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Metabolic Rates Can Drive Individual Differences in Information and Insurance Use under the Risk of Starvation

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ABSTRACT: Variation in how individuals invest in acquiring information (sampling) and in insuring themselves against potential negative consequences of uncertainty (e.g., by storing energy reserves) has been suggested to underlie consistent individual differences in suites of behavioral traits. However, the key drivers of individual differences in information use remain poorly understood. We use dynamic programming to explore how existing variation in metabolic rates (MRs) affects the use of sampling and insurance under starvation risk. Our analysis reveals nonlinear effects of MRs on diurnal patterns of sampling and insurance. Individuals with low MRs accrue reserves quickly, because they invest in sampling and are able to exploit profitable options when they arise. Individuals with intermediate MRs initially lose reserves, because sampling, while optimal, is relatively expensive; however, they later build reserves due to efficient exploitation of alternative foraging options. Sampling rarely pays for individuals with the highest MRs, which show relatively constant levels of energy reserves throughout the foraging period. Thus, individual variation in MRs on the scale observed in natural populations can lead to important differences in investment in sampling and insurance and may underpin consistent individual differences in suites of other behavioral traits, including individual differences in behavioral responsiveness.

Keywords: managing uncertainty, responsiveness, energy budget, foraging, sampling.

Introduction

Individuals from the same population often differ in the degree to which they value information. For example, individuals show marked differences in the extent to which their behavior is guided by environmental stimuli (Benus et al. 1991; Aron and Aron 1997; Belsky et al. 2007; Frost et al. 2007; Jones and Godin 2010; Morand-Ferron et al. 2011), which is assumed to reflect underlying differences in how individuals invest in sampling environmental cues

(Verbeek et al. 1994). Additionally, several studies have reported direct evidence that individuals differ in how much they invest in sampling (Krebs et al. 1978; Shettleworth et al. 1988; Morand-Ferron et al. 2011), in how they value personal information versus social information (Marchetti and Drent 2000; Kurvers et al. 2010), or in their willingness to choose options with greater uncertainty in outcome (i.e., variance sensitivity or risk sensitivity; Byrnes et al. 1999; Kuhnen and Chiao 2009; Mathot et al. 2009). These differences in how individuals value information are taxonomically widespread and have been reported in birds (Verbeek et al. 1994; Kurvers et al. 2010; Morand-Ferron et al. 2011), fish (Frost et al. 2007; Jones and Godin 2010), and mammals (Benus et al. 1991), including humans (Aron and Aron 1997; Belsky et al. 2007; Kuhnen and Chiao 2009). There is growing interest in understanding how such differences arise as well as in the role they may play in generating consistent individual differences in other behaviors (i.e., personality) and behavioral responsiveness (i.e., plasticity; Wolf et al. 2008, 2011; Dubois et al. 2010; Mathot et al. 2012).

Given that information is necessary for individuals to respond adaptively to changing conditions (Dall et al. 2005), understanding how intraspecific variation in information use can arise and persist is a key challenge. Theoretical work suggests that individual variation in sampling and behavioral responsiveness can evolve when the payoffs for behavioral responsiveness are negatively frequency dependent (Wolf et al. 2008; Dubois et al. 2010), a conclusion that has been supported by at least two empirical studies (Mathot et al. 2011; Morand-Ferron et al. 2011). However, it remains unclear what proximate mechanism may underlie individual differences in responsiveness. One recently proposed notion is that individuals differ consistently in how they manage uncertainty and that this in turn affects how they respond to changing environmental conditions (Mathot et al. 2012).

Two tactics that have been studied extensively in the

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context of managing uncertainty are sampling and insurance (Dall and Johnstone 2002). Sampling (i.e., gathering and storing information about) relevant features of the environment reduces uncertainty (Stephens 1987; Dall and Johnstone 2002). Sampling allows individuals to track environmental change and therefore to exploit options that are the most profitable and to avoid options that are not. Individuals can also act to minimize the potential consequences of environmental uncertainty by investing in “insurance” (Dall and Johnstone 2002; Dall 2010). For example, energy stores will buffer an individual against the negative fitness consequences of unpredictably occurring poor foraging periods (Dall 2010). Individual differences in the use of either sampling or insurance will affect both an individual’s ability and its incentive to respond to changing conditions (Mathot et al. 2012).

Theoretical studies have identified several extrinsic factors that shape the adaptive use of sampling and insurance. Greater use of insurance is favored when there is greater unpredictability in foraging conditions (Houston and McNamara 1993). The optimal level of sampling is affected by both the rate at which options change states and the ratio of the costs of missing out on productive opportunities (overrun error costs) to the costs of sampling unproductive options (sampling error costs; Stephens and Krebs 1986; Stephens 1987). Empirical studies confirm the predicted effects of environmental stochasticity on optimal levels of sampling (Shettleworth et al. 1988) and insurance (Bednekoff and Krebs 1995), at least when considering the behavior of the average individual in a population. However, there is growing awareness that within populations, individuals often differ consistently in their behavior (Bell et al. 2009), referred to as animal personality (Dingemanse et al. 2010). Recently, it has been suggested that consistent individual differences in the use of sampling and insurance as means of managing environmental uncertainty may underpin consistent individual differences in a range of other behavioral traits (Mathot et al. 2012).

Despite the potential significance of individual differences in the use of sampling and insurance, the origin and maintenance of such variation remain poorly understood. Individual variation in metabolic rates (MRs) has received a great deal of attention as potentially underlying consistent individual differences in a wide range of behaviors (Biro and Stamps 2008, 2010; Careau et al. 2008; Houston 2010). Consistent individual differences in MRs have been reported in several taxa, with MRs often differing severalfold among individuals from the same population (Speakman et al. 2004; Biro and Stamps 2010; Burton et al. 2011). In this article, we do not address the origin or maintenance of variation in MRs, which has been discussed extensively elsewhere (Biro and Stamps 2010; Houston 2010; Burton et al. 2011; Konarzewski and Ksi-

ązek 2012; White and Kearney 2012; Wolf and McNamara 2012). Instead, we ask what consequences individual differences in MRs (within the naturally occurring range) have for the adaptive use of sampling and insurance.

Individual differences in MRs may be expected to generate consistent individual differences in the use of sampling and insurance for several reasons. All else being equal, having greater energetic needs will alter the balance between the costs and benefits of any behavior that affects energy acquisition or energy expenditure. Optimal investment in sampling is set by the ratio of the costs of overrun errors to sampling errors (Stephens 1987), and the magnitude of these costs is likely to differ between individuals as a function of their MRs. For an individual with a high MR, both missing out on the opportunity to exploit a variable option when it is in a good state (overrun errors) and sampling a variable option when it is in a bad state (sampling errors) may be relatively more costly compared with the same errors for individuals with low MRs, given their higher overall energy requirements. However, because energy expenditure increases with increasing metabolic rate, the low amount of food obtained from sampling errors may be sufficient to meet the energy expenditure of a low-MR individual but not a high-MR individual, thus allowing low-MR individuals to remain on a positive energy budget but placing high-MR individuals on a negative energy budget. If energy deficits are costly, then individuals with high MRs may be expected to show lower investment in sampling behavior compared with individuals with low MRs as a means of minimizing the ratio of sampling to overrun errors.

Similarly, MRs may influence the relative value of insurance as a means of mitigating environmental uncertainty. For an individual with a high MR, the same amount of energy reserves (i.e., fat) provides a smaller buffer against uncertainty compared with an individual with lower energy requirements, and the possibility of building up energy reserves may also be more restricted given the constantly higher rate of energy expenditure. At the same time, if individuals with lower MRs sample more, they may be in a better position to exploit productive opportunities when they arise and therefore be better able to build energy reserves. Because sampling and insurance are not mutually exclusive, and because the use of one of these tactics will have consequences for the value of the alternative tactic, we use a stochastic dynamic optimization approach to explore how MRs simultaneously shape insurance and sampling behaviors. Elucidating factors that can underpin individual differences in sampling and insurance may provide novel insights into the origin and maintenance of individual differences in responsiveness.

The Model

We extend the model of Dall and Johnstone (2002) of state-dependent sampling in a changing environment to explicitly consider the impact of variation in MRs (within the observed range for a range of taxa) on optimal investment in information use. We develop a dynamic programming model of the choice between two foraging options. One choice provides a consistent alternative to an option that is sometimes better and sometimes worse. These choices can be thought of as alternative foraging patches, prey types, foraging tactics, and so on. All foraging returns are stochastic, and in this way foragers are always at risk of an energetic shortfall. Our aim is to explore how individual differences in MRs shape the use of sampling and insurance in the face of environmental uncertainty. Terms and baseline values are defined in table 1.

Behavior is modeled as a sequence of decisions made at times $t = 1, 2, \dots, T_{\max}$. An individual is characterized by its metabolic rate when active (M) and the state of its energy reserves at t , $X(t) = x$. The value M is scaled to the population mean, so that values explored range from 0.5 to 1.5. This represents a scenario in which “low” and “high” M individuals have energy expenditures that are 50% lower and 50% higher, respectively, than the energy expenditure of “intermediate” M individuals, which is comparable to the range observed in empirical studies for a wide range of taxa (Speakman et al. 2004; Burton et al. 2011).

Energy expenditure for animals at rest is assumed to be $0.3 \times M$, the metabolic rate while active, following previously published estimates (Daan et al. 1990; Ricklefs et al. 1996). Energy reserves can take values ranging from $X_{\text{crit}} = 0$ to $X_{\text{max}} = 100$. If a forager’s reserves drop to

X_{crit} , the forager is assumed to die from starvation. To survive from the end of one foraging period until the beginning of the next foraging period, individuals must accrue enough reserves to sustain their metabolic requirements over the nonforaging period, which is of equal duration to the foraging period (T_{\max}). Foraging animals are assumed to behave so as to maximize their fitness F at T_{\max} , the end of the foraging period (e.g., dusk for diurnal foragers), given their energetic requirements over the nonforaging period. We assume that the payoff from surviving to the subsequent foraging period is an increasing but decelerating function of the forager’s state at T_{\max} . Specifically, the terminal fitness payoff is a function of the forager’s energy reserves, metabolic rate, and the duration of the nonforaging period, such that

$$F(x, T_{\max}) = \begin{cases} 0, & x - (T_{\max} \times 0.3 \times M) \leq X_{\text{crit}} \\ \Omega \frac{x - (T_{\max} \times 0.3 \times M)}{x - (T_{\max} \times 0.3 \times M) + x_0}, & T_{\max} \times 0.3 \times M < x \leq X_{\text{max}} \end{cases} \quad (1)$$

The variable Ω refers to the maximum fitness value of carrying reserves into the immediate future (i.e., over the nonforaging period). Here, $\Omega = 1$ as $x \rightarrow \infty$ of this function, with $F(x, T_{\max}) = \Omega/2$ when $x = X_{\text{crit}} + x_0$ (Dall and Johnstone 2002). This models a very general situation in which survival and condition at the end of the foraging period have nonnegligible consequences for reproductive value (Cuthill and Houston 1997).

At each point t during the foraging period, the model animal must decide which of the two options to forage on. If the forager chooses option 1, the forager finds food with expected energetic value e_1 with a probability P and no food with a probability of $1 - P$. Alternatively, if the

Table 1: Model parameters

Term and baseline value	Definition
$T = 60$	Length of foraging period and of nonforaging period
t	Unit of time at which behavioral decisions are made
$X(t) = x$	State of energy reserves of forager at time t
$X_{\text{crit}} = 0$	Minimum level of reserves for survival
$X_{\text{max}} = 100$	Maximum level of reserves that can be stored
$I(t) = i$	State variable representing information about the system; it is the expectation that option 2 is in a good state
$X_{\text{init}} = 5, 10, 15, \text{ or } 20, I_{\text{init}} = .5$	Initial states for computation of expected optimal behavior
e_1, e_2	Net energy gained per food encounter from options 1, 2
P	Probability of encountering food on option 1
g, b	Probabilities of finding food on option 2 when in good, bad state: $g > P > b$
$\mu_1 = P \times e_1, \mu_2 = [(g + b) \times e_2]/2$	Mean amount of food obtainable per time step from options 1, 2
$\alpha, \beta = .8$	Probability that option 2 remains in good, bad state
$C(x)_{\text{day}} = M + r \times x$	Metabolic costs to individual of carrying x reserves while foraging
$C(x)_{\text{night}} = .3 \times M$	Metabolic costs to an individual at rest
$r = M/X_{\text{max}}$	Rate at which metabolic costs accrue with x

forager chooses option 2, it finds food with expected energy value e_2 . Option 2 varies between good states (g) and bad states (b), such that when option 2 is in a good state, the probability of finding food is g and the probability of finding no food is $1 - g$. When option 2 is in a bad state, the probability of finding food is b , and the probability of finding no food is $1 - b$. If option 2 is in a good state at time t , then the probability that it remains in a good state at time $t + 1$ is α , and the probability of switching to a bad state is $1 - \alpha$. Similarly, the probability that option 2 remains in a bad state at $t + 1$ when already in a bad state at t is β , and the probability that it switches to a good state is $1 - \beta$. Thus, the model forager is offered a choice between two options with stochastic returns: option 1 is consistently stochastic, and option 2 varies in stochasticity over time. Furthermore, whenever an animal has not chosen option 2, it has incomplete information about the current state of that option and can gain information only by sampling it. For simplicity, we assume that foragers can easily discriminate between the good and bad states of option 2 once it has been chosen (see Dall and Johnstone 2002 for further justification).

An animal's current information on option 2 can be defined as $I(t) = i$, which is the expectation that the probability of finding food on option 2 is g . We assume that the probability of change is symmetric between states of option 2 such that $1 - \alpha = 1 - \beta$. In this way, the information obtained from experiencing option 2 when good versus bad is equal. A forager's information regarding the state of option 2 can range from 0 to 1, such that when a forager has no information regarding the state of option 2, $i = 0.5$ (the information updating functions are given in app. A; apps. A–C available online).

Following Dall and Johnstone (2002), we set up the foraging problem to be similar to Stephens (1987), so that the mean value of option 1 is intermediate to option 2 when in its good or bad state, such that $b \times e_2 < P \times e_1 < g \times e_2$. Additionally, parameter values are set so that the long-term returns from option 2 are less than those from option 1: $[(g + b) \times e_2]/2 < P \times e_1$. This ensures that blind exploitation of option 2 is penalized and that tracking of option 2 should occur only when it pays to reduce uncertainty by gathering information (see Dall and Johnstone 2002 for further discussion).

Fat is metabolically inactive (Daan et al. 1990). Thus, we do not assume any additional energetic costs associated with carrying more energy reserves during the nonforaging period. However, carrying extra energy reserves while active may impose energetic costs to foragers, and we assumed that foragers incur metabolic costs (C) at each time step in the foraging period at a rate (r) with increasing energy reserves (x):

$$C(x, M) = M + r \times x. \quad (2)$$

We set r equal to M/X_{\max} , which corresponds to a doubling of foraging metabolic costs when a forager carries reserves equal to X_{\max} . This level of cost implies that consuming food always yields a net energy profit to the forager. The resultant state dynamics are detailed in appendix A.

We find the strategy that maximizes the animal's fitness at T_{\max} , specified by equation (1). A strategy is a rule for choosing between the actions available to the forager during a foraging bout based on its energetic state and its current information on the system. Since the fitness consequences of an action depend on future actions, we solve for the optimal strategy numerically, using dynamic programming (Houston and McNamara 1999). The dynamic programming equations are also given in appendix A.

Results

We characterize sampling behavior as choosing the variable option when the forager has no information regarding the current state of the variable option (good vs. bad, $i = 0.5$). Figure 1 illustrates the finding that sampling behavior is expected under two general sets of conditions. First, individuals are expected to sample when they are in poor energetic condition early in the foraging period (lower left regions of graphs), because the only means of achieving sufficient energy intake is by tracking the variable option in order to capitalize on it when it is in a good state ("sampling for survival"). At intermediate reserves, foragers are expected to exploit the predictable option (option 1). Although the expected payoff from option 1 is higher than that from blind exploitation of option 2, successfully tracking option 2 so that it can be exploited when it is in a good state would provide the highest payoff. Thus, the lack of sampling for individuals with intermediate energy reserves cannot be accounted for solely by the fact that option 1 has a higher mean value than option 2; rather, it indicates that at intermediate levels of energy reserves, sampling errors are relatively more costly than overrun errors. Once a forager has acquired some threshold level of reserves, the use of sampling is again expected (upper left regions of graphs; "sampling as a luxury"), because by tracking the variable option, they have the opportunity to end the foraging period in a very high energetic state, if they are able to exploit it efficiently when it is in a good state, while at the same time being able to afford the risk of exploiting the variable option while it is in a bad state. The level of reserves that favors sampling changes throughout the foraging period. Generally, sampling is expected under a narrower set of conditions as the end of the foraging period approaches, because sampling becomes less

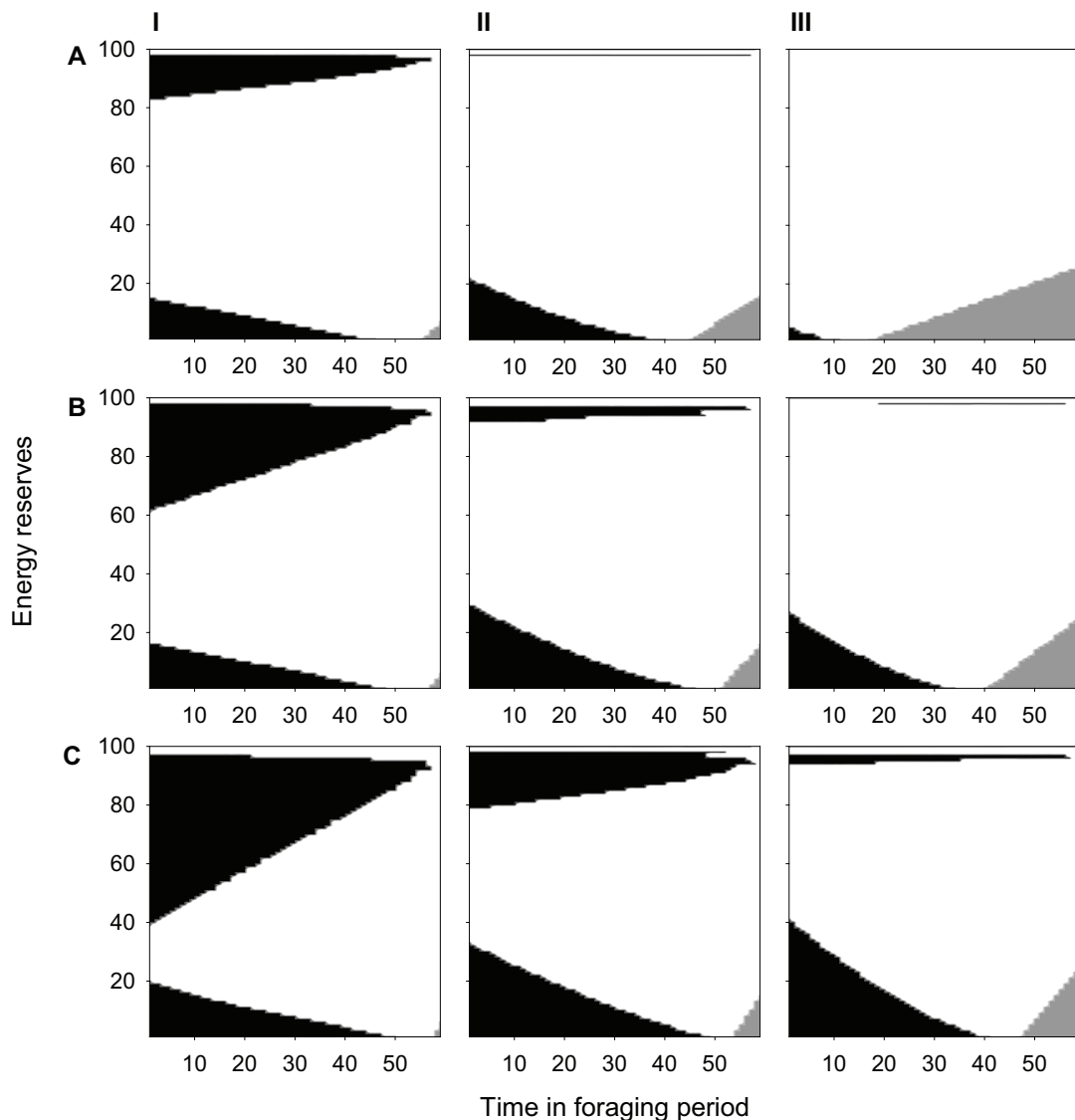


Figure 1: Optimal decision matrices for individuals when metabolic rate is low (*I*; $M = 0.5$), intermediate (*II*; $M = 1$), or high (*III*; $M = 1.5$) and food abundance is low (*A*; $e_1 = e_2 = 3$), intermediate (*B*; $e_1 = e_2 = 4$), or high (*C*; $e_1 = e_2 = 5$). Black areas show combinations of parameter values that are predicted to favor sampling, gray areas indicate combinations of parameter values where foragers are unable to achieve the required level of energy reserves for survival over the nonforaging period, and white areas indicate combinations of parameter values where foragers are expected to choose the less variable foraging option. Parameter values: $g = 0.7$, $b = 0.2$, $P = .5$. Values of other parameters are given in table 1.

valuable as there is less opportunity (time) for individuals to capitalize on any information they gain via sampling.

Moving from left to right across the panels in figure 1 illustrates the finding that MR has opposing effects on the two sampling zones. Sampling as a luxury always decreases with increasing MR. In contrast, increasing MR has non-linear effects on the use of sampling for survival. At low food abundance (fig. 1A), intermediate MR foragers have the highest use of sampling for survival. This result arises

because although sampling for survival provides the opportunity to exploit the variable option while it is in a good state and thus to obtain a higher intake rate, it also incurs a risk of sampling errors. For high-MR foragers, the need to accrue reserves much earlier in the foraging period under conditions of low food abundance means that there is little time to recover from sampling errors. Consequently, the combination of parameter values favoring sampling for survival is relatively restricted. How-

ever, as food abundance increases, high-MR-rate individuals are less time constrained to build reserves and thus have greater opportunity to recover from sampling errors, and sampling for survival is expected under a wider combination of parameter values. Consequently, at high food abundance (fig. 1C), sampling for survival always increases as a function of MR. Moving from top to bottom down each column of panels in figure 1 illustrates the effect of food abundance on the optimal use of sampling. Individuals are able to build energy reserves relatively more easily under conditions of high food abundance, which makes sampling errors relatively less costly. This results in a higher use of sampling, in terms of both sampling as a luxury and sampling for survival.

To understand the implications of these optimal decision rules for expected behavior, we determined the likelihood that foragers following the optimal strategy would be in a particular state (energy reserves) at any given time in the foraging period and hence which foraging option (stable or variable) they would be expected to exploit after specifying the initial state (x_{init} ; Houston and McNamara 1999). Figure 2 shows that under conditions of low food abundance ($e_1 = e_2 = 3$), individuals with intermediate MRs spend the greatest proportion of time on the variable option across a wide range of initial energy reserves. Generally, both intermediate- and low-MR individuals begin by sampling the variable option, while high-MR individuals exploit the predictable option. Differences in investment in sampling combined with differences in energy expenditure result in nonlinear effects of MR on the accumulation of energy reserves. Low-MR individuals accrue reserves the most rapidly, while high-MR individuals maintain relatively stable levels of reserves. Intermediate-MR foragers spend the greatest proportion of time on the variable option across a range of food abundances (app. B). Only at very high food abundance ($e_1 = e_2 = 5$) do high-MR foragers spend a higher proportion of time on the variable option compared with intermediate-MR foragers.

Discussion

There is growing interest in understanding why individuals should differ in the way they value information and in the role these differences may play in generating consistent individual differences in behavior and behavioral responsiveness. However, proximate causes of consistent individual differences in the use of tactics for managing uncertainty remain unexplored. Our analysis reveals that variation in MRs can strongly affect the optimal use of both sampling and insurance. Increasing MRs changes the range of conditions under which sampling is favored, resulting in differences in the types of resources exploited

(variable vs. predictable) and diurnal patterns of mass change as a function of an individual's MR. These results provide formal support for earlier suggestions that variation in MRs may be an important factor underlying consistent individual differences in behavior (Biro and Stamps 2008, 2010; Careau et al. 2008).

Our analyses reveal two general sets of conditions under which sampling is expected. The first is when the danger of starving to death in a foraging period is minimal (termed sampling as a luxury). This is illustrated by our results in several ways. First, all else being equal, foragers with lower MRs—and thereby at lower risk of energetic shortfall—are expected to sample under a wider range of conditions compared with individuals with high MRs. Additionally, as the overall abundance of food increases, so does the range of parameter space where sampling is expected. Finally, within each panel of figure 1, a region of sampling behavior is expected when foragers have accrued some threshold level of energy reserves. These results are consistent with suggestions that a stable rule for managing (food) uncertainty adaptively is “insurance first and foremost, and information if affordable” (Dall and Johnstone 2002, p. 1524).

One important distinction between our analysis and previous work by Dall and Johnstone (2002) is that we incorporate into our time horizon the requirement that foragers accrue enough reserves to survive a nonforaging period. This results in a second set of conditions under which sampling is expected, that is, when the risk of energetic shortfall is sufficiently great that the only means of achieving the required energy intake is by tracking and exploiting the variable option when it is in a good state (fig. 1, *lower left*; sampling for survival). This result is reminiscent of variance- or risk-sensitive foraging behavior, in which preference for the more variable foraging option is expected when the risk of energetic shortfall is high (McNamara and Houston 1996; Mathot et al. 2009). However, dynamic variance-sensitive analyses predict variance-prone behavior for individuals with low reserves at the end of the foraging period, while our analyses predict sampling of the variable option by foragers with low energy reserves at the beginning of the foraging period. This difference is due to the fact that in our analyses, the uncertainty associated with the variable option is not entirely irreducible (Dall and Johnstone 2002; Dall 2010), because experiencing it in either a good state or a bad state at time t provides information about the likelihood of it being in a good or bad state at time $t + 1$. Thus, there is an advantage to sampling early in the day, because there is a longer window of opportunity to benefit from any information acquired compared with sampling later in the day. This is analogous to previous studies showing that greater investment in sampling is expected when foragers have a

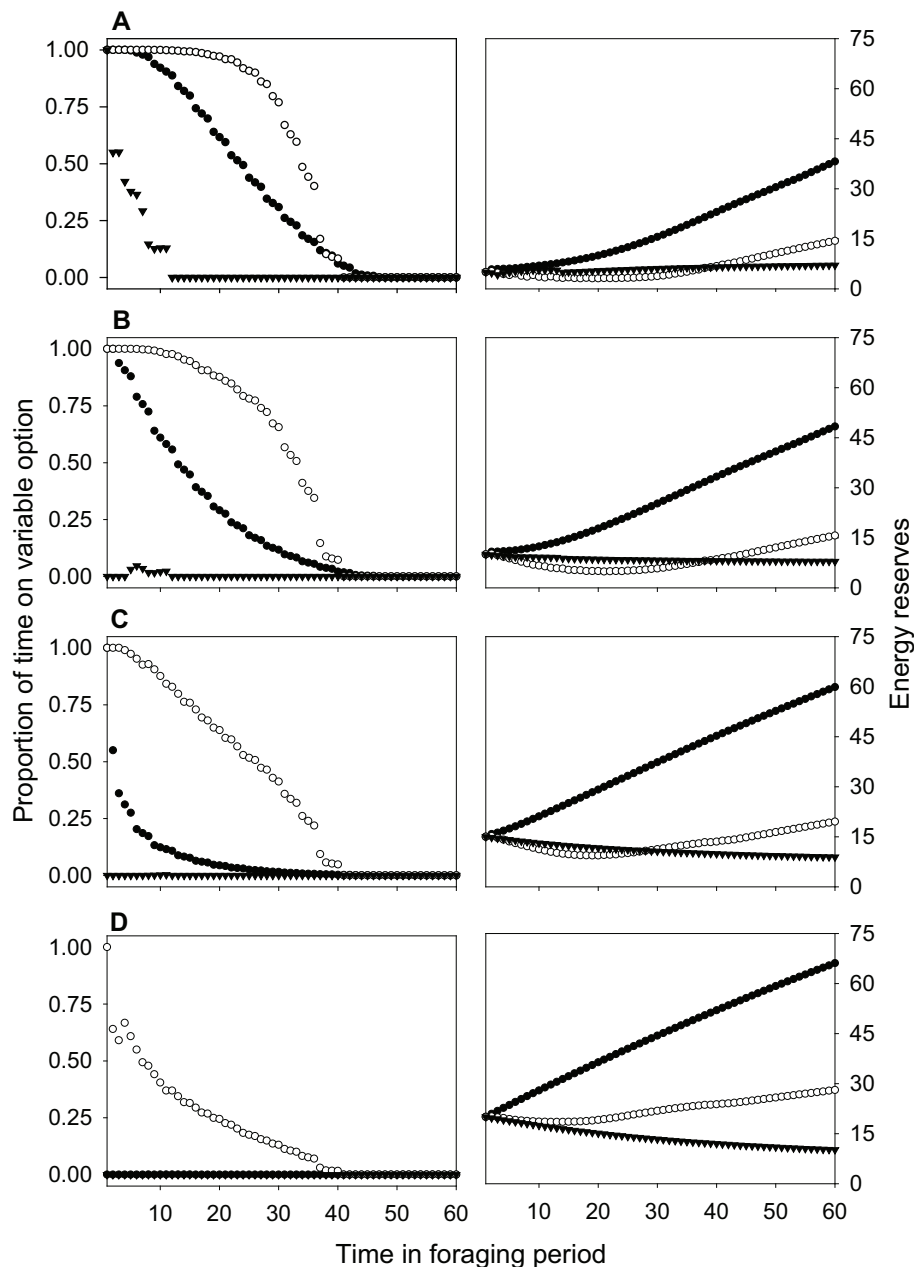


Figure 2: Outcome of differences in optimal sampling policies (found by stochastic dynamic programming; see text) on diurnal patterns in the mean proportion of time individuals are expected to forage on the more variable option (*left panels*) and mean energy reserves (*right panels*) they carry as a function of energy reserve levels at the start of the foraging period: $x_{\text{init}} = 5$ (A), $x_{\text{init}} = 10$ (B), $x_{\text{init}} = 15$ (C), $x_{\text{init}} = 20$ (D). Foragers with low ($M = 0.5$), intermediate ($M = 1.0$), and high ($M = 1.5$) metabolic rates are shown with filled circles, empty circles, and filled triangles, respectively. Parameter values: $e_1 = e_2 = 3$, $g = 0.7$, $b = 0.2$, $P = .5$. Values of other parameters are given in table 1.

low expectation of foraging interruptions (Dall et al. 1999) or a longer life expectancy (Eliassen et al. 2007). In contrast, variance-sensitive models assume that the variable option fluctuates between good and bad states in an entirely unpredictable fashion (Stephens and Krebs 1986),

providing no comparable benefit from early exploitation of the variable option.

Our analyses reveal that between-individual differences in metabolic rates on the scale observed in natural populations produce large differences in the optimal use of sam-

pling behavior. Sampling as a luxury always decreases with increasing MR, because higher reserves are needed for high-MR individuals before the cost of sampling errors becomes affordable. In contrast, the effect of MR on sampling for survival varies as a function of food abundance. At low food abundances, high-MR individuals sample for survival under a more restrictive set of conditions, because their higher energetic demands mean that they are more time constrained to acquire energy reserves and, consequently, that they have less opportunity to recover from sampling errors when they are in a poor state. However, once food abundance is sufficiently high that high-MR individuals are less time constrained to acquire energy reserves, sampling for survival increases as a function of MR.

Differences in optimal sampling behavior as a function of individual differences in MRs lead to MR-related differences in diurnal (or nocturnal) patterns of resource use and energy acquisition (fig. 2). Exploitation of the variable resource changes nonlinearly with increasing MR, such that intermediate-MR individuals spend the greatest proportion of time exploiting the variable resource (fig. 2). Differences in investment in sampling and exploitation of the variable food resource, combined with differences in energy expenditure, result in MR-related differences in patterns of mass change throughout the foraging period. Both low- and intermediate-MR individuals initially show high levels of exploitation of the variable option when initial energy reserves are low ($x_{\text{init}} \leq 15$). The energetic needs of low-MR individuals relative to food abundance are sufficiently low that such individuals pay a relatively low cost for sampling errors and are therefore able to continuously accrue energy reserves. In contrast, the MR of intermediate individuals relative to food abundance is such that sampling error costs are comparatively high, resulting in initial losses in energy reserves under high investment in sampling. Later in the foraging period, as information about the state of the variable option accumulates, both low- and intermediate-MR foragers are able to exploit the variable option efficiently, resulting in a steady accumulation of energy reserves. High-MR foragers defend themselves against losses in energy reserves by exploiting the constant foraging option almost exclusively throughout the foraging period.

Our analyses indicate that high MR-foragers experience reduced energy gains compared with low- and intermediate-MR foragers, suggesting a fitness cost of possessing a higher MR. This is due to the fact that we model the energetic costs of only higher metabolic rates. However, if we assume that higher metabolic rates confer foraging advantages in the form of increased foraging efficiency, the qualitative pattern remains even if its quantitative details change (see app. C). Although our results predict MR-related differences in the accumulation of energy reserves across the foraging

period, we caution against inferring implications of this variation for MR-related differences in long-term fitness for at least two reasons. First, we consider only the consequences of existing variation in MRs for optimal use of sampling and insurance in a foraging context. Higher metabolic rates may provide a range of benefits in other contexts, including higher growth and/or fecundity (Biro and Stamps 2008). Additionally, the relationship between MR-related differences in the accumulation of energy reserves and fitness may be complicated by the fact that differences in energy reserves can have both positive and negative fitness associations depending on the context. For example, higher fat reserves will reduce an individual's probability of energetic shortfall (positive fitness effect) but may simultaneously reduce an individual's ability to evade predators (negative fitness effect).

The role of stable differences in physiology, including individual differences in metabolic rates, in generating consistent individual differences in behavior has received a lot of attention in recent years (Biro and Stamps 2008, 2010; Réale et al. 2010; Wolf and McNamara 2012). Differences in energetic needs are thought to shape the expression of behaviors associated with energy acquisition and expenditure. More recently, individual differences in strategies for managing uncertainty have been recognized as a potentially important factor underlying individual differences in a wide range of behavioral traits and in behavioral plasticity (Mathot et al. 2012). This work unifies these two ideas by showing that individual differences in MRs in the range observed in natural populations (Speakman et al. 2004; Burton et al. 2011) can lead to dramatic differences in how individuals value information and thus in how they invest in managing uncertainty. This result also builds on previous work by Wolf and colleagues (2008) by providing a putative proximate mechanism for individual differences in responsiveness. Empirical studies are now needed to test our model predictions. This would require controlling the predictability of alternative foraging options available to individuals (see Krebs et al. 1978; Shettleworth et al. 1988) as well as tracking mass trajectories of individuals of known metabolic rates throughout the foraging period. It would also be worthwhile to investigate whether asymmetries among individuals in their propensity to acquire information carry over in group contexts, where individuals also have the possibility of acquiring information socially.

Although our model addressed differences in sampling and information use in a foraging context, there is growing evidence that such individual differences can occur in a wide range of contexts. For example, females may differ consistently in the number of males sampled before selecting a mate (Bensch and Hasselquist 1992) or in the proportion of their young resulting from extrapair matings

(While et al. 2009; Reid et al. 2011), which can be viewed as a form of insurance against mate infertility or genetic incompatibility (Kempnaers and Dhondt 1993).

One interesting extension of this work would be to evaluate whether variation in MRs can account for individual differences in sampling behavior in nonforaging contexts, where the payoffs for sampling are in a currency that relates less directly to MR.

Acknowledgments

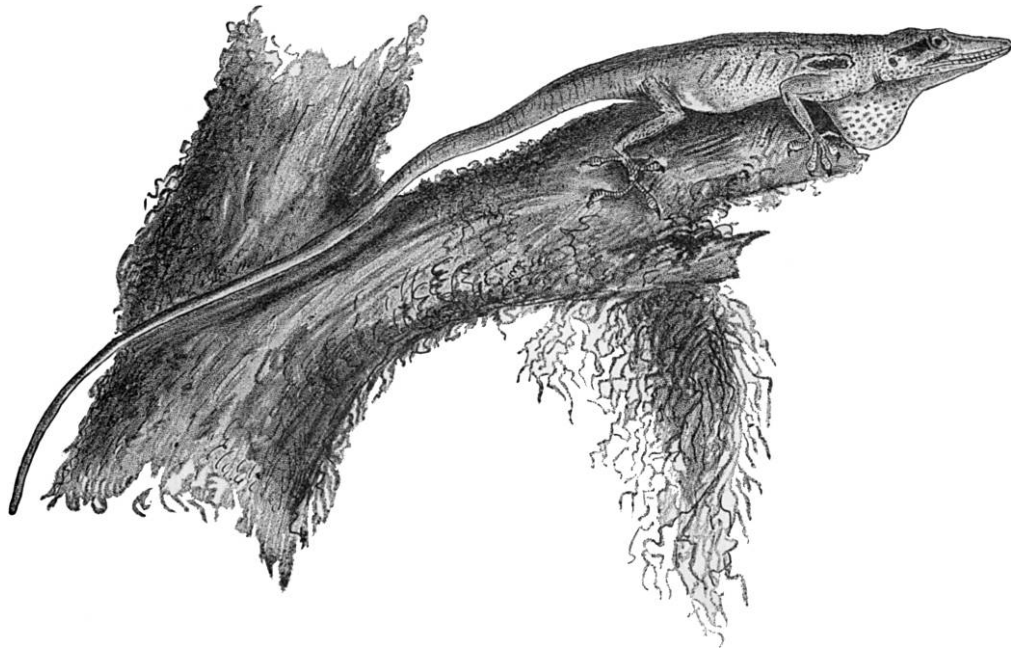
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“[I]t must be remembered, and it is a fact not commonly known, that [...] the chameleon has an uncompromising enemy in the domestic cat. This animal, I have been informed upon undoubted authority, will, when the opportunity presents itself, pass anything, meat, birds, and even fish, if there is the slightest chance of securing one of these lizards, of which they seem to be so inordinately fond. The cat will stalk one, just as we all have seen them attack some unsuspecting sparrow. Should the lizard be on the trunk of a tree, and low down near the ground, and the cat miss it in her spring, she will frequently, in her disappointment, chase it up the tree, where of course the reptile wins in such an unequal race.” From “Observations on the Habits of the American Chameleon (*Anolis principalis*)” by R. W. Shufeldt (*American Naturalist*, 1883, 17:919–926).