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Temporal Variation in Danger Drives Antipredator Behavior: The Predation Risk Allocation Hypothesis

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ABSTRACT: The rapid response of animals to changes in predation risk has allowed behavioral ecologists to learn much about antipredator decision making. A largely unappreciated aspect of such decision making, however, is that it may be fundamentally driven by the very thing that allows it to be so readily studied: temporal variation in risk. We show theoretically that temporal variability in risk leaves animals with the problem of allocating feeding and antipredator efforts across different risk situations. Our analysis suggests that an animal should exhibit its greatest antipredator behavior in high-risk situations that are brief and infrequent. An animal should also allocate more antipredator effort to high-risk situations and more feeding to low-risk situations, with an increase in the relative degree of risk in high-risk situations. However, the need to feed leaves an animal with little choice but to decrease its allocation of antipredator effort to high-risk situations as they become more frequent or lengthy; here, antipredator effort in low-risk situations may drop to low levels as an animal allocates as much feeding as possible to brief periods of low risk. These conclusions hold under various scenarios of interrupted feeding, state-dependent behavior, and stochastic variation in risk situations. Our analysis also suggests that a common experimental protocol, in which prey animals are maintained under low risk and then exposed to a brief "pulse" of high risk, is likely to overestimate the intensity of antipredator behavior expected under field situations or chronic exposure to high risk.

Keywords: antipredator behavior, decision making, foraging behavior, predation risk, vigilance.

The existence of predators influences decisions about feeding, activity levels, and reproduction made by a diverse array of vertebrate and invertebrate prey (Dill 1987; Lima and Dill 1990; Sih 1994). This pervasive influence of predators on prey behavior follows from the fact that an animal's behavioral options that maximize energy intake, access to mates, and so forth, often expose it to an increased risk of predation. One might thus expect that animals should (in some way) be able to weigh the risk of predation against various benefits when deciding which behavioral option to pursue. Hundreds of studies now provide evidence that animals possess such abilities (Lima 1998*b*). Collectively, these studies provide insight into not only animal behavior but also the nature of predator-prey interactions (Abrams 1995; Sinclair and Arcese 1995; Ruxton and Lima 1997) and their ecological consequences (Werner 1992; Wooster and Sih 1995; Lima 1998*a*).

Progress in understanding decision making under the risk of predation can be attributed to the fact that animals respond quickly to changes in the risk of predation over time. Such temporal variation in risk is, in fact, an unavoidable aspect of most natural environments. Risk may vary seasonally (Werner 1986; Lucas et al. 1996), across a lunar cycle (Daly et al. 1992; Kotler et al. 1994), within a day (Dodson 1990; Fenn and Macdonald 1995), or even minute to minute during an encounter with a predator (Dill and Gillett 1991; Sih 1992). Thus, the fact that animals are able to detect and respond to temporal variation in the risk of predation (e.g., Kats and Dill 1998) is not surprising. Less obvious, however, is the fact that the nature of this temporal variation itself can fundamentally influence antipredator decision making.

Here, we develop the "risk allocation hypothesis," which is based on the idea that animals feeding under temporal variation in the risk of predation face a problem in the optimal allocation of antipredator behavior across various states of risk. We also argue that such temporal variation in risk can actually drive much of the antipredator behavior observed in nature. We illustrate this general allocation problem in a simple environment with two states of risk, high and low. It is intuitively clear that animals should allocate relatively more of their antipredator effort to the high-risk situation, and ample evidence suggests

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that animals will do so (see Lima 1998*b*). However, the question here concerns the nature of such "risk allocation." If the periods of high risk are brief, then a foraging animal might choose to stop feeding completely and ride out the "pulse" of high risk in a state of heightened antipredator behavior; the lost feeding may then be shifted to low-risk periods. Alternately, if high-risk periods are frequent or lengthy, then an animal has little choice but to feed under high risk; under such conditions, however, we might expect intense feeding efforts during the infrequent low-risk periods. In short, the crux of the risk allocation hypothesis is that the antipredator efforts exhibited in each state of risk are not independent but are inextricably linked.

Empirical and theoretical research has failed to appreciate the risk allocation problem resulting from temporal variation in risk. In fact, we know of no empirical work that examines whether an animal's response to predation risk at one time period depends on the risk experienced at other times. Similarly, models of antipredator decision making tend to treat risk as a constant over time, despite the fact that the theory is applied to situations in which risk might vary markedly. Even models with time-varying risk treat such variation as an environmental given rather than an important entity in itself (e.g., Clark and Levy 1988; McNamara et al. 1994; but see Clark 1994). Models of state-dependent decision making (Mangel and Clark 1988) perhaps come closest to dealing with the risk allocation problem (see also McNamara and Houston 1994). This is particularly true for models in which temporal changes in energy reserves determine predation risk and thus the temporal pattern of daily feeding behavior (Bednekoff and Houston 1994*a*, 1994*b*; McNamara et al. 1994); even in this context, the risk allocation problem remains unexplored.

We take as our theoretical starting point the Risk Spreading Theorem (RST) of Houston et al. (1993). The RST provides the nonintuitive result that the feeding effort minimizing predation risk over a fixed time interval is constant and independent of the actual level of risk. Under these conditions, an animal should feed at the lowest rate (or, conversely, at the maximal antipredator effort) that will still allow it to meet some energetic requirement over the time interval in question. Actual levels of risk influence behavior only when non-predation-related factors (e.g., time constraints, interruptions to feeding, reproductive considerations, etc.) are introduced into the analysis (Houston et al. 1993). Such factors clearly could be important determinants of behavior but are not necessarily associated with foraging under predation risk. In contrast, we show that one need only introduce temporal variation in risk into the RST to explain the fact that animals are sensitive to the level of predation risk. We argue that such variation in risk (and the resulting risk allocation problem) is a fundamental reason why animal decision making is so clearly influenced by different levels of risk. After describing this modification to the RST, we then elaborate further on the risk allocation phenomenon by considering the effects of interruptions in feeding and state-dependent decision making. We also apply our general theory to the effects of temporal variation in group size on antipredator vigilance. Finally, we discuss the implications of our results for the design and interpretation of behavioral experiments on antipredator behavior.

Models and Results

Basic Model

We analyze a situation in which an animal feeds over some time, T, in order to gain a given amount of energy, E, required for survival. The animal spends some known proportion, p, of its time in a relatively dangerous situation and the remainder $(1 - p)$ of its time in a less dangerous situation. The problem for the animal is to decide how much foraging effort (or, alternatively, how much antipredator effort) to allocate across these two risk states such that survival is maximized, given that it must meet its energetic requirement, E, by the end of T.

An animal has control over the proportion of its time that it spends feeding during a given risk state. We denote these feeding efforts in the high- and low-risk states by f_H and f_L, respectively $(0 \leq f \leq 1)$. Feeding effort is related to predator detection, since an animal will be less likely to detect predatory attack as f increases. Following Houston et al. (1993), we assume that an animal fails to detect attack with probability f^2. This formulation assumes diminishing returns in predator detection with increasing vigilance (see Lima 1987). When f is high, vigilance is low, and a relatively small decrease in feeding (increase in vigilance) adds greatly to predator detection; when f is low, vigilance is already high, and additional vigilance adds relatively little to predator detection. We later consider the more general situation in which the probably of failing to detect attack is given by f^b.

We assume that attacks occur according to a simple Poisson process at rates α_H and α_L for the high- and low-risk situations, respectively. Thus, the overall probability of surviving the time interval T is the product of the probabilities of surviving feeding while in the two risk states. In symbols,

$$P(\text{survival}) = \exp(-\alpha_H f_H^2 pT) \exp[-\alpha_L f_L^2 (1 - p)T],$$

which rearranges to

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$$P(\text{survival}) = \exp\{-T[\alpha_H f_H^2 p + \alpha_L f_L^2(1-p)]\}. \quad (1)$$

As in the Risk Spreading Theorem of Houston et al. (1993), this simple formulation assumes no state dependence in risk and that feeding proceeds uninterrupted over the interval (0, T).

A key point here is that f_H and f_L are linked because the animal is feeding to meet the energetic requirement, E. This functional relationship can be expressed as

$$f_H \epsilon p T + f_L \epsilon (1-p) T = E, \quad (2)$$

where ϵ is the rate of energy intake while the animal is actually feeding (i.e., per amount of foraging effort, assumed equal across risk states). Defining $R = E/(\epsilon T)$ as the average rate of foraging that must prevail in order to meet E, equation (2) rearranges to

$$f_H p + f_L(1-p) = R. \quad (3)$$

Our goal is thus to maximize (1) subject to the requirement (3). This is equivalent to minimizing the exponent in equation (1) subject to (3). Doing so yields the optimal feeding efforts in the high-risk and low-risk states:

$$f_H^* = \frac{R}{(\alpha_H/\alpha_L)(1-p) + p}, \quad (4)$$

$$f_L^* = \frac{R}{(1-p) + (\alpha_L/\alpha_H)p}. \quad (5)$$

The crux of the risk allocation hypothesis, that temporal variability in predation risk drives risk-dependent antipredator behavior, follows from equations (4) and (5). Consider first the case where $\alpha_H = \alpha_L$; here, $f_L^* = f_H^* = R$, indicating that optimal behavior under an invariant risk of predation is not dependent upon the level of risk itself. This is actually the result obtained in the single-risk-state version of the RST developed by Houston et al. (1993). However, if $\alpha_H > \alpha_L$, then the level of risk does matter. More precisely, the ratio of α_H/α_L matters. As the "attack ratio" α_H/α_L increases, f_H^* decreases and f_L^* increases. That is, as the attack ratio increases, more feeding effort is allocated to the low-risk situation and less to the high-risk situation. We note further that the ratio of feeding efforts varies as the inverse of the attack ratio ($f_H^*/f_L^* = \alpha_L/\alpha_H$) independently of the value of p, which nonetheless has a marked influence on feeding efforts; this inverse relationship breaks down when the feeding effort in the low-risk situation is maximal ($f_L^* = 1$).

It is perhaps more intuitive to illustrate this risk allocation phenomenon in terms of antipredator behavior per se rather than feeding effort. As suggested earlier, we can do this most easily using antipredator vigilance. The optimal proportion of time that an animal spends vigilant for predators (v^*) is effectively $v^* = 1 - f^*$, since f can easily be interpreted as the proportion of time that an animal is feeding with its head down (e.g., Lima 1990; Packer and Abrams 1990). A plot of optimal vigilance against attack ratio (fig. 1) illustrates key points of our risk allocation hypothesis. As attack ratio increases, the amount of vigilance allocated to the high-risk situation increases, as one might expect; less vigilance is allocated to the low-risk situation, reflecting the benefit of shifting more feeding to the low-risk situation with increasing α_H/α_L.

This risk allocation phenomenon is accentuated considerably as the proportion of time spent in the high-risk situation increases, as indicated by the greater divergence in optimal vigilance between low- and high-risk situations with increasing p (fig. 2). As p increases, there are fewer opportunities to feed in the low-risk situation and more time is spent at high risk. Accordingly, with increasing p, progressively less vigilance (more feeding) is allocated to the low-risk situation. In fact, v_L^* actually drops to 0 for high attack ratios and p values. In other words, an animal should take maximal advantage of safe feeding opportu-

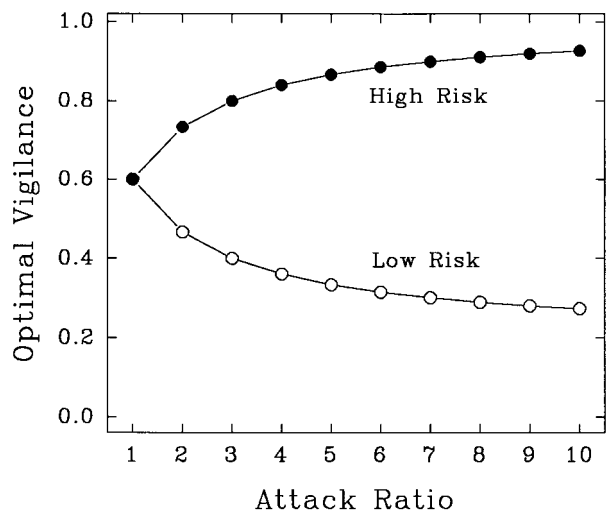

Figure 1: Risk allocation as influenced by attack ratio (α_H/α_L). Results are given for expected vigilance in high-risk (*solid circles*) and low-risk (*open circles*) situations. Both curves emanate from the level of vigilance expected in an environment with no temporal variation in risk ($\alpha_H = \alpha_L$). The values of R (average intake rate necessary to meet energetic requirement) and p (proportion of time in the high-risk state) are set at 0.4 and 0.5, respectively.

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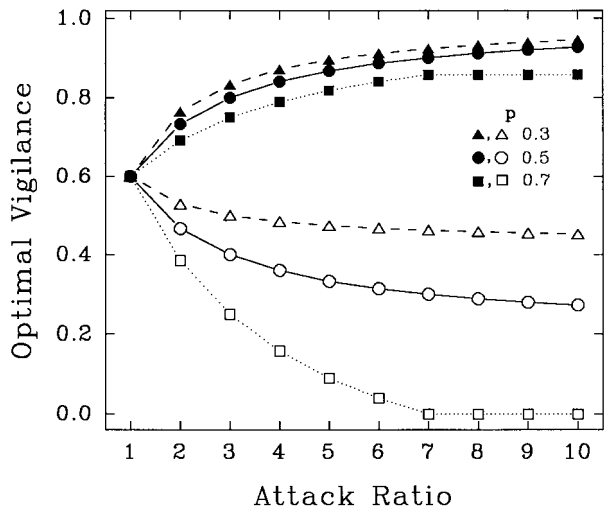

Figure 2: Risk allocation as influenced by attack ratio (α_H/α_L) and proportion of time in the high-risk state (p). Results are given in terms of expected vigilance in high-risk (*solid symbols*) and low-risk (*open symbols*) situations. For all cases, the value of R (average intake rate necessary to meet energetic requirement) is set at 0.4.

nities that are brief or infrequent. A less intuitive effect of increasing p is a concomitant decrease in vigilance in both low- and high-risk situations (fig. 3). This result also reflects the fact that more time must be spent feeding under high risk as p increases: maintaining high vigilance under chronically high risk is impossible if the overall energetic requirement is to be met. Note that vigilance decreases more steeply in the low-risk situation with increasing p (fig. 3), reflecting the greater allocation of feeding to the low-risk situation as p increases.

The above results can be generalized for any situation in which failure to detect attack can be described by the power function f^b, rather than f^2, as we have so far assumed. For $b > 1$, or the case of diminishing returns in predator detection with increasing vigilance, equation (4) generalizes to

$$f_H^* = \frac{R}{(\alpha_H/\alpha_L)^{1/(b-1)}(1-p)+p}.$$

This form of f_H^* provides behavior qualitatively similar to that described in figures 1 and 2, including the dependence of optimal behavior on the attack ratio rather than the absolute values of attack rates. However, for $1 < b < 2$, the divergence in feeding efforts between the two risk states can be much more accentuated than indicated above (where $b = 2$). For the unlikely case of $b = 1$, optimal behavior means feeding only in the low-risk situation at $f_L^* = R/(1-p)$, with $f_H^* = 0$ (there is no attack ratio–dependent effect when $b = 1$). The case of $b < 1$ implies that animals are likely to fail to detect attack under all but the most minimal feeding efforts; that is, a considerable investment in vigilance is required before realizing any ability to detect predators. This situation does not seem biologically realistic, but if it were to occur, all feeding would be done at the maximal effort ($f = 1$).

Overall, our results stress the practical importance of an appreciation for the interdependence of antipredator behavior across all risk situations experienced by an animal. For example, consider a situation in which the attack ratio is increasing due to an increase in α_H over a constant α_L. If one were studying vigilance solely in the low-risk situation, one might be hard-pressed to explain why vigilance is changing despite no apparent change in local predation risk (α_L). Similarly perplexing results might occur due to changes in overall risk allocation following unappreciated changes in p.

Interrupted Feeding

We have so far considered the risk allocation phenomenon in an environment in which feeding is not interrupted. In reality, of course, feeding could be interrupted by a variety of phenomena. Following Lima (1987) and Houston et al. (1993), we consider the effects of major interruptions to feeding. Here, interruptions terminate future feeding opportunities, and thus an animal that has not already met

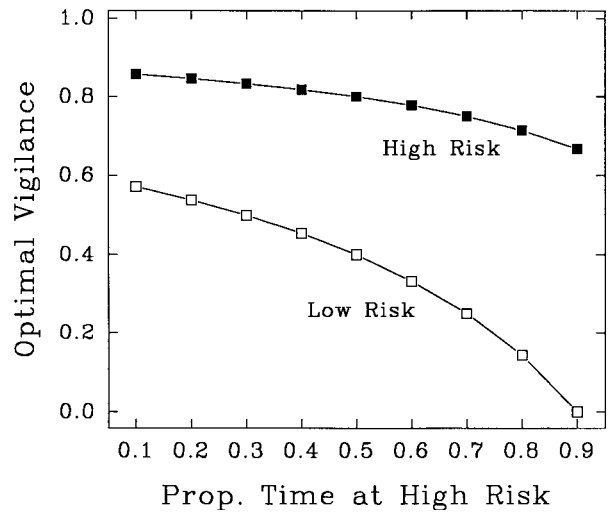

Figure 3: Vigilance in high-risk (*solid symbols*) and low-risk (*open symbols*) situations as influenced by the proportion of time spent in the high-risk state (p). Values of R and the attack ratio (α_H/α_L) are set at 0.4 and 3.0, respectively.

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its requirement, E, will not survive. Sudden snowstorms might have such an effect on small, wintering birds. Houston et al. (1993) show that the optimal feeding strategy under the threat of such interruptions is to feed faster and to stop feeding before the interval $(0, T)$ has expired. We define this stopping time as $\tau \leq T$ and $d = \tau/T$ as the proportion of available time spent feeding. We assume further that a nonfeeding animal $(f = 0)$ is safe from predators.

The overall probability of survival is the product of the probabilities of avoiding starvation due to interruptions and avoiding being killed during both high- and low-risk situations. We assume that interruptions occur with constant probability per unit time at rate γ. Thus, the probability of finishing feeding before being interrupted is $\exp(-\gamma dT)$. The probabilities of avoiding predation are as derived in equation (1), with the exception that the time, T, is multiplied by the proportion, d; this assumes a well-mixed sequence of high- and low-risk periods such that the overall proportions of period types is the same regardless of when the interruption occurs. With these assumptions, the overall probability of survival is

$$P(\text{survival}) = \exp(-\gamma dT)\exp(-\alpha_{\mathrm{H}} f_{\mathrm{H}}^2 p dT) \exp[-\alpha_{\mathrm{L}} f_{\mathrm{L}}^2 (1-p) dT], \tag{6}$$

where all symbols are as defined previously. Equation (6) is maximized subject to the requirement that the animal meets its target energetic requirement by time $\tau = dT$. This requirement can be expressed by a simple modification to equation (3): $f_{\mathrm{H}} p + f_{\mathrm{L}}(1-p) = R/d$. A determination of optimal feeding efforts in the high- and low-risk periods (as per eqq. [4] and [5]) yields the following:

$$f_{\mathrm{H}}^* = \frac{R/d}{(\alpha_{\mathrm{H}}/\alpha_{\mathrm{L}})(1-p) + p},$$

$$f_{\mathrm{L}}^* = \frac{R/d}{(1-p) + (\alpha_{\mathrm{L}}/\alpha_{\mathrm{H}})p}.$$

The only difference between these optimal feeding efforts and those derived earlier (eqq. [4] and [5]) is that interruptions effectively increase R by a factor of $1/d$. This means that, with the possibility of interruptions, animals must feed faster by a factor of $1/d$ in order to terminate feeding at time $\tau \leq T$. One would thus expect an overall increase in feeding (and decrease in antipredator behavior) with a decrease in the overall proportion of available time spent feeding (d). This effect can be seen in figure 4, in which we once again express behavior in terms of a simple measure of vigilance ($v^* = 1 - f^*$). This figure also illustrates the basic risk allocation phenomenon seen in figures 1 and 2: optimal vigilance levels in low- and high-risk situations diverge considerably as the attack ratio increases. This allocation effect is accentuated with decreasing d. In fact, with adequately low d, optimal risk allocation leaves the animal with zero vigilance in the low-risk situation (all-out feeding) and the maximum vigilance possible (given the energetic requirement) in the high-risk situation.

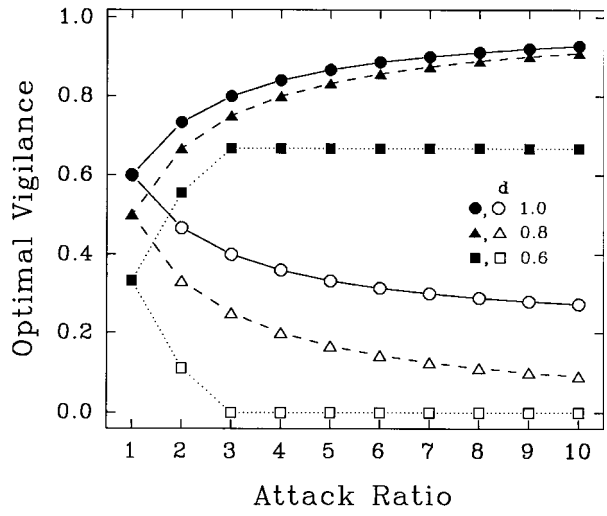

Figure 4: Risk allocation as influenced by attack ratio ($\alpha_{\mathrm{H}}/\alpha_{\mathrm{L}}$) and feeding interruptions; greater values of d (the proportion of available time used for feeding) indicate increasingly severe interruptions. Results are given in terms of expected vigilance in high-risk (*solid symbols*) and low-risk (*open symbols*) situations. For $d = 0.6$, optimal vigilance in the low-risk situation drops to zero for attack ratios ≥ 3; beyond this point, vigilance in the high-risk situation holds at a constant value, since no further feeding can be allocated to the low-risk situation. Values for R and p are set at 0.4 and 0.5, respectively.

We can also use equation (6) and the optimal feeding efforts to determine the optimal stopping time (τ^*) or, equivalently, the optimal value of d ($d^* = \tau^*/T$). Doing so yields

$$d^* = \frac{R}{\sqrt{\gamma[(1-p)/\alpha_{\mathrm{L}} + p/\alpha_{\mathrm{H}}]}}. \tag{7}$$

Taking partial derivatives, we see that $\partial d^*/\partial\gamma < 0$ and $\partial d^*/\partial\alpha_i > 0$, indicating intuitively that d^* (or τ^*) decreases with increasing probability of interruption (increasing γ) and increases with increasing attack rate. The relative importance of predation risk and feeding interruption in determining d^* can be illustrated by reformulating equation (7) as

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$$d^* = \sqrt{\beta_{d=1}/\gamma}, \tag{8}$$

in which

$$\beta_{d=1} = \frac{R^2}{(1-p)/\alpha_L + p/\alpha_H};$$

$\beta_{d=1}$ is essentially the predation-related death rate in equation (1) when $d = 1$. Thus equation (8) indicates that $d^* < 1$ only when γ exceeds $\beta_{d=1}$. In other words, interruptions come into play in determining optimal risk allocation only when the rate of interruptions exceeds the overall death rate caused by predators in the absence of interruptions. In many realistic situations, the predator-driven death rate will likely exceed that from interruptions (McNamara and Houston 1990); hence, an animal may often behave as if $d = 1$ and spread its feeding over the entire interval $(0, T)$.

State Dependence

The allocation of risk should be responsive to changes in an animal's energetic state over time. Here, we consider a situation in which variation in an animal's energetic reserves reflects stochastic variation in the sequence of high- and low-risk periods experienced over time. Periods of high risk imply periods of reduced feeding (Lima 1998*b*), several of which in close temporal proximity can significantly lower energetic reserves.

We make use of the technique of stochastic dynamic programming (Mangel and Clark 1988) to determine optimal antipredator behavior as a function of time, energetic state, and risk situation. We translate the logic of the basic analytical model into a dynamic programming framework as follows. At any point in time, a forager with energetic reserves at level X finds itself in either the high- or low-risk situation and chooses to feed with effort $0 \le f \le 1$. Since dynamic programming works with discrete intervals of time and state, we assume that our foragers actually have the option of feeding at efforts of 0, 0.1, 0.2, … , 1.0, which we assume yield 0, 1, 2, … , or 10 units of energy, respectively. A forager expends e units of energy per time interval regardless of its behavior or energetic state. The forager starves if reserves fall to zero. Regarding predation, a given time interval is high risk (H) with probability p, and low risk (L) with probability $1 - p$, independently of the risk situation in the previous time interval. The per-interval probabilities of attack in the two risk situations are a_H and a_L. As before, f^2 is the probability of failing to detect attack. Thus, the probability of death during a given time interval is the product $a_i f^2$, which does not depend on reserve level.

Using dynamic programming, we find the optimal foraging effort in both high- and low-risk situations by working backward from a terminal reward (Mangel and Clark 1988) in which all survivors with nonzero reserves are of equivalent fitness. The dynamic programming equation is

$$F(X, r, t) = \max_{0 \le f \le 1} (1 - a_r f^2) [pF(X + 10f - e, \mathrm{H}, t + 1) + (1 - p)F(X + 10f - e, \mathrm{L}, t + 1)].$$

The function F denotes fitness from time t until the end of the interval, T, which is the product of the probability of avoiding predation in the current interval and the expected fitness during subsequent time intervals. For each combination of energetic state (X), risk situation ($r =$ L or H) and time (t), optimal behavior is the value of f maximizing $F(X, r, t)$. The dynamic programming equation was solved numerically for time intervals successively farther from the terminal reward until a stable behavioral policy was reached (stationarity; see Mangel and Clark 1988). Stationary behavior is that which maximizes long-term survival and is independent of the form of terminal reward that is used. Stationary behavioral policies emerged quickly, usually within 30 steps from the end of the interval, T.

The dynamic programming results (table 1), expressed as before in terms of vigilance, broadly reflect the basic analytical results. In particular, the phenomenon of risk allocation is once again apparent. As the attack ratio a_H/a_L increases from unity, vigilance levels in high- and low-risk situations diverge considerably. As seen in the analytical model, all-out feeding (zero vigilance) is again observed in the low-risk situation with high values for attack ratio and proportion of time in the high-risk situation (p). An effect of energetic state is also apparent, with energetically well-off animals investing more in vigilance (and less in feeding) than other animals (see also McNamara and Houston 1992). Generally, animals feed only if their energetic reserves are relatively low, with the exception of the nearly all-out feeding in the low-risk situations mentioned above.

Perhaps the most striking effect in table 1 confirms our analytical result that attack ratios rather than absolute levels of risk influence the allocation of antipredator behavior among risk states; increasing a_H and a_L 100-fold while maintaining constant attack ratios has virtually no impact on the optimal behavioral policy (cf. top and bottom halves of table 1). However, this result applies to stationary behavior. Absolute levels of risk may come into play as the end of the time interval approaches, or with the sort of energetic-reserve-dependent predation suggested for

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Table 1: Optimal proportion of time spent vigilant for animals feeding under a stochastic sequence of high- and low-risk periods, as a function of energetic state, attack ratio a_H/a_L, proportion of time spent in the high-risk state (p), and risk state

		Energetic state (% maximum reserves)									
a_H/a_L[a] and p	Risk[b]	5	10	15	20	25	30	35	40	45	50
1/1:											
.3	Both	.7	.9	.9	.9	1.0	1.0	1.0	1.0	1.0	1.0
.7	Both	.7	.8	.8	.8	.8	.9	.9	.9	.9	.9
3/1:											
.3	H	.7	.9	.9	1.0	1.0	1.0	1.0	1.0	1.0	1.0
	L	.7	.8	.9	.9	.9	1.0	1.0	1.0	1.0	1.0
.7	H	.7	.8	.8	.8	.8	.9	.9	.9	.9	.9
	L	.4	.4	.5	.5	.6	.6	.7	.7	.7	.7
6/1:											
.3	H	.7	.9	.9	1.0	1.0	1.0	1.0	1.0	1.0	1.0
	L	.5	.7	.8	.8	.9	.9	1.0	1.0	1.0	1.0
.7	H	.7	.8	.8	.8	.8	.9	.9	.9	.9	.9
	L	.0	.1	.2	.2	.3	.4	.4	.5	.5	.5
10/1:											
.3	H	.7	.9	.9	1.0	1.0	1.0	1.0	1.0	1.0	1.0
	L	.5	.6	.7	.8	.8	.9	.9	1.0	1.0	1.0
.7	H	.7	.8	.8	.8	.8	.9	.9	.9	.9	.9
	L	.0	.0	.0	.0	.0	.1	.1	.2	.3	.4
100/100:											
.3	Both	.7	.9	.9	.9	1.0	1.0	1.0	1.0	1.0	1.0
.7	Both	.7	.8	.8	.8	.8	.9	.9	.9	.9	.9
300/100:											
.3	H	.7	.9	.9	1.0	1.0	1.0	1.0	1.0	1.0	1.0
	L	.7	.8	.9	.9	.9	1.0	1.0	1.0	1.0	1.0
.7	H	.7	.8	.8	.8	.8	.9	.9	.9	.9	.9
	L	.4	.4	.5	.5	.6	.6	.7	.7	.7	.7
600/100:											
.3	H	.7	.9	.9	1.0	1.0	1.0	1.0	1.0	1.0	1.0
	L	.5	.7	.8	.8	.9	.9	1.0	1.0	1.0	1.0
.7	H	.7	.8	.8	.8	.8	.9	.9	.9	.9	.9
	L	.1	.1	.2	.2	.3	.4	.4	.5	.5	.5
1000/100:											
.3	H	.7	.9	.9	1.0	1.0	1.0	1.0	1.0	1.0	1.0
	L	.5	.6	.7	.8	.8	.9	.9	1.0	1.0	1.0
.7	H	.7	.8	.8	.8	.8	.9	.9	.9	.9	.9
	L	.0	.0	.0	.0	.0	.1	.2	.2	.3	.4

Note: Results apply only to the period of stable, survival-maximizing behavior (stationarity; see "State Dependence"). Results are shown only for energy reserves ≤50% of maximum; vigilance levels beyond this point are generally near maximal (except for very high p values). In all cases, $e = 4$ units, and the maximum reserve level was set at 40 units.

[a] a values $\times 10^{-4}$ per time interval.

[b] "Both" signifies that the results apply to both high- and low-risk situations; H = high-risk situation, L = low-risk situation.

some birds (Witter and Cuthill 1993; Gosler et al. 1995; Metcalfe and Ure 1995).

The Group Size Effect in Antipredator Vigilance

We close with a brief application of the risk allocation hypothesis to a ubiquitous behavioral phenomenon: the vigilance group size effect. In virtually all social birds and mammals that have been studied, an increase in group size causes individual group members to become less vigilant for predators (Elgar 1989; Roberts 1996). For these animals, group size, and thus predation risk, varies considerably over short time periods (e.g., Roberts 1995). In-

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deed, this fluctuation in group size makes it possible to measure the group size effect in the first place. Entirely unappreciated, however, is the possibility that variability in group size (or predation risk) may be a major driving force behind the group size effect itself.

We model the effects of variation in group size by considering an animal that feeds solitarily for a proportion of time, s, and in a pair for $1 - s$. For heuristic ease (and without loss of generality), we consider the optimal behavior of a focal animal with reference to a specific feeding effort by its occasional companion. We denote the feeding effort of the focal animal by f_s when solitary and f_p when in a pair; the feeding effort of its companion is ϕ. As before, we assume that an animal's feeding effort represents the proportion of time spent with its head down and that f^2 (or ϕ^2) represents the probability that it will not detect attack. Here, we assume that attack rates on solitary and paired foragers are equal at rate α (as in Lima 1987; McNamara and Houston 1992) and focus on variation in risk as represented by variation in group size. With these assumptions, the overall probability of survival for our focal animal is

$$P(\text{survival}) = \exp(-\alpha f_s^2 sT)$$
$$\exp\{-\alpha[(f_p^2\phi^2)/2](1 - s)T\},$$

which is the product of the probabilities of survival when solitary and when in a pair; in the exponent of the latter, the product $f_p^2\phi^2$ represents the probability that both members of the pair fail to detect attack, and the 2 in the denominator represents a 50% chance that the focal animal is killed in a successful attack (the dilution of risk). Proceeding as in earlier sections, the optimal feeding effort of the focal bird, when alone, is

$$f_s^* = \frac{R}{(2/\phi^2)(1 - s) + s} \tag{9}$$

and, when in a pair,

$$f_p^* = \frac{R}{(1 - s) + (\phi^2/2)s}. \tag{10}$$

It is easy to show that, since $\phi \leq 1$, then $f_p^* > f_s^*$ for all values of s. In other words, the optimal feeding effort in a pair is higher than when alone. This result translates into lower vigilance when feeding in a pair. This standard result of decreasing vigilance with increasing group size is realized only when groups vary in size over time. Under such conditions it is optimal to allocate less vigilance to the low-risk situation (paired) and more vigilance to the high-risk situation (solitary). If group size were fixed over time, then risk would not vary and the optimal feeding effort would be given by the standard risk-spreading theorem: from equations (9) and (10), $f_p^* = f_s^* = R$ if the focal bird were to always feed alone ($s = 1$) or in a pair ($s = 0$).

Discussion

Temporal changes in the risk of predation are a fact of life for most animals, and hundreds of studies demonstrate that animals respond quickly and adaptively to changes in the risk of predation (Kats and Dill 1998; Lima 1998*b*). Indeed, behavioral ecologists have gained a good understanding of antipredator decision making by studying these responses to changing risk. Largely unappreciated by behavioral ecologists, however, is the fact that temporal variation in risk may be a fundamental driving force behind predation-risk-dependent behavior. As a consequence of this variation in risk, animals are generally faced with the problem of how to best allocate feeding and antipredator efforts across different risk states.

The crux of the risk allocation hypothesis is that antipredator responses are not simply situation specific. In other words, optimal behavior in a given situation depends upon the broader temporal context in which risk varies. If high-risk periods are relatively brief and infrequent, then an animal may allocate a great deal of antipredator behavior to such situations, with the bulk of its feeding effort allocated to low-risk situations. This low-risk feeding effort may be particularly intense when high-risk periods are long or frequent. Such an intense low-risk feeding effort allows for greater antipredator effort during the long periods of high risk (in which the animal must feed).

Our simple model does not cover all situations with variable risk. We assumed that animals are likely to experience many changes in risk state over a given time interval. This assumption is important to the conclusion that only the ratio of attack rates will influence behavior. For some animals, however, risk may vary on a longer timescale, perhaps even on a scale approaching entire life spans for some short-lived creatures. We also assumed implicitly that an animal can withstand periods of low feeding (high predation risk) without a great risk of starvation. If either of these assumptions does not hold, then animals must deal with periods of high- or low-risk as if they are effectively long-term situations. That is, they will not face the sort of risk allocation problem that we have modeled. Overall, however, our risk allocation hypothesis will likely apply to a great many animals faced with temporal variability in the risk of predation.

The risk allocation hypothesis suggests that particular caution must be used in interpreting and designing experimental studies on antipredator decision making. Such

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caution is especially warranted when using a common experimental protocol under which animals are exposed to a brief "pulse" of high risk, preceded and followed by extended periods of low risk. Under these circumstances, animals, especially those in good energetic condition, may adopt a degree of antipredator behavior that could not be sustained for long (see also Clark 1994; McNamara and Houston 1994). The risk allocation hypothesis indicates that such heightened antipredator behavior is not typical of field situations or chronic exposure to high risk. In fact, there is a growing realization that the degree of antipredator behavior expected under realistic field conditions may be overestimated by laboratory experiments (Abramsky et al. 1996; Irving and Magurran 1997; Wolff and Davis-Born 1997; see also Lima 1998*b*).

A specific example of this "pulse of risk" problem arises when measuring the energetic equivalence of the risk of predation (Abrahams and Dill 1989; Utne et al. 1993; Kennedy et al. 1994; Grand and Dill 1997; see also Kotler and Blaustein 1995). The basic idea behind energetic equivalence is that predation risk can be expressed in terms of the energetic benefit that an animal is willing to forgo to avoid predation. This willingness to forgo feeding is typically measured during relatively brief exposures to high predation risk. However, as mentioned above, an animal might forgo a good deal of feeding during a brief exposure to high risk. Thus, if feeding behavior is examined only during this high-risk period, then one might conclude erroneously that avoiding risk is worth a great deal of energy. Clearly, any measure of the energetic equivalence of risk will reflect the temporal context in which predation risk varies (see also Moody et al. 1996).

Risk allocation complications may also arise when applying theory to real-world situations. Since the majority of theoretical work on antipredator behavior takes risk (attack rates, etc.) to be constant over time, theoretical expectations may generally underestimate behavioral responses to (temporary) high risk and overestimate such responses to (temporary) low risk. One of us provides an example of this sort of problem. Based upon a "constant risk" model, Lima (1987) concluded that vigilance should be minimal in a visually obstructive environment in which the only method of detecting predators involves time-consuming scanning; such scanning is too costly because it greatly increases overall exposure to predators. Nevertheless, Metcalfe (1984) found that sandpipers engage in much vigilance in visually obstructive environments. Lima (1987) explained this contradiction by assuming that sandpipers are attacked more frequently in such environments. However, it seems likely that these sandpipers fed only briefly in the presence of visual obstructions and thus could afford to allocate considerable antipredator effort to this risky situation.

Our theory of risk allocation assumes that animals have a reasonably accurate perception of whether they are in a high- or low-risk situation. Indeed, there are many unambiguous cues available to detect an increase in risk. The scent of predators provides excellent information on current risk (Kats and Dill 1998) for many aquatic creatures. Changes in illumination during the lunar cycle may signal differing levels of risk (Kotler et al. 1994). For social animals, changes in risk due to changes in group size are easily detectable. Recent encounters with predators may also signal an increase in risk. Assessing a lowering of risk is probably more difficult for many animals, especially when determining whether a predator is still in the immediate area (Sih 1992). Nevertheless, a huge literature (see Lima and Dill 1990; Lima 1998*b*) suggests that animals can and do make the sorts of assessments necessary for risk allocation to be observed in nature.

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