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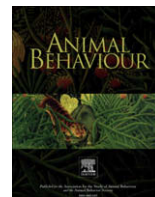
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Review

The paradox of risk allocation: a review and prospectus

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Predation is one of the most important selection pressures acting on prey behaviour. While numerous studies have shown that when predation risk is high, prey tend to increase vigilance and reduce foraging effort, until recently, few studies have looked at how the temporal pattern of risk influences antipredator behaviour. The risk allocation hypothesis predicts that as predation risk fluctuates over time (e.g. as predators come and go), the intensity of prey vigilance and foraging should depend on both the level of risk and the proportion of time that predators are present. If predators are usually absent, prey can meet their energy demands during safe periods, and thus respond strongly during the rare times when predators are present. In contrast, if predators are almost always present, prey might need to forage actively even though predators are present, a counterintuitive prediction for many behavioural ecologists. In this review, we present and highlight the paradoxical nature of the risk allocation model. We then review studies that empirically tested the model. These studies provide only mixed support for the model. Importantly, we identify factors that help to explain why some studies supported the model and others did not. In particular, we find that studies that gave prey more time to assess and learn the risk regime had a higher probability of yielding results that supported the model. Finally, we suggest extensions of the model framework to incorporate broader and more complex ecological contexts.

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Because of the unforgiving nature of predation, prey animals are under intense selection to detect and avoid predators (Lima & Dill 1990; Lima 1998a, b). Predation affects many aspects of a prey individual's life, including life history, morphology and behaviour (Chivers & Smith 1998; DeWitt et al. 1999; Hoverman et al. 2005). For the past 30 years, behavioural decisions made under the risk of predation have been a major topic of interest in behavioural ecology (Lima & Dill 1990; Caro 2005; Bednekoff 2007). Most studies have investigated changes in prey behaviour in the presence versus absence of predation risk (Lima 1998a). However, predation is by nature highly variable in space and time. Predators come and go on a moment-to-moment basis or on a diurnal, lunar or seasonal cycle, and the effect of this aspect of predation risk has been widely overlooked by behavioural ecologists (Sih et al. 2000a; Ferrari et al. 2008a).

Many studies have provided evidence that prey respond to variation in predation risk, adjusting their behaviour to adaptively balance the fitness effects of energy intake and predation risk

(reviewed in Lima 1998a). However, most of the research has focused on this aspect of decision making under relatively short periods of time (i.e. short-term behavioural changes due to the presence of an immediate threat). Until recently, few studies have investigated longer-term effects of variation in predation risk on prey decision making, more specifically whether the response of a prey animal to a predation threat depends on the risk experienced by the individual at other times. An animal's recent history of food consumption and predation risk will probably affect trade-offs between foraging activity and predator avoidance. For instance, studies have shown that when an animal is food deprived, it will show less response to a predation threat than when it is satiated (Lima & Dill 1990; Lima 1998b). Until recently, however, how different temporal patterns of risk affect prey behaviour within a longer time frame has received little attention. About a decade ago, Lima & Bednekoff (1999) proposed a new model, the predation risk allocation hypothesis, to predict the dynamics of how prey vigilance should depend on the temporal pattern of predation risk. This paper has been quite influential. As of 18 February 2009, Lima & Bednekoff (1999) have been cited 204 times, more often by a wide margin than any paper published in 1999 in *Animal Behaviour*, *Behavioral Ecology* or *Behavioral Ecology and Sociobiology* (ISI Web of Science). As might be expected, several experimental studies have tested the risk allocation model directly (see Table 1) or indirectly (see Griffin et al. 2005; Baird & Baird 2006; Gude et al. 2006; Creel et al. 2008).

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Table 1
Empirical tests of the risk allocation model

Study species	Source	Measure	Manipulate	Risk	Food stress?	Pre-exposure	Results (+match, –no match to predictions)			
							Risk ratio		<i>p</i>	
							Low risk	High risk	Low risk	High risk
Marine snails <i>Littorina scutulata</i> <i>L. sitkana</i>	Hamilton & Heithaus 2001	Proportion moving (/10)	<i>p</i>	Caged crabs, <i>Cancer productus</i> , <i>C. magister</i>	No	2 days	N/A	N/A	–	+
Freshwater snail <i>Physa gyrina</i>	Sih & McCarthy 2002	Microhabitat position and activity	<i>p</i>	Live crayfish, <i>Orconectes juvenilis</i>	No	3 days	N/A	N/A	+	+/–
Rusty crayfish <i>Orconectes rusticus</i>	Pecor & Hazlett 2006	Shelter use, time moving, time eating	<i>p</i> and risk ratio (DW, PO, AC)	Snapping turtle, <i>Chelydra serpentina</i>	Yes	2 days	N/A	–	N/A	–
Virile crayfish <i>Orconectes virilis</i>	Pecor & Hazlett 2003	Shelter use, time moving, time eating	<i>p</i> and risk ratio (DW, PO, AC)	Snapping turtle, <i>Chelydra serpentina</i>	No	1 day	N/A	–	N/A	–
Larval damselfly <i>Ischnura elegans</i>	Slos & Stoks 2006	Sit-and-wait foraging and walking	<i>p</i> and risk ratio (no. of live predators)	Conspecifics, 1–2 pumpkinseed sunfish, <i>Lepomis gibbosus</i>	No	65 days	+	–	+	–
Rainbow trout <i>Oncorhynchus mykiss</i>	Mirza et al. 2006	Line crosses, feeding strikes	<i>p</i> and risk ratio (DW, heterosp.AC, consp. AC)	Alarm cues from brook charr, <i>Salvelinus fontinalis</i>	No	2 days	–	+	–	+
Perch <i>Perca fluviatilis</i>	Vainikka et al. 2005	Spine erection, movement, shoaling	Predictability of risk	Northern pike, <i>Esox lucius</i>	No	0 h	N/A or –	N/A or –	N/A or –	N/A or –
Convict cichlid <i>Archocentrus nigrofasciatus</i>	Foam et al. 2005	Time moving, distance to neighbour, vertical area use	<i>p</i> and risk ratio (100% vs 20% AC)	Conspecific AC	No	3 days	–	–	+	+
Convict cichlid <i>Archocentrus nigrofasciatus</i>	Brown et al. 2006	Area use, time moving, foraging rate	<i>p</i> and risk ratio (AC concentration)	Conspecific AC	No	3 days	+	+	+	+
Convict cichlid <i>Archocentrus nigrofasciatus</i>	Ferrari et al. 2008c	Area use, time moving, foraging rate	<i>p</i> and predictability	Conspecific AC	No	3 days	N/A	N/A	+	+
Flatfish <i>Parophrys vetulus</i> <i>Lepidopsetta polyxystra</i> <i>Hippoglossus stenolepis</i>	Boersma et al. 2008	Posture, burial, activity, foraging and latency to feed	<i>p</i>	Model flounder predator	Yes	1–5 days	N/A	N/A	N/A	+
Frog tadpole <i>Rana lessonae</i>	Van Burskirk et al. 2002	Proportion moving (/20)	<i>p</i> and risk ratio (no. of live predators)	Caged dragonfly larvae, <i>Aeshna cyanea</i>	No	2 days	–	+	–	–
Common frog tadpole <i>Rana temporaria</i>	Laurila et al. 2004	Proportion moving (/14)	<i>p</i>	Dragonfly larvae, <i>Aeshna</i> spp.	No	3 days	N/A	N/A	–	–
Field vole <i>Microtus agrestis</i>	Koivisto & Pusenius 2003	Number of seeds eaten	<i>p</i> and risk ratio (Live predator vs faeces)	Caged least weasel, <i>Mustela nivalis</i>	Yes	27.5 h	–	+	–	–
Bank vole <i>Clethrionomys glareolus</i>	Sundell et al. 2004	Number of seeds eaten and patch use	Risk ratio (distance of live predator)	Caged least weasel, <i>Mustela nivalis</i>	No	12 h	–	+	–	–

DW: distilled water; AC: alarm cue, PO: predator odour; N/A: not applicable.

The goal of this paper is to review and synthesize insights from tests of the risk allocation hypothesis. We first present Lima & Bednekoff's (1999) model, its assumptions and predictions, including a counterintuitive prediction that we dub the 'paradox of risk allocation'. We then review empirical tests of the model's

predictions and find that some tests corroborate the model's predictions, while others do not. Importantly, we identify factors that explain some of this variation in fit to predictions. Finally, we highlight several aspects of the risk allocation model in need of further consideration, and discuss how temporal variation in

predation risk can be investigated in different contexts such as competition and reproduction.

LIMA & BEDNEKOFF'S RISK ALLOCATION MODEL

This model is based on the concept that prey adaptively allocate their foraging efforts, and therefore, their exposure to predation across high-risk and low-risk situations. Prey behaviour in any situation should depend on the overall risk experienced by prey, more specifically, the duration of high-risk versus low-risk situations and the relative level of risk associated with each of them. The model predicts that as the duration of exposure to risk increases, prey should decrease their overall vigilance (during periods of both high and low risk) since long periods of sustained vigilance may result in unacceptable decreases in energy intake. Moreover, animals exposed to long periods of high risk should forage particularly actively during brief periods of safety, compared to prey exposed to infrequent risk. The model also predicts that as the risk associated with high-risk situations increases, prey should increase their antipredator response, but will consequently increase their foraging effort in low-risk situations to compensate for the loss of foraging opportunities.

The basis of this model is that an individual feeds over a given period of time to gain a threshold amount of energy necessary to survive. The period available to feed is divided into a proportion of time with high predation risk (i.e. dangerous situations, p) and periods of low predation risk (i.e. safer situations, $1 - p$). The model assumes that prey decide the duration and intensity of foraging (resource gain) and vigilance (predator avoidance) in these two situations. To maximize fitness, prey should adaptively allocate these two behaviours, keeping in mind that they must obtain the required amount of energy before the end of their feeding period to survive. The model assumes the usual trade-off that an individual's increased vigilance comes with a cost of reduced foraging and vice versa.

According to the risk allocation model, the prey's foraging rate and, by extension, its vigilance depends on two factors: the proportion of time spent in high-risk situations (p) and the attack ratio. The attack ratio (α_H/α_L) represents the ratio of attacks per unit time in high-risk (α_H) versus low-risk (α_L) situations. In other words, this ratio reflects how much more dangerous the high-risk situations are compared to the low-risk situations. Predictions of the model then focus on effects of different risk regimes that we will discuss using the following terminology. Within any given risk environment, predators come and go such that prey experience high versus low risk periods. High risk environments are ones where either high risk periods are more frequent (e.g. predator density is high 90% of the time, as opposed to where predator density is high only 10% of the time), or where attack rates are particularly high during high risk periods (i.e. where the attack ratio is high).

The Paradoxical Nature of the Risk Allocation Hypothesis

One main prediction of the risk allocation model is that prey that are usually exposed to long periods of sustained high risk (i.e. a high-risk environment) should be less vigilant and forage more (in both high- and low-risk periods) than prey that usually face lower predation risk. This prediction runs counter to the typical behavioural ecology dogma that prey exposed to higher predation risk should be less active (more vigilant) than prey exposed to lower risk. We thus refer to this as 'the paradox of the risk allocation hypothesis'.

Several field studies support the usual view that prey populations co-existing with dangerous predators show a stronger response to predation threats than prey from populations without predators. For example, Woodward (1983) compared the activity level of several

anuran species and found that larval amphibians from low-risk, ephemeral ponds were almost always in motion, whereas larvae from high-risk, permanent ponds were almost always stationary. When exposed to predators, this behavioural dichotomy between the two populations resulted in much higher predation rates on temporary pond species. Similarly, Giles & Huntingford (1984) showed that stickleback from high-predation environments responded with stronger antipredator responses to both predatory fish (pike) and bird (heron) models than stickleback from low-predation environments. Other studies have observed similar patterns (Mathis et al. 1993; Sih et al. 2000b; Ferrari et al. 2007a).

However, yet other studies have contradicted the usual dogma (see Table 1). In these studies, prey that were held in environments that were usually highly risky showed higher foraging activity, or less response to predators than prey that were held in environments that were usually safe. Most interestingly, in several cases, prey that experienced high risk most of the time showed relatively high activity during those periods of high risk (Hamilton & Heithaus 2001; Sih & McCarthy 2002; Mirza et al. 2006; Slos & Stoks 2006). That is, prey responded to being in a more dangerous world by being more active. This counterintuitive pattern can be explained by the risk allocation model. Next, we discuss these studies along with other tests of risk allocation in more detail.

PREDICTIONS AND TESTS OF THE RISK ALLOCATION HYPOTHESIS

Literature Search

To identify studies testing the risk allocation hypothesis, we used the ISI Web of Science to search for all publications in which 'risk allocation hypothesis' appeared in the title, abstract or keywords. The 37 articles resulting from this search were then individually browsed to determine whether the authors performed a test of the risk allocation model, either through direct laboratory manipulation or through observational field studies. We identified 15 experimental and four observational studies testing the risk allocation model. The 15 experimental studies are summarized in Table 1.

Manipulating the Attack Ratio

A frequently tested set of predictions of the risk allocation model involves effects of variation in the attack ratio α_H/α_L . If the level of risk does not differ between periods of 'high risk' and periods of 'low risk' ($\alpha_H/\alpha_L = 1$), then prey should display similar foraging efforts across risk periods, allowing it to meet its energy requirements independently of the actual risk. However, as the attack ratio increases (i.e. as the high-risk periods become more dangerous compared to low-risk periods), prey should increase vigilance in high-risk periods and decrease vigilance during periods of lower risk (Fig. 1). This prediction matches the results of many studies demonstrating an increase in antipredator behaviour in response to an increase in perceived risk (e.g. threat-sensitive predator avoidance: Helfman 1989; Ferrari et al. 2007b, 2008b); however, to compensate for the loss of foraging opportunities in high-risk periods, prey should decrease vigilance and, thus, increase foraging effort during periods of low risk. In theory (Lima & Bednekoff 1999), changing the absolute value of attack rates in the two periods (α_H and α_L) does not change the optimal level of vigilance as long as the attack ratio is constant.

Nine studies have empirically tested the above predictions of the model (Table 1). Three studies found no support, five studies found partial support and one study found full support for the predictions tested. One reason why prey might not show antipredator behaviour that matches an optimality model is if the prey

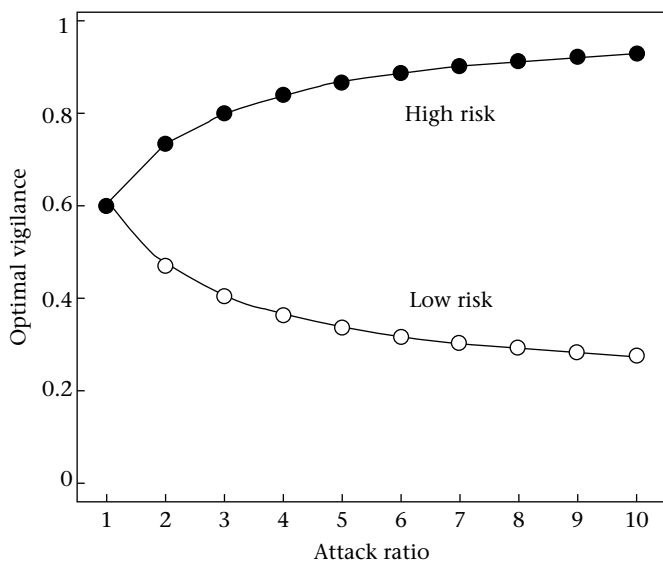


Figure 1. Risk allocation as influenced by attack ratio (α_H/α_L). Results are given for expected vigilance in high-risk (solid circles) and low-risk (open circle) situations (from Lima & Bednekoff 1999).

do not receive cues that allow them to evaluate variation in risk. Here, we present the relevant studies in groups organized by the method used to provide prey with cues about predation risk.

Several studies used caged predators to vary perceived risk. Van Burskirk et al. (2002) varied the risk ratio by exposing *Rana lessonae* tadpoles to 0, 1 or 4 caged predatory dragonfly larvae (*Aeshna* spp., fed tadpoles to generate predation cues). As predicted, they found that as the risk ratio increased, the activity of the tadpoles decreased in periods of high risk. However, they did not find the increase in activity expected in periods of low risk. Sundell et al. (2004) manipulated risk ratios for bank voles, *Clethrionomys glareolus*, by keeping caged least weasels, *Mustela nivalis nivalis*, either 1 or 3 m away from the food source. Similarly, Koivisto & Pusenius (2003) presented field voles: *Microtus agrestis*, with either caged least weasels (high-risk ratio) or fresh weasel faeces (low-risk ratio). As expected, visual and auditory cues from predators represented the greatest threat to the voles, indicating the presence of the predator, whereas weasel scents only elicited mild responses. In both cases, voles' foraging effort was lower during high-risk periods than during low-risk periods when exposed to high-risk ratio. However, contrary to the predictions of the risk allocation model, this pattern disappeared when the risk ratio was lowered.

An alternative way to supply chemical cues without a caged predator is through direct addition of different chemicals in the prey's environment. For example, Pecor & Hazlett (2003, 2006) exposed crayfish (*Orconectes* spp.) to distilled water, the odour of a snapping turtle, *Chelydra serpentina*, or the odour of crushed conspecifics. Previous work (Hazlett 1999) showed that crayfish displayed a higher antipredator response to the odour of crushed conspecifics than to the odour of snapping turtles. In both experiments, Pecor & Hazlett (2003, 2006) failed to find any results predicted by the risk allocation model. Along similar lines, Mirza et al. (2006) exposed rainbow trout, *Oncorhynchus mykiss*, to alarm cues of conspecifics, alarm cues from brook charr, *Salvelinus fontinalis*, or distilled water. Rainbow trout respond to conspecific alarm cues with a greater intensity than when exposed to heterospecific cues (Mirza & Chivers 2001). The results of this experiment indicated that as the risk ratio increased, trout increased the intensity of their antipredator response in periods of high risk, but did not decrease it in periods of low risk. Another way to use chemical cues to

manipulate risk is to expose prey to different concentrations of the cues (Foam et al. 2005; Brown et al. 2006). Increased concentrations of alarm cues have been shown to elicit increased antipredator responses in some prey (Ferrari et al. 2005, 2008b). Brown et al. (2006) found full support for the effect of increased risk ratio on antipredator behaviour and foraging of cichlids, while Foam et al. (2005) found no effect of the risk ratio on the behaviour of cichlids in low- or high-risk periods.

Chemical cues may pose problems for prey and for investigators testing the risk allocation model. Chemicals used to create different risk environments decay over time, consequently decreasing the level of perceived risk (Ferrari et al. 2007c). Moreover, unless cues are provided continuously, a single presentation of cues might not affect prey as much as would be predicted. Chemical information is by nature often unreliable in either space or time as chemical cues may persist in the environment long after the predator is gone. Hence, aquatic prey might respond to a burst of chemicals in their environment, but quickly disregard it in the absence of further evidence of the presence of a predator nearby.

Overall, experiments manipulating the risk ratio rarely found full support for the risk allocation model but instead often showed partial support. Interestingly, in several cases, the prediction of decreased activity (increased vigilance) in the high-risk period was upheld, but the predicted increase in activity during the low-risk period was not. That is, contrary to predictions, animals often did not compensate for reduced activity during risky periods with increased foraging during safe periods.

Manipulating the Duration of High- and Low-risk Periods

The second variable manipulated while testing the risk allocation model is p , the proportion of time that prey experience high risk. Individuals exposed to short periods of high risk (low p) can obtain their energy by foraging at moderate rates during periods of safety, while displaying very high levels of vigilance during the brief periods of high risk. However, as p increases, the time window available for foraging decreases; prey should thus show very high foraging efforts during the brief periods of safety (Fig. 2). If the short periods of safety do not allow prey to meet their energy demands, then prey must feed moderately actively even during periods of high risk in order to obtain food. As noted earlier, the risk allocation model

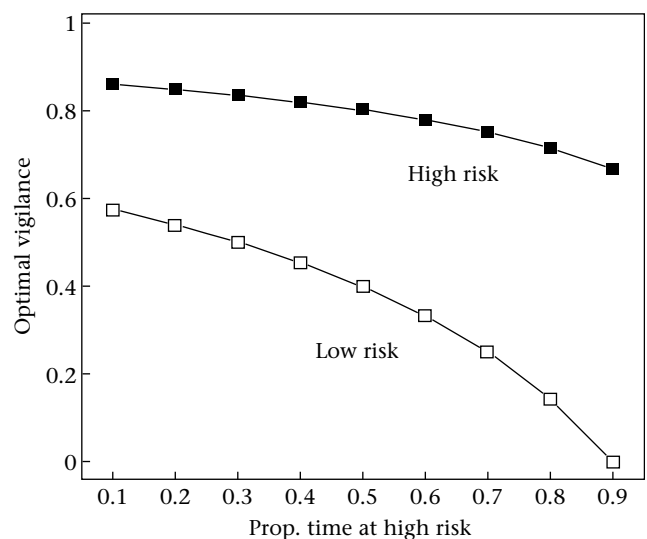


Figure 2. Vigilance in high-risk (solid squares) and low-risk (open squares) situations as influenced by the proportion of time spent in high-risk state (p) (from Lima & Bednekoff 1999).

thus features the paradoxical prediction that prey should be less vigilant if they live in environments that are typically more risky.

Thirteen studies investigated this prediction of the risk allocation model, six failed to support the predictions, four found partial support and three found full support for the model. In several studies, prey were exposed to alternating periods of low or no risk followed by periods of high risk. For example, [Hamilton & Heithaus \(2001\)](#) exposed marine snails (*Littorina* spp.) to high-risk periods (i.e. in the presence of caged predatory crabs, *Cancer* spp.) for 0, 2, 6, 18, 22 or 24 h per day. Similarly, [Van Burskirk et al. \(2002\)](#) exposed tadpoles to high-risk periods for 4, 12 or 20 h per day. While [Hamilton & Heithaus \(2001\)](#) found partial support for the risk allocation model in periods of high risk (snails increased foraging as p increased), [Van Burskirk et al. \(2002\)](#) found no effect of p on the activity of tadpoles. [Sih & McCarthy \(2002\)](#) tested the risk allocation model by exposing freshwater snails (*Physa gyrina*) to a pulse (2 h) of either high-risk or low-risk predation, given a background level (22 h) at the other risk level. As predicted by the risk allocation model, snails were basally less active in the high-risk than in the low-risk environment. Moreover, a pulse of 'safety' for snails in the high-risk environment elicited a burst in activity, and a pulse of risk in the low-risk environment elicited a decrease in the activity, although not as sharp as expected.

Some studies have exposed animals to different frequencies of risk, as an approximation of p , arguing that even though the risk allocation model does not specifically address encounter frequency, an increase in encounter frequency would necessarily lead to an increase in the time spent under predation risk. For instance, [Pecor & Hazlett \(2003, 2006\)](#) exposed crayfish to risk either once every 6 h or once every 12 h using chemical cues. Similarly, [Laurila et al. \(2004\)](#) exposed *Rana temporaria* tadpoles to visual or chemical cues of larval dragonfly every day or every 3 days. Using this methodology, neither study found an effect of p on the activity of the prey. [Foam et al. \(2005\)](#), [Brown et al. \(2006\)](#) and [Ferrari et al. \(2008c\)](#) also manipulated risk frequency instead of directly manipulating p . To better simulate natural patterns of risk, all three studies exposed cichlids (*Archocentrus nigrofasciatus*) to risk cues in a series of three pulses, each separated by a 10 min period ([Foam et al. 2005](#)). All three studies found full support for the predictions of the risk allocation model.

These tests hinge on manipulating the prey's perception of both immediate risk, and their long-term risk regime. To minimize prey uncertainty, experimenters should facilitate the assessment of risk by the prey. When dealing with visual or caged predator risk cues, one can either move the prey (e.g. switch the prey between habitats with and without predators: [Hamilton & Heithaus 2001](#); [Sih & McCarthy 2002](#); [Van Burskirk et al. 2002](#)) or remove the risk. For example, [Koivisto & Puseenius \(2003\)](#) either exposed or removed the weasel from the view of the bank voles but found no effect of p on the foraging activity of voles in these conditions. When dealing with chemical cues, [Foam et al. \(2005\)](#), [Brown et al. \(2006\)](#) and [Ferrari et al. \(2008c\)](#) conducted 100% water changes to provide prey with a 'risk-free' environment. In contrast, [Pecor & Hazlett \(2003, 2006\)](#) did not perform water changes. As they pointed out, the absence of water changes might have made the assessment of high-risk and low-risk periods more difficult for the prey, which might partly explain why their results failed to support the risk allocation model. Overall, with the exception of the three cichlid studies, manipulations of p only partially matched the predictions of the risk allocation model, finding a predicted change in prey behaviour in either the high-risk or the low-risk periods, but not both.

TOWARDS EXPLAINING MIXED RESULTS

A closer look at the experimental tests of the risk allocation model suggests that part of the variation in fit of results to

predictions can be explained by how well the test conditions fit the model's key assumptions regarding energy limitation, and the requirement that prey must know their environmental risk regime. We next discuss these points in more detail.

Some of the cases where results failed to corroborate the risk allocation model's predictions might be explained by the fact that, contrary to the model's assumptions, animals were apparently not 'living on the edge' in terms of meeting their energy demands. The basic model assumes that the relationship between overall energy intake during the entire period (combining periods of high and low risk) and fitness is a step function with a discrete energy threshold ([Lima & Bednekoff 1999](#); but see [Bednekoff & Lima 2004](#); [Bednekoff 2007](#) for different functions). Animals that take in less energy than the threshold have no fitness, while energy intake above the threshold yields no further gains in fitness. Given that assumption, over the entire period, animals should forage just enough to meet their energy demands. They can respond to changes in their risk regime by reallocating their overall foraging activity between periods of higher and lower risk, but they cannot afford to reduce their overall foraging activity. If they reduce their foraging activity during periods of higher risk, they must compensate by foraging more actively during periods of lower risk. In fact, as noted earlier, several studies found that when the risk ratio increased, animals reduced their activity during the high-risk period (as predicted), but failed to show the predicted compensatory increase in foraging activity during the low-risk period. This implies that they were not energy stressed.

To better match the risk allocation model's assumption of energy limitation, tests should examine the behaviour of animals held, ideally in the long term, under conditions where their fitness is clearly energy limited. Interestingly, only three of the 15 studies in [Table 1](#) energetically stressed their animals prior to testing the model ([Koivisto & Puseenius 2003](#); [Pecor & Hazlett 2006](#); [Boersma et al. 2008](#)). While it may be an avenue to pursue, present results are inconclusive with regards to the effect of food limitation on the likelihood of finding support for the risk allocation model (chi-square likelihood ratio: $\chi^2_1 = 0.33$, $P > 0.5$). Six of 12 studies without food restriction found support for the risk allocation model, while one of three studies restricting food availability found support for the risk allocation model. However, even in these three cases, the duration of energy stress was probably too short (1–5 days) to influence the animals' long-term condition. Future research should compare risk allocation for animals held in different long-term rearing regimes that result in different energy states.

Another assumption of the model is that prey must have perfect information about the risk regime. First, they must know whether they are currently in a period of high versus low risk. Determining the presence of a predator (i.e. defining a period as high risk) is probably easier than obtaining absolute knowledge that the predator is absent and that the level of risk is now low. Prey uncertainty regarding the absence of predators might often cause prey to display high levels of vigilance even after a predator has left the area ([Sih 1992](#)). In addition, prey must have an accurate assessment of the proportion of time that they will be experiencing high versus low risk over the long term (i.e. prey must know p). The periods of high and low risk set by an experimenter might differ from the prey's perception of high- and low-risk periods, and the common assumption that prey have perfect knowledge regarding the risk they are exposed to is probably not true ([Lima & Steury 2005](#)).

One way to decrease prey uncertainty about p is to provide prey with a longer period of pre-exposure to the risk pattern. With longer pre-exposure times, prey should be able to better allocate their vigilance and foraging efforts across periods. The 15 studies listed in [Table 1](#) that tested the effect of p on prey behaviour varied in duration of pre-exposure from no pre-exposure up to 65 days.

Interestingly, longer pre-exposures tended to be associated with a higher likelihood of detecting an effect of p on prey behaviour (chi-square likelihood ratio: $\chi^2_1 = 4.67$, $P < 0.05$). Five of six studies with pre-exposures of 3 or more days found some effect of p on prey behaviour (including all three studies that best fit the model's predictions), whereas only two of eight studies with pre-exposures less than 3 days found effects of p on prey behaviour.

A surrogate for the stability of p is the predictability of risk. Do prey allocate vigilance and foraging differently if predation risk is predictable as opposed to unpredictable? A predictable risk should lead to prey displaying minimal vigilance behaviours during predictable low-risk periods and displaying the strongest anti-predator behaviours during high-risk periods. Conversely, an unpredictable predation risk should result in prey displaying constant vigilance behaviour, with suboptimal foraging rates during periods of safety, but displaying antipredator behaviours of lower intensity during periods of risk. Vainikka et al. (2005) exposed perch to either constant (predictable) or unpredictable risk by pike (*Esox lucius*). They found no evidence that predictability affected behaviour. However, the experiment was conducted over a 10 h period without pre-exposure to the risk, and the constant and the unpredictable risk were alternated every 2 h, which seems to defeat the purpose of providing prey with either an entirely constant or totally unpredictable environment. Ferrari et al. (2008c) conducted the only other study to test the effect of predictability of predation risk in the context of the risk allocation model. Their results are somewhat ambiguous, but they did suggest an effect of predictability on the behaviour of cichlids exposed to low-risk but not to high-risk cues.

Overall, our analysis of the 15 studies in Table 1 suggests that many of the examples of tests that provided little or no fit to the risk allocation model's predictions can be explained by the notion that these tests violated one or more of the crucial assumptions of the model: (1) that animals should be energy limited; and (2) that animals have had enough time to assess the risk regime (either the risk ratio, or the proportion of time that predation risk is high versus low). In particular, when animals were given more time to evaluate the risk regime, in most cases, they showed at least a partial fit to the model's predictions.

FUTURE DIRECTIONS

Temporal variation in risk should influence a broader range of behaviours and behavioural outcomes than just vigilance and foraging per se. Animals also trade off vigilance against mating and reproductive demands, competition and territorial defence, and so on (Lima 1998a). A body of existing theory and empirical work analyses optimal behaviour in situations where animals account not just for the foraging/risk trade-off but also for competition (i.e. ideal free models with predation risk; Houston et al. 1993; Sih 1998; Bednekoff & Lima 2004). Modifying the risk allocation model to address ideal free competitive behaviour under temporally varying predation risk should prove useful. Another existing body of work looks at how predation risk influences mating behaviour and sexual selection (e.g. Crowley et al. 1991; Endler 1995). Extending the risk allocation framework to examine how temporal variation in predation risk might influence mating tactics should also prove exciting. Finally, predation risk influences not just prey behaviour but also community or even ecosystem dynamics (Sih 1987; Schmitz et al. 2008). Risk often generates strong nonconsumptive effects of predators on prey, and even on the prey of prey (e.g. carnivores can have large positive effects on plants by reducing herbivore activity; Preisser et al. 2005). Another future direction of study thus involves examining how temporal variation in risk influences the nonconsumptive effects of risk on community and

even ecosystem dynamics. Temporal variation in risk is ubiquitous. The risk allocation framework provides a start towards understanding how prey should respond to this temporal variation; however, much remains to be done.

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