**QUEEN'S
UNIVERSITY
BELFAST**

Luck in Food-finding Affects Individual Performance and Population Trajectories

Wilson, R. P., Neate, A., Holton, M. D., Shepard, E. L. C., Scantlebury, D. M., Lambertucci, S. A., Di Virgilio, A., Crooks, E., Mulvenna, C., & Marks, N. (2018). Luck in Food-finding Affects Individual Performance and Population Trajectories. *Current Biology*, 28(23), 3871-3877.e5. <https://doi.org/10.1016/j.cub.2018.10.034>

Published in:
Current Biology

Document Version:
Peer reviewed version

Queen's University Belfast - Research Portal:
[Link to publication record in Queen's University Belfast Research Portal](#)

Publisher rights

Copyright 2018 Elsevier Ltd.

This manuscript is distributed under a Creative Commons Attribution-NonCommercial-NoDerivs License

(<https://creativecommons.org/licenses/by-nc-nd/4.0/>), which permits distribution and reproduction for non-commercial purposes, provided the author and source are cited.

General rights

Copyright for the publications made accessible via the Queen's University Belfast Research Portal is retained by the author(s) and / or other copyright owners and it is a condition of accessing these publications that users recognise and abide by the legal requirements associated with these rights.

Take down policy

The Research Portal is Queen's institutional repository that provides access to Queen's research output. Every effort has been made to ensure that content in the Research Portal does not infringe any person's rights, or applicable UK laws. If you discover content in the Research Portal that you believe breaches copyright or violates any law, please contact openaccess@qub.ac.uk.

Luck in Food-finding Affects Individual Performance and Population Trajectories

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

Rory P. Wilson^{1*}, Andrew Neate², Mark D. Holton³, Emily L. C. Shepard¹, D. Michael Scantlebury⁴, Sergio A. Lambertucci⁵, Agustina di Virgilio^{5,6}, Elaine Crooks², Christina Mulvenna⁴, and Nikki Marks⁴

¹Swansea Lab for Animal Movement, Biosciences, College of Science, Swansea University, Singleton Park, Swansea SA2 8PP, UK.

²Department of Mathematics, College of Science, Swansea University, Singleton Park, Swansea SA2 8PP, UK.

³Department of Computer Science, College of Science, Swansea University, Singleton Park, Swansea SA2 8PP, UK

⁴School of Biological Sciences, Institute for Global Food Security, Queen's University Belfast, Belfast BT9 7BL, UK.

⁵Grupo de Investigaciones en Biología de la Conservación, Laboratorio Ecotono, INIBIOMA (CONICET-Universidad Nacional del Comahue), Bariloche, Argentina.

⁶Grupo de Ecología Cuantitativa, INIBIOMA (CONICET-Universidad Nacional del Comahue), Bariloche, Argentina.

* Correspondence: r.p.wilson@swansea.ac.uk (R.P.W.)

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).

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.

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 *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.

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, $C=1$.

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 [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).

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- (red lines) and Magellanic penguins (blue lines) using data on the metabolic rates of 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 then 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 16/20 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 costs 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 rates substantially (red histogram) cf. Supplemental Figure S4.

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_s -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.

ACKNOWLEDGEMENTS

We thank SANParks and the Department of Wildlife and National Parks, Botswana for allowing our research in the Kgalagadi Transfrontier Park (Permit Number 2006-05-01 MGLM) and Mr H. McKay and Mr W. Wright for their co-operation. The study was made possible by various grants; a Leverhulme early career fellowship (ELCS), Fundación BBVa, PICT_BID-2014-0725 (SAL), the National Geographic Global Exploration Fund

(#GEFNE89-13) the Royal Society (2009/R3 JP090604), NERC (NE/I002030/1) (DMS), and the Royal Society/Wolfson Lab refurbishment scheme (RPW). We also thank the Lewis Foundation, South Africa, The Howard G. Buffet Foundation, National Geographic, Kanabo Conservation Link, Comanis Foundation, Panthera and the Kruger Park Marathon Club for financial support. We appreciate the support by DAERA, the Nature Conservancy and S. Gary for the sheep work and Gus Mills for help with the cheetahs.

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.

REFERENCES

1. Pyke, G.H., Pulliam, H.R., and Charnov, E.L. (1977). Optimal foraging: a selective review of theory and tests. *The quarterly review of biology* 52, 137-154.
2. Côté, S.D., Rooney, T.P., Tremblay, J.-P., Dussault, C., and Waller, D.M. (2004). Ecological impacts of deer overabundance. *Annu. Rev. Ecol. Evol. Syst.* 35, 113-147.
3. Yasué, M., Quinn, J.L., and Cresswell, W. (2003). Multiple effects of weather on the starvation and predation risk trade-off in choice of feeding location in Redshanks. *Functional Ecology* 17, 727-736.
4. Janetos, A.C., and Cole, B.J. (1981). Imperfectly optimal animals. *Behavioral Ecology and Sociobiology* 9, 203-209.
5. Darwin, C., and Bynum, W.F. (2009). *The origin of species by means of natural selection: or, the preservation of favored races in the struggle for life*, (Penguin).
6. McNamara, J., and Houston, A. (1990). Starvation and predation in a patchy environment. In *Living in a Patchy Environment*, B. Shorrocks and I. Swingland, eds. (Oxford University Press).
7. Sims, D.W., Southall, E.J., Humphries, N.E., Hays, G.C., Bradshaw, C.J., Pitchford, J.W., James, A., Ahmed, M.Z., Brierley, A.S., and Hindell, M.A. (2008). Scaling laws of marine predator search behaviour. *Nature* 451, 1098.

8. Estabrook, G.F., and Dunham, A.E. (1976). Optimal diet as a function of absolute abundance, relative abundance, and relative value of available prey. *The American Naturalist* 110, 401-413.
9. Houston, A.I., and McNamara, J.M. (1999). *Models of adaptive behaviour: an approach based on state*, (Cambridge University Press).
10. Haerter, J.O., Mitarai, N., and Sneppen, K. (2016). Food web assembly rules for generalized Lotka-Volterra equations. *PLoS computational biology* 12, e1004727.
11. Rands, S.A., Cowlshaw, G., Pettifor, R.A., Rowcliffe, J.M., and Johnstone, R.A. (2003). Spontaneous emergence of leaders and followers in foraging pairs. *Nature* 423, 432.
12. Houston, A., Clark, C., McNamara, J., and Mangel, M. (1988). Dynamic models in behavioural and evolutionary ecology. *Nature* 332, 29-34.
13. Caraco, T., Martindale, S., and Whittam, T.S. (1980). An empirical demonstration of risk-sensitive foraging preferences. *Animal Behaviour* 28, 820-830.
14. Wilson, R.P., Jackson, S., and Thor Straten, M. (2007). Rates of food consumption in free-living Magellanic Penguins *Spheniscus magellanicus*. *Mar Ornithol* 35, 109-111.
15. Mills, M., Broomhall, L.S., and du Toit, J.T. (2004). Cheetah *Acinonyx jubatus* feeding ecology in the Kruger National Park and a comparison across African savanna habitats: is the cheetah only a successful hunter on open grassland plains? *Wildlife Biology* 10, 177-186.
16. Ruxton, G.D., and Houston, D.C. (2004). Obligate vertebrate scavengers must be large soaring fliers. *Journal of theoretical biology* 228, 431-436.
17. Lambertucci, S.A., Trejo, A., Di Martino, S., Sánchez-Zapata, J.A., Donazar, J.A., and Hiraldo, F. (2009). Spatial and temporal patterns in the diet of the Andean condor: ecological replacement of native fauna by exotic species. *Animal Conservation* 12, 338-345.
18. Smith, B.R., and Blumstein, D.T. (2008). Fitness consequences of personality: a meta-analysis. *Behavioral Ecology* 19, 448-455.
19. Gorman, M.L., Mills, M.G., Raath, J.P., and Speakman, J.R. (1998). High hunting costs make African wild dogs vulnerable to kleptoparasitism by hyaenas. *Nature* 391, 479.
20. Scantlebury, D.M., Mills, M.G., Wilson, R.P., Wilson, J.W., Mills, M.E., Durant, S.M., Bennett, N.C., Bradford, P., Marks, N.J., and Speakman, J.R. (2014). Flexible energetics of cheetah hunting strategies provide resistance against kleptoparasitism. *Science* 346, 79-81.
21. Williams, T.D. (1995). *The penguins: Spheniscidae*, Volume 2, (Oxford University Press, USA).
22. Crawford, R., Altwegg, R., Barham, B., Barham, P., Durant, J., Dyer, B., Geldenhuys, D., Makhado, A., Pichegru, L., and Ryan, P. (2011). Collapse of South Africa's penguins in the early 21st century. *African Journal of Marine Science* 33, 139-156.
23. Crawford, R., Williams, A., Hofmeyr, J., Klages, N., Randall, R., Cooper, J., Dyer, B., and Chesselet, Y. (1995). Trends of African Penguin *Spheniscus demersus* populations in the 20th century. *South African Journal of Marine Science* 16, 101-118.
24. Sherley, R.B., Underhill, L.G., Barham, B.J., Barham, P.J., Coetzee, J.C., Crawford, R.J., Dyer, B.M., Leshoro, T.M., and Upfold, L. (2013). Influence of local and regional prey availability on breeding performance of African penguins *Spheniscus demersus*. *Marine Ecology Progress Series* 473, 291-301.
25. Cooper, J. (1977). Energetic requirements for growth of the jackass penguin. *African Zoology* 12, 201-213.
26. Nagy, K.A., Girard, I.A., and Brown, T.K. (1999). Energetics of free-ranging mammals, reptiles, and birds. *Annual review of nutrition* 19, 247-277.
27. Williams, R.J., and Martinez, N.D. (2004). Limits to trophic levels and omnivory in complex food webs: theory and data. *The American Naturalist* 163, 458-468.
28. Castro, G., Stoyan, N., and Myers, J. (1989). Assimilation efficiency in birds: a function of taxon or food type? *Comparative Biochemistry and Physiology Part A: Physiology* 92, 271-278.
29. Leeuw, J.d., and Bakker, J. (1986). Sheep-grazing with different foraging efficiencies in a Dutch mixed grassland. *Journal of Applied Ecology*, 781-793.
30. Fryxell, J.M., Wilmschurst, J.F., and Sinclair, A.R. (2004). Predictive models of movement by Serengeti grazers. *Ecology* 85, 2429-2435.
31. Grant, C., and Scholes, M. (2006). The importance of nutrient hot-spots in the conservation and management of large wild mammalian herbivores in semi-arid savannas. *Biological Conservation* 130, 426-437.
32. Fortin, D., Merkle, J.A., Sigaud, M., Cherry, S.G., Plante, S., Drolet, A., and Labrecque, M. (2015). Temporal dynamics in the foraging decisions of large herbivores. *Animal Production Science* 55, 376-383.

33. Bryant, D., and Bryant, V. (1988). Assimilation efficiency and growth of nestling insectivores. *Ibis* *130*, 268-274.
34. Williams, T.M., Wolfe, L., Davis, T., Kendall, T., Richter, B., Wang, Y., Bryce, C., Elkaim, G.H., and Wilmers, C.C. (2014). Instantaneous energetics of puma kills reveal advantage of felid sneak attacks. *Science* *346*, 81-85.
35. Elgmork, K., and Kaasa, J. (1992). Food habits and foraging of the brown bear *Ursus arctos* in central south Norway. *Ecography* *15*, 101-110.
36. Carbone, C., Mace, G.M., Roberts, S.C., and Macdonald, D.W. (1999). Energetic constraints on the diet of terrestrial carnivores. *Nature* *402*, 286-288.
37. Anderson, R.A., and Karasov, W. (1981). Contrasts in energy intake and expenditure in sit-and-wait and widely foraging lizards. *Oecologia* *49*, 67-72.
38. Schaller, G.B. (2009). *The Serengeti lion: a study of predator-prey relations*, (University of Chicago Press).
39. Byers, J., Hebets, E., and Podos, J. (2010). Female mate choice based upon male motor performance. *Animal Behaviour* *79*, 771-778.
40. Wilson, R.P., Griffiths, I.W., Mills, M.G., Carbone, C., Wilson, J.W., and Scantlebury, D.M. (2015). Mass enhances speed but diminishes turn capacity in terrestrial pursuit predators. *Elife* *4*, e06487.
41. Gaillard, J.-M., Festa-Bianchet, M., and Yoccoz, N.G. (1998). Population dynamics of large herbivores: variable recruitment with constant adult survival. *Trends in Ecology & Evolution* *13*, 58-63.
42. Prevedello, J.A., Dickman, C.R., Vieira, M.V., and Vieira, E.M. (2013). Population responses of small mammals to food supply and predators: a global meta-analysis. *Journal of Animal Ecology* *82*, 927-936.
43. Hempson, G., Illius, A., Hendricks, H., Bond, W., and Vetter, S. (2015). Herbivore population regulation and resource heterogeneity in a stochastic environment. *Ecology* *96*, 2170-2180.
44. Msuha, M.J., Carbone, C., Pettorelli, N., and Durant, S.M. (2012). Conserving biodiversity in a changing world: land use change and species richness in northern Tanzania. *Biodiversity and Conservation* *21*, 2747-2759.
45. Carbone, C., Pettorelli, N., and Stephens, P.A. (2010). The bigger they come, the harder they fall: body size and prey abundance influence predator-prey ratios. *Biology Letters*, rsbl20100996.
46. Fryxell, J.M., Sinclair, A.R., and Caughley, G. (2014). *Wildlife ecology, conservation, and management*, (John Wiley & Sons).
47. Wilson, R.P., Shepard, E., and Liebsch, N. (2008). Prying into the intimate details of animal lives: use of a daily diary on animals. *Endangered Species Research* *4*, 123-137.
48. Wilson, R., Steinfurth, A., Ropert-Coudert, Y., Kato, A., and Kurita, M. (2002). Lip-reading in remote subjects: an attempt to quantify and separate ingestion, breathing and vocalisation in free-living animals using penguins as a model. *Marine Biology* *140*, 17-27.
49. Wilson, R.P., Holton, M. D., di Virgilio, A., Williams, H., Shepard, E.L.C., Lambertucci, S., Quintana, F., Sala, J.E., Balaji, B., Lee, E.S., Strivastava, M., Scantlebury, D.M., Duarte, C.M. (2018). Give the machine a hand: A Boolean time-based decision-tree template for rapidly finding animal behaviours in multi-sensor data. *Methods in Ecology and Evolution* *In Press*.
50. Wilson, J.W., Mills, M.G., Wilson, R.P., Peters, G., Mills, M.E., Speakman, J.R., Durant, S.M., Bennett, N.C., Marks, N.J., and Scantlebury, M. (2013). Cheetahs, *Acinonyx jubatus*, balance turn capacity with pace when chasing prey. *Biology letters* *9*, 20130620.
51. Shipley, L.A., Gross, J.E., Spalinger, D.E., Hobbs, N.T., and Wunder, B.A. (1994). The scaling of intake rate in mammalian herbivores. *The American Naturalist* *143*, 1055-1082.
52. Wilson, R. (1986). *The Jackass Penguin (Spheniscus demersus) as a pelagic predator*. Volume PhD. (University of Cape Town), p. 193.
53. Wilson, R.P., Puetz, K., Bost, C.A., Culik, B.M., Bannasch, R., Reins, T., and Adelung, D. (1993). Diel dive depth in penguins in relation to diel vertical migration of prey: whose dinner by candlelight? *Marine Ecology Progress Series* *94*, 101-104.