



CHICAGO JOURNALS



The University of Chicago

---

A Reassessment of the Predation Risk Allocation Hypothesis: A Comment on Lima and Bednekoff.

Author(s): Guy Beauchamp and Graeme D. Ruxton

Source: *The American Naturalist*, Vol. 177, No. 1 (January 2011), pp. 143-146

Published by: [The University of Chicago Press](#) for [The American Society of Naturalists](#)

Stable URL: <http://www.jstor.org/stable/10.1086/657437>

Accessed: 08/08/2014 09:48

---

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at <http://www.jstor.org/page/info/about/policies/terms.jsp>

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.



*The University of Chicago Press, The American Society of Naturalists, The University of Chicago* are collaborating with JSTOR to digitize, preserve and extend access to *The American Naturalist*.

<http://www.jstor.org>

## A Reassessment of the Predation Risk Allocation Hypothesis: A Comment on Lima and Bednekoff

Guy Beauchamp<sup>1,\*</sup> and Graeme D. Ruxton<sup>2</sup>

1. Faculty of Veterinary Medicine, University of Montréal, P.O. Box 5000, Saint-Hyacinthe, Québec J2S 7C6, Canada; 2. Division of Ecology and Evolutionary Biology, Faculty of Biomedicine and Life Sciences, University of Glasgow, Glasgow G12 8QQ, Scotland, United Kingdom

Submitted March 18, 2010; Accepted August 30, 2010; Electronically published November 30, 2010

---

*Keywords:* antipredator behavior, cognitive constraints, predation risk allocation hypothesis, time horizon.

---

### Introduction

The predation risk allocation hypothesis was proposed more than 10 years ago to explain the allocation of antipredator effort to situations when predation risk or danger varies temporally (Lima and Bednekoff 1999). Unlike most previous theory, the hypothesis acknowledges that danger can vary temporally, with alternating states of high and low risk. The crux of the model is the assumption that foragers must accumulate a fixed amount of resources during a fixed period of time and that to do so, animals should allocate vigilance, and thus indirectly foraging effort, differentially between periods with high or low risk.

Two predictions can be made from the theory. Given a fixed proportion of time spent in each risk state, a higher proportion of foraging should take place during the relatively safer periods when the ratio of attacks between high-risk and low-risk states increases (i.e., when the range of predation risks is more exaggerated). Another prediction is derived by fixing the attack ratio and varying the proportion of time spent in each risk state. As proportionately more time is spent under high risk, foragers are expected to be less vigilant in both high-risk and low-risk states, with most of the foraging performed in the low-risk state. Under chronic high risk, foragers must allocate some foraging in the high-risk state to accumulate their fixed resource requirements. This leads to the initially counterintuitive prediction that chronic high risk reduces investment in antipredator behavior when in the high-risk state.

Acceptance of the model has been swift, as shown by

\* Corresponding author; e-mail: [guy.beauchamp@umontreal.ca](mailto:guy.beauchamp@umontreal.ca).

the 450+ citations the article has garnered over the years. More important, the hypothesis has been tested repeatedly (see Ferrari et al. 2009 for a recent review). While the results have been mixed thus far, enthusiasm for the model is still strong. Here we highlight some underappreciated assumptions of the model and of the empirical tests of this hypothesis. First we examine how broadly the model can be applied in ecological settings. Then we identify constraints faced by foragers that may act to limit the generality of the model. Finally, we point the way forward for further theoretical developments and new empirical tests of the model.

### Model Assumptions

The model considers situations with contrasting risk, usually labeled high and low risk. At any point in time, the forager is aware of whether it is in a high- or low-risk state, but it cannot influence whether the risk is high or low at any point or predict when the risk state will change. The probability of a high-risk state occurring is constant over time. Further, the forager cannot control the fraction of the time for which the risk is high, nor can it retreat to some protective area when risk is high or quit the situation early if it collects sufficient resources beforehand. Foragers can control only the amount of time allocated to vigilance in each risk situation and are thus considered passive with respect to the pattern of risk experienced.

Taking all these factors into account, the sort of situation to which the theory might apply is a mammalian herbivore out foraging in the middle of a wide savannah. That is, it applies to situations where the focal prey cannot influence its intrinsic risk by selecting particular microhabitats according to whether it currently perceives predation risk as high or low. Thus, the focal forager must be essentially immobile, or the habitat must be homogenous and not offer any refuges from predation or other microhabitats that differ in inherent predation risk from other available microhabitats. High-risk situations might correspond to

times when the focal forager detects the alarm calls of others or other indirect cues of predator presence. There could easily be selection for enhanced vigilance in response to detecting such cues, with this translating into enhanced vigilance in times of high predation risk (Creel et al. 2008). However, the model does not apply to many situations where there is more control over predation risk. For example, animals often “know” (i.e., have been selected or learn over time to behave as if they know) that feeding farther from protective cover involves greater predation risk or that foraging at the beginning or end of the day is more risky. Many foragers can manipulate their predation risk, at least in part (Caro 2005). For example, birds can often select from simultaneously available foraging microhabitats that vary in their proximity to cover (Sansom et al. 2009). Such situations, again, are not represented by the existing theory. Further, the model does not apply to animals that can quit foraging early and retreat to protective cover; Lima and Bednekoff’s animals must stay until the end of the time period.

Active risk management can lead to drastically different predictions. For instance, a forager in a risky situation may reduce vigilance to spend as little time as possible exposed to predators and flee to cover during the remainder of the high-risk period (Beauchamp and Ruxton 2007). In such a case, vigilance is lower, not higher, in high-risk situations. Similarly, animals may forage in larger or denser groups, which provide greater protection (Krause and Ruxton 2002), leading again to a prediction of lower vigilance in riskier situations (because high risk triggers an increase in group size). All empirical tests of the model so far have been conducted in the laboratory, where individuals experience risk rather passively. A challenge that we foresee will be to determine how to apply the model to natural settings, where foragers are more likely to manage predation risk actively, say, by selecting from available microhabitats that vary in inherent predation risk in response to internal factors (such as food reserves) or external factors (such as the alarm calls of others). In addition, tests of the hypothesis should exploit natural settings, given the assumption that animals must know the predation risk regime perfectly. In the laboratory, animals may not be provided with sufficient time to learn a risk regime that they have not been exposed to previously (Sih et al. 2000).

### Cognitive Constraints

The model does not specify how individuals are expected to evaluate the proportion of time spent in low- or high-risk states. Through natural selection, animals may come to react optimally to the sequence of high- and low-risk states, but this would require that the proportion of time spent in each risk state be stable over many generations.

Such a view would probably invalidate laboratory experiments of the hypothesis unless the risk regime was absolutely similar to the one in which animals evolved. In their review of the hypothesis, Ferrari et al. (2009) argue that animals probably learn the risk regime through repeated exposures to periods of high and low risks.

In the unpredictable-risk scenario presented above, estimates of this proportion must be based on information collected over several cycles of high- and low-risk states. In the end, animals in a given risk state should adjust their current antipredator responses in anticipation of changes in future risk based on their earlier pattern of exposure to risk. The simplest scenario would consist of a predictable sequence of low- and high-risk states, which is fine as long as we assume that foragers experience risk passively (as noted above). Many empirical tests of the model have considered this simplified risk scenario (Ferrari et al. 2009).

In general, several hours separate periods of high and low risk, at least in empirical tests of the hypothesis that have been published. However, the psychological literature reveals that anticipation of future events based on earlier exposure is unlikely to alter current behavior unless future events occur within minutes. Rats, for instance, will work hard to obtain vanishing resources despite the fact that all their food could be obtained from a rich patch that materializes only 15 min later (Timberlake et al. 1987). That is, they were unaffected by the availability of future foraging opportunities beyond a time horizon of 15 min. The concept of a time horizon for integrating foraging information has also been studied in other species, and the horizon was found to be shorter in one bird species, longer in monkeys, and the longest in human adults (Roberts 2002). Most empirical tests of the risk allocation hypothesis have been conducted with fish or invertebrate species for which the existence and magnitude of extended foraging time horizons are not known.

The concept of foraging time horizon is related to the idea that animals discount future events because intervening uncontrollable events are more and more likely to reduce the likelihood of obtaining these future rewards. The value of future rewards is expected to be strongest when close in time and to decrease in an exponential-like fashion with delay (Green and Myerson 1996). Beyond a certain point, the value of future rewards becomes vanishingly small, thus delineating the foraging time horizon. Such time discounting has also been related to lack of self-control, or impulsiveness, which is common in most animals (Logue 1988). Given that this window in time is rather small, we should not expect major adjustments in antipredator effort unless the switch to a period of contrasting risk is very close at hand. Therefore, while the model does not specify the amount of time between risk

situations, it would appear that for many species it should be very short.

An inability to integrate events beyond a certain time horizon certainly raises doubts about the ability of foragers to foresee changes in the current state of risk. This static view of risk, in which current behavior is informed only by a limited amount of information, clashes with the dynamic view of predation risk emphasized by the risk allocation hypothesis. We suggest that animals stuck in time are not good candidates to learn and/or react to temporal changes in predation risk.

### Future Directions

Our foregoing discussion suggests that the ecological relevance of the risk allocation hypothesis may be narrower than it first appears. In addition, cognitive constraints faced by animals may limit their ability to react optimally to temporal changes in predation risk.

Where do we go from here? One avenue is to test the hypothesis while ignoring our reservations about constraints or applicability to different systems. After all, if the consensus after many tests is that the predictions hold, then we should not be too concerned that the hypothesis is unrealistic; all models are only an approximation of reality. Several tests have been conducted so far, and the results have been mixed. Nevertheless, assumptions of the model have not always been met. In their review of the empirical tests of the hypothesis, Ferrari et al. (2009) note that animals in those tests have not always been food stressed. This means that the theory's assumption that foraging must take place over the whole time period is not mimicked in the experiment.

Trivial explanations for some predictions have not always been ruled out. As pointed out by some authors (e.g., Brown et al. 2006), repeated exposure to predators or indirect predatory cues without any obvious death risk may lead to habituation, which represents a fading of responses to risk with time. Therefore, the prediction that foragers previously exposed to more risk should adjust their responses to a pulse of high risk to a lesser extent than those previously exposed to lower risk is similar to that expected under the habituation hypothesis. To rule out such habituation effects, it is important to ensure that the amplitude of the response to high risk after repeated exposures does not change over time.

Another trivial explanation that has not been considered thus far is that antipredator behavior is adjusted to current hunger levels regardless of how long individuals are expected to spend in high- and low-risk states. We suggest that temporal variation in danger can influence current antipredator responses in animals that are unaware of the risk regime. For instance, when facing long periods with

high risk, which must hinder the acquisition of resources, animals will forage more in low-risk situations simply because they are hungrier, irrespective of their knowledge of temporal risk distribution. To be convincing, an empirical test must be able to show that animals have learned about the temporal distribution of risk and are not trivially responding to multiple exposures to harmless risk (habituation) or to their level of satiation.

A simple way to control for hunger level would consist of this procedure: animals all experience a low-risk state before facing either a higher-risk or the same low-risk state. The assumption here is that animals need to forage under each risk state to acquire their fixed food requirements and that they cannot escape from risk. At the end of this sequence, all animals are provided with food to compensate for lower food intake in the high-risk situation. After a suitable time lapse to ensure that foragers are hungry and, more important, all equally hungry, all individuals repeat the cycle anew. After several such cycles, individuals are tested in the low-risk state to determine whether the anticipation of higher risk later, with a low expected food intake rate, entices foragers to increase their current food intake rate.

Another avenue would be to develop the model further to examine the consequences of allowing active responses to risk and to integrate cognitive constraints. Many optimal foraging models beyond the risk allocation hypothesis have been developed without considering the cognitive abilities of animals. Behavioral ecologists have been urged several times to include cognitive constraints in their models, and integration of mechanistic and functional considerations can greatly expand the scope of models (Kacelnik and Bateson 1996). The reservations that we have discussed certainly warrant a more critical look at the relevance of the predation risk allocation hypothesis.

### Literature Cited

- Beauchamp, G., and G. D. Ruxton. 2007. Dilution games: use of protective cover can cause a reduction in vigilance for prey in groups. *Behavioral Ecology* 18:1040–1044.
- Brown, G. E., A. C. Rive, M. C. O. Ferrari, and D. P. Chivers. 2006. The dynamic nature of antipredator behavior: prey fish integrate threat-sensitive antipredator responses within background levels of predation risk. *Behavioral Ecology and Sociobiology* 61:9–16.
- Caro, T. M. 2005. *Antipredator defenses in birds and mammals*. University of Chicago Press, Chicago.
- Creel, S., J. A. Winnie Jr., D. Christianson, and S. Liley. 2008. Time and space in general models of antipredator response: tests with wolves and elk. *Animal Behaviour* 76:1139–1146.
- Ferrari, M. C. O., A. Sih, and D. P. Chivers. 2009. The paradox of risk allocation: a review and prospectus. *Animal Behaviour* 78: 579–585.
- Green, L., and J. Myerson. 1996. Exponential versus hyperbolic dis-

counting of delayed outcomes: risk and waiting time. *American Zoologist* 36:496–505.

Kacelnik, A., and M. Bateson. 1996. Risky theories: the effects of variance on foraging decisions. *American Zoologist* 36:402–434.

Krause, J., and G. D. Ruxton. 2002. *Living in groups*. Oxford University Press, Oxford.

Lima, S. L., and P. A. Bednekoff. 1999. Temporal variation in danger drives antipredator behavior: the predation risk allocation hypothesis. *American Naturalist* 153:649–659.

Logue, A. W. 1988. Research on self-control: an integrating framework. *Behavioral and Brain Sciences* 11:665–709.

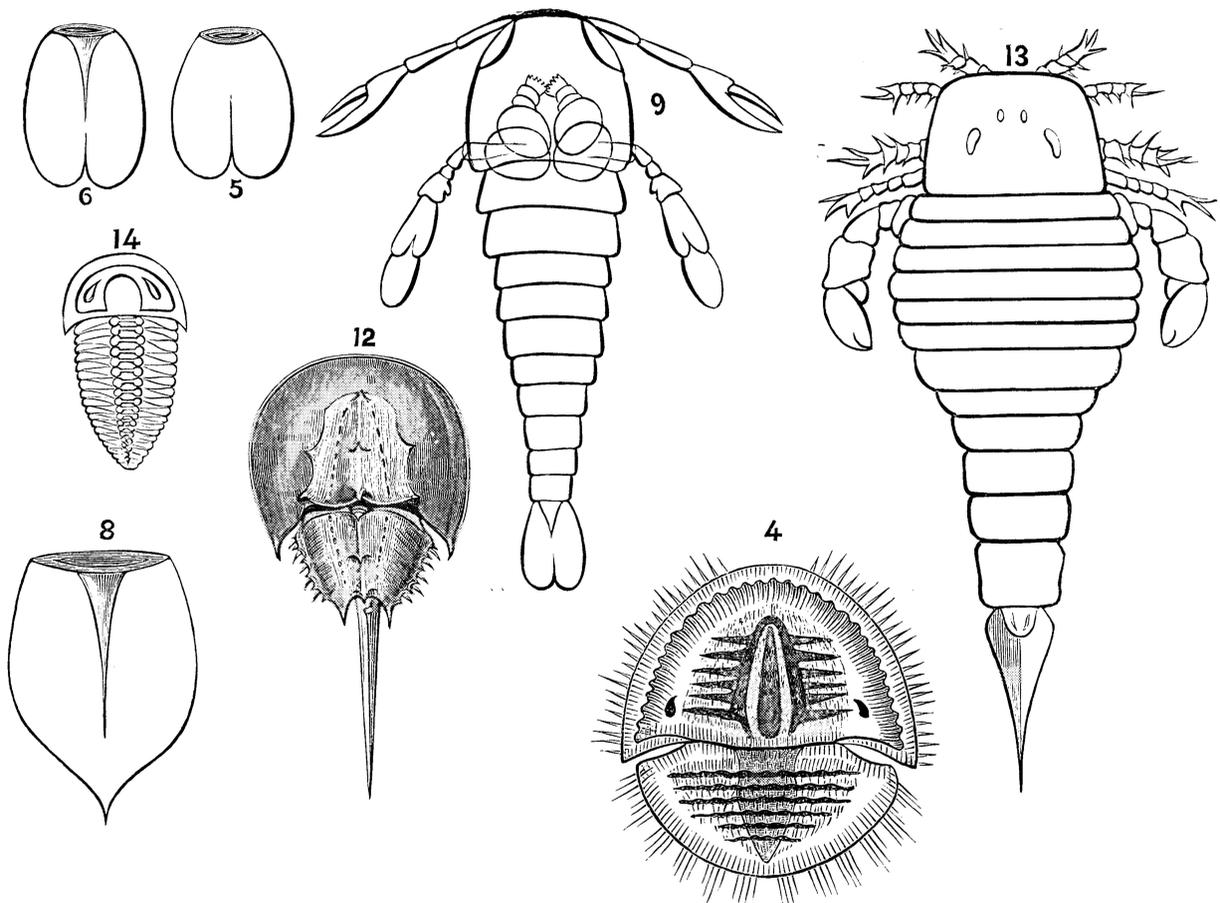
Roberts, W. A. 2002. Are animals stuck in time? *Psychological Bulletin* 128:473–489.

Sansom, A., J. Lind, and W. Cresswell. 2009. Individual behavior and survival: the roles of predator avoidance, foraging success, and vigilance. *Behavioral Ecology* 20:1168–1174.

Sih, A., R. Ziemba, and K. C. Harding. 2000. New insights on how temporal variation in predation risk shapes prey behavior. *Trends in Ecology & Evolution* 15:3–4.

Timberlake, W., D. J. Gawley, and G. A. Lucas. 1987. Time horizons in rats foraging for food in temporally separated patches. *Journal of Experimental Psychology: Animal Behavior Processes* 13:302–309.

Associate Editor and Editor: Mark A. McPeck



*Limulus polyphemus* (Horse Foot Crab, Horseshoe Crab, or King Crab). 4, Young *Limulus* just out of the egg. 5, Terminal tail joint, *Pterygotus banksii*. 6, Terminal tail joint, *Pterygotus bilobus*. 8, Terminal tail joint, *Pterygotus ludensis*. 9, *P. bilobus*. 12, *L. polyphemus*, 1 year old. “The anterior edge of its enormous cephalic shield is not unlike in form the sausage, or mincemeat knife of our kitchens.” 13, *Eurypterus remipes*. 14, *Sao hirsutus*, a trilobite. From “The Horse Foot Crab” by S. Lockwood (*American Naturalist*, 1870, 4:257–274).