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BEHAVIORAL ECOLOGY - ORIGINAL PAPER

Change your diet or die: predator-induced shifts in insectivorous lizard feeding ecology

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Abstract Animal feeding ecology and diet are influenced by the fear of predation. While the mechanistic bases for such changes are well understood, technical difficulties often prevent testing how these mechanisms interact to affect a mesopredator's diet in natural environments. Here, we compared the insectivorous lizard *Acanthodactylus beershebensis*' feeding ecology and diet between high- and low-risk environments, using focal observations, intensive trapping effort and fecal pellet analysis. To create spatial variation in predation risk, we planted "artificial trees" in a scrubland habitat that lacks natural perches, allowing avian predators to hunt for lizards in patches that were previously unavailable to them. Lizards in elevated-risk environments became less mobile but did not change their microhabitat use or temporal activity. These lizards changed their diet, consuming smaller prey and less plant material. We suggest that diet shifts were mainly because lizards from risky environments consumed prey items that required shorter handling time.

Keywords *Acanthodactylus beershebensis* · Crossover hypothesis · Foraging · Handling time · Mobility

Introduction

Diet (i.e., types, sizes and amounts of food items) is influenced by many aspects of animal biology, including morphology, physiology, behavior and habitat choice (Pyke et al. 1977; Houston and Shine 1993). Attempts to reduce the probability of being killed by a predator (i.e., predation risk) may alter decisions made by animals about where to feed (Abramsky et al. 1996, 2002), when to feed (Bouskila 1995; Kotler et al. 2002), how to feed (Lima et al. 1985), and on what to feed (Dill and Fraser 1984; Rothley et al. 1997). Consequently, the risk of predation may directly or indirectly change an animal's diet.

The behavioral mechanisms underlying prey dietary responses to predation risk are well understood due to numerous empirical studies that used simplified environments to test discrete responses (e.g., Dill and Fraser 1984; Lima 1985; Houtman and Dill 1998). Under natural conditions, various aspects of prey feeding ecology might interact and alter dietary changes that are expected based on these mechanisms when acting alone. For example, hungry prey could accept greater risk and hence adopt behaviors that deviate from the predicted mechanistic responses to elevated predation (Skutelsky 1996). Thus, to understand the consequences of chronic predation risk on prey diet, feeding ecology should be explored under natural field conditions when all organisms are allowed to move and interact freely.

Most field studies that use such empirical approaches have focused on herbivores (e.g., Schmitz 1998; Christianson and Creel 2008). The effect of a chronic increase in

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predation on mesopredator (medium-sized predator that top predators can prey upon) feeding ecology and diet has rarely been studied in manipulative field experiments (but see Martín and Salvador 1993). This is not surprising when considering the technical difficulties of manipulating top predator activity while allowing the focal mesopredator and its prey to move and forage in their natural habitat.

Here we report the results of a controlled and replicated field experiment designed to test the consequences of a persistent increase in avian predation on the insectivorous lizard, *Acanthodactylus beershebensis'* (Moravec et al. 1999) feeding ecology and diet. We added perches to homogeneous scrubland, allowing avian predators to perch and hunt for lizards in patches that were previously unavailable to them (Hawlena and Bouskila 2006). Consequently, this manipulation locally enhanced the risk of predation by altering the spatial activity of indigenous predators but did not change other determinants of patch quality (e.g., shade, food or shelter) and did not confine the movements of the focal organisms. Using fecal pellet analysis, intensive trapping effort and direct observations, we compared the lizard time allocation, microhabitat use and diet composition between environments of high and low (i.e., control) predation pressures.

Generating predictions

We integrated well-established hypotheses of prey feeding responses to predators with natural history information to generate realistic yet testable predictions for lizard dietary responses to risk of avian predators in a natural environment. Theory posits that animals forage in areas and during times that maximize their energy gain per unit time but that do not considerably compromise other needs (Stephens and Krebs 1986). Spatial or temporal changes in the risk of predation may alter the food-safety balance and may force animals to partially or completely avoid areas or time windows of high foraging efficiency if their exploitation entails significant danger (Schmitz et al. 1997). In our system, lizards retreat to bush cover when threatened. Thus, we expect lizards from increased predation habitats to stay longer in or around bushes. During summer months, lizards used bimodal activity to evade the extreme temperatures of midday. Southern grey shrike (*Lanius meridionalis*), the main lizard predator in this habitat, has a similar daily activity mode (Ward and Pinshow 1995). In risky environments, lizards are expected to shift their activity toward the thermally less favorable time of midday, when the risk of shrike predation is reduced.

A mobile prey has a higher probability of being detected and attacked by a visually oriented predator (Lima 1998; Sheffield et al. 2001) and suffers from reduced abilities to detect and escape predator attacks (Fleishman 1986; Lima and Bednekoff 1999). Thus, under increased predation risk the active forager *A. beershebensis* is predicted to adopt a more stationary foraging mode. A mesopredator's foraging mode is an important determinant of its diet (Vitt and Pianka 2007). The predator-prey crossover hypothesis (Huey and Pianka 1981) predicts, based on variation in encounter rates, that ambush foragers should mainly feed on widely foraging organisms while more mobile foragers should prey on stationary prey. Consequently, we predict that a lizard that reduces its movements to minimize the risk of predation will feed on prey that is more mobile.

Insect size is often positively correlated to handling time and is used as a rough approximation of energy value to an insectivore (Schoener 1971). Optimal foraging theory predicts that a predator should consume a prey item when the net energy gained per unit time by consuming it is greater than the expected gain by skipping it and searching for a better prey (Stephens and Krebs 1986). The handling time required to consume arthropods that are much smaller than allowed for by the lizards' maximal prehension and processing abilities is negligible (Griffiths 1980). Thus, active foragers are expected to feed on all small arthropods encountered while actively searching (Fig. 1, Eat everything area). Above a certain prey size threshold, consumption requires longer handling time and may include a risk of injury due to prey defense. When prey consumption incorporates handling costs, the predator is expected to feed on an arthropod size that maximizes their energy gain per unit handling time without considerably compromising safety (Lima and Valone 1986) (Fig. 1, Trade-off area). Under increased predation risk, handling time becomes more costly (Brown 1988; Brown and Kotler 2004) and lizards should shift their preferences (i.e., within the trade-off area) to prey upon smaller arthropods. Consequently, the maximal prey size consumed by lizards under elevated risk of predation is expected to be smaller than the maximal prey size of lower-predation-risk lizards. However, based on the acknowledged negative association between animal size and abundance (Cyr et al. 1997), we assumed that most arthropod prey available to lizards would be much smaller than the threshold size that accompanied handling costs (Fig. 1, Eat everything area). Consequently, based on prey availability, we expect to find a decrease in maximal prey size consumed by lizards in increased predation environments, but to find no effect of predation on average prey size consumed by those lizards. Reduced searching effort (due to lower lizard mobility) by lizards from increased risk environments may lead to under-representation of relatively bigger, hence rarer, prey items in the lizards' diet, reinforcing the expected reduction in maximal prey size.

Prey feeding selectivity is acknowledged to be based on the prey danger–profitability relationship (Houtman and Dill 1998). When more profitable prey items are more

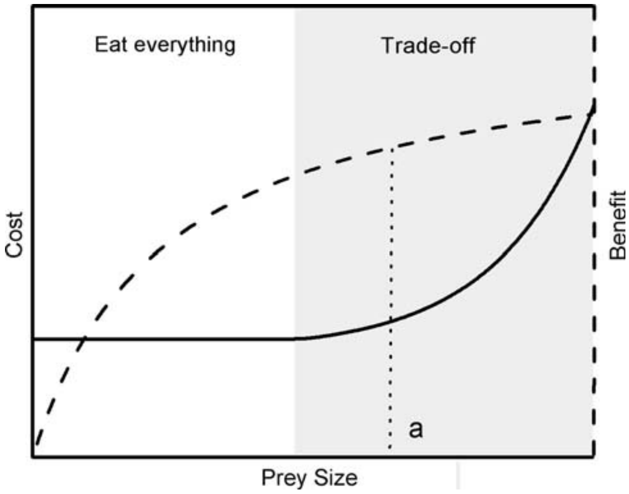

Fig. 1 A conceptual model to predict prey size distribution in an active mesopredator's diet. The *broken line* represents the energetic benefits of consuming a prey and the *solid line* represents the accompanying costs of searching and handling the prey (risk of predation; traveling, missed opportunity, injury). Prey that are much smaller than allowed for by the maximal prehension and processing abilities of the predator require almost no time to consume. Thus, we assume no additional cost on top of the basic cost of active searching (represented by the *horizontal section* of the cost curve). When no additional costs are included all prey items should be consumed (*Eat everything* area). Above a certain threshold, a positive association between prey size and handling time is expected, generating a trade-off situation in which increased energy gain bears accompanying costs (e.g., missed opportunities, risk of predation, risk of injury). The mesopredator should prefer prey of a size that will maximize its overall gains when considering the potential costs (*dotted line*). Under increased risk levels this optimal prey size (*a*) will shift to the left and the predator should prefer prey of a smaller size

dangerous to consume (i.e., cost embedded with size), as in our system, a decrease in the selection of preferred prey items is expected under elevated levels of predation. Consequently, we predict that lizards reared under increased predation should become less selective, consuming a diet that is more diverse.

In summary, in this study we specifically tested the following predictions regarding whether lizards under increased predation will: (1) forage in safer microhabitat (bushes) and during less dangerous periods (midday), (2) reduce mobility and consequently consume prey that are more mobile, (3) prefer prey of smaller maximal size and consume a more diverse diet.

Materials and methods

Study area and experimental animals

We conducted the field experiment in a loess scrubland in the Northern Negev Desert, Israel (N31°14′, E34°38′). *A. beershebensis* is an insectivorous lizard with mean adult snout-vent length (SVL) of 64.5 mm (SE = 0.5, $n = 35$) and 60.4 mm (SE = 0.5, $n = 41$) for males and females, respectively. *A. beershebensis* usually hatch in late May and their lifespan rarely exceeds 1 year. Previous studies showed that *A. beershebensis* is an active forager (Hawlena et al. 2006), but no prior dietary data were available. The main lizard predators in this area are the two resident avian predators southern grey shrike and common kestrel (*Falco tinnunculus*). We found lizard remains in 57% of shrike pellets and in 53% of kestrel pellets during summer months (May–September). *A. beershebensis* constituted at least 37% of the recovered lizards (D. Hawlena, unpublished data). Shrikes hunt almost exclusively from perches; therefore, they can prey on lizards only within the vicinity of natural or human-made perches (Yosef 1993). Kestrels hunt using perches and by hovering, but the latter is less efficient than the former (Sheffield et al. 2001). The study area is dominated by a small woody perennial shrub *Noea mucronata*, creating an open landscape with a small number of perches available for birds.

Experimental design

We modified the habitat to increase predation by adding small groups of artificial trees to the homogeneous scrubland, allowing predatory birds to hunt with greater efficiency in the manipulated patches. This manipulation locally increased hunting activity of resident predatory birds without changing the predator number or identity. We selected five areas of homogeneous scrubland located at least 300 m from each other. The home range of *A. beershebensis* is small (on average, 607 m^2 ± SE = 85 m^2, $n = 20$) thus the five plots were independent replicates. In each of the chosen locations, we set up two 80 × 80-m subplots separated by a 30-m buffer. In one randomly selected subplot in each pair, sixteen 1.5-m metal poles were erected to attract avian predators. The paired pole-free subplot served as a control. We attached barbed wire connected to a 50 × 50-cm metal frame to the pole tops to mimic thorny branches, creating suitable locations for shrikes to perch and to impale their prey. We assessed the effectiveness of these structures in attracting hunting shrikes by comparing the time shrikes spent in manipulated versus control subplots. We observed each plots for 2 h and calculated the time shrikes were present in each subplot as the average of three observations. Shrikes spent significantly more time in manipulated subplots (17.9% ± SE = 2.5% of total survey time) than in control subplots (2.2% ± SE = 0.8%) (Hawlena and Bouskila 2006). This enhanced presence of predators also led to a 68% reduction in *A. beershebensis*' survival.

In each plot we buried a grid of 64 pitfall traps (10-l buckets buried flush with the ground), that were spaced

10 m apart. In this way we were able to trap lizards indiscriminately and to simultaneously sample all subplots. We captured the lizards for 3 consecutive days each month from September 1999 (1 month after adding the perches) until September 2001. Between trapping periods, the pitfalls were tightly closed with lids. We collected all lizards individually into cloth bags, marked them individually, and released them at the exact location of capture within 24 h. Lizards often defecated while in the cloth bag or during measurements. We collected the fecal pellets into small Eppendorf tubes with 70% ethanol for subsequent analysis of diet. During trapping periods, the pitfalls were checked at least once every 2 h. We recorded the time from sunrise in which every lizard was collected.

Focal observation

The same observer (D. H.) observed all lizards during August and September 2000. The observer wore similar clothing to reduce possible artifacts in lizard responses due to differences in observer characteristics. We conducted all observations between 0730 and 1030 hours to decrease the variation in lizard activity resulting from non-foraging behaviors. We located a lizard either in an increased predation ($n = 12$) or control plot ($n = 18$) by random search and then observed it, from a distance of approximately 4 m, for 23 min. We deleted the first 3 min of every observation during analysis to decrease variation resulting from transient behaviors before habituation of the lizard to the observer (Hawlena et al. 2006). We observed lizard behavior in three plots and in different locations within each subplot to reduce chances for pseudoreplication due to repeated observation of the same individuals.

We recorded the foraging mode and the microhabitat use on a palm-top with the software FIT (Held and Manser 2005). This software enabled us to record event times while observing lizard behavior continuously. We observed only lizards with intact tails in order to decrease variability associated with changes in activity that may result from tail autotomy (Martín and Salvador 1993). We omitted observations of lizards that were engaged in thermoregulation or lizards that showed a strong response to the observer (i.e., escape behavior and intensive refuge use) from the analysis. We calculated two foraging mode indices, movements per minute (MPM) and proportion of time spent moving (PTM), to quantify the lizard foraging behavior (Perry 2007). We estimated lizards microhabitat use by calculating the percent of time spent in open gaps between shrubs (PTO). We considered a lizard in a shrub when at least part of it was concealed under the shrub canopy. We measured ambient temperature at the beginning and the end of every observation and used the averages of these values during data analysis.

Diet analysis

We analyzed the content of 327 fecal pellets, collected from 291 different lizards, under a binocular dissecting microscope. Fecal pellet analysis is a standard method to quantify diet without compromising lizard well-being (e.g., Suarez et al. 2000). Diet reconstruction based on fecal pellet analysis can be biased against small and soft prey items that are likely to be destroyed by digestive processes (Pincheira-Donoso 2008). To minimize this possibility we carefully searched for body parts of small and soft-bodied prey taxa that are less likely to be digested (e.g., head capsules in insect larvae and chelicerae and fragments of cephalic region in spiders). Diet reconstruction based on such meticulous fecal pellet analysis was found to be highly comparable to diet reconstruction based on gastric contents removed from dissected stomachs (V. Pérez-Mellado, unpublished data). We identified prey items to order or family level. We measured the length of intact or nearly intact prey items to estimate prey size. An average prey size was then calculated with only measurable prey items. This assessment may be biased against small prey sizes, making the results more conservative. This is because we expected a decrease in maximal prey size but no effect on the average prey size consumed by lizards from increased predation subplots. Diet composition was described by the relative prey presence, that is, the percentage of individual lizards consuming a given prey type and prey abundance, as the percentage of a given prey type relative to the total prey number.

Data analysis

Lizard activity

We combined all lizard trapping data from the 4 summer months (June, July, August and September) of 2000 and 2001. We included individuals that were trapped multiple times in one trapping session only once to avoid pseudoreplication. We divided the trapping times to three intervals that correspond to morning (sunrise until 1000 hours), midday (next 5 h) and evening activity (remaining time until sunset) and compared the activity levels using a G- test.

Focal observation

We log10-transformed behavioral indices (PTM, MPM and PTO) prior to statistical tests to achieve homogeneity of the variance. We examined the effect of ambient temperature on all behavioral variables using linear regressions. We used one-way ANOVA to compare lizard foraging mode (PTM and MPM) and microhabitat use (PTO) between increased predation and control plots. Because the data were log10 transformed, we present the mean and the 95%

confidence intervals of the inverse log10 of the behavioral indices (Sokal and Rohlf 1995).

Prey mobility

We categorized the mobility of all taxa occurring in the lizard diet to seven mobility categories following Perry (2007). We then used prey composition and movement index for each prey type to calculate a single value (termed H_j), which represents the weighted average of the locomotor tendencies of all items in the fecal pellets of an individual lizard. This value can be mathematically expressed as $H_j = \Sigma M_i F_i$, where M_i is the movement index of prey type i and F_i is the percentage of each prey type in the diet of lizard j. The summation is carried out over all prey types in the diet of a lizard. We averaged H_j when we had multiple fecal pellet samples from the same individual to avoid pseudoreplication. We used an ANOVA to compare H_j between increased predation and control subplots. Because we were concerned that high variation between individual feces pellets may swamp general responses, we used the mobility values assigned to each prey item to construct a table of frequencies of overall mobility values for experimental and control subplots (Table 1). We used a G-test to compare these frequencies.

Prey size selection

We used the average prey size and the maximal prey size recovered in each lizard's fecal pellets to examine the effect of elevated risk of avian predation on lizard prey size selection. Both parameters were log10 transformed prior to statistical tests to achieve homogeneity of variance. We compared the average and maximal prey size eaten by individual lizards between increased predation and control plots using a G-test. To do so we divided the prey size categories into 3-mm size classes following Diaz and Carrascal (1990) and Martín and Salvador (1993). Lizard maximal prey size is often correlated with the lizard SVL. Thus, we repeated the analyses with and without statistical correction for lizard SVL and found no qualitative differences between the two.

Table 1 Overall distribution of prey mobility values in diets of increased predation and control lizards

Mobility value (Perry 2007)	Control (%)	Predation (%)
0	2.6	0.6
1	2.3	2.6
2	18.6	18.4
3	63.5	71.0
3.5	5.2	3.7
4	3.7	0.6
5	2.5	2.0
6	1.5	1.2

For the maximal prey size, only Coleoptera sample sizes were big enough to allow separate analysis of a specific taxon. We compared the maximal Coleoptera size distribution between increased predation and control plots using the same procedure used for the general comparison of size distribution.

Prey diversity

We estimated prey diversity as trophic niche amplitude (B), by means of Levin's niche breadth (Levins 1968). We compared niche breadths between experimental and control environments using a delete-one jack-knife resampling procedure (Magurran 1988). Thus, B-values were recalculated by excluding each fecal sample in turn and generating pseudovalues (VPi), which were normally distributed. However, since we found non-homogeneous variances (Levene test, $F = 9.27$, $P = 0.003$) we compared the distributions of pseudovalues using Welch ANOVA. For all analyses significance tests were two-tailed at $\alpha = 0.05$.

Results

We found no difference in daily activity time during the 4 summer months between increased predation risk (morning, 74.6%; noon, 5.9%; afternoon, 19.5%) and control subplots (morning, 70.8%; noon, 3.0%; afternoon, 26.3%)($G = 5.007$, $df = 2$, $P = 0.082$). Ambient temperature had no effect on the three behavioral indices PTM, MPM or PTO ($R^2 = 0.005$, $P = 0.692$; $R^2 = 0.027$, $P = 0.377$; $R^2 = 0.002$, $P = 0.832$; respectively), consequently we did not have to correct for ambient temperature when comparing lizard behaviors between groups. Lizards from elevated predation subplots were less mobile [28.38, 95% confidence interval (CI) 23.29–34.51%] than lizards observed in control subplots (38.37, 95% CI 32.81–44.88%) (PTM; $F_{1,29} = 6.07$, $P = 0.02$). But no differences in the movement frequency (control, 1.61, 95% CI 1.34–1.92; predation, 1.61, 95% CI 1.25–1.98) (MPM; $F_{1,29} = 0.01$, $P = 0.907$) or the percent time spent in open microhabitat (control, 54.9%, 95% CI 44.9–64.9%; predation, 42.4%, 95% CI 29.9–55.0%) (PTO; $F_{1,29} = 1.97$, $P = 0.169$) were found between lizards observed in increased predation and control subplots. We found no difference in prey mobility index between increased predation and control subplots (control, 301.5 ± 5.6; predation, 297.7 ± 6.7) ($F_{1,\ 245} = 0.20$, $P = 0.659$). However, we found a highly significant difference in prey mobility between treatments when the frequency of mobility values was compared between treatments

($G = 38.95$, $df = 7$, $P < 0.001$; Table 1). Average prey size consumed by lizards did not differ between elevated predation and control subplots ($G = 4.471$, $df = 3$, $P = 0.192$). Lizards inhabiting elevated predation environments ate prey of small size (0.1–3 mm) more than did lizards from control subplots ($G = 8.756$, $df = 3$, $P = 0.033$; Fig. 2a). Similarly, lizards inhabiting increased predation subplots consumed beetles (Coleoptera) of a smaller maximal size (0.1–3 mm) than control lizards ($G = 7.454$, $df = 1$, $P = 0.006$; Fig. 2b) that ate bigger beetles (3.1–6 mm). Comparison of the seven taxa that contributed at least 1% to *A. beershebensis*' diet revealed highly significant differences in overall pattern of relative abundance between increased predation and control plots ($G = 31.366$, $df = 6$, $P < 0.001$; Fig. 3). Formicidae were the most common prey items consumed by both lizards from control (67.12%) and increased predation subplots (69.32%). Isoptera were the second most common prey items consumed by both lizards from control and increased predation subplots (19.17 and 19.14%, respectively). Lizards inhabiting the control subplots consumed more seeds (2.62%) than lizard inhabiting increased predation subplots (0.52%). We found no difference in prey diversity between lizards in increased predation and control subplots (predation subplot, −0.965 ± 0.06; control subplot, −0.947 ± 0.04; $F_{1,319} = 0.056$, $P = 0.814$).

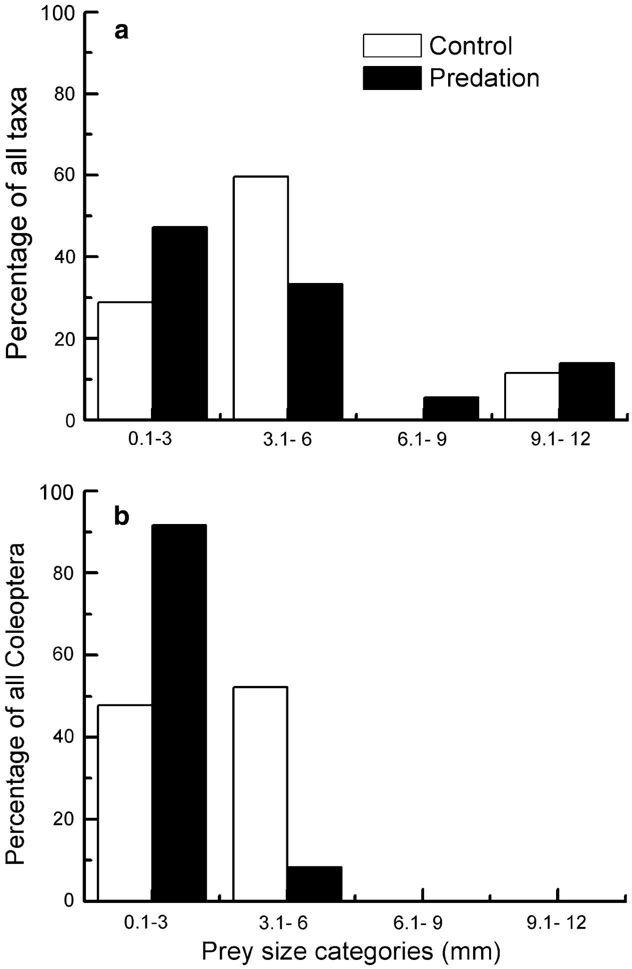

Fig. 2a, b Comparison of maximal prey size distribution between increased predation and control plots. **a** Comparison of all taxa. **b** Comparison of Coleoptera

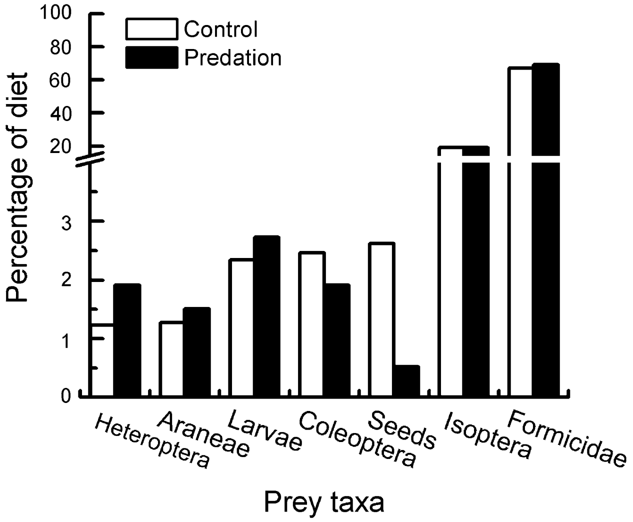

Fig. 3 Comparison of the relative abundance of prey taxa that constitute more than 1% of *A. beershebensis'* diet between increased predation and control plots

Discussion

Our experimental design enabled resident avian predators to hunt with greater efficiency in patches they could hardly use before, creating similar risk to that experienced by lizards in patches with natural perches. As a result, we were able to test the consequences of realistic variation in predation risk on various aspects of lizard feeding ecology and diet. Lizards inhabiting risky patches became more stationary but did not significantly alter their movement frequency, microhabitat use, or daily activity. Despite the more stationary foraging activity, lizards exposed to elevated risk did not consume more mobile prey. A persistent elevated predation risk induced changes in lizard diet composition and the maximal prey size consumed but we found no difference in diet diversity.

It is widely acknowledged that prey species can decrease the risk of a predator attack by reducing activity in places or during times that encompass high danger, and by adopting more cautious behavior (Lima and Dill 1990). Thus, our results are surprising not because we detected a significant reduction in lizard movement in response to elevated predation risk but because we did not reveal strong temporal or spatial changes in lizard activity with increased predation risk. Many empirical investigation of predator-prey interaction expose prey to short and often unrealistic intense pulses of predation that favor extreme and very costly defensive responses. We believe that the chronic but realistic nature of our manipulation constrained lizards from compromising other risks (e.g., starvation and heat exposure) to reduce the risk of predation, weakening expected defense responses that involve changes in microhabitat use and time of activity.

As predicted, lizards reduced their movements in the predation treatments. Consequently, and based on the hypothesized negative association between predator and prey mobility (predator-prey crossover hypothesis; Huey and Pianka 1981), we expected lizards within increased predation environments to consume more mobile prey. We did not detect differences in prey mobility when comparing the mobility index of individual lizard diets, but found small yet significant differences when comparing the frequencies of mobility categories between the two treatments. Although significantly altered, the differences in diet composition were inconsistent with the predator-prey crossover hypothesis (Table 1). We suggest that the observed diet shift partially resulted from confounding factors (e.g., prey size, quality or defense capabilities) that affected lizard prey choice independently from prey mobility (e.g., Martín and Salvador 1993). Previous evaluation of the crossover hypothesis found supportive evidence when using between-species comparisons (Perry 2007 for Lacertidae). It is possible that a 10% change from the baseline of species active foraging, found in the current study, was not enough to generate significant dietary changes based on mobility alone. Lizards exposed to elevated predation risk may delay attack on detected prey to allow evaluation of associated risks (Martín and Avery 1997). Possibly, such a delay may reduce the probability of capturing mobile prey, balancing the predicted change according to the predator-prey crossover hypothesis.

A chronically elevated risk of predation induced changes in the relative abundance of major prey taxa in *A. beershebensis*' diet (Fig. 3). Although statistically significant, these changes were not bigger than a ~2% change for all taxa. *A. beershebensis* specializes on Formicidae and Isoptera that, together, comprised 86.3 and 88.5% of their diet in the control and increased predation environments, respectively. These results are consistent with dietary analyses of other insectivorous desert lizards and particularly *Acanthodactylus* species (Pérez-Mellado 1992). In our study site, most species of ants and termites are of small size and fall in the "eat everything" area of Fig. 1. Consequently, we found no difference in the average prey size between lizards in increased predation and control environments. However, as predicted by our simple prey size selection model, we found that maximal prey size consumed by lizards in increased predation subplots was smaller than that consumed by lizards in the control subplots. Differences in beetle sizes were a major determinant of this trend. Coleoptera are generally characterized by a particularly hard exoskeleton and hard elytra (forewings). Thus, the handling time required to consume this abundant prey group is expected to be larger than for most other prey of similar size (Diaz and Carrascal 1993; Martín and Salvador 1993). Avoidance of larger Coleoptera by lizards in the increased predation plots may account for beetles making up a lower percentage of their diet than lizards in control subplots (Fig. 2b). During summer months 81% of the shrike pellets included beetles. Thus, it is possible that increased shrike predation on large beetles could contribute to the decline of maximal beetle size consumed by lizards from increased predation subplots. Shrikes in the study site hunted mostly large Tenebrionidae beetles that often are much bigger than the lower prey size threshold of 10 mm found elsewhere (Hodar 2006). The fact that the largest beetle size recovered from *A. beershebensis*' fecal pellets was 5 mm suggests that even if some degree of competition exists it is unlikely to account for the strong variation in maximal prey size consumed by lizard from increased predation and control subplots.

The occurrence of relatively big food items (>6 mm; mostly Hymenoptera and Arachnida) in the diet of increased predation lizards (Fig. 2a) may suggest a shift in feeding behavior that our simple model did not account for. Predators that can carry their prey and consume it in a refuge are expected to do so if the energetic benefit of consuming it exceeds the costs of traveling, the risk of predation and the missed opportunity costs (Lima and Valone 1986). Consequently, instead of skipping big prey items and searching for prey that require less handling time to consume (as we predicted), lizards may carry big but profitable prey items and consume them in safety.

In spite of the observed changes in diet composition, we found no differences in prey diversity. Here too, this may be explained by *A. beershebensis*' specialization on ants and termites that conceal smaller changes in diet.

It was surprising that lizards from increased predation and control subplots differed in the amount of plant material they consumed. Plant material often includes relatively small amounts of protein. Consumption of plant material is widespread among insectivorous lizards, but is mainly confined to species inhabiting islands (Pérez-Mellado and Corti 1993). It was hypothesized that this is mainly a result of arthropod scarcity and low predation levels in those habitats (Olesen and Valido 2003). We manipulated avian predators to hunt in our experimental subplots, consequently increasing the risk of predation and reducing lizard density (Hawlena and Bouskila 2006). Thus, our finding that lizards in risky patches consumed less plant material than lizards from low risk yet more competitive environments provides the first experimental support for the low-predation component of this hypothesis.

Experiments that test discrete components of prey feeding ecology in simplified environments provide a profound understanding of the behavioral mechanisms underlying prey dietary responses to predation risk (e.g., Dill and Fraser 1984; Lima 1985; Houtman and Dill 1998). In this study, we show that actual dietary changes under natural field conditions may vary from predicted responses that are based on isolated mechanisms. This could indicate that a simplistic experimental approach may not be enough to reveal realistic changes in mesopredator diet and consequently may fail to reveal cascading effects on community structure, ecosystem function and character divergence (Preisser et al. 2005; Andersson et al. 2006; Schmitz 2008). We demonstrated that a mechanistic approach that integrates well-established behavioral mechanisms of animal feeding ecology can be a useful way to produce meaningful and realistic predictions and that natural field manipulation is a credible way to test those predictions. We believe that, together, these complimentary conceptual and empirical approaches can facilitate the incorporation of predator-induced dietary changes into wider ecological and evolutionary concepts.

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