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Luck in Food-finding Affects Individual Performance and Population Trajectories

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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 the environment and food distribution. Typically, differences between individuals in the rate of food acquisition are attributed to varying competencies [3] even though food encounter rates are known to be probabilistic [4]. 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 [5] through behavioural strategies [6] to population dynamics and food web structure [7]. However, although some work recognizes the importance of variation in rates of energy accumulation [8] and how animal condition depends on foraging decisions [9], 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 [10], which does not necessarily equate with linear rates of food

procurement across a population [4]. 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' [4]. 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 [11]). 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 (Figure 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 of the species considered (Figure 1). They were followed by the Magellanic penguins *Spheniscus magellanicus* (high power, pursuit piscivores that typically ingest dozens of prey items per trip [12]). 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 [13]) and the Andean condors *Vultur gryphus* (low power, scavenging carnivores that also, at best, encounter a single, high quality, food item per foraging trip [14]) 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 (Figure 1. See also Figure S1).

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 (Figure S1). A simple mathematical model using a binomial process 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. Using these three distinct P_s values as a basis to simulate the number of food items accumulated for three hypothetical species (Figure S2A – cf. Figure 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 (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. 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.15]. 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 (Figure 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. Of particular note, however, 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 (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. It also highlights why the higher foraging costs and low energy reserves of apex-carnivores, such as wild dogs *Lycaon pictus* [16] and cheetahs [17], which have been described as 'living on an energetic knife edge' should be associated with dramatically increased individual ruin probabilities (Figure 3. See also Figure S4), and that animals with lower rates of food acquisition taking higher value food items are more vulnerable to a given reduction in prey availability (Figure S4).

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 *Spheniscus demersus* and Magellanic penguins. Magellanic penguins have a large, stable population operating in an area with minimal commercial fishing pressure [18] while African penguins have a dramatically decreasing population, reportedly due to intense competition with commercial fishing fleets [19]. Using our estimated 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, 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 [20] or that they remain at sea during the night, during which they cannot forage [18], and incur substantial extra energy costs which have to be made good the next day. In this case, the provisioning rate is less than half that of the birds that were lucky enough to have acquired enough food within the first day (Figure 4).

Animal lifestyle and P_s values

Giving food acquisition a probabilistic P_s value within a gambler's 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 [21]. This latter condition is met by lower trophic level foodstuffs, most notably plants [22], that are typically the domain of herbivores, with low energetic gain per unit time [23]. Such animals are anticipated to have foraging success most affected by the energetic value in their foods [24]; reason enough though, for herbivores to be selective in what they eat [25], provided they balance returns with probabilities of encounter as they move to lower P_s values [26]. The nutritional or energetic value of different foodstuffs [22] 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 [27]) which need to be abundant (with high P_s values), to species with the lowest P_s values (e.g. large cats and scavengers) that feed on large prey items [14, 28]. Omnivorous animals, such as bears, may have variable P_s values, consuming food items of highly variable energetic value [29]. This may make them less susceptible to probabilistic failure than the more specialized apex predators due to the diversity of their diet. 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 and scavengers, are subject to selection pressure to minimize the metabolic costs of all activities [30]. For non-foraging behaviours, this may explain why large carnivores spend so much time 'resting' [31] while many herbivores can engage in energetically taxing behaviour, such as males rutting and engaging in high speed chases to demonstrate fitness to females [32]. During foraging, it may explain why many mega-carnivores rely on low-cost sneak attacks on prey [28], and why cursorial predators, which rely on high power pursuit tactics, such as cheetahs [17] and wild dogs [16], should incur severe energetic penalties when subject to probabilistic failure [16]. 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 [33], but this brings with it complications in prey-catching during active pursuits [34] and still leaves small-bodied young susceptible to starvation.

Previous work has shown the complexities of the factors affecting population processes [35] and, within these, the fundamental role of food acquisition in breeding success has been repeatedly emphasized [36], 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 [18] while the other is in serious decline [19], with all the evidence pointing to the consequences of excessive fishing as the prime cause [19]. 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 [37] may affect animals differentially according to the encounter probabilities of finding food. This might explain, for example, why Carbone et al. [38] 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 [39].

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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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Figure captions

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). See also Figure S1.

Figure 2. The success time (T_s) required to accumulate a target energy.

(A) Distribution of T_s to accumulate 3000 units of energy using the probability of food encounter per second search (P_s) from our study species. The mean rate of energy accumulation is kept constant across species by varying the energy return in a single food item (G); $G = 3$ for the sheep, $G = 5$ for the penguin, and $G = 3750$ for the condor. (B) The mean success time (blue line) and variation around it (orange and green lines; σ denotes the standard deviation) required to accumulate 3000 units of energy for a range of P_s values. Here, G is scaled to keep the mean rate of energy accumulation constant. (C) Standard deviations in T_s, for a range of target energies (which may represent non-foraging costs such as breeding) plotted over a range of P_s. The size of energy reward, G, is scaled to keep the mean rate of energy accumulation constant.

Figure 3. Probability of foraging ruin, P_R, for apex predators.

P_R is given for a range of initial energy values and probabilities of food encounter, P_s, in a scenario where one food encounter represents foraging success and the cost of foraging $C = 1$. See also Figure S4.

Figure 4. Likelihood of reproductive ruin due to variation in time taken to acquire food in two penguin species.

Modelled rates of energy gain for 20 African penguins (red lines) and 20 Magellanic penguins (blue lines) using data on the metabolic rates for different activities and time budgets of breeding adults, amounts of food needed by chicks according to age (for 35 day-old chicks), and probabilities of prey encounter. We assume adults

persist with neutral energy balance, here indicated by the 0 line (adult penguin threshold), which is crossed during foraging. Energy is assumed to be acquired probabilistically. Both species easily recoup their lost body energy (where they cross the adult threshold/green line) within the first foraging day. The Magellanic penguins also easily gain all the energy needed for their chicks (blue horizontal line) (cf. blue frequency histogram) but 16 of the 20 individual African penguins fail to do so (black lines). If these birds remain at sea to make up the difference, they pay the elevated metabolic cost of this, have to pay the consequent extended stay once at the nest, but cannot even acquire a time-corrected amount of food for the chicks due to limitations in stomach size. All this decreases the provisioning rate substantially (red histogram) cf. Figure S4.

STAR*Methods

Deposited Data

All input data

Method Details

EXPERIMENTAL MODEL AND SUBJECT 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), 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 [40]) 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 [41] 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. 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 [42]. 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 [43]. 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 [42] 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. 41], 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 [44] so the P_s-values should be seen within this context. It is an oversimplification to preclude handling times and food gathering success for our modelling process (see below). For example, if a large carnivore makes a large kill, it may not resume hunting for several days. In contrast, if it fails, it will continue to hunt, so that this process will affect the inter-individual variance in kill rates. We attempted to mitigate for some of this by identifying, as far as possible, proper foraging behaviour (see above) but the approach is undoubtedly imperfect. In addition though, lack of hunting success may also reduce body condition, which could, in turn, promote lack of foraging success, effectively changing the P_s-value of the animal in question.

METHOD DETAILS

A simple probabilistic model for foraging

Consider an animal foraging for food, whereby foraging is defined as periods of time during which animals are actually searching for food rather than, for example, commuting to a foraging site or handling food.

Making these assumptions, we divide time into discrete steps of equal length which we number as step n=1, 2, 3, …, N. Nominally, these would be e.g. seconds. At each time step, the animal is either successful at finding food or it finds nothing. Suppose the reward for successfully acquiring a food item is a gain in energy of value G and that the cost of foraging per time step is given by C. We let;

  a) $F(n)$ denote the number of food items collected up to, and including, time step n,

  b) $E(n)$ denote the amount of energy gained up to, and including, time step n,

  c) $S(n)$ denote the total energy reserves of the animal at time step n.

We suppose that the probability of success at each time step is given by P_s and the probability of failure at each time step is given by 1- P_s. If, at time n, the animal is successful, we set $X(n) = 1$ and if it is unsuccessful we set $X(n) = 0$. Our model is then given by the equations;

$$F(n) = \sum_{j=1}^{n} X(j), \quad E(n) = G \sum_{j=1}^{n} X(j), \quad S(n) = u - nC + G \sum_{j=1}^{n} X(j)$$

where u denotes the initial energy reserves of the animal. These types of models are known as "Binomial Processes" and full details of their study can be found in [45]. (An extensive mathematical theory for models generalising $S(n)$ also already exists, having been developed to study the mathematics of random storage problems and the theory of insurance [46]).

For given values of P_s, u, G, C and N, our model can be simulated for the first N time steps as follows;

> $F(0) = 0; E(0) = 0; S(0) = u$
> FOR $n = 1$ TO N
>> $X(n) = 1$ with probability P_S OR $X(n) = 0$ with probability $1 - P_S$
>> $F(n) = F(n-1) + X(n)$
>> $E(n) = E(n-1) + G \times X(n)$
>> $S(n) = S(n-1) - C + G \times X(n)$
> END FOR

This approach has been used to generate the data in Figures 4, S2A, and S3

Exact formulae are known for many properties of this model[1]. The mean rate of energy accumulation is $P_s G$, and the mean net rate of energy accumulation is $(P_s G - C)$. If we let T_{Search} denote the search time the animal spends between consecutive successes, then the mean search time is given by $\frac{1}{P_s}$ and the variance in the search times is $\frac{(1-P_s)}{P_s^2}$. Therefore, in our model, as P_s decreases, both the average and variance in the search time will increase, with disproportionate changes when P_s is already small (see Figure S2B.).

Suppose that the animal has an energy accumulation target of M units of energy. Given that a successful forage results in a reward of G units of energy, the animal will reach its target when it has accumulated k successes, where k is the smallest integer greater than $\frac{M}{G}$. If we let T_s denote the success time required for an animal to achieve k successes, then the probability that $T_s = n$ is given by;

$$\binom{n-1}{n-k} P_s^{\,k} (1 - P_s)^{n-k}$$

(see Figure 2B), the mean success time is $\frac{k}{P_s}$ and the variance in the success time is $\frac{(1-P_s)k}{P_s^2}$ (see Figure 2C).

Suppose we consider two different species of foraging animals with the same mean rate of accumulation of energy $\mu = P_S G$, the same energy accumulation target M but differing values of P_S. Then, the variance in the energy accumulated in n time steps by each species is $\mu^2 n \left(\frac{1}{P_S} - 1 \right)$ while the mean success time is $\frac{M}{\mu}$ and variance in the success time is $\frac{(1-P_S)M}{P_S \mu}$ where, for mathematical simplicity, we assume that $\frac{M}{G}$ is an integer. Thus, as the probability of success P_S decreases towards 0, the average length of time taken to forage, and the variance in both the energy gain and time taken to forage will increase disproportionately (see Figure 2B).

We can also use $S(n)$ to consider two different ruin scenarios:

1. The animal could forage indefinitely until it has either reached a given success target or run out of energy (i.e. until $S(n) \leq 0$), with the latter considered as *individual ruin.*

2. The animal could be required to accumulate enough energy in a fixed time period to sustain its offspring. That is, it is restricted to forage for, at most, a fixed period of time of length *N*, stopping once the required success target is reached, with failure to reach the target before reaching the end time considered as *reproductive ruin.*

As an example, calculating the probability of individual ruin is straightforward in the case where only one success is sufficient to reach the success target. Such a situation corresponds to most apex predators. In this scenario, given that the animal begins foraging with some initial energy *u* and loses *C* units of energy for each unsuccessful attempt, the only way for individual ruin to occur is if the animal experiences exactly z successive losses where z is the smallest integer greater than u/C. Therefore, the ruin probability P_R (see Figure 3) here is;

$$P_R = (1 - P_S)^z$$

Estimating P_S

The value of P_S for a given species can be estimated using data accumulated from the animal-attached tags collating the time between the acquisition of food items. If our model for food accumulation as described above holds with the discrete time steps taken as 1 second long, then an estimator $\widehat{P}_S$ for the parameter P_S is given by;

$$\widehat{P}_s = \frac{1}{\overline{T_{Search}}}$$

where $\overline{T_{Search}}$ denotes the sample mean of the search time in the collected data for each individual species. For the data collected we have the following results ($\widehat{P}_s$ given to 1 significant figure):

Animal	$\overline{T_{Search}}$ (seconds)	$\widehat{P}_s$
Sheep	22	0.05
Penguin	33	0.03
Cheetah	27,055	0.00004
Condor	24,903	0.00004

The sheep P_s values are notably close to those of the penguin because the mean search times are similar, even though the inter-bite/prey frequency distributions are very different (Figure 1). This is because the sheep occasionally had much longer periods between bites (which are not shown in Figure 1 for scaling reasons). We have no *a priori* reason to preclude these long periods from our analysis although it is possible (even likely) that the animals were engaging in activities other than searching for food. The effect of precluding long intervals is appreciable: By simply excluding all inter-bite durations greater than 100 s for sheep, for example, the mean search time decreases to 10 s and raises the P_s-value to around 0.1. Similarly, excluding all inter-bite intervals greater than 50 s and 10 s produces P_s-values of 0.1 and 0.5, respectively (with mean inter-bite durations of 7.1 s and 2 s, respectively). This demonstrates the importance of determining when an animal is actually searching for food but also highlights the particular case of herbivores within this context. Importantly though, changes in P_s-values change the variation in outcomes less for higher values than for low ones (cf. Figure 2).

Modelling foraging energetics in penguins

In brief, we used 5 key parameters 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).

Details on the five key parameters used to inform the model are;

(1) <u>The probability of encountering prey</u> was taken to be 0.03/s for Magellanic Penguins using data presented in this work. The equivalent figure for African Penguins (P_s = 0.006) was derived from data collected in 1981, equating distance swum underwater with mass of food ingested [47, 48] from 15 birds. The distance swum during foraging was converted to time spent foraging by using a swim speed of 2.02 m/s [49] and mean dive and pause durations of 43 s and 18 s, respectively [49]. The mass of food ingested by each individual was converted to number of prey by dividing the total mass ingested by the mean prey mass (see below).

(2) <u>The energy value of food items</u> used data on the primary prey of Magellanic Penguins, which was *Sprattus sprattus* at the study site [12] which had a metabolizable energy of 2.18 kJ/g (wet mass) from Ciancio et al. [50] with a mean size of 2.8 g, giving a metabolizable energy of 6100 J per mean prey. The primary prey of African Penguins at the time (and location) that the prey ingestion *versus* distance swum data were collected, was Cape Anchovy *Engraulis japonicus/capensis* with a modal length of 85 mm [51], which equates to a prey mass of 4.54 g. Since these anchovies have a

metabolizable energy content of 5.13 kJ/g [52], a single prey item yields 23290 J of energy.

(3) <u>The power costs for foraging</u> were split into two basic activities; underwater swimming and surface resting. Estimations for power to swim underwater as a function of speed (v) were taken from Luna-Jorquera & Culik [53], derived from the congeneric Humboldt Penguin *Spheniscus humboldti*, where mass-specific power = $2.954v^3$-$6.354v^2$+$5.818v$+ RMR, using a mass-specific RMR in water for African Penguins of 11.3 W [52] and that of Magellanics to be 5.9 W [53, 54]. Correcting these to normal swim speeds of 2.02 m/s for the African Penguins [49] and 2.1 m/s for Magellanic Penguins [54], and accounting for dive *versus* surface pause durations (of 43:18 s for African Penguins [49] and 74:15 s for Magellanic Penguins [54, 55]), results in total bird power requirements for foraging African Penguins of about 44 W, while those for Magellanic Penguins are estimated to be *ca.* 62 W.

(4) <u>The power costs for not foraging</u> are the costs of the birds on land, for which the costs were taken to be 14.5 W for the African Penguin [52] and 15.2 W for the Magellanic Penguin [53, 56].

(5) <u>The total energy allocated to all activities that are not foraging</u> is primarily composed of (i) the total energy spent on land by multiplying the power costs for being on land (see above) by the time spent on land per chick-provisioning period considered and (ii) any energy that is gathered for the brood. With respect to (i), we assumed that adults only foraged during daylight [18, 57]. With respect to (ii), Cooper [20] gives data for the mass of food ingested by wild African Penguin chicks growing notably slowly. These data were fitted with an inverse logistic equation by Wilson [47] to give; Mass ingested/day = $235/(1+6e^{-0.08A})$, where A is the age in days. We adopted this, and multiplied it by 4/3 for Magellanic Penguin chicks (because the adult birds weigh 4 kg and adult African Penguins weigh 3 kg [18] and we expect food requirements of chicks to scale approximately) to describe food requirements of individual chicks in the brood, which nominally contains two chicks in both species [18]. We assumed a metabolizable energy content of 5130 J/g wet weight for Cape Anchovy [52] and 2180 J/g wet weight for sprat [50] which was added to the total energy allocated to non-foraging activities. Both African and Magellanic

Penguins have brood-rearing periods that last about 60 days [18] and the susceptibility of chicks to death via starvation varies with age [47].

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. For our example, we used adults feeding chicks that were 35 days old (approximately half-way through the chick-rearing period). Penguins do not forage at night [57] 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.

Model flow and key parameters used to inform the model predicting breeding ruin in penguins

The model was based on the following coding;
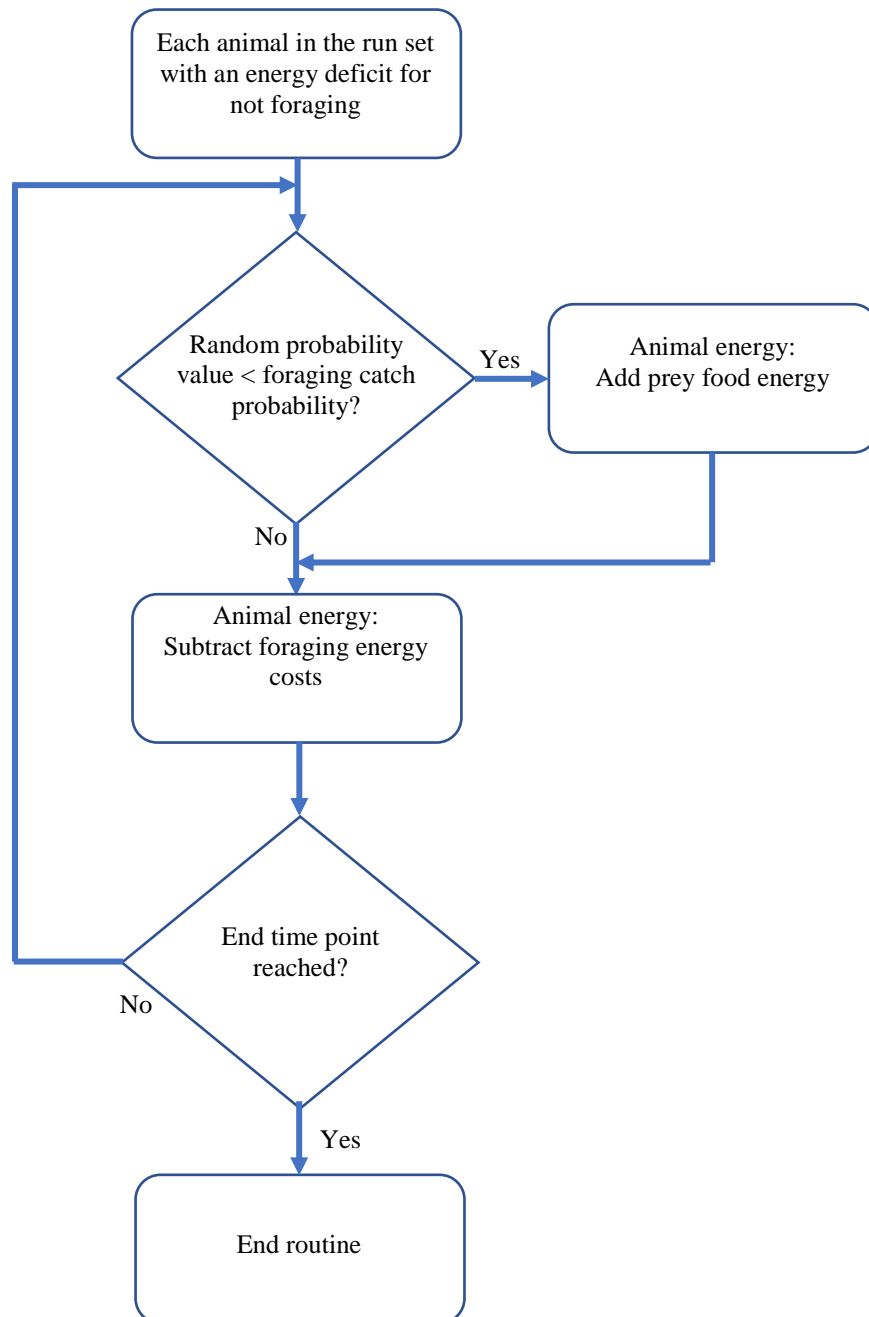
DATA AND SOFTWARE AVAILABILITY

The software used in the work follows the protocols indicated above.

The data on feeding rates have been deposited in the Dryad repository and can be accessed via; link xxxxxxx. doi:10.5061/dryad.g7k8j6v
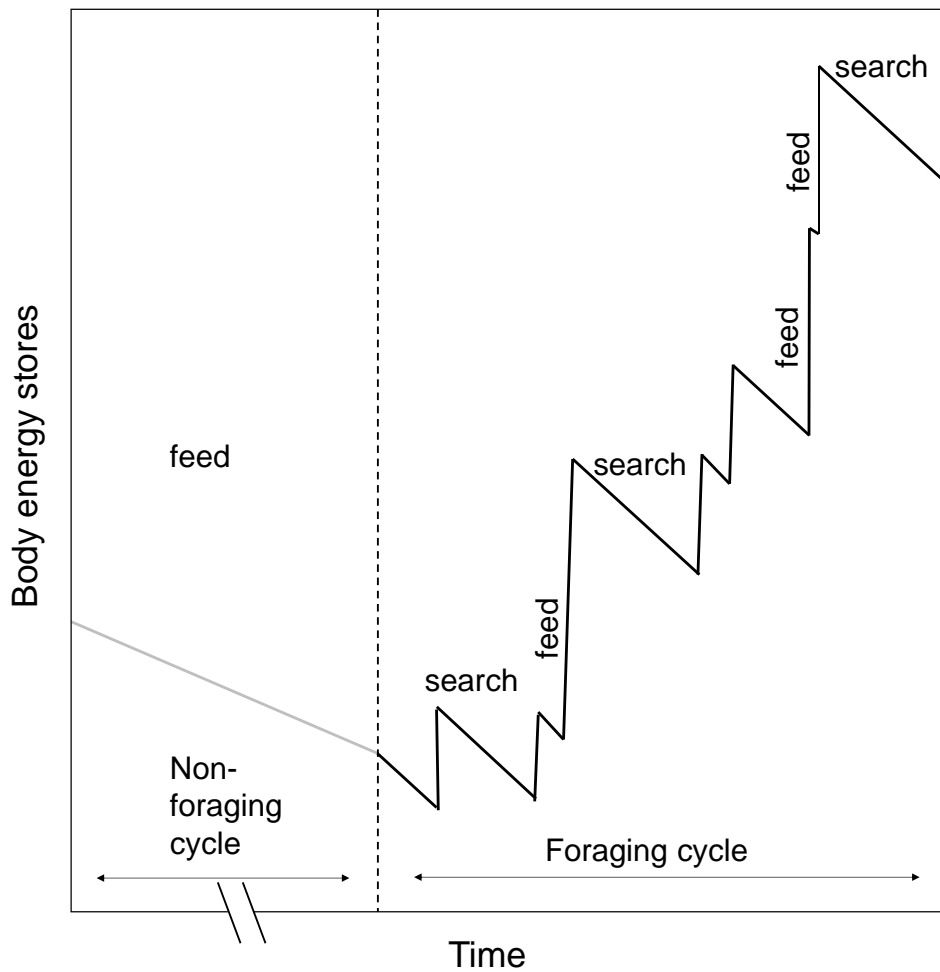
Figure S1. Schematic diagram illustrating changes in overall body energy reserves over time for a foraging animal, Related to Figure 1.

During the non-foraging cycle (grey line), there is only energy expenditure with no energy acquisition. Subsequently, during foraging, although energy is lost during searching, the energy acquired by feeding normally more than compensates for this. Typically, an animal will search for a period and then ingest food before searching again. The variability in the search durations, represented by their frequency distributions is a measure of the time-based probability of success. The energy contained within each food item is a measure of the reward while the energy expended to acquire it is the cost, with the ratio of these two latter terms representing the net energy gain over time.
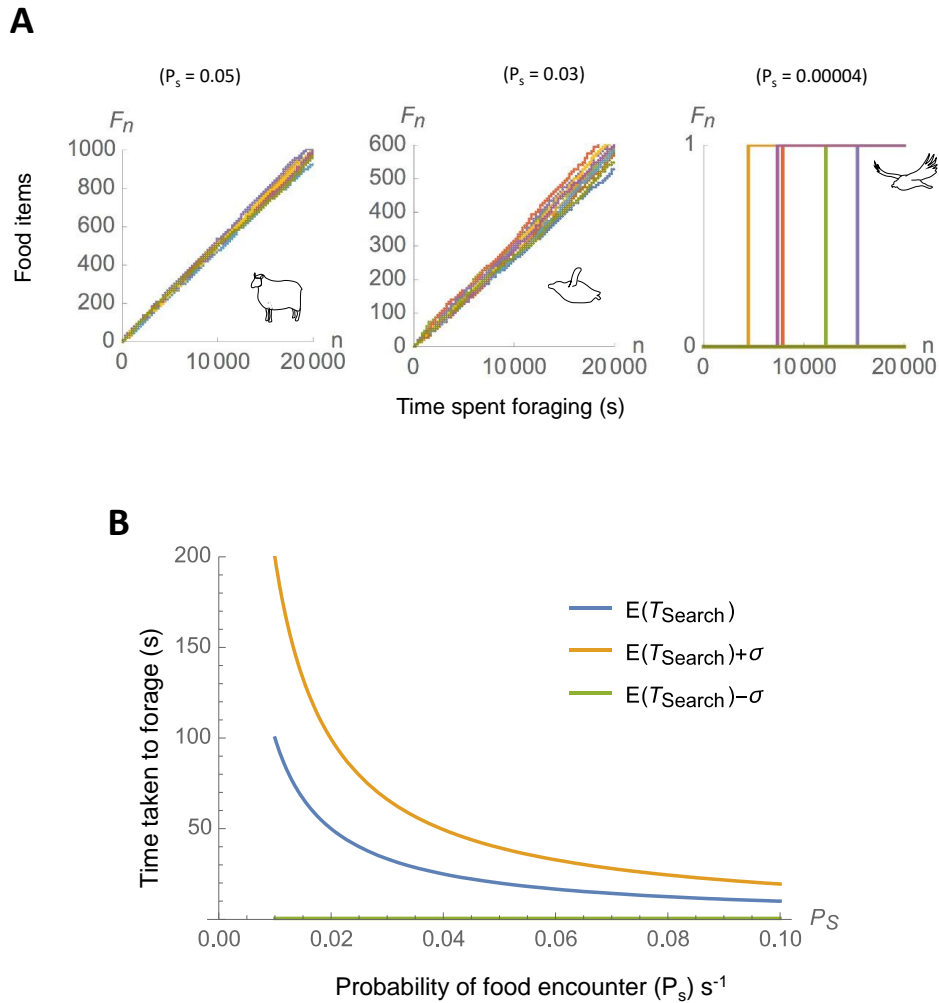
Figure S2. Accumulation of food items and time taken to forage for animals with different probabilities of finding food, Related to STAR Methods.

A. Predicted accumulation of food items over time by 10 individuals of three different animals foraging with varying probabilities of food encounter per unit time (P_s). The right hand panel has a low probability, like the condor or cheetah, the middle panel a medium probability, like the penguin, while the left hand panel has a high probability, like the sheep.

B. Mean of the search times T_{Search} for each success in finding a food item for a range of values of the probability of success. σ denotes the standard deviation of the distribution of T_{Search}.
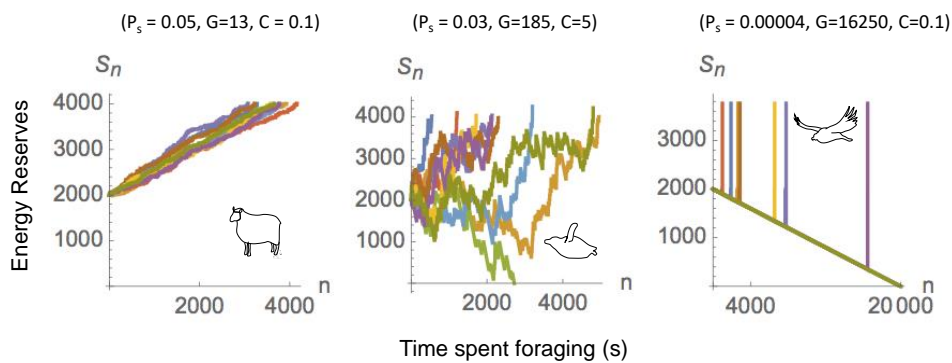
Figure S3. Simulations of energy reserves (S_n) over time showing intra- and interspecific variation, Related to STAR Methods.

Simulations were run for 10 individuals of three different animals foraging with varying probabilities of food encounter per unit time (P_s), gains per success (G) and costs per unit time (C). Each example has the same mean net rate of energy gain (0.55), energy target (4,000 units) and initial energy allocation (2,000 units). 'Ruin' has occurred when the energy reserves reach 0.
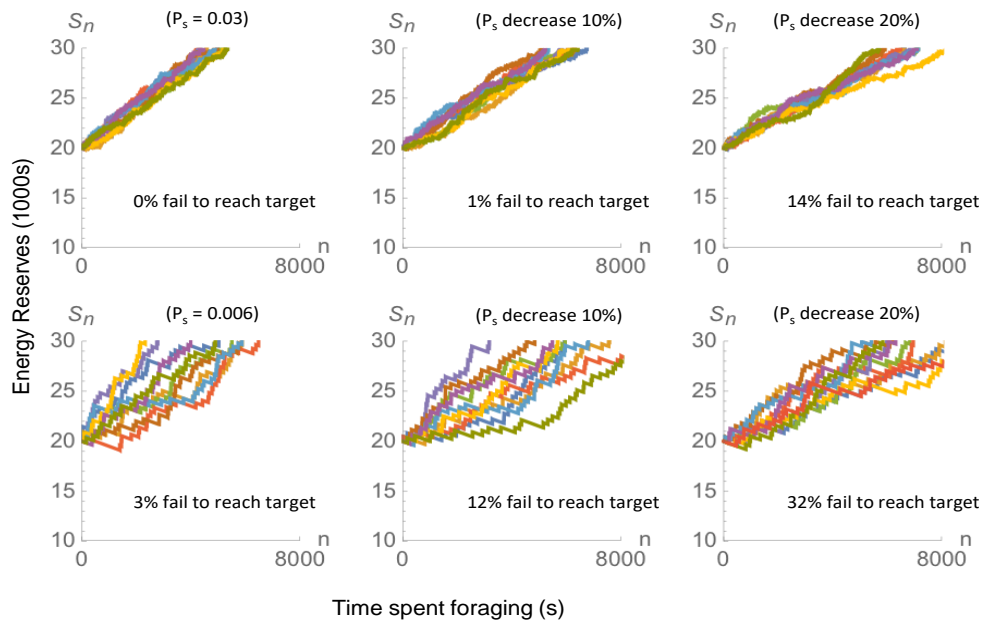
Figure S4. Simulations of energy reserves (S_n) over time for two populations as P_s is reduced, Related to Figure 3

Simulations were run for 500 individuals (10 are shown) of two different animals to illustrate the effect on populations subject to a reduction in P_s. The top row shows an animal with $G = 100$, $C = 1$ and initial $P_s = 0.03$, which is then reduced by 10% and 20%. The bottom row shows an animal with $G = 500$, $C = 1$ and initial $P_s = 0.006$, then reduced by 10% and 20%. Each initial example has the same mean net rate of energy gain (2), energy target (30,000 units) and initial energy allocation (20,000 units). The percentage of individuals in the simulation failing to reach the energy target within 8,000 s is recorded. Both populations appear stable initially but a reduction in the P_s value in the second scenario leads to a greater proportion failing to reach the target due to increased variance.