DISPATCH

Ecology: Luck, Scarcity and the Fate of Populations

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An animal's choice of diet plays a large part in determining whether it will find food during a period of searching. This has profound implications for the likelihood of reproductive success or starvation and many other important questions in ecology.

Energy is the fundamental currency of life [1]. Many organisms obtain their energy by consuming others; thus, consumption is one of the most important — and most studied — interactions for ecological and evolutionary dynamics and the focus of some of the earliest mathematical models in ecology [2,3]. Early models of consumer–resource or predator–prey interactions were often powerful, general, simple and deterministic. Since then, awareness of the importance of luck has increased, exposing how chance events like finding food, or encountering predators or bad weather, can play an important role in determining the fates of individuals and populations [4–6]. Despite this, standard results that many ecologists take for granted – such as the ecological drivers of diet breadth and specialisation, and insights into the stability of predator–prey interactions – lean heavily on a small number of early deterministic models. In a recent paper in *Current Biology*, Rory Wilson and colleagues [7] show the link between diet and chance, highlighting the profound effects of diet in determining the fates of individuals and populations in changing environments.

As a foundation for their analyses, Wilson and colleagues [7] make use of recent advances in biologging, an area of development within which they have long been at the forefront. They used data from four different species (domestic sheep, Magellanic penguins, cheetahs and Andean condors), multiple individuals of which had been fitted with triaxial accelerometers and magnetometers as components of 'daily diaries' used to monitor many aspects of animal movement and behaviour [8]. As their names suggest, triaxial accelerometers record acceleration in three planes, whilst magnetometers indicate orientation. When analysed carefully [9], data from these devices can be used to infer characteristic patterns of movement associated with many behaviours, and so to reconstruct the activities and feeding behaviour of animals during periods of monitoring. In addition, the penguins were fitted with Hall sensors, an ingenious device used to measure jaw-angle and, thereby, to reveal the frequency of food ingestion [10]. Using this technology, the team were able to determine how long individuals of the focal species spend looking for each consecutive item of food before they can eat.

Ecologists working on herbivores are often interested in their bite rates in different habitats [11], whilst carnivore ecologists often pay close attention to the frequency with which their subjects make kills [12]. However, the idea of comparing these rates among species with very different diets is novel. By doing so, Wilson and colleagues [7] show that sheep, which feed almost continuously on low-value vegetation, had fairly linear increases in cumulative intake with time, and very little difference between individuals. At the other end of the spectrum, Andean condors are scavengers that might search for days for a new food source. During the period of monitoring, condors varied over two orders of magnitude in their food search times. The result is that, over time and simply by chance, the cumulative intake of condors could show massive variation between individuals.

Based on their findings about the variation in food search time, Wilson and colleagues [7] use simple models to show that preying on rarer, high-value food is inherently risky. This is because the high uncertainty in time taken to find food can lead to a greater proportion of foragers failing to gain the energy required to finance costly activities, such as reproduction and offspring provisioning. This is particularly pronounced when less food is available, increasing the mean search time and its variance. In less and less productive areas, populations that rely on high value but scarce resources will show rapid increases in the proportion of individuals failing to acquire enough resources to survive and breed.

Wilson and colleagues [7] use simulations to show that there are pronounced differences in the vulnerability of different penguin species to declines in food availability (Figure 1). Intriguingly, they also suggest that their findings regarding luck in finding food could help to explain a mysterious macroecological pattern relating the abundance of predators to that of their prey. The pattern had been identified previously [13], based on data on the densities of mammalian carnivores and their prey. For a given relative decrease in prey availability, declines in abundance of the largest carnivores were over five times greater than those of the smallest carnivores – and the relationship between the abundance of predators and that of their prey was strongly linked to the predator's body mass [13]. Further work would be required to show that the findings of Wilson and colleagues [7] predict the observed relationship, but the link between predator size, prey size and, thus, likely inter-individual variability in foraging success is a compelling suggestion (Figure 2).

The study by Wilson and colleagues [7] could prompt reconsideration of many other biological phenomena. In general, given the importance of meeting requirements during the energetically demanding periods of reproduction and offspring provisioning, the role of luck and its link to diet might help to explain strategies to reduce the effects of chance during those critical periods. For example, predictability of food supplies is thought to have played a strong role in driving the evolution of lactation [14]. Similarly, unpredictability of food encounter has been linked to the emergence of capital breeding, in which reproduction is financed from stored energetic capital rather than by reliance on concurrent energy acquisition (which, by contrast, is referred to as 'income breeding') [15]. Diet might thus be expected to play a role in the consistency of reproductive output and the contrasting phenomenon of year-skipping [16]. Buffering against chance is linked to the benefits of food-sharing in social mammals [17] and has also been invoked in the context of alloparenting within human hunter-gatherer societies [18]. As such, diet and predictability of resources are likely to have played a strong role in the evolution and maintenance of sociality.

The link between diet and luck highlighted by Wilson and colleagues [7] also adds an additional level of interest to the dietary choices of animals. Standard models of diet choice focus on the 'profitability' of prey (its energy content divided by the time taken to subdue it, if necessary, and ingest it) and show that it is the mean rate of encounter with more profitable prey that determines whether less profitable prey will be incorporated into the diet [19]. Wilson and colleagues [7] show that variance in encounter rate could also be highly influential. The obvious implication is that, when the most profitable prey are of high energetic value but relatively rare, consideration of variance in encounter rates would suggest that foragers could buffer against that by adopting a generalist diet — even where mean encounter rates, alone, would suggest that a specialist diet would be optimal.

Clearly, the range of phenomena that could be linked to the relationship between diet, luck and variance is broad. The findings of Wilson and colleagues [7] and their presentation of, not only a theoretical framework, but also hard-bought empirical data, should prompt renewed interest in this field. More empirical data on a wider range of species could enable advances in relation to a broad range of biological questions.

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Figure legends]

Figure 1. Penguins, diet and population dynamics.

Magellanic penguins (A) and African penguins (B) are highly similar congeners but differ in their diets and vulnerability to declining food resources [7]. African penguins take prey that is approximately four times as energetically rich as that taken by Magellanic penguins, but do so with a correspondingly lower frequency. That results in greater inter-individual variability in the foraging success of African penguins. Wilson

and colleagues [7] suggest that this could help to explain the sustained decline in the African penguin population of South Africa's western cape, where they compete with intensive commercial fishing activities.
Photo (A) by D. Faulder (https://tinyurl.com/y8er6kd3), photo (B) by Martyn Smith (https://tinyurl.com/ycqhaewc); both images released under a CC BY 2.0 license (https://creativecommons.org/licenses/by/2.0/).

Figure 2. Prey size, variance, and the abundance of terrestrial carnivores.
Data on terrestrial mammalian carnivores from the least weasel (A) to the polar bear (C) were collated by Carbone *et al.* [13]. The abundances of the largest carnivores were strongly affected by the abundances of their prey, whilst those of small carnivores were relatively weakly influenced by prey availability (B, after [13]). Starting from an environment with ample resources, successive reductions in prey availability lead to a rapid increase in the proportion of a population failing to gain the energy required to survive and breed when that population utilises rare, high quality prey (panel D, blue line). This effect is more abrupt for populations utilising prey of intermediate value and frequency of encounter (panel D, green line) and highly abrupt for those reliant on low quality but frequently-encountered prey (panel D, red line). Assuming that most field data come from situations more like the left side of the graph, this suggests that the role of luck highlighted by Wilson and colleagues [7] could explain why small predators (feeding on small but relatively common prey) might show much less impact of prey declines than do large predators (feeding on large but relatively uncommon prey).
Photo (A) by Ashley Buttle (https://tinyurl.com/y9yk3sty), photo (C) by Orion Wiseman (https://tinyurl.com/y99s7f3k); both images released under a CC BY 2.0 license (https://creativecommons.org/licenses/by/2.0/).

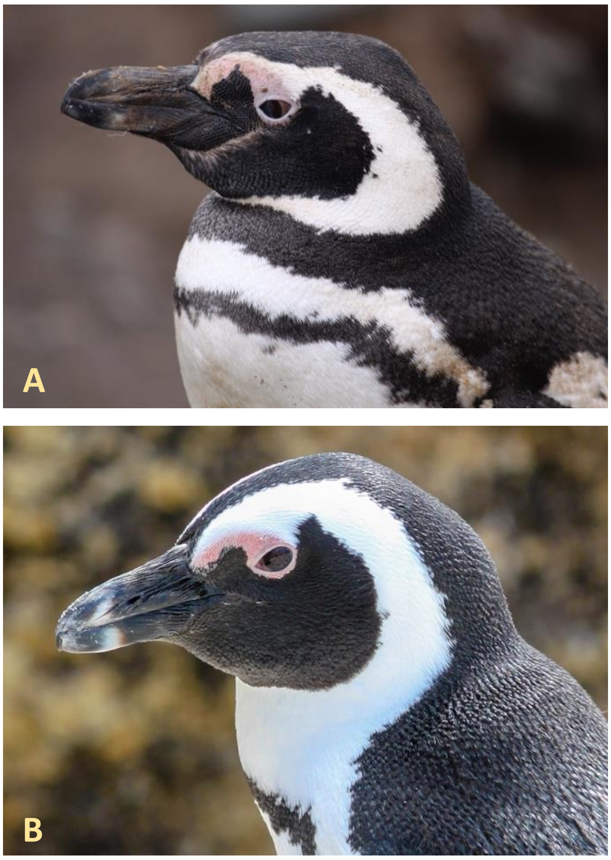

Figure 1

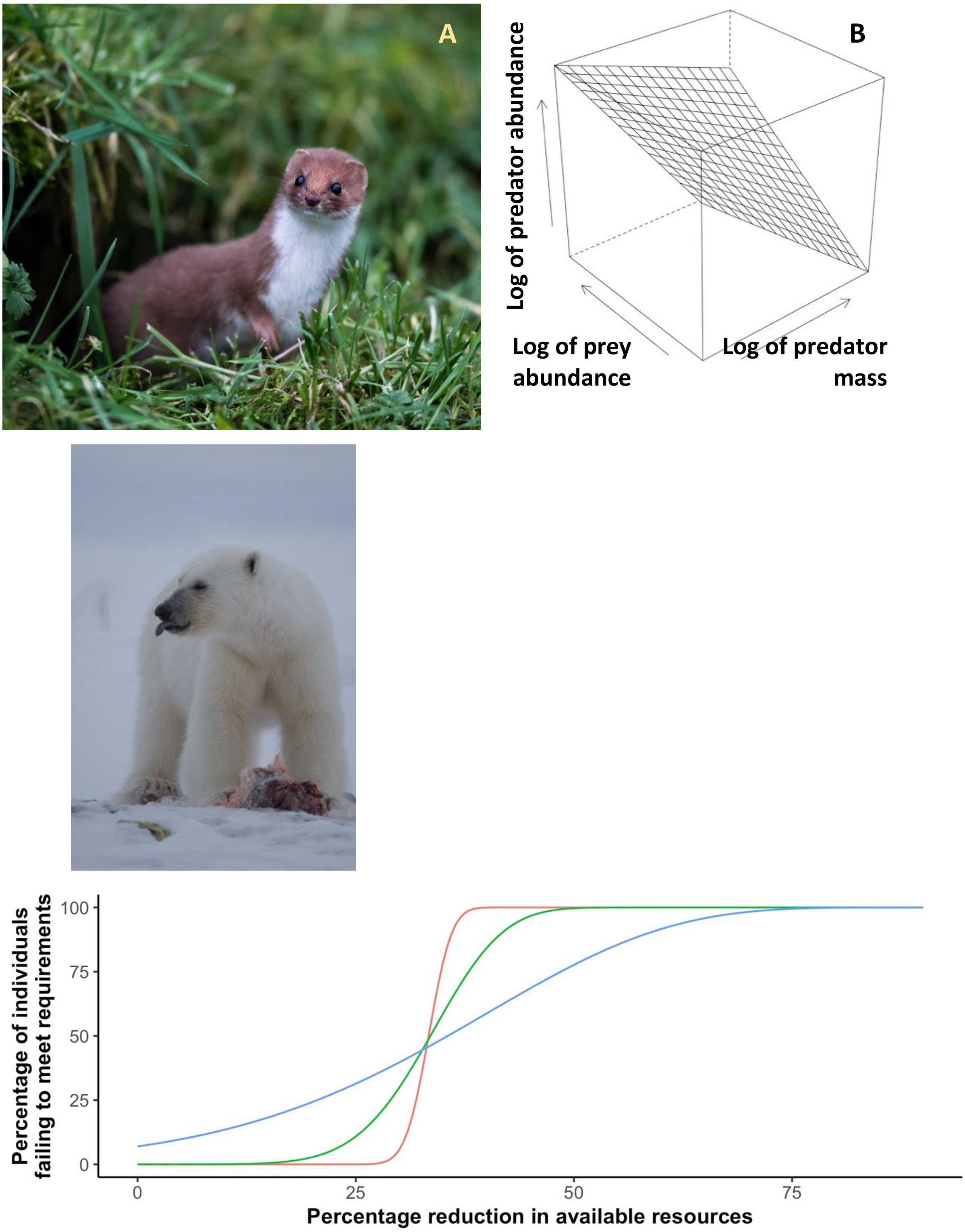
A
B
Log of predator abundance
Log of prey abundance
Log of predator mass
Percentage of individuals failing to meet requirements
100
75
50
25
0
0
25
50
75
Percentage reduction in available resources

Figure 2