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Research

Bird predation alters infestation of desert lizards by parasitic mites

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Theory predicts that predators can reduce parasite abundance on prey by reducing prey density and through disproportionate predation on heavily infested individuals. We experimentally tested this prediction by examining the effects of bird predation on parasitic mite infestation of the prey lizard *Acanthodactylus beershebensis*. We manipulated predation by adding perches to arid scrubland, allowing avian predators to hunt for lizards in a habitat the birds would not normally use. Host density influenced parasite abundance in hatchlings, but not in older aged individuals and parasite abundance did not affect lizard host survival. Contrary to expectation mite abundance on adult lizards increased under low predation intensities. We explain these results by suggesting a novel hypothesis based on the assumption that the two components of predation, i.e. actual removal of prey and risk, exert contradictory effects on macroparasite abundance.

Predators and parasites can have substantial effects on prey/host population dynamics (Price et al. 1986, Lima and Dill 1990, Lehmann 1993, Poulin 1999). Both kinds of natural enemies are common in ecological systems and often impose simultaneous threats to victims. Yet, possible combined effects of predators and parasites on shared prey and especially the effect that predators may impose on parasites mediated through prey are not well understood (Hudson et al. 1992, Lass and Bittner 2002, Murray 2002, Steen et al. 2002).

Host and macroparasite abundance are often positively correlated, especially when parasites have minor affects on host fitness (Dobson 1990). Accordingly, loss of prey/potential hosts due to direct predation should indirectly cause a reduction in parasite abundance (Choo et al. 2003, Packer et al. 2003). Furthermore, disproportionate predation on infested prey is expected to enhance this effect (Hudson et al. 1998, Hall et al. 2005). This prediction, however, has never been explicitly tested.

We used an experimental system comprised of predator (birds), prey/host (lizard) *Acanthodactylus beershebensis* that responds both numerically and behaviorally to changes in its avian predators activity (Hawlena and Bouskila 2006, Hawlena and Pérez-Mellado 2009) and ectoparasites (trombiculid mites) with prevalence of 92.9–100% on *A. beershebensis*. We created spatial variation in predation intensities by adding perches to homogenous scrubland, thereby inducing indigenous avian predators to perch and hunt for lizards in patches that were previously unavailable to them. Using intensive trapping we tested the prediction that increased

predation indirectly reduces macroparasite abundance and two basic assumptions underlying this prediction: (a) host density and macroparasite abundance are positively correlated; and (b) heavily infested hosts suffer higher predator mortality than lesser infested and un-infested hosts.

Predictions

Theory (Dobson 1990) suggests that there should be an asymptotic relationship between host density and parasite abundance (Fig. 1a). While this relationship is useful for identifying patterns in the field, it does not, in its current form, amenable to making explicit comparisons between treatment and control conditions in experiments. We therefore modified the baseline model to make explicit predictions for field testing.

The baseline model predicts that decreasing host density due to predation should lead to reductions in parasite abundance (Fig. 1a). However, the degree of reduction in parasite abundance should vary nonlinearly with the intensity of predation on prey. Accordingly, we can deduce that as the difference in prey/host number between no-predator control conditions (N_c) and predation level i (N_{pi}) increases (i.e. predation intensity N_c–N_{pi} increases) there should be a corresponding increase in the magnitude of decline in parasite burden (i.e. the difference between parasite load on hosts in control conditions [P_c] and in predation conditions [P_{pi}]). This process generates a positive exponential relationship between predation intensity and decline in parasite burden (Fig. 1b).

Methods

Study system

We conducted the field experiment in a loess scrubland in the northern Negev desert, Israel (31°14'N, 34°38'E). The habitat is characterized by a matrix of bare crusted soil with microphytic communities and distinct patches of small perennials with a mound of herbaceous understory (e.g. macrophytic Eldridge et al. 2002). The low-lying woody shrub *Noea mucronata* comprised 97% of all perennial shrubs in this habitat. The prey/host lizard *A. beershebensis* usually hatches in late spring and lives less than a year. Hatchlings undergo short dispersal period about two weeks post hatching but later present strong site fidelity. In our study area, *A. beershebensis* is usually parasitized by four species of trombiculid mites, *Pentidonis agamae*, *Matacarus maroccanus*, and two undescribed species of the genus *Matacarus*. The main lizard predators in this area are the southern grey shrike *Lanius meridionalis* and the common kestrel *Falco tinnunculus*. Both avian predators are important lizard predators in arid and semi-arid habitats throughout their distribution ranges (Hodar 2006, Padilla et al. 2007). In our field site, we found lizard remains in 57% of shrike pellets and in 53% of kestrel pellets during summer months (May–September) (Hawlena and Pérez-Mellado 2009). Shrikes hunt almost exclusively from perches; therefore, they can prey on lizards only within the vicinity of perches. Kestrels hunt from perches but can also hunt while hovering, but then their efficiency declines (Sheffield et al. 2001). Thus, predation on lizards in this habitat occurs mostly in the vicinity of the few *Lycium europaeum* (a deciduous shrub up to 3 m tall) and *Asphodelus microcarpus* (a flowering perennial geophyte that grows in clusters and produces a 1-m-tall flower stalk from which the birds hunt), and around the even fewer acacia trees *Acacia raddiana*.

Experimental design

We conducted the experiment in five replicate 190×80 m plots of homogenous habitat, located at least 300 m from each other. Given that *A. beershebensis* have small home ranges (on average, $607 \pm SE = 85$ m^2, n = 20, i.e. a 24–32 m diameter for a circular home range), the five plots effectively represent independent replicates. We divided each of the five plots into paired 80×80 m subplots, separated by a 30 m buffer zone to create control and treatment subplots. We enhanced predation pressure by experimentally adding small groups of artificial trees that could be used by birds as hunting perches in the otherwise perch free habitat. We constructed the artificial trees by erecting sixteen metal poles (artificial trees) of 1.5 m height in one randomly selected subplot from each pair (treatment plot). We attached to the top of each pole barbed wire connected to a 0.5×0.5 m metal frame to mimic thorny branches. The paired subplot was used as a control. We found strong philopatry of lizards to a subplot (after dispersal) as only five of 546 marked individuals (<1%) were recaptured in a subplot adjacent to that in which they were originally captured and marked. Time budget analysis, done to verify that the treatments did indeed enhance predator presence, revealed that avian predators spent more time in all treatment subplots (17.9% $\pm$ SE = 2.5% of total survey time) than in the paired control subplots (2.2% $\pm$ SE = 0.8%) (Hawlena and Bouskila 2006). This enhanced presence of predators also led to a 68% reduction in *A. beershebensis* survival.

In each subplot we buried a grid of 64 pitfall traps (10 l buckets buried flush with the ground), that were spaced 10 m apart. We captured the lizards for three consecutive days each month for two years. Low recapture rates prevented calculating lizard density using standard mark recapture methods. Instead, we used the minimal number of lizards known to be alive (from here on MNA) as our density measure.
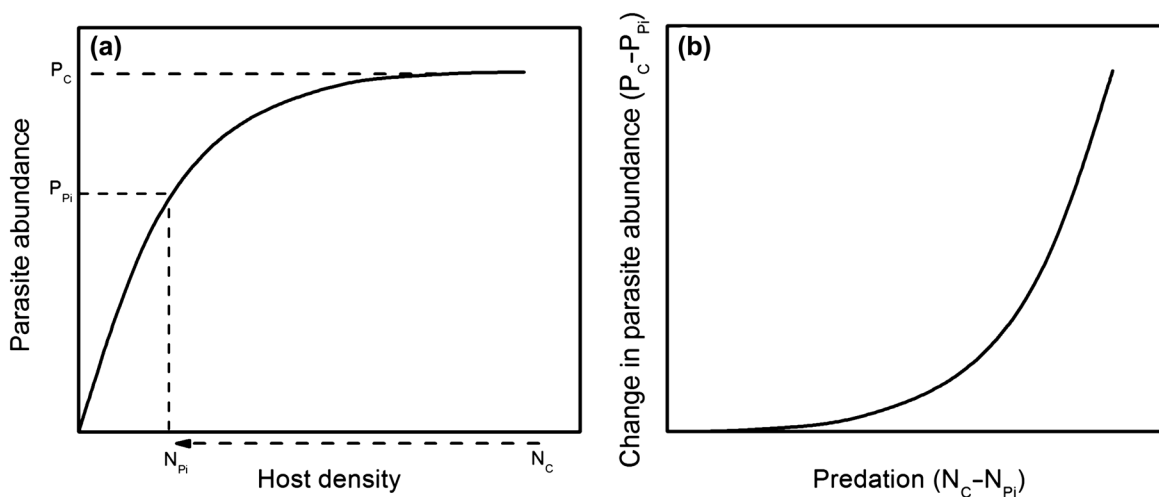

Figure 1. The predicted relationship between predation intensity and change in parasite abundance. (a) Based on well acknowledged asymptotic relationship between host density and parasite abundance (Dobson 1990), host density due to predation intensity (N_{pi}) will cause lower parasite abundance (P_{pi}). (b) Plotting the changes in prey density due to predation (N_c–N_{Pi}; predation intensity) against the corresponding changes in parasite abundance (P_c–P_{Pi}) will result in an exponential relationship.

We marked the lizards individually by toe clipping and measured lizard body length (snout–vent length, SVL, to the nearest 1 mm) using a transparent ruler and body mass to the nearest 0.1 g with an electronic field scale. Mites on *A. beershebensis* are usually located in pockets behind legs (especially in the posterior axillae) and under large ventral scales. We estimated parasite abundance (mites per lizard) by counting individual mites using a magnifying glass ($\times 10$) (Casher et al. 2002). Since the majority of *A. beershebensis* live less than a year, all lizards with similar body length belong to the same age cohort. This enabled us to define lizards that were trapped during June as hatchlings (mean SVL = 34.76, SD = 4.07), trapped during July as juveniles (mean SVL = 53.67, SD = 5.88) and trapped during October as adults (males: mean SVL = 61.71, SD = 7.2; female: mean SVL = 59, SD = 3.3). The determination of sex was possible only for adult lizards. Studies in the same experimental system found that hatchling densities in treatment subplots were significantly lower than in the paired control subplots (reflecting density differences in the parental cohort), but that spatial redistribution soon after the June trapping period concealed those differences. Differences in lizard densities between neighboring subplots started to open wide again due to variation in predator activity soon after lizard settled in their new home ranges. This unique population dynamics allowed to compare mite responses to differences in lizard densities due to indirect (hatchling) or direct (juvenile and adult) predator activity and to examine the responses of juvenile mite abundance to variation in predation intensity soon after dispersal to that of adults that experienced predation for already more than four months. We expected smaller effect of predation on parasite abundance in juveniles relatively to adult lizards.

Data analysis

Parasite abundance per host typically follows a negative binomial distribution (Anderson and May 1978). To facilitate parametric statistical analysis, we square-root transformed the data on parasite abundance per host to meet normality and homogeneity of variance assumptions of parametric statistics. The transformed data did not deviate significantly from normality (Kolmogorov–Smirnov tests; d = 0.059, DF = 188, p = 0.2 for hatchlings, d = 0.040, DF = 126, p = 0.2 for juveniles; and d = 0.062, DF = 180, p = 0.087 for adults).

We tested the prediction that increased predation indirectly reduces macroparasite abundance using two complementary procedures. First, we used mixed model analysis of variance (ANOVA) with treatment (increased predation vs control) as a fixed factor and plot identity and year as random factors to examine if predation affects parasite abundance. We were able to use results from successive cohorts as independent replicates without committing pseudoreplication since *A. beershebensis* lives less then a year and because of the hatchling spatial redistribution during the dispersal period. But, intensity of parasite infestation may also depend on host body size and physiological condition (Hawlena et al. 2005). We therefore evaluated the potential need to account for dependence of parasite load on lizard SVL, absolute mass and body condition index (i.e. residuals of a linear regression

between SVL and body mass) by regressing the number of mites on each individual lizard against these three measurements. We repeated the same procedure for hatchlings (SVL: $R^2 = 0.011$, p = 0.214; mass: $R^2 = 0.013$, p = 0.179; body condition: $R^2 = 0.007$, p = 0.312), juveniles (SVL: $R^2 < 0.001$, p = 0.945; mass: $R^2 = 0.021$, p = 0.11; body condition: $R^2 = 0.006$, p = 0.387), and adults (SVL: $R^2 < 0.001$, p = 0.983; mass: $R^2 = 0.01$, p = 0.373; body condition: $R^2 = 0.045$, p = 0.057) and found no effect of these variables on parasite abundance on any age group, indicating that it was unnecessary to correct mite abundance per host for these traits. Lizard sex has been reported to have significant effects on parasite abundance (Klukowski and Nelson 2001); so we added sex as a fixed factor in the adult mixed model ANOVA.

Second, we a priori chose an exponential model (predicted relationship; Fig. 1b) to examine the relationship between predation intensity and the corresponding change in lizard parasite abundance and compared it to a linear model. The numerical change in prey abundance due to predation was calculated as $\frac{N_c - N_p}{N_c + N_p}$, where N_c was *A. beershebensis* MNA in the control subplot and N_p was MNA in the paired predation subplot. Similarly, we calculated changes in parasite abundance as $\frac{P_c - P_p}{P_p + P_c}$, where P_c was parasite abundance in the control subplot and P_p was parasite abundance in the paired predation subplot. A negative change in parasite abundance means that mite abundance was elevated under increased predation. We repeated the same procedure for the three age classes. Because in two treatment subplots we found no adult lizards the adult models are based only on eight data points.

Theory predicts asymptotic relationship between host density and parasite abundance (Dobson 1990; Fig. 1a). To test this assumption we a priori chose a logarithmic model (predicted association) and compared it against linear model (simple reference association) on data for hatchlings, juveniles, and adults independently.

We used multiple logistic regression to test the assumption that heavily infested hosts suffer higher predator mortality than lesser infested and un-infested hosts (Janzen and Stern 1998). We treated the first five-month interval (June –October) as an episode of mortality. In the basic logistic regression models we included parasite abundance as a covariate and treatment (increased predation vs control) as a factor. We present only the results of the best models identified using the backward conditional procedure. Significance tests were two-tailed at $\alpha = 0.05$. For all analyses we used SPSS 13.0.

Results

Predation intensity had a significant effect on hatchling parasite abundance ($F_{1,140} = 4.953$, p = 0.028). As predicted, hatchlings in increased predation plots harbored fewer mites (8.13; 95% CI 5.94–10.67) than did hatchlings from the control plots (11.45; 95% CI 9.54–13.54). Nevertheless, one month later we no longer found a net effect of predation on juvenile parasite abundance ($F_{1,4.1} = 0.062$, p = 0.815). Similarly, we did not find a net predation effect on adult parasite abundance ($F_{1,29.9} = 0.034$, p = 0.856).
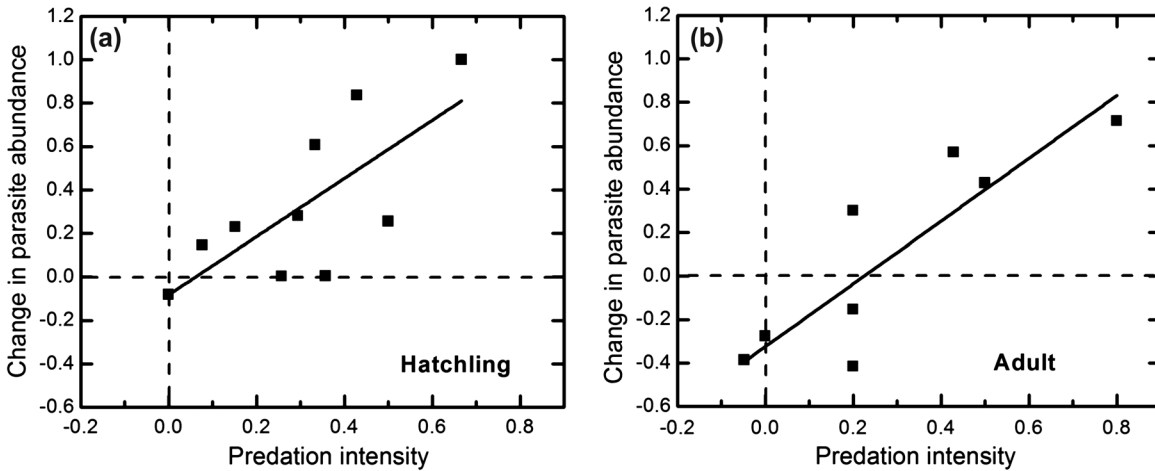
Figure 2. The observed relationship between predation intensity and change in parasite abundance on hatchling (a) and adults (b). Predation intensity was calculated as $\dfrac{N_c - N_p}{N_c + N_p}$, where N_c was the number of prey individuals in the control subplot and N_p was the number of individuals in the paired predation subplot. The change in parasite abundance was calculated as $\dfrac{P_c - P_p}{P_p + P_c}$, where P_c was parasite abundance in the paired control subplot and P_p was parasite abundance in the predation subplot.

The relationship between predation intensity and the change in parasite burden on hatchling lizard were significant using both exponential ($R^2 = 0.526$, DF = 8, p = 0.018) and linear ($R^2 = 0.529$, DF = 8, p = 0.017; Fig. 2a) models. There was no relationship between predation intensity and change in mite abundance for juvenile lizards (linear: $R^2 = 0.001$, DF = 8, p = 0.930; exponential $R^2 = 0.001$, DF = 8, p = 0.938). But, there was again a significant relationship for adult lizards using both exponential ($R^2 = 0.737$, DF = 6, p = 0.006) and linear ($R^2 = 0.750$, DF = 6, p = 0.005; Fig. 2b) models. The linear model explained slightly more of the variation for the same number of model parameters; hence we make the conservative conclusion that the relationship is linear.

A striking outcome is that under low predation intensities, parasite burden on lizards in the experimental plots (i.e. increased predation) was higher than in the control plots, i.e. low predation had enhanced parasite load. This trend was reversed under moderate to higher predation intensities (Fig. 2b).

Only hatchling minimal number known to be alive had a significant effect on mite abundance. The logarithmic model ($R^2 = 0.691$, DF = 18, p < 0.001; Fig. 3) explained the variation of this relationships better than did the linear model ($R^2 = 0.544$, DF = 18, p < 0.001). We found no significant relationships between juvenile or adult MNA and average mite abundance using either logarithmic (juveniles: $R^2 = 0.023$, DF = 18, p = 0.519; adults: $R^2 = 0.002$, DF = 16, p = 0.869) or linear (juveniles: $R^2 = 0.029$, DF = 18, p = 0.476; adults: $R^2 = 0.002$, DF = 16, p = 0.851) models.

We found no significant effect of mite abundance on lizard survival using logistic regression (Wald statistics = 0.965; DF = 1; p = 0.834).

Discussion

Theory predicts that predation should decrease prey macroparasite abundance (Packer et al. 2003). This prediction is based on two assumptions. First, host density is positively associated with macroparasite transmission rate and consequently with parasite abundance (Anderson and May 1978, Krasnov et al. 2002), and hence any predation that diminishes prey/host population size should lead to lower macroparasite abundance. Second, disproportionate predation on heavily infested prey reduces the average macroparasite load per individual (Hudson et al. 1998, Hall et al. 2005).

This study revealed inconsistent results regarding the prediction and the two assumptions underlying it. We found unidirectional negative effect of avian predators on hatchling parasite abundance, offering first experimental support for the prediction that loss of prey/potential hosts due to direct predation should indirectly cause a reduction in parasite abundance (Choo et al. 2003, Packer et al. 2003). We, also,
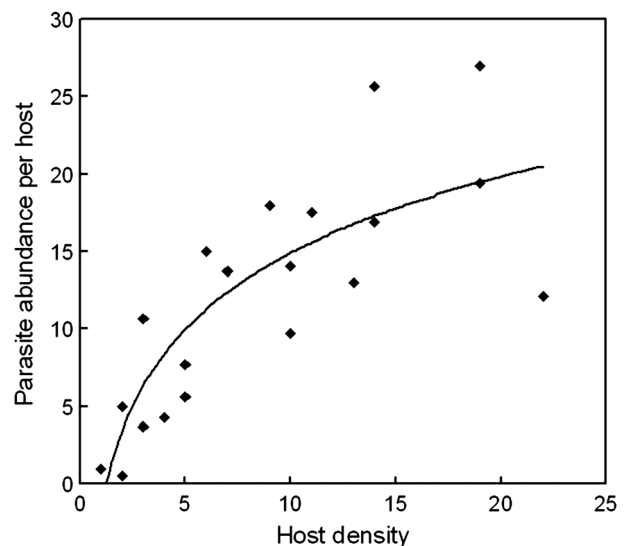

Figure 3. The relationship between hatchling density and mite abundance before dispersal.

found an asymptotic association between hatchling density and mite abundance that confirmed the basic assumption underlying this prediction. Contrary to expectation, the exponential model did not describe the association between predation intensity and the change in parasite abundance much better than did a linear model.

The effect of predation on hatchling parasite abundance reflected the numerical effect of avian predation on the parental cohort and not an acute response of the hatchling to contemporary variation in predator activity (Hawlena and Bouskila 2006). We expected to find similar results when examining the direct consequences of predation on juvenile and adult lizard mite abundance. To our surprise, we did not find unidirectional negative effect of predation on mite infestation in neither juveniles nor adults, although, elevated avian predator activity was observed in all treatment subplots. Contrary to expectation mite abundance on adult lizard increased under low predation intensities and decreased under higher predation intensities. Also, we did not find support for the two well acknowledged assumptions underlining the Packer et al. (2003) hypothesis. First, host density had no effect on mite abundance in either juvenile or adults. This cannot simply be a statistical artifact, because of variation in sample sizes (Poulin 2007), since hatchling sample size (n = 147) was bigger than that of juveniles (n = 126) and of that of adults (n = 81). Thus, we suggest that environmental factors that were not present soon after hatching (e.g. perceived predation risk) became important later in season, altering the predicted association between host density and parasite abundance. Second, in both treatment and control subplots we did not detect reduced survival of heavily parasitized lizards although heavily infested, hosts are expected to suffer higher mortality due to disproportionate predation against them and even though macroparasite can directly impair their host fitness (Lehmann 1993). We suggest that in our system, trombiculid mites have a low effect on lizard fitness components and on lizard behavior, as in several other studies that explored the effect of ticks and mites on lizard fitness (Bull and Burzacott 1993, Abell 2000).

Our results were inconsistent with the predicted unidirectional reduction in macroparasite abundance and with the two assumptions underlying it. This inconsistency suggested a need to consider greater biological detail to account for cases in which macroparasite have relatively moderate effect on their host fitness and for situations in which contemporary predator activity is affecting the prey/host population. Packer et al. (2003) considered the consumption effects of predators as the prominent effect on prey parasite abundance. However, the mere risk of predation introduces nonconsumptive effects that may change the nature of prey behavior (Lima 1998), that may decouple the direct relationship between predation and parasite burden. Accordingly, the role of predation risk in mediating the relationship between predation and parasite abundance may need to be considered.

Prey responding to predation risk alters their spatial locations and activities, often at the cost of fully engaging in essential behaviors such as foraging and thermoregulation (Abramsky et al. 1996, Brown and Kotler 2004, Martin and Lopez 2005). Lower resource acquisition may in turn impair important physiological characteristics, such as body condition and immunocompetence (Folstad and Karter 1992, Downes 2001). This altered behavior and physiological condition can affect parasite transmission rate, reproduction and survival, which may then influence parasite abundance (Moore 2002). Hosts that suffer from lower body condition and impaired immune-response, or those that occupy predation risk free patches that are favorable habitats for parasites can become highly susceptible to mactoparasite infestation (Talleklint-Eisen and Eisen 1999, Main and Bull 2000, Casher et al. 2002, Cox et al. 2005, Hawlena et al. 2005). As a result, we propose that at a given host density, an increase in predation risk that will induce antipredator responses may cause a parasite burden on hosts that is higher in the face of predation than in its absence. This suggested tradeoff between the risk of predation and the risk of parasitism was confirmed for many predator–prey–parasite systems (Relyea 2005), but was not yet established for macroparasites. We hypothesize that higher risk may increase parasite burden, but this is increasingly compensated by higher losses of prey to direct predation. The net result of increasing predation pressure (consumptive and perceived predation) can be an increase or decrease in parasite abundance, depending on the magnitude of the impact imposed by each component of predation pressure on the prey (Appendix 1). This net effect however is a hump-shaped relationship between parasite abundance and prey density (Appendix 1).

In conclusion, our experimental results were inconsistent with unidirectional negative effect of predation on parasite abundance predicted by theory. Instead, we found slight increases in adult lizard parasite abundance under low predation pressure. We propose that this effect arises from predation risk effects that are not considered in current theory. We offer a new model of the relationship between predation and parasite abundance that accounts for such risk effects. Future studies should examine the suggested mechanisms in greater detail, by separating the perceived risk effect of predation on parasite abundance from the consumption (numerical) effect of predation. This step is necessary to include predator–prey–parasite relationship into broader evolutionary ecological concepts.

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Appendix 1

Graphical representation of the combined effect of consumptive and none-consumptive components of predation on prey parasite abundance

Graphic representation that demonstrates the way we combine both components of predation (numerical and behavioral responses) to predict the general effect of predation on prey-parasite abundance. The solid curve describes the well acknowledged asymptotic relationship between prey density and parasite abundance (Dobson 1990). Predation risk is predicted to generate an increase in mean parasite burden per host under a given density, resulting in a family of dotted asymptotic curves. Each of these curves represents the effect of different risk levels on mean parasite burden per host. The increase in parasite abundance as a function of increased risk of predation gradually diminishes. Although the mechanism for this maximal parasite abundance is still controversial, its existence is widely acknowledged (Krasnov et al. 2002). This is the reason for plotting the dotted curves with decreasing distances between them. Under natural conditions, both factors operate together and thus the combined effect will be the intercept of the vertical line emerging from the new reduced densities of the host (Np_1; Np_2) and the appropriate risk curve. Under low predation pressure parasite abundance is predicted to increase P_{p1} and under high predation pressure parasite abundance is predicted to decrease. The dashed line represents this combined relationship.