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Creel S 2011. Toward a predictive theory of risk effects: hypotheses for prey attributes and compensatory mortality. *Ecology* 92: 2190–2195

<http://dx.doi.org/10.1890/11-0327.1>

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Toward a predictive theory of risk effects: hypotheses for prey attributes and compensatory mortality

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Abstract. Risk effects, or the costs of antipredator behavior, can comprise a large proportion of the total effect of predators on their prey. While empirical studies are accumulating to demonstrate the importance of risk effects, there is no general theory that predicts the relative importance of risk effects and direct predation. Working toward this general theory, it has been shown that functional traits of predators (e.g., hunting modes) help to predict the importance of risk effects for ecosystem function. Here, I note that attributes of the predator, the prey, and the environment are all important in determining the strength of antipredator responses, and I develop hypotheses for the ways that prey functional traits might influence the magnitude of risk effects. In particular, I consider the following attributes of prey: group size and dilution of direct predation risk, the degree of foraging specialization, body mass, and the degree to which direct predation is additive vs. compensatory. Strong tests of these hypotheses will require continued development of methods to identify and quantify the fitness costs of antipredator responses in wild populations.

Key words: antipredator response; body mass; compensatory mortality; dilution of risk; foraging strategy; group size; nonconsumptive effect; predation; risk effect.

INTRODUCTION

Predators can limit prey by direct killing or by risk effects, which are the costs of antipredator responses (Peckarsky et al. 1993, 2008, Boonstra et al. 1998, Creel and Christianson 2008). Responses to risk can be morphological (Tollrian and Harvell 1999) or behavioral (Lima 1998), including changes in habitat use (Anholt and Werner 1999, Creel et al. 2005, Heithaus and Dill 2006), vigilance (Armitage 2004, Winnie and Creel 2007), foraging (Kotler et al. 1993, Lima and Bednekoff 1999), aggregation (Boesch 1991, Krause and Ruxton 2002, Caro 2005, Creel and Winnie 2005), movement patterns (Sih and McCarthy 2002), and sensitivity to environmental conditions (Winnie et al. 2006). The costs of these responses can be manifest by reduced survival, growth, or reproduction (Peckarsky et al. 1993, 2008, Ruxton 1997, Creel et al. 2007, Pangle et al. 2007). Recent empirical research has shown that risk effects on prey dynamics can be as large as direct effects, or even larger (Schmitz et al. 1997, Nelson et al. 2004, Preisser et al. 2005, Pangle et al. 2007). Logic and data both suggest that risk effects play a part in most predator–prey interactions. Nonetheless, many analyses of predation as a limiting factor still consider only direct effects, particularly in studies focusing on conservation and management, and particularly, in studies of vertebrates.

There is no general theory for the expected relative magnitudes of direct and risk effects, though recent

research has begun to consider this question, and to identify ecological factors that might determine the relative importance of direct predation and risk effects (Heithaus et al. 2007, Creel and Christianson 2008, Schmitz 2008). For example, Schmitz (2008) described differences in the responses of grasshopper prey to spiders with different modes of hunting (active pursuit vs. sit-and-wait), and suggested that classifying predator–prey interactions by the hunting mode of the predator is a productive way to predict the strength of risk effects. Schmitz concluded that “we must begin to consider the mechanisms by which predators hunt their prey in order to develop clearer understanding of predator effects on ecosystems and to develop effective ecosystem conservation efforts. An appealing feature of framing theory using hunting mode as a functional trait is that it may offer generalizable understanding about the source of contingency in prey responses to predators. Moreover, hunting mode is a trait that is readily ascertained through natural history observation of predators in the field.”

As with grasshoppers preyed upon by spiders, vertebrate prey face different risks from predators with different tactics, and their antipredator responses vary accordingly (e.g., antelope responding to stalkers vs. coursers, or solitary vs. pack hunters; Fitzgibbon and Fanshawe 1989, Scheel 1993, Creel and Creel 2002, Caro 2005, Stankowich and Coss 2006, 2007). Because the strength and type of antipredator responses ultimately determine the importance of risk effects, these studies support the argument that consideration of hunting mode will help to frame theory about the strength of risk

Manuscript received 24 February 2011; revised 6 June 2011; accepted 18 July 2011. Corresponding Editor: R. W. Ruess.

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effects. Other aspects of interactions between predators and prey also have strong effects on the strength of antipredator responses, and should be considered in developing a general framework to predict the importance of risk effects. In predicting the strength of antipredator responses and the magnitude of risk effects, we must consider attributes of the prey and of the environment, in addition to attributes of the predator (which include hunting mode and hunting group size). For example, vigilance has been studied in many birds and mammals, and factors demonstrated to affect vigilance include group size (Elgar 1989, Hunter and Skinner 1998), age and sex (Childress and Lung 2003, Winnie and Creel 2007), body condition (Ovadia and Schmitz 2002, Heithaus et al. 2007), position within the group (Hamilton 1971, Keys and Dugatkin 1990, Hunter and Skinner 1998, Stankowich 2003), habitat type (Lima 1987, Scheel 1993), time of day (Elgar 1989, Scheel 1993), and local environmental conditions (Elgar 1989, Lima and Dill 1990). These studies clearly demonstrate that animals adjust their level of vigilance in response to their own condition, the size and composition of the group that they occupy, and in response to the local environment. We know much less about the ways that animals respond to variation in the type of threat that they face, simply because many studies have examined antipredator responses to simulated risk or in response to the immediate presence or absence of only one natural predator. This approach has been productive for some questions, but it gives little scope to ask whether the strength of antipredator response is sensitive to aspects of risk such as the predator's hunting mode, the distance to predators, the size of the hunting group, or cues about the predators' state of satiation. It is likely that prey assess risk as a continuous variable (rather than dichotomizing risk into periods of safety and danger) and that attributes of the predator, the prey, and the environment all play a role in determining the strength of response.

We know little about the relative importance of the attributes of predators, prey, and the environment in determining the strength of antipredator responses, and still less about the manner in which these responses carry costs that affect prey dynamics. To my knowledge, only one study has applied formal model selection to data from the wild to examine the relative importance of these factors. Liley and Creel (2008) found that the best supported models of antipredator responses by elk included several attributes of the threat from wolves (e.g., distance, number of hunters, recent kill or not), several attributes of the prey group (e.g., herd size, herd composition, spatial configuration, and physical condition), and several attributes of the local environment that affect the likelihood of detection or escape (distance to protective cover, snow depth, and snow condition). Of these variables, properties of the prey group had the strongest effects on vigilance. This is perhaps not surprising, because attributes of the prey themselves

affect all of their interactions with predators. Consequently, I suggest that it will be useful to develop and test general hypotheses about the ways that functional traits of prey might affect the relative importance of nonconsumptive risk effects. In this note, I consider the effects of compensatory mortality, prey group size and dilution of risk, the degree of foraging specialization, and body mass. My intention is to stimulate further thought and empirical research on factors that determine the relative importance of risk effects and direct killing. To develop a truly general predictive theory for the importance of risk effects will require a better understanding of the relationship between antipredator responses and their fitness costs.

RISK EFFECTS WITH COMPENSATORY DIRECT MORTALITY

Mortality due to predation can increase a population's total death rate (additive mortality) or be compensated by density-dependent decreases in the death rate due to other factors, thus having little effect on overall mortality (compensatory mortality). Williams et al. (2002) and Lebreton (2007) provide excellent reviews of compensatory and additive predation. Formally, predation is fully additive when the regression of total mortality on the predation rate (with slope $\hat{\beta}$ and intercept $\hat{m}(0)$) yields

$$\frac{\hat{\beta}}{1 - \hat{m}(0)} = 1.$$

When

$$\frac{\hat{\beta}}{1 - \hat{m}(0)} = 0$$

a harvest is fully compensatory up to a threshold predation rate $\hat{m}(0)$, the rate of mortality with no harvest, which defines the maximum scope of compensation via "substitution of risk" (Fig. 1).

With models of predation that consider only the effects of direct killing, compensatory predation has no effect on prey dynamics when the killing rate, k , is less than $\hat{m}(0)$ (Fig. 1). With substitution of risk, other forces of mortality decline as the rate of predation increases, and mean survival holds constant. When we consider risk effects in addition to direct killing, we must recognize that natural selection acting on an individual's antipredator responses is indifferent to the fact that others are more likely to survive after the individual dies. The strength of selection on antipredator behavior depends on the killing rate (k), and this is equally true when $k < \hat{m}(0)$ and when $k > \hat{m}(0)$. Consequently, the proportion of predation's limiting effect on prey that is composed of risk effects will increase steadily as the rate of direct predation rises from 0 to $\hat{m}(0)$ (Fig. 1). Assuming that risk effects are positively correlated with the rate of direct predation in this context (Creel and Christianson 2008), Fig. 1 illustrates two cases in which risk effects increase in a linear manner as the predation

FIG. 1. If direct predation is compensatory due to substitution of risk, other forces of mortality decline as the rate of predation increases, so that mean survival initially holds constant as the killing rate increases. Because the benefit of antipredator behavior depends on the killing rate itself (not on mean survival), the proportion of predation's total effect that is due to risk effects should increase as the killing rate increases, up to the maximum scope for compensation by substitution of risk. When the direct mortality due to predation is completely compensatory through substitution of risk, mean survival does not decrease until the rate of predation (kill rate) exceeds the rate of mortality in the absence of predation ($m_{(0)}$) (left-hand axis and dotted line). If the strength of antipredator responses is proportional to the rate of predation, then risk effects become a larger proportion of predation's total effect on prey dynamics as the killing rate increases from 0 to $m_{(0)}$ (right-hand axis and bars). The cross-hatched bars show a case in which risk effects are 2/3 as strong as direct effects. The shaded bars show a case in which risk effect effects are twice as strong as direct effects.

rate increases, with slopes of 0.67 (risk effects are weaker than direct effects) and 2 (risk effects are stronger than direct effects), to show that the basic result is not sensitive to this variation. For species with high mortality rates in the absence of predation (i.e., r -selected species), the scope for compensation is large ($\hat{m}(0) \rightarrow 1$), so the relative importance of risk effects will increase across a wider range of predation rates (k).

Prediction.—Risk effects will comprise an increasing proportion of predation's limiting effect when direct predation is compensatory and the direct predation rate approaches the maximum scope for compensation through substitution of risk. This effect is most important for prey species with a high rate of mortality in the absence of direct predation (i.e., r -selected prey).

RISK EFFECTS AND DILUTION OF DIRECT PREDATION RISK: PREY GROUP SIZE

Antipredator responses can be active or passive. Active responses include vigilance, movement to safer habitats, and deterrence behaviors such as stotting, flight, and physical resistance. Most models of antipredator behavior (Illius and FitzGibbon 1994, Caro 2005) assume that active responses carry costs that affect survival or reproduction. These costs can be energetic (Brown et al. 1999, Christianson and Creel 2008, 2010) or mediated by other physiological mechanisms such as stress responses, and empirical research often (but not

always) confirms that antipredator responses carry costs (Boonstra and Singleton 1993, Creel et al. 2007, 2009, Rayor and Uetz 1990). The primary passive response to predation risk is a shift in patterns of aggregation. In some instances, prey may disaggregate into smaller groups when the risk of predation is high, to reduce the probability that they will be detected or attacked (Creel and Winnie 2005). More often, group size increases in response to risk.

Even if active defenses do not decrease the probability that someone within the group will be detected, attacked, and killed, joining larger groups in response to predation risk is often favored by dilution of risk (Hamilton 1971). Fig. 2 illustrates a case in which this pattern holds, for impala (*Aepyceros melampus*) hunted by African wild dogs (*Lycaon pictus*) (Creel and Creel 2002). Upon being encountered by wild dogs, the "corporate risk" of an entire impala herd increases with herd size (Fig. 2). Larger impala herds are also encountered by wild dogs more often than expected under the hypothesis that herd size does not affect the encounter rate (Creel and Creel 2002). Thus, the active responses of large herds are less effective than those of small herds at reducing herd-level predation rates. Nonetheless, the individual risk of predation is lower for impala in large herds, through dilution of risk (Fig. 2). In this example, individual-level predation risk is more strongly affected by passive dilution than by active

antipredator behavior. It is plausible to hypothesize that passive responses carry lower costs than active antipredator behavior. (Indeed, this hypothesis provides one explanation for the ubiquity of grouping as an antipredator strategy.) If so, then we might hypothesize that risk effects will be weak in species that rely mainly on aggregation to reduce predation risk, and that (all else equal) risk effects will be inversely related to group size.

Prediction.—Risk effects will comprise a small proportion of predation's limiting effect when the primary antipredator responses of prey are passive, as is the case with dilution of risk. Risk effects will be inversely related to group size. These predictions assume that the costs of passive defenses are less than the costs of active antipredator responses, an assumption that requires testing in the wild.

RISK EFFECTS AND PREY FORAGING STRATEGIES

Many species respond to predation risk by reducing their use of habitats in which they are easily detected or otherwise more vulnerable to predation (Peckarsky et al. 1993, Sih 1997, Creel et al. 2005, Heithaus and Dill 2006). The use of different habitats can have a direct influence on diet composition (Christianson and Creel 2006), so shifts of habitat in response to risk can drive changes in diet (Christianson and Creel 2008) with nutritional or energetic costs (Christianson and Creel 2010).

A set of prey species will often vary in their degree of morphological and physiological specialization to a particular foraging strategy. Using ungulates as an example, some species (such as African buffalo *Syncerus caffer*, wildebeest *Connochaetes taurinus*, and zebra *Equus quagga*) are almost completely specialized grazers, dependent on graminoids and forbs. Other species (such as the black rhinoceros *Diceros bicornis* or giraffe *Giraffa camelopardalis*) are almost pure browsers, dependent on woody vegetation. Others (such as impala or elk, *Cervus elaphus*) are mixed feeders, capable of large shifts in the proportion of graze and browse in their diet (Christianson and Creel 2006). When faced with the presence of a predator, mixed feeders can engage in habitat shifts that are strong enough and persistent enough to produce a substantial change of diet (Christianson and Creel 2008, 2010). Specialized feeders have less scope to employ such responses (though they might engage in short-term responses that reduce the rate of feeding [Lima and Dill 1990, Lima and Bednekoff 1999]). Thus, it is reasonable to hypothesize that a larger proportion of predation's effect on dietary specialists will be via direct killing, and that risk effects will be relatively more important for dietary generalists.

Prediction.—Risk effects will be more important in dietary generalists than in species whose morphological and physiological adaptations do not allow them to alter diet composition in response to predation risk.

FIG. 2. The likelihood of a kill occurring when impala are hunted by African wild dogs in the Selous Game Reserve (data from Creel and Creel 2002). The left-hand panel shows that corporate risk, the risk that at least one herd member will be killed, increases as herd size increases. The right-hand panel shows that, through dilution of risk, individual risk decreases as herd size increases.

RISK EFFECTS AND PREY BODY MASS: AN EVOLUTIONARY PERSPECTIVE

In some prey guilds, larger prey species are vulnerable to fewer predators (e.g., ungulates; Sinclair et al. 2003), suggesting that predation can select for increased body size. In other guilds, smaller prey are less vulnerable (e.g., plankton; Brooks and Dodson 1965), but the direction of this selection gradient is not important for the argument that follows. Consider a thought experiment in which two prey species, A and B, are initially killed at the same rate by a single predator. Species A evolves to become larger than species B. This increase in size reduces the rate of direct predation on species A, although there might be other costs associated with increasing (or decreasing) body mass. Observed at some point after this evolutionary response, species A is less likely to respond to variation in predation risk on short (ecological) time scales, having already responded on an evolutionary time scale, in a manner that reduced the fitness benefits of short-term responses to predators. Thus, within a guild of ecologically similar prey species, if body mass affects the risk of direct killing, it is reasonable to hypothesize that body mass will alter risk effects in a parallel fashion.

Prediction.—For a set of prey species that faced common predation risks over evolutionary time, morphological traits (such as increased or decreased body mass) that reduce the risk of direct killing will also reduce risk effects. This pattern will cause the predation-related fitness effects of such traits to be larger than is revealed by consideration of direct killing rates alone.

ATTRIBUTES OF PREDATORS, PREY, AND THE ENVIRONMENT AND THE IMPORTANCE OF RISK EFFECTS

A comprehensive theory for the effects of predation on prey dynamics must account for direct killing and risk effects (Preisser et al. 2005, Creel and Christianson 2008, Schmitz et al. 2008, Peckarsky et al. 2008). Substantial data show that risk effects are often strong, and can be stronger than direct effects (Schmitz et al. 1997, Preisser et al. 2005, Pangle et al. 2007, Peckarsky et al. 2008), but we do not have a general framework that predicts the importance of risk effects across systems. Schmitz (Schmitz 2008) has proposed that "an appealing feature of framing theory using hunting mode as a functional trait is that it may offer generalizable understanding about the source of contingency in prey responses to predators." I agree, but when the goal is to understand the relative importance of risk effects and direct predation, functional traits of the prey may offer an even more direct general framework. For a prey species that faces multiple predators, the functional traits of each predator affect only some antipredator responses, but the prey's own traits affect all of them.

For a general framework predicting the relative importance of risk effects and direct predation, it will be necessary to clarify the relative importance of attributes of predators, prey, and the environmental in determining the strength of antipredator responses (Liley and Creel 2008). It will also be necessary to develop better methods to quantify how antipredator responses translate into effects on survival and reproduction in the wild. Methods that can detect risk effects do not necessarily allow us to quantify the relative importance of risk effects and direct killing, in terms of their effects on prey dynamics. For example, we can infer that risk effects are important when a chain is established from the presence of a predator to behavioral responses by the prey, to physiological costs of the behavioral response, to demographic costs, and finally to changes in prey dynamics. Even with such data, field studies have rarely (if ever) yielded direct estimates of the proportion of predation's total effect on prey dynamics that was due to risk effects vs. direct killing. Determining the demographic costs of antipredator responses remains a thorny problem for observational studies (Peckarsky et al. 1993, Schmitz 1998, Boonstra et al. 1998, Creel et al. 2007, Pangle et al. 2007, Creel and Christianson 2008). To further develop and test a predictive theory of the importance of risk effects, two steps will be important. First, we must develop and apply methods that relate antipredator responses (which vary on short time scales) to their fitness costs (which are manifest over longer time scales). Studies that integrate behavioral, physiological, and demographic data will be useful for this purpose, because predictable physiological mechanisms often drive the fitness costs of antipredator behavior. Such data will allow the second step, which is to more clearly define the quantitative form of trade-offs between direct killing and risk effects

(Creel and Christianson 2008). Fundamentally, it is the shape of this trade-off curve that predicts the importance of risk effects.

ACKNOWLEDGMENTS

This research was supported by NSF award IOS-0642393. I am grateful to Jim Estes for helpful comments on the manuscript, and to Dave Christianson, John Winnie, and Paul Schuette for many constructive discussions of risk effects.

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