Prey Under Stochastic Conditions Should Probably Overestimate Predation Risk: A Reply to Abrams

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PREY UNDER STOCHASTIC CONDITIONS SHOULD PROBABLY OVERESTIMATE PREDATION RISK: A REPLY TO ABRAMS

Abrams (1994) has analyzed a set of deterministic models for optimal foraging effort when foragers have small deviations from perfect information about their risk of predation. He states that either overestimation or underestimation of predation risk may be adaptive, depending on the derivatives of starvation and reproduction as functions of foraging effort. Finally, Abrams concludes that if there is no cost to obtaining more information about predation risk (or the cost is small), increased accuracy of estimation is favored. When comparing our dynamic model (Bouskila and Blumstein 1992) with his, Abrams emphasizes points that he interpreted as different from his conclusions. We argue here that the results of Abrams are not fundamentally different from ours; the simplified model that Abrams used is not sufficiently similar to our dynamic model to compare them directly; and under stochastic conditions, overestimating predation risk is favored when errors are moderate to large, while at small errors, both over- and underestimation may be favored.

Although we (Bouskila and Blumstein 1992) discussed situations in which underestimation is better than overestimation (pp. 170–171), Abrams ignores these situations in his discussion. In addition, he ignores the fact that the cost of obtaining more information was essential for the interpretation of the results of the dynamic model and that we took great care to state so. Obviously, if perfect information about the risk of predation could be obtained without cost (which we assume is unlikely), animals with perfect information about the risk of predation would fare better than animals with an erroneous estimate of the risk. Our results do not contradict this statement, but because the differences in mortality were small (table 1), the advantages to a perfectly informed animal were irrelevant when the cost of perfect information was considered.

In an attempt to understand the results of our stochastic state variable model, Abrams uses a simpler deterministic model (which he considers analogous). Abrams concludes from the analysis of his simpler model that the results of the state variable model are not general. To do so, Abrams dismissed stochasticity as unimportant (thus justifying the translation to a deterministic model). We disagree with the validity of the translation and with some unwarranted interpretations of the dynamic model. First, while Abrams correctly assumes that the dynamic model predicts that individuals with high energy reserves should stay in the safe patch as the time horizon approaches, this stay is not necessarily "a small part of the total season" as he supposes (p. 326). For example, individuals with medium levels of energy reserves are predicted to stay in the safe patch 60%–75% of the time units (fig. 1). Moreover, the timing for the switch to the safe patch is

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TABLE 1

An Example of Values Plotted Earlier (Bouskila and Blumstein 1992)

Percentage Error	Probability of Death
100	.6245868
90	.1685641
80	.1654472
70	.1654446
60	.1654398
50	.1654280
40	.1654280
30	.1643974
20	.1641523
10	.1641518
0	.1641518
−10	.1641518
−20	.1641529
−30	.1641530
−40	.1641530
−50	.1641649
−60	.1641649
−70	.1641649
−80	.1641657
−90	.1641657
−100	.1642357
−110	.1642357
−120	.1642357
−130	.1642408
−140	.1642408
−150	.1645769
−160	.1699567
−170	.1699567
−180	.1699567
−190	.1699567
−200	.1724254

Note.—These values correspond to fig. 1 in Bouskila and Blumstein (1992).

determined by the interaction of foraging success in early periods (stochastic events) and decisions of the forager (which are based on the consequences of those events). Thus, the strategy of the foragers (i.e., the patches in which they forage) may not be approximated accurately for all error levels by a simple deterministic model. Consequently, the unconfirmed assertion that the "probabilities of mortality reported in the figures in B&B can be approximated through a deterministic model" (p. 326) remains exactly that.

Second, Abrams incorrectly claims that the probability of starvation in the dynamic model is related to foraging effort (i.e., the time spent in the risky patch) by a step function (also see Mangel and Clark 1988). While the terminal fitness function in our model (Bouskila and Blumstein 1992) is a step function, the probability of starvation is a gradually declining function of time spent in the risky patch. This is caused by the stochasticity in finding food, an important element in the dynamic model, albeit ignored by Abrams.

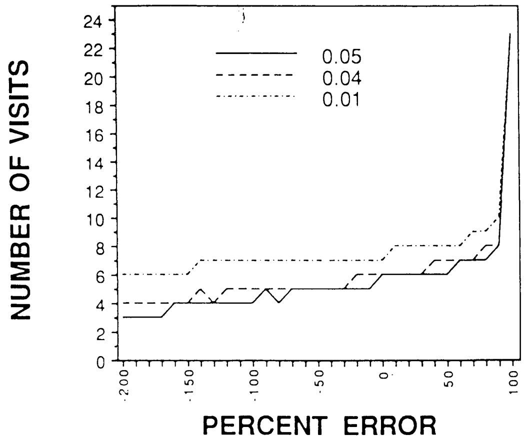

FIG. 1.—Number of time units spent in the risky patch as a function of error in the perception of predation risk in that patch. Different lines depict different values of the true predation risk. These plots correspond to the probabilities of mortality described elsewhere (fig. 2 of Bouskila and Blumstein 1992) ($X[t = 0] = 13$).

Third, Abrams states that in the dynamic model, the time spent in the risky patch is "independent of the number of predators in that patch" (p. 325). However, the level of risk in the patch (the number of predators, in Abrams's terminology) has an effect on the strategy of the individual in the stochastic model (fig. 1). There are even differences in strategies between individuals who differ in their level of error in estimation of predation risk. Contrary to Abrams's assertion, these differences are often seen and are not restricted to the cases when the risky patch is perceived as the safer of the two. Because time and the number of predators in the risky patch are independent in Abrams's deterministic model, his model is a poor approximation of the dynamic model he tried to understand.

We (Bouskila and Blumstein 1992) focus our state variable model on animals in a nonreproductive period and use a step function to describe the relationship between terminal fitness and energy reserves of the animals. The model has been extended (Bouskila 1993) to animals with different terminal fitness functions. These models with sigmoidal and exponential fitness functions still show that at moderate and large errors, there are advantages to animals that overestimate predation risk. For small errors (up to 10%–40%), underestimation is favored. When underestimation was favored in the earlier model (Bouskila and Blumstein 1992), this too occurred only at small errors. Because we assume that the cost of accurate information will lead to moderate and large errors in the estimation of predation risk, our models predict that animals in the real world are likely to overestimate.

Previous analysis (Bouskila 1993) resulted in ranges with a relatively small effect of errors, but these tolerance zones were less flat than in our earlier model (Bouskila and Blumstein 1992). This outcome suggests that everything else being equal, we would expect animals with general, continuous terminal fitness functions to use rules that provide more accurate information than rules used by nonreproductive individuals. However, the cost of obtaining information may not be the same for all animals. For instance, a gravid lizard moves more slowly than a male or nongravid female (Shine 1980). Gathering information may thus be more costly for a gravid female, at least in terms of predation cost. It is the interaction between the cost of information and the cost of making errors that shapes selection and determines how accurate rules of thumb can be (Bouskila 1993); Abrams seems to agree with us on this point. This is where state variable models can be especially useful, because they allow state-dependent considerations. Finally, we take issue with Abrams's gratuitous comment concerning "the lack of sufficient sensitivity analysis" (p. 326) of the model: our model (Bouskila and Blumstein 1992) is specifically limited to animals in a nonreproductive period so that fitness can be identified with viability. These animals are analogous to time minimizers (Schoener 1971), and only in later work (Bouskila 1993) was the model extended to energy maximizers (Schoener 1971). Every model only applies to the conditions set up in its assumptions.

When Abrams refers to humans and domestic animals, he actually proposes a new model in which predation risk is state-dependent. This could indeed be of importance in many situations, but then one must face the problem of untangling state and information in predation risk. In his analysis, Abrams assumes no dependence of predation risk on state of the organism.

We agree with Abrams that bank voles' use of scent as an indication for high predation risk (Jedrzejewski and Jedrzejewska 1990) may imply that visual information about the risk from weasels is seldom available. Nevertheless, we consider this an example of the costs associated with acquiring information: voles that would attempt to obtain more accurate information are not likely to survive and make use of this information. Similarly, in the other studies we (Bouskila and Blumstein 1992) have mentioned (Leger and Owings 1978; Seyfarth et al. 1980; Kotler 1984; Endler 1987; Møller 1988), elements used by prey animals as a cue for high predation risk (e.g., illumination level, conspecific alarm calls) are likely to lead to an overestimation of predation risk. Alternative, and more accurate, cues are probably too costly to use.

Abrams notes that "many of the more commonly assumed relations do imply that overestimation of risk will be favored" (p. 327). Perhaps the most important question concerning "evidence from the real world" is, How do we identify those biological cases in which the third derivative of the starvation versus risk relationship is positive (and thus underestimation is predicted)? Here again, dynamic state variable models are useful, because they specifically identify measurable parameters and states that need to be determined in order to predict behavior.

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LITERATURE CITED

Abrams, P. A. 1994. Should prey overestimate the risk of predation? American Naturalist 144:317–328.

Bouskila, A. 1993. Predation risk and competition in a community of rodents and snakes. Ph.D. diss. University of California, Davis.

Bouskila, A., and D. T. Blumstein. 1992. Rules of thumb for predation hazard assessment: predictions from a dynamic model. American Naturalist 139:161–176.

Endler, J. A. 1987. Predation, light intensity and courtship behaviour in *Poecilia reticulata* (Pisces: Poeciliidae). Animal Behaviour 35:1376–1385.

Jedrzejewski, W., and B. Jedrzejewska. 1990. Effect of predator's visit on the spatial distribution of bank voles: experiments with weasels. Canadian Journal of Zoology 68:660–666.

Kotler, B. P. 1984. Risk of predation and the structure of desert rodent communities. Ecology 65:689–701.

Leger, D. W., and D. H. Owings. 1978. Responses to alarm calls by California ground squirrels: effects of call structure and maternal status. Behavioral Ecology and Sociobiology 3:177–186.

Mangel, M., and C. W. Clark. 1988. Dynamic modeling in behavioral ecology. Princeton University Press, Princeton, N.J.

Møller, A. P. 1988. False alarm calls as a means of resource usurpation in the great tit *Parus major.* Ethology 79:25–30.

Schoener, T. W. 1971. Theory of feeding strategies. Annual Review of Ecology and Systematics 2:369–404.

Seyfarth, R. M., D. L. Cheney, and P. Marler. 1980. Vervet monkey alarm calls: semantic communication in a free-ranging primate. Animal Behaviour 28:1070–1094.

Shine, R. 1980. "Costs" of reproduction in reptiles. Oecologia (Berlin) 46:92–100.

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