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Life in a multi-predator environment: some considerations for anti-predatory vigilance

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Animals live in environments with many types of predators, yet studies of animal behavior under the risk of predation focus almost exclusively on single-predator environments. This is especially true in an important area of study: anti-predatory vigilance. A simple exploration of vigilance shows that several "single-predator" expectations may not apply in a multi-predator environment. Two cases of vigilance are identified: predator-specific vigilance, in which the detection of a given predator requires a particular mode of vigilance, and non-specific vigilance, in which one mode of vigilance suffices for all predators. In both cases, and contrary to the single-predator situation, vigilance in a multi-predator environment may respond little or even negatively to increasing attack rates. Furthermore, predator-specific vigilance may be directed exclusively towards the most abundant predator in the environment; the "ignored" predators are nonetheless important determinants of vigilance. Finally, most studies usually focus on the most dangerous predator faced by the animal in question, but in doing so ignore the role of additional, seemingly innocuous predators as important determinants of vigilance. Studies adopting a "multi-predator" perspective promise to shed much light on the study of anti-predator behavior in general.

1. Introduction

Most animals live in environments containing several types of predators (e.g., hawks, owls, canids, snakes, etc.) covering the spectrum from extremely dangerous to relatively innocuous. Despite the large and growing literature on animal decision making under the risk of predation (Lima & Dill 1990), surprisingly few studies address the behavioral conflicts facing life in a multi-predator environment (but see Power 1984, Rahel & Stein 1988, Schlosser 1988, Soluk & Collins 1988, Brown 1989, Huang & Sih 1991, Daly et al. 1992, Kotler et al., in press). In fact, virtually all of the many laboratory studies on such decision-making deal only with one, usually dangerous predator (but see Heads 1985, Savino & Stein 1989), and even behavioral studies in the field make only passing mention (if that) of the multi-predator nature of the environment. Here, I present a mathematical exploration of some of the ways in which different types of predators may combine to influence behavioral decision making under the risk of predation.

My focus is on anti-predatory vigilance in animals feeding under the risk of predation, the many studies of which (for a review see Elgar 1989) provide few (if any) exceptions to the above neglect of multiple predators. Experimental studies of vigilance that manipulate predatory attacks themselves (e.g., Caraco et al. 1980) invariably focus on only one type of predator. In fact, the actual identity of important predators is usually a matter of speculation in most studies of vigilance (e.g., Ekman 1987, Lima 1987a, see Elgar 1989). Thus entities like predatory attack rates are treated abstractly, often with the implication that there is only one main predator, or that all predators can in some way be combined across types. This focus on single predators is also true of theoretical treatments of anti-predatory vigilance (e.g., Pulliam et al. 1982, Lima 1987b), which explicitly or implicitly assume only one type of predator in the environment.

Below, I show that many of the intuitive expectations of the single-predator paradigm may not apply to vigilance in a multi-predator situation. For instance, contrary to single-predator expectations, vigilance may not respond positively nor monotonically to increasing attack rates. Situations also exist in which vigilance is directed towards only one type of predator, yet nonetheless influenced by other predators. I also show how several, apparently innocuous predators may in combination induce substantial anti-predatory vigilance, even in the absence of any identifiably dangerous predator.

2. Model

To appreciate fully the vigilance effects of multiple predators, one must specify in some detail many behavioral aspects of predator-prey interactions; these include escape, detection, time exposed to attack, etc. Thus models abstractly treating vigilance as the proportion of time spent vigilant (e.g., Parker & Hammerstein 1985, Motro & Cohen 1989, Packer & Abrams 1990, Lima 1990) are not adequate for present purposes. Therefore, I base the following model on that in Lima (1987b), which is similar in several respects to that of Pulliam et al. (1982); this class of models, despite its drawbacks (Lima 1990), provides a simple basis upon which to analyze some potentially complex behavioral phenomena. McNamara & Houston (1992) present an excellent discussion of the relationships among various models of anti-predatory vigilance.

The feeding animal in question faces the following situation. Predatory attacks occur as a poisson process at a given rate (see below), and feeding can be interrupted (for the remainder of the day) at any time by events (such as poor weather) that occur at rate γ. Vigilance (or scanning) allows for the detection of predatory attack; higher rates of scanning dictate a higher probability of predator detection. However, because scanning and food ingestion are mutually exclusive, vigilance detracts from energy intake rate and vice versa. Thus an increase in vigilance lengthens both the time necessary to meet a given metabolic need, and the time actually exposed to attack. Thus the level of vigilance maximizing the overall probability of survival represents a trade-off among these competing demands.

For convenience, I assume a non-breeding animal for whom maximizing fitness is equivalent to maximizing the probability of daily survival. As such, the model applies most closely to small, wintering endothermic animals which face high metabolic demands and large potential costs of energetic shortfall. The general results, however, should apply to several other creatures. Furthermore, my analysis is directed more towards the predatory environment than the forager's social environment. Thus I assume a solitarily-feeding animal and will not address directly the many additional behavioral complications arising in socially-foraging animals (see Kaitala et al. 1989, Motro & Cohen 1989, Packer & Abrams 1990, McNamara & Houston 1992).

2.1. Non-specific vigilance

This case applies when attacks by any predator are detectable during any given scan; in other words, scanning applies simultaneously to all potential predators. This assumption is relaxed in the next section.

The probability of surviving a given day is the product of the probabilities of avoiding being killed and avoiding starvation. Following Mc-

Namara & Houston's (1992) simplification of Lima (1987b), that treats attacks as a poisson process,

$$P(survival) = e^{-D(\lambda)T(\lambda)}\, e^{-\gamma T(\lambda)} \qquad (1)$$

where the first and second exponential functions represent the probabilities of avoiding predation and starvation, respectively. In Eq. (1), λ is the rate at which scans are initiated from the non-vigilant state (e.g., when searching for and ingesting food), $T(\lambda)$ is the time necessary to finish daily feeding (including time spent vigilant). The function T is given by (see Lima 1987b)

$$T(\lambda) = \frac{(1/\lambda + s + 2m)M}{E/\lambda t} = [1 + (s + 2m)\lambda]\,\frac{Mt}{E}$$

where s is the time to complete a scan, m is the time to initiate or terminate a scan (during which predator detection is not possible), E is the energy content of a single food item, and t is the time necessary to consume it; the factor Mt/E is the time necessary, regardless of time spent vigilant, to handle the M/E food items that must be ingested to meet a daily metabolic need M. The function $D(\lambda)$ is the "death rate", through which I will discuss the main points concerning the detection of multiple predators.

The goal here is to find the λ maximizing (1). Eq. (1) can be rearranged to

$$P(survival) = e^{-[\gamma + D(\lambda)]T(\lambda)}. \qquad (2)$$

This indicates that maximizing (1) is equivalent to minimizing the exponent in (2), or

$$[\gamma + D(\lambda)]\,[1 + (s + 2m)\lambda]\,\frac{Mt}{E}. \qquad (3)$$

Inspection of (3) indicates that the optimal scanning rate is independent of M, E, and t (see also McNamara & Houston 1992), or more precisely, the Mt/E time units necessary to meet the metabolic need M. This somewhat counter-intuitive result reflects the fact that the animal has no control over this "metabolic" time cost; optimal behavior concerns the time above and beyond Mt/E that results directly from vigilance and thus is under the animal's control. Note that this treatment assumes that the animal is unlikely to be limited by daylength in meeting the need M. If daylength is a strong constraint in meeting a metabolic need, then a dynamic programming approach (McNamara & Houston 1992) would be in order. Such an approach might also be used to essentially give the animal control over M as well.

The "death rate" $D(\lambda)$ contains the crux of the argument concerning predator detection in a multi-predator environment. For the case of non-specific vigilance in an environment with n types of predators, $D(\lambda)$ is given by

$$D(\lambda) = \sum_{i=1}^{n} \alpha_i P_i(K \mid A) \qquad (4)$$

where, for the ith predator, α_i is the attack rate and $P_i(K|A)$ is the probability of being killed given attack. As developed in Lima (1987b) and adapted to the multi-predator situation,

$$P_i(K \mid A) = [1 - p(\lambda)]\, e^{-\lambda \tau_i}$$

where $p(\lambda) = s/(1/\lambda + s + 2m)$ is the proportion of time spent vigilant (e.g., with the head up) and τ_i is the critical time period during which a scan must be initiated in order to detect attack and escape successfully. Thus $P_i(K|A)$ is the probability that the animal does not initiate a scan during τ_i given that it was not vigilant at the time of attack. Combining all of this into (4),

$$D(\lambda) = [1 - p(\lambda)] \sum_{i=1}^{n} \alpha_i e^{-\lambda \tau_i}.$$

Predators differing in τ_i values differ in the threat they pose to a feeding animal; larger values in a sense imply less dangerous predators. One might conveniently relate predatory threat to attack speed, but several factors (even in very simple escape processes) can combine to produce a particular τ_i value. Thus in the interest of generality, I present the results below in terms of τ_i values rather than predator attack speeds, etc. The Appendix contains a simple expression for τ_i and some attack and escape speeds that might yield the τ_i values used in the analysis below; the reader may find these useful in interpreting the results.

2.2. Predator-specific vigilance

In the case of predator-specific vigilance, scans directed toward a particular predator cannot detect the attack of another predator. To keep the analysis tractable, I assume an environment containing only two types of predators. Thus predator detection involves two scanning rates, λ_1 and λ_2, concerning predators 1 and 2, respectively. Optimal behavior is still determined via minimizing (3), with the modifications that $D(\lambda)$ is replaced by $D(\lambda_1,\lambda_2)$, and the remaining λ replaced by the combined scanning rate of $\lambda_c = \lambda_1+\lambda_2$.

Relative to the previous case, however, $P_i(K|A)$ is considerably more complex for two reasons. First, if predator 1 attacks and a scan is initiated during τ_1, detection will not occur if that scan was directed toward predator 2 (and vice versa). Second, predator 1 will not be detected if the foraging animal is scanning for predator 2 at the time of attack; however, the attack may still be detected if, after terminating the "predator 2" scan, a scan for predator 1 is initiated before the critical τ_1 period has elapsed.

Before presenting an expression for $P_i(K|A)$, I note the following: (i) $exp(-\lambda_c\tau_i)$ is the probability that no scan of any sort is initiated during τ_i; (ii) $1-p(\lambda_c)$ is the probability that the feeding animal is non-vigilant at the time of attack; (iii) $w_j = \lambda_j/\lambda_c$ is both the probability that a given scan is directed toward predator $j \neq i$, and the proportion of vigilance directed towards predator $j \neq i$; and (iv) $U(\lambda_1,\lambda_2)$ represents the probability of detecting an attack that began while scanning for the "wrong" predator. Given these entities,

$$P_i(K \mid A) = [1 - p(\lambda_c)]\,[e^{-\lambda_c\tau_i} + (1 - e^{-\lambda_c\tau_i})\,w_j] + w_j\,p(\lambda_c)\,U(\lambda_1,\lambda_2). \qquad (5)$$

The first term in (5) represents the probability of being killed by predator i given attack while not vigilant; the second represents the probability of being killed if attack occurs while scanning for the wrong predator.

The derivation of U is straightforward. Recall that scans are of length s, and assume that scans are of the same length for a given predator. Given an attack while scanning for the wrong predator, the time of attack (x) within the interval (0, s) is a uniform random variable with the simple probability density function of $1/s$. Assuming $\tau_i > s$ and attack at time x, the feeding animal has $s-x$ time units remaining in the scan, and thus $\tau_i-(s-x)$ time units in which to detect the attack. As before, attack will not be detected if no scan is initiated, or if the scan is for the other predator. Thus, reasoning as above and integrating over the entire scan duration,

$$U(\lambda_1,\lambda_2) = \frac{1}{s}\int_0^s [e^{-\lambda_c[\tau_i-(s-x)]} + w_j\,(1 - e^{-\lambda_c[\tau_i-(s-x)]})]\,dx$$

which rearranges to

$$U(\lambda_1,\lambda_2) = \frac{1-w_j}{s}\int_0^s e^{-\lambda_c[\tau_i-(s-x)]}dx + \frac{w_j}{s}\int_0^s dx\,.$$

After integration and rearrangement,

$$U(\lambda_1,\lambda_2) = \frac{1-w_j}{s\lambda_c}\,[e^{-\lambda_c(\tau_i-s)} - e^{-\lambda_c\tau_i}] + w_j.$$

Thus, substituting U into (5) yields $P_i(K|A)$, which, in turn, is substituted into (4) to yield $D(\lambda_1,\lambda_2)$.

3. Results and discussion

Analyzing anti-predatory vigilance in a multi-predator environment requires numerical analyses of the above equations. Optimal behavior is expressed via the proportion of time spent scanning given the optimal scanning rate (λ^*): $p/(1/\lambda^* + s + 2m)$. (This measure is equivalent to the "observable" scanning rate when $s = 1$; see Lima 1987b, Pulliam et al. 1982.) In two-predator environments ($n = 2$), unless otherwise stated, parameters for predator 2 will be set at $\alpha_2 = 1 \times 10^{-5}$ s^{-1} and $\tau_2 = 1.0$ s. Parameter values set at $s = 1.0$ s, $m = 0.1$ s, $\gamma = 5 \times 10^{-6}$ s^{-1} will hold throughout. Note that during the great majority of days, feeding will not be interrupted, and can be completed easily within a 10 h day. Furthermore, attack rates given below are chosen such that predatory

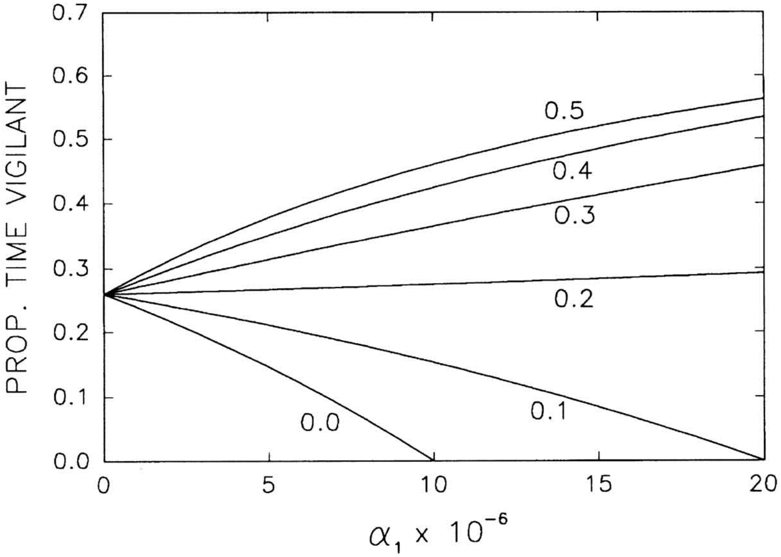

Fig. 1. Overall proportion of time spent vigilant as a function of α_1 for non-specific vigilance. Numbers indicate values of τ_1 for a particular curve.

attack is relatively infrequent on a daily basis. The above parameters are meant to be representative for a small, wintering bird. However, the qualitative results below are not strongly parameter-specific.

3.1. Non-specific vigilance

Here, any given scan detects attack by all potential predators in the environment. Figure 1 shows the vigilance effects of attack rate (α_1) for various levels of predatory threat (τ_1) imposed by predator 1. Note first that all lines emanate from the same point at $\alpha_1 = 0$, which represents optimal vigilance in an environment containing only predator 2. In such a single-predator environment, an increase in attack rate leads to an increase in vigilance (e.g. Lima 1987b, McNamara & Houston 1992). This is certainly an intuitive result, but it holds in this simple two-predator situation (Fig. 1) only for relatively high values of τ_1. When predator 1 is relatively "dangerous" (small τ_1), vigilance actually decreases with α_1. This decrease is easily understood for the case of $\tau_1 = 0$, in which the attack of predator 1 is virtually undetectable; under such circumstances, *decreasing* vigilance is the only reasonable response, since minimizing the probability of being killed by predator 1 requires minimizing time spent exposed to attack. Thus extremely dangerous predators may paradoxically have a strong negative influence on vigilance in a multi-predator environment.

The region in Fig. 1 in which vigilance is insensitive to predator attack rate (e.g., $\tau_1 = 0.2$ s) has many interesting empirical implications, for it may easily lead one astray in interpreting experimental results. For instance, if such behavioral insensitivity were observed in experimentation, one might reasonably conclude that the forager is either unconcerned about predator 1, or basing its vigilance solely on the characteristics of predator 2. Furthermore, a researcher focusing solely upon the more dangerous predator 1 ($\tau_1 < \tau_2$), without appreciating the multi-predator nature of the environment, might conclude that vigilance is not anti-predatory in nature because it does not respond to obvious changes in attack rates.

To date virtually all studies experimentally increasing the perceived risk of attack report an increase in vigilance (see Elgar 1989). However, these studies actually manipulate the perception of an *imminent* attack to which animals respond in the short-term (e.g., Caraco et al. 1980, Sullivan 1984, Glück 1987). The current model addresses vigilance over the long-term, and I am not aware of any experimental work addressing the role of attack rates on such a time scale. In any case, the above decrease or "neutrality" in vigilance with increasing attack rates remains an interesting theoretical possibility.

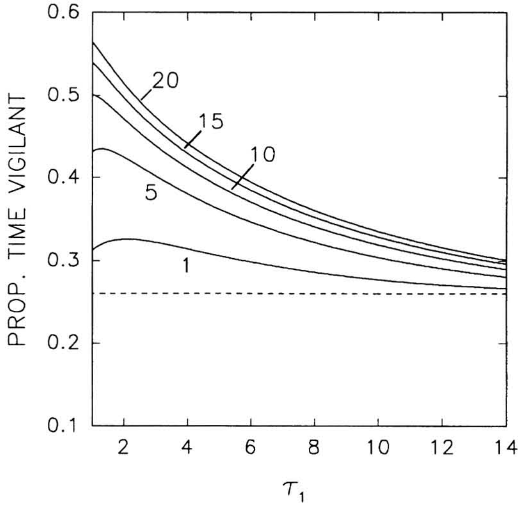

Fig. 2. Overall proportion of time spent vigilant as a function of τ_1 over the range $\tau_1 > \tau_2 = 1.0$. Non-specific vigilance is assumed. Numbers indicate values of $\alpha_1 \times 10^{-6}\ s^{-1}$ for a particular curve.

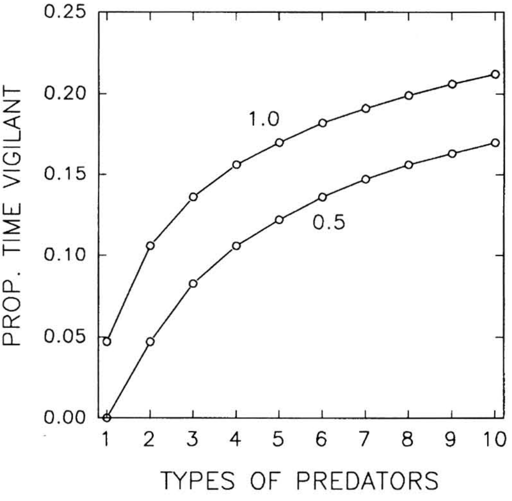

Fig. 3. Overall proportion of time spent vigilant as a function of the number of types of predators present in the environment. Non-specific vigilance is assumed. Numbers refer to values of $\alpha_1 \times 10^{-6}\ s^{-1}$ for a particular curve. These values apply to every predator in the environment, thus the overall attack rate increases as predators are added to the environment.

I began this study with the expectation that vigilance would be influenced mainly by the most dangerous predator in the environment, and that a simple rule-of-thumb would suffice concerning vigilance in a multi-predator environment: focus on the most dangerous predator, and vigilance for this predator will be ample for the detection of all others. While such a rule appears reasonable, it is valid only under extreme circumstances.

Fig. 2 shows a plot of vigilance as a function of increasing τ_1 (decreasing predatory threat from predator 1) for various predator 1 attack rates. The dashed line refers to optimal vigilance when focusing only on predator 2, which in this case is the most dangerous predator ($\tau_2 = 1$; $\tau_1 > \tau_2$). As one might expect, predator 1 has a major impact on vigilance when $\tau_1 \approx \tau_2$. However, predator 1 continues to have such an effect even when τ_1 becomes relatively large. This holds even when $\alpha_1 = 1 \times 10^{-6}$, which implies an attack by predator 1 once every 24 days on average. Thus predator 1 can be ignored only when τ_1 becomes very large. The Appendix contains some representative values of predator and prey speeds that might lead to large τ values. Under reasonable assumptions, $\tau_1 > 5$ s can imply prey escape speed an order of magnitude greater than attack speed, yet predator 1 may still have a major impact upon vigilance in such circumstances. Clearly, my proposed rule-of-thumb focusing on the most dangerous predator may be dangerously in error.

The results in Fig. 2 suggest that several apparently "innocuous" predators may combine to induce substantial anti-predatory vigilance in their potential prey. To underscore this possibility, consider several identical types of "feeble" predators for whom $\tau_i = 10$ s; this might correspond to attack speeds well under prey escape speed (Appendix). Fig. 3 shows that even a few such predators in the environment may induce substantial anti-predatory vigilance. Note that attack rates used in Fig. 3 are exceedingly low. For instance, assuming a 12 h feeding period, the average time between attacks by a given type of predator is 24 and 47 days, respectively, for attack rates of 1 and $0.5 \times 10^{-6}\ s^{-1}$; these values increase only to one attack every 3 and 5 days, respectively, when as many as 10 types of predators are present in the environment.

Thus, several innocuous predators may have a major impact upon anti-predatory vigilance,

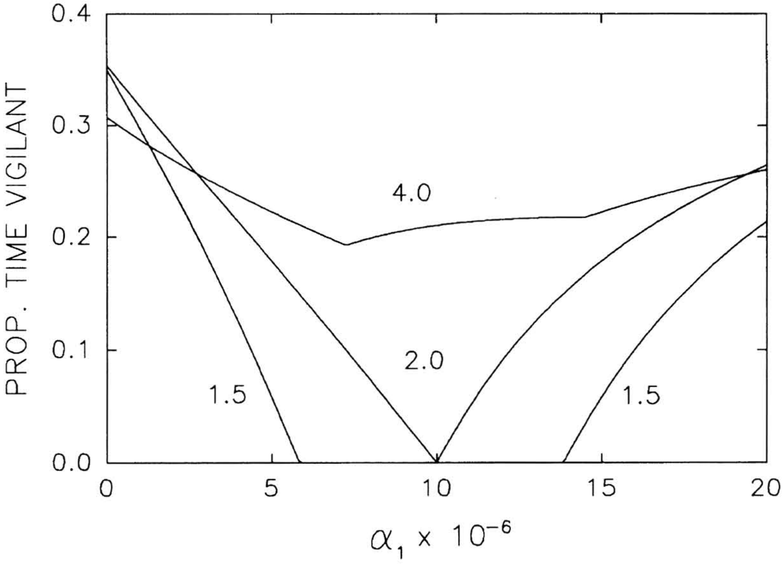

Fig. 4. Overall proportion of time spent vigilant as a function of α_1 for predator-specific vigilance. Numbers indicate values of τ (common to both predators) for a particular curve.

even if there is no identifiably dangerous predator in the environment. Such environments are probably common in nature, especially with the demise of most higher-trophic-level predators in many areas. For instance, small birds such as juncos (*Junco* spp.) face their greatest threat from bird-eating hawks (*Accipiter* spp.), which have declined greatly in eastern North America. Nevertheless, these birds winter in areas with many "low-level" threats such as *Buteo* hawks, owls, cats, and canids. If the above analysis has any bearing on reality, these predators may in combination be a major factor in junco anti-predatory vigilance. Similar situations undoubtedly apply to several other creatures, perhaps even those not thought to have any serious predators (Brown & Alkon 1990, Sweitzer & Berger 1992).

3.2. Predator-specific vigilance

For small terrestrial vertebrates, scans directed towards avian predators (attacking from the sky) may not effectively detect attacks from mammalian predators lying in ambush in nearby vegetation; small fish feeding near the water's surface may not detect attack from avian predators when scanning the water column for piscivorous fish. Little is known about such matters of predator detection (Lima 1990), but these scenarios imply predator-specific vigilance. Assuming predator-specific vigilance in a two-predator environment, vigilance involves two scanning rates (one for each type of predator). As before, I express the results in terms of the overall proportion of time spent scanning given optimal behavior: $s/(1/\lambda_c^* + s + 2m)$. I also assume two predators identical in τ values to better illustrate some of the odd effects below.

Fig. 4 shows plots of vigilance vs. predator 1 attack rate for several τ values. Immediately apparent from these plots is a non-monotonic relationship between overall vigilance and attack rate. Vigilance is minimal or non-existent in the region where $\alpha_1 \approx \alpha_2$ (at 10 × 10^{-6}), despite the continuous increase in α_1. This unusual relationship reflects the fact that the overall probability of being killed given attack [$P(K|A)$] is minimized by devoting all vigilance to only the higher-attack-rate (e.g. more abundant) predator unless attacks rates are roughly equal. This can be seen by determining the scanning rates minimizing $P(K|A)$ for a particular combined scanning rate ($\lambda_c = \lambda_1 + \lambda_2$).

$P(K|A)$ is given by

$$P(K \mid A) = \sum_{i=1}^{2} \frac{\alpha_i}{\alpha_1 + \alpha_2} P_i(K \mid A)$$

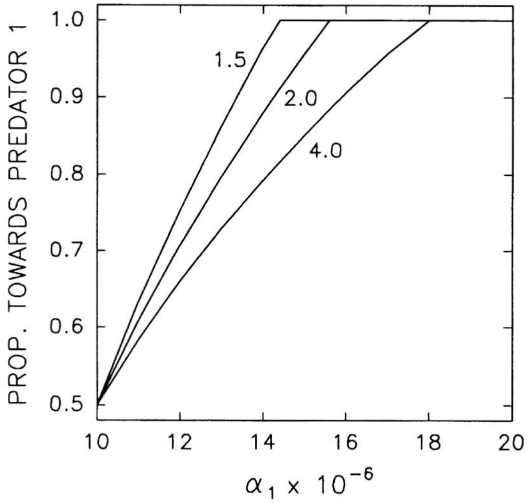

Fig. 5. Proportion of vigilance directed toward predator 1 as a function of α_1. This proportion minimizes the probability of being killed given an attack for the fixed combined scanning rate of $\lambda_c = 0.5\ s^{-1}$. Numbers indicate values of τ (common to both predators) for a particular curve. Shown are the relationships over the range $\alpha_1 > \alpha_2$.

where $\alpha_i/(\alpha_1+\alpha_2)$ is the probability that a given attack involves predator i. Fig. 5 shows, as a function of α_1, the proportion of vigilance devoted to predator 1 $[\lambda_1/(\lambda_1+\lambda_2)]$ that minimizes $P(K|A)$. Only when $\alpha_1 = \alpha_2$ (= 10×10^{-6}) is vigilance partitioned equally between predators. As α_1 diverges from α_2, the proportion of vigilance devoted to predator 1 increases sharply, especially for small τ values. In other words, vigilance will usually be devoted exclusively to the more abundant predator. Thus vigilance over the descending portion of a curve in Fig. 4 is actually devoted entirely to detecting predator 2 (the more abundant predator); since attack by predator 1 will not be detected, vigilance declines with increasing α_1 for the same reason it declined in Fig. 1 for small τ_1. Likewise, over the ascending curve all vigilance is devoted entirely to predator 1 (at this point the increasingly more abundant predator).

For $\tau = 4.0$ s, the distinct central region of the curve straddling $\alpha_1 = \alpha_2$ (at 10×10^{-6}) indicates vigilance split between both predators. Such regions are possible for large τ values since minimizing $P(K|A)$ via "exclusive" vigilance becomes less likely as τ increases (Fig. 5). It may seem paradoxical that vigilance in this region of "simultaneous" vigilance should be minimal compared with regions of exclusive vigilance. However, simultaneous vigilance is relatively ineffective because scanning is split between the two predators, and thus not detecting either very efficiently. As seen in Lima (1987b), vigilance is generally depressed under such circumstances; a strategy lowering vigilance and thus the overall time spent exposed to predatory attack is favored.

Nothing even resembling the results in Fig. 4 has been reported in the literature on anti-predatory vigilance. Perhaps this indicates that cases of predator-specific vigilance are rare in nature. I suspect, however, that the lack of corroborating information may reflect the lack of studies examining the effects of long-term attack rates (see above) that are actually addressed in models of vigilance. Furthermore, predator-specific vigilance by definition implies a multi-predator environment; the lack of studies in such environments greatly restricts any data that might be applied in the present case. Any conclusions regarding the prevalence of predator-specific vigilance would be premature at best.

4. Conclusions

The most immediate conclusions that I can offer concern qualitative differences between expectations of single vs. multi-predator approaches to vigilance. Of particular interest is the fact that "multi-predator" vigilance may not respond positively to increasing attack rates as it does in a single-predator environment. Furthermore, certain less-abundant predators requiring specific modes of vigilance may even be "ignored" by a foraging animal, yet influence vigilance nonetheless. Without a need for predator-specific vigilance, it is generally not a good idea to ignore innocuous predators and focus only on those more abundant or dangerous. Just a few innocuous predators, in fact, may combine to induce substantial vigilance in their potential prey. In any case, these qualitative conclusions should be amenable to empirical investigation. While the experimental tractability of a single-predator environment is clear, two- or three-predator systems should also be manageable in both laboratory and field studies of vigilance.

Is an assumption of non-specific vigilance generally more valid than one of predator-specific vigilance? Virtually all studies to date assume, at least implicitly, non-specific vigilance, but the validity of this is far from clear. I suspect that similar predators may be grouped into one "class" or the other. For instance, a particular mode of scanning may detect aerial predators, while another mode may detect ground predators, etc. While a strict distinction between classes of predator detection is unlikely, the above results should provide a good starting point for empirical investigations.

Multi-predator environments have been neglected in studies of anti-predator behavior generally, and in anti-predatory vigilance in particular. I hope that a fresh look at vigilance from a multi-predator perspective will provide further insight into this important field of behavioral ecology. Such a perspective will also help integrate behavioral studies of predator-prey interactions with those at the population and community levels of organization, which routinely consider several types of predators over several trophic levels (e.g., Menge & Sutherland 1987, Schoener 1989, Polis 1991).

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Appendix

For an example of how τ might reflect characteristics of predator and prey, consider the "standard" situation in which a prey animal feeds a given distance c away from a refuge to which it flees when attacked. Assume that predators can approach to a distance d from the prey before initiating attack. Let the speed of predator and prey be v_{pred} and v_{prey}, respectively. The time needed to initiate/terminate a scan is given by m. Adapting the derivation for τ in Lima (1987b) to the present case,

$$\tau = \frac{d}{v_{pred}} - c\left(\frac{1}{v_{prey}} - \frac{1}{v_{pred}}\right) - m, \quad v_{pred} > v_{prey},$$

or

$$\tau = \frac{d}{v_{pred}} - m, \quad v_{pred} \leq v_{prey}.$$

Assume c = 5 m, $d = 10$ m, and $m = 0.1$ s. Table 1 indicates the predator attack speed corresponding to various τ values for a given prey escape speed, v_{prey}.

Table 1. Some predator attack speeds (m/s) implied by various combinations of τ and prey escape speed (v_{prey}, m/s).

v_{prey}	τ (s): 0	0.1	0.2	0.5	1.0	2.0	4.0	10.0	15.0
5.0	13.6	12.5	11.5	9.4	7.1	4.8	2.9	1.35	0.93
10.0	25.0	21.4	18.8	13.6	9.4	5.8	3.3	1.42	0.96
15.0	34.6	28.1	23.7	16.1	10.5	6.2	3.9	1.44	0.97