Foraging mode switching: the importance of prey distribution and foraging currency

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Foraging methods are highly variable, but can be grouped into two modes: searching and ambush. While research has focused on the functioning of each mode, the question of how animals choose which to use has been largely neglected. Here we consider a forager that exploits prey that are patchily distributed in space and time. This forager can either sit and wait for prey to appear or search for prey, which is more likely to result in encounters with prey but costs more energy and/or exposes the forager to greater predation risk. The currency that natural selection appears to have optimized will be determined by the additional costs of searching and whether there is a risk of starvation. We therefore compare the predictions of models based on currencies that consider only energy and predation risk to state-dependent models in which energy reserves are used to trade off predation rate, starvation rate and investment in growth. The choice of currency qualitatively affects how mode should change when prey abundance and prey patchiness increase. We show how differing prey distributions can explain variation in effects of experimentally increasing prey abundance. Our work has several implications for the study of foraging mode, population dynamics and the methods used to assess population size.

Food is usually spatially and temporally clumped, and effective foraging strategies must take this heterogeneous distribution into account. Foraging strategies can usefully be divided into two broad types. The first is to search actively for prey. Optimal foraging theory (Stephens & Krebs, 1986) has provided great insights into how foragers should choose among different prey (Krebs, Erichsen, Webber, & Charnov, 1977), adjust their search trajectories in response to clumped hidden prey (Prins & van Langevelde, 2008) and stop searching in the current patch to travel to another (Stephens, 2007). The second main foraging method, which can only be used when consuming mobile prey, is to sit and wait for prey to approach ('ambush' predation). Many foragers use this method (Cooper, Vitt, Caldwell, & Fox, 2001; Huey & Pianka, 1981; Johansson, 1991; Killen, Brown, & Gamperl, 2007; Scharf, Lubin, & Ovadia, 2011), which is more likely to be successful if a location can be found where prey arrive frequently, such as spiders waiting on flowers that attract pollinating insects (Morse, 2000). Research

on this mode of foraging has concentrated on understanding how sit-and-wait foragers choose foraging sites (Scharf et al., 2011), how they choose when to move between sites (Huey & Pianka, 1981) and the physiological correlates of sit-and-wait foraging as an obligate life history strategy (Lourdais, Gartner, & Brischoux, 2014).

Some animals are highly adapted for one of these two modes of foraging (Lourdais et al., 2014 and references therein), but many species switch flexibly between them. Among the African felids, for example, the cheetah, *Acinonyx jubatus*, lion, *Panthera leo*, and leopard, *Panthera pardus*, all make use of both foraging modes, differing in their relative use of the two (Turner, 1997). The optimal exploitation of patchily distributed prey has some commonality with the flexible use of ambush versus searching, but there are important differences. While the extensive literature on patch departure decisions and area-restricted search can be viewed as exploring a choice between waiting and moving, such models assume that decisions are driven by the spatial structuring of prey into patches and restricted information about food availability in the current patch (Stephens, 2007). However, many animals can see their prey and so are fully informed about the profitability of the current patch, and many prey are not found in discrete patches. Scavengers are especially obvious examples of such animals, since

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they seek individual prey items which may appear while they are waiting, or they can actively search for them. Furthermore, the short timescales involved in the approaches described above do not account for the likelihood that while active searching might bring benefits in enhanced encounter rates with prey, it is likely to increase costs: both metabolic and in greater exposure to predators. The relative magnitudes of these costs and benefits will be influenced by both the state of the focal organism and aspects of its environment. To our knowledge, few theoretical approaches have attempted to include these effects on foraging behaviour (see Bednekoff, 2007 for an overview). Our understanding of how animals decide whether to search or wait is less advanced than for other aspects of foraging theory, and since foraging mode clearly affects the distribution and/or behaviour of other species (Huey & Pianka, 1981), this is an important gap in our understanding of species interactions.

Norberg (1977) showed that a forager that has the 'aim' of minimizing the foraging time to achieve a given gain should respond to an increase in prey abundance by switching to a more costly but more rewarding strategy. This tactic is intuitively appropriate for endotherms that must meet a given metabolic need to stay alive, and experimental tests on endotherms tend to support this prediction (Rudolph, 1982). Ectotherms may instead maintain a minimum prey encounter rate (Helfman, 1990), but experiments on ectotherms known to use both foraging modes reveal a mixture of responses when prey abundance increases: switching from search to ambush (Anthony, Formanowicz, & Brodie, 1992; Formanowicz, 1982; Inoue & Matsura, 1983; Johansson, 1991), switching from ambush to search (Hirvonen, 1999; Huey & Pianka, 1981) or maintaining ambush at all prey densities (Greeff & Whiting, 2000; Johansson, 1991), and in one case predators switched from ambush to searching as prey abundance increased and back to ambush at very high prey densities (Hirvonen, 1999). This variability may occur because different ectotherms will have faced different selective pressures on their foraging behaviour (Griffiths, 1980), such as whether searching requires increased energy use or entails a higher risk of predation. Furthermore, different studies have used different prey and have manipulated prey abundance in various ways. Predators should respond to the distribution of their food, in addition to its abundance, and since experimenters may inadvertently alter prey distribution when altering prey abundance, we might expect differences between experiments in predator responses.

To understand the variability in foraging mode we make three biologically motivated developments. (1) We relax the assumption that the forager knows where the other patches of prey are, and therefore deciding to move gives no guarantee of finding food. We assume instead that the food distribution exhibits both spatial and temporal autocorrelation, and any strategy must take this into account. That is, we assume that the prey temporal distribution is independent of the spatial distribution encountered by the forager, such as may occur if prey move in a different spatial plane from predators (e.g. small mammalian carnivores accessing birds that forage on the ground) or arrive randomly and are consumed (e.g. scavengers on benthic carrion, birds preying on bees at flowers). (2) We assume that the metabolic cost and predation risk while searching for prey can be greater than the metabolic cost and predation risk while waiting. This assumption is likely to be true very generally (Bautista, Tinbergen, & Kacelnik, 2001; Bautista, Tinbergen, Wiersma, & Kacelnik, 1998; Berger & Gotthard, 2008; Cooper & Sherbrooke, 2013; Helfman & Winkelman, 1991; Lourdais et al., 2014; Williams & Yeates, 2004; Wood, Stillman, Wheeler, Groves, Hambly, et al., 2013). (3) Optimal foraging theory is based on the concept of natural selection as a fitness-maximizing algorithm, where fitness is assumed to depend on

the dominant costs and benefits associated with behavioural options. The combination of the dominant costs and benefits is known as the 'currency'. Because the types of foraging costs and the particular requirements of any animal determine the currency its behaviour will be selected to maximize, we explore how the predictions of foraging models depend on the currency that an optimal strategy maximizes. We find the optimal strategy, which may be state-dependent, given four critical characteristics of the environment: the abundance of prey items, the number of prey in the patches, the spatial clumpiness of the patches and the size of prey items. Given the variability in previously reported experimental results, we are especially concerned with how the foraging currency and prey distribution should affect whether an increase in prey abundance favours an increase or a decrease in the propensity to search actively. Our analysis enables us to explain the variation among experimental results, make predictions for future experimental tests and explain differences between species and environmental conditions in observed foraging behaviour.

MODELS AND RESULTS

General Overview

We assess behaviour in a generic system where at any one time a solitary forager is in one of two exclusive states: either in a patch of prey or not. We assume that the animal knows without error whether it is currently in a patch of prey. Patches of prey occur in a world consisting of an infinite one-dimensional series of interconnected potential patch locations, which contain a total of γ prey items at all times. That is, prey are replenished continuously and are eaten by other predators, and the focal forager has a negligible impact on overall prey abundance and distribution. This would apply in situations in which prey and predator populations are stable and prey are mobile, and so the per capita prey abundance and distribution experienced by individual predators are unchanging.

When in a patch of prey, the forager makes the binary decision θ whether to eat a prey item ($\theta = F$) or rest ($\theta = R$, if its reserves are sufficiently high). If the forager chooses to feed then it consumes a prey item and gains an amount of energy drawn stochastically from a symmetrical distribution with mean c. Owing to prey movement and competition from other predators, there is a probability ϕ per time step that a patch will become exhausted (i.e. be empty on the next time step) whether the forager eats or not. This implies that the number of prey in a patch is Poisson distributed (with the mean number of prey in a patch equal to $1/\phi$). We refer to ϕ as patch transience and $1/\phi$ as patch size. Thus, prey are clumped such that most locations are empty but patches of prey each consist of a variable number of food items. In Fig. A1 (Appendix 1) we show the distribution of the number of prey per location for some representative values of ϕ.

If there are currently no prey at its current location the forager decides whether to search for prey ($\delta = S$) or wait for prey to arrive ($\delta = W$). The consequences of this decision depend on the probability of finding prey under the chosen option, the energetic costs until the next decision time and the associated predation risk.

Assuming that the density of food in the environment is fixed at γ then every time a patch is exhausted prey must appear in another location. The proportion of locations that contain a prey patch depends on the size of patches and is $\gamma\phi$. Therefore $(1-\gamma\phi)$ of the possible locations do not contain prey at any given moment. Assuming that $\gamma \leq 0.5$ and time steps are sufficiently short that patches of prey cannot both appear and disappear from a location in the same time step, then if a forager waits at a location where there was no prey at the last time step, the probability that prey