P_s$ affected inter-individual variation in terms of energy accumulated during foraging (even if the mean rate of energy gain was held constant), with, again, disproportionately increasing variation for decreasing $P_s$ (Supplemental data 1). This means that some individuals in a population of foragers can be successful in terms of energy accumulation, and others markedly less so, even without invoking inter-individual differences in foraging abilities, which is normally suggested as the source of such variation [e.g.18]. It is particularly relevant that species taking more improbable food (such as apex predators or scavengers) are subject to an increasing element of (entirely unselective) detriment to an extent determined by their $P_s$ value.

This approach also demonstrates how decreasing $P_s$ substantially increases the variance in the times taken for species to reach a fixed energy target (Supplemental data 1) (Fig. 2). This is most germane in species seeking to provision their young with a set amount of energy within a particular time period, as is the norm. As before, this effect is most marked in animals feeding on food with low probabilities of acquisition (Figure 2B), such as apex predators, but of particular note is how this effect is exacerbated by the additional costs of breeding for a fixed $P_s$ value (Figure 2C).
Generally, the increased costs of reproduction will force animals to forage for longer, further increasing the foraging energy expended. Incorporation of these additional costs into our model for our three hypothetical species illustrates the huge variation between
individuals and species in the accumulation of energy reserves for reproduction according to \( P_s \) (Supplemental Figure S3). This variation defines the likelihood of ‘foraging ruin’, in which an animal uses up all of its energy available for reproduction during foraging due to repeated failure (Supporting data 1). It also highlights why the higher foraging costs and low energy reserves of apex-carnivores, such as wild dogs \textit{Lycaon pictus} [19] and cheetahs [20], which have been described as ‘living on an energetic knife edge’ should be associated with dramatically increased individual ruin probabilities (Figure 3), and that animals with lower rates of food acquisition taking higher value food items are more vulnerable to a given reduction in prey availability (Supplemental Figure S4).

![Figure 3. Probability of foraging ruin, \( P_R \), for apex predators.](image)

\( P_R \) is given for a range of initial energy values and probabilities of food encounter \( P_e \), in a scenario where one food encounter represents foraging success and the cost of foraging, \( C=1 \).

Our explicit example of how reproductive ruin is affected by probabilistic food encounter capitalizes on our data, together with other information on the ecological energetics, of African \textit{Spheniscus demersus} and Magellanic penguins. Magellanic
penguins have a large, stable population operating in an area with minimal commercial fishing pressure [21] while African penguins have a dramatically decreasing population, reportedly due to intense competition with commercial fishing fleets [22-24]. Using our estimate data of a $P_s$ of 0.03 for Magellanic penguins and calculating an equivalent value for African penguins to be 0.006, and combining these with data on the species-specific energy expenditures together with the energetic values of prey and the chick growth requirements (Supplemental information 4), allowed us to illustrate the marked divergence in the accumulation of energy by birds from the two species over foraging time (Figure 4). Specifically, the inter-individual variation in the Magellanic penguin was minimal, with all modelled animals acquiring enough food to meet all their energetic needs, including those of the brood, within a single day at sea. By contrast, although all modelled African penguins could acquire enough energy for the adult needs within a day, most could not acquire adequate food for their chicks in this time (Figure 4). This means either that the birds return to the nest with inadequate food to sustain appropriate chick growth [25] or that they remain at sea during the night, during which they cannot forage [21], and incur substantial extra energy costs which have to be made the next day. In this case, the provisioning rate is less than half the birds that were lucky enough to have acquired enough food within the first day (Fig. 4).
Animal lifestyle and $P_s$ values

Giving food acquisition a probabilistic $P_s$ value within a gamblers context for animals is important because it indicates how the energy of food items must relate to their abundance if animals are to breed successfully, or even survive. Generally, we expect $P_s$ values to reflect both food abundance and food quality: A low $P_s$ necessitates a high energetic gain from the foodstuff because all energy demands must be met by few food
encounters. Conversely, a higher $P_s$ means that food must be abundant [26]. This latter condition is met by lower trophic level foodstuffs, most notably plants [27] that are typically the domain of herbivores, with low energetic gain per unit time [28]. Such animals are anticipated to have foraging success most affected by the energetic value in their foods [29, 30]; reason enough though, for herbivores to be selective in what they eat [31], provided they balance returns with probabilities of encounter as they move to lower $P_s$ values [32]. The nutritional or energetic value of different foodstuffs [27] will tend to lead to carnivores generally having lower $P_s$ values than herbivores. However, this will be affected by prey size: Strategies will range from species that have multiple encounters with high quality, but small, prey (e.g. insectivores [33]) which need to be abundant (with high $P_s$ values), to species with the lowest $P_s$ values, that feed on large prey items (e.g. large cats and scavengers [17, 34]). Omnivorous animals, such as bears, may have variable $P_s$ values, consuming food items of highly variable energetic value [35]. This may make them less susceptible to probabilistic failure than the more specialized apex predators due to the diversity. Indeed, a specific benefit of omnivory, which is poorly dealt with by traditional models of diet choice [1], is that it partially deals with variance in food encounter rates due to the differential occurrence of the assorted components of the diet.

The implication is that animals operating with a low probability of food acquisition per unit time, such as many apex predators [36], are subject to selection pressure to minimize the metabolic costs of all activities [37]. For non-foraging behaviours, this may explain why large carnivores spend so much time ‘resting’ [36, 38] while many herbivores can engage in energetically taxing behaviour, such as males rutting and engaging in high speed chases to demonstrate fitness to females [39]. During foraging, it may explain why many mega-carnivores rely on low-cost sneak attacks on prey [34], and why cursorial predators, which rely on high power pursuit tactics, such as cheetahs [20] and wild dogs [19], should incur severe energetic penalties when subject to probabilistic failure [19]. Some mitigation of these effects may be achieved by species with lower $P_s$ having greater capacity for surviving longer periods without food, something enhanced by greater body size [16], but this brings with it complications in
prey-catching during active pursuits [40] and still leaves small-bodied young susceptible to starvation.

Previous work has shown the complexities of the factors affecting population processes [41, 42] and, within these, the fundamental role of food acquisition in breeding success has been repeatedly emphasized [42, 43], although the precise mechanistic link between energy gain and population success with respect to food has been unclear. As such, the biological relevance of gambler’s ruin for reproduction within and between similar species is likely to be profound, most particularly where food is rare because this detrimentally affects a greater proportion of the population based on ‘luck’ alone. This point is aptly illustrated by our two study Spheniscus penguins, one of which has a stable population [21] while the other is in serious decline [22, 23], with all the evidence pointing to the consequences of over-fishing as the prime cause [24]. Critically, we note how inter-individual variation in food encounter rates, presumably a direct consequence of food abundance, affects the rate at which food can be bought back to the nest (Figure 4).

Conclusions

This work illustrates how a systematic, non-selective proportion of populations can incur detriment with increasingly rare food, and provides a framework to consider how the reproductive success of apex predators and scavengers is likely to be dramatically different to that of species taking common food. It also highlights how even small changes in ecosystem functioning stemming from anthropogenic activities [44] may affect animals differentially according to the encounter probabilities of finding food. This might explain, for example, why Carbone et al. [45] found that larger carnivores show the most dramatic declines in numbers to decreasing prey abundance. Whilst there is no doubt that changes to animal populations in the Anthropocene are the result of complex processes, we suggest that the use of probabilistic frameworks relating reproductive ruin to foraging have an important role to play in our understating of population processes. Indeed, this may prove pivotal for assessing and predicting
population well-being as well as in helping formulate conservation plans as environmental conditions change [46].

STAR-Methods

Deposited Data

All input data

Method Details

Determination of food ingestion

‘Foraging’ is a general term used within a variety of contexts. We consider foraging to be all time consecrated to the process of searching for, and securing (but generally not handling unless it is virtually instantaneous (see supplementary information 1)), food. Thus, animals such as penguins and cheetahs may be able to see potential food, but these potential food items only become relevant to this study once they were secured. Seven Magellanic penguins at Cabo Virgenes, Argentina, during 2002 were equipped with Daily Diary loggers (DDs [47]) recording, at 6 Hz, dive depth and swim heading as well as Hall sensor-based jaw angle loggers which recorded, at 20 Hz, all prey items swallowed [48] during a single foraging trip for these birds at sea. These birds were considered to be foraging after they had ingested their first prey item and engaged in dives in excess of 5 m. Equivalent data were derived for the African penguin (see Supporting data 3). Six domestic sheep were studied, each for a full day, three in Patagonia, Argentina in 2014 and three in Northern Ireland during 2016, with bites of food being evident as a clear signal recorded by tri-axial accelerometers and/or magnetometers (in DDs), logging data at 40 Hz, attached to their heads [49]. As with the penguins, the sheep were considered to be foraging from the first bite of food. Seven condors, caught in Argentina during 2010-2014, were studied using DDs
recording pressure, tri-axial acceleration and tri-axial magnetic field intensity at 20 or 40 Hz for periods up to 10 days. These tags showed flight and feeding via characteristic changes in recorded pressure, acceleration and magnetic field intensity (cf. 40). They were assumed to be foraging in all flights except those immediately following feeding during which the birds were considered to be returning to roosting sites. Six cheetahs in the Kgalagadi Transfrontier Park, South Africa, were caught and fitted with tri-axial accelerometers recording at 30 Hz [50]. These animals were followed continuously during the day and occasionally at night for 4-6 days each, to document all hunting behaviours. The acceleration data were used for periods when the animals could not be observed, benefitting from matched acceleration signatures with activity gained during the observations. Animals were assumed to be foraging during all walking, stalking and chasing behaviours [49] except when walking occurred immediately after prey capture.

We note that there was appreciable difference in the handling time of food between the different species studied. For the condors and cheetahs, we did not include any handling within the foraging (food searching) time. For the penguins, the time taken to ingest a single prey item was typically <2 s [cf. 48], which is a small fraction of the inter-fish duration, implying that food acquisition (searching and then capturing) was the primary factor affecting inter-prey durations. However, for the sheep, the most likely explanation for most of the inter-bite durations (see frequency distribution in Figure 1) was actually food processing [51] so the P Experienced values should be seen within this context.

Modelling foraging energetics in penguins

We used 5 key parameters (Supporting data 3) to determine the percentage of breeding penguins (African or Magellanic) that manage to raise one, or two, chicks successfully to fledging. These are:

1. The probability of encountering prey (taken to be 0.006/s and 0.03/s for African and Magellanic Penguins, respectively)

2. The energy value of individual food items (taken to be 23290 J and 6104 J for African and Magellanic Penguins, respectively)
(3) The power costs of foraging (taken to be 44 W and 62 W for African and Magellanic Penguins, respectively)
(4) The power costs of not foraging (taken to be 14.5 W and 15.2 W for African and Magellanic Penguins, respectively)
(5) The total minimum mass of food that should be allocated to each chick to keep them alive varied between 206 g/d and 2191 g/d for African Penguins, for the smallest and largest chicks, respectively, and 275 g/d and 2921 g/d for Magellanic Penguins, for the smallest and largest chicks, respectively (because chick food requirements vary with chick size).

We ran a model that incorporated all the above parameters which started with a foraging penguin having, as a target, to acquire enough energy to pay for the total energy allocated to all non-foraging activities (including acquiring food for its chicks) as well as the energetic costs of its own foraging within a certain time period. During foraging, the model allowed the parent bird to find prey based on probabilities per unit time as described above and gained energy appropriately. Both penguin species typically provision chicks <40 days old, by having one parent foraging while the other broods, with roles switching when the foraging bird returns from sea [52]). For older chicks, both parents forage simultaneously, spending generally enough time at the nest to feed the brood before returning to sea. Penguins do not forage at night [53] so any adult that does not acquire enough food to feed the brood appropriately within one day foraging may spend the night at sea, incurring higher metabolic costs, before resuming foraging the next day. This process decreases the frequency of provisioning greatly and is incorporated within the model.

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AUTHOR CONTRIBUTIONS

RPW conceived the original idea, which was enhanced by discussions with all authors. MDH provided concepts for the animal-attached tags and programming for data analysis. AN and EC formulated the maths while RPW, ELCS, SAL, ADV, RL, CM, NM and DMS provided data. All authors discussed and developed the ideas and helped write the manuscript.

DECLARATION OF INTERESTS

The authors declare no competing interests.

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