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Novel predator recognition by Allenby's gerbil (*Gerbillus andersoni allenbyi*): do gerbils learn to respond to a snake that can "see" in the dark?

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Unlike desert rodents from North America, Allenby's gerbil (*Gerbillus andersoni allenbyi*) from the Negev Desert, Israel has evolved with snakes that do not have heat-sensitive sensory pits that enhance night vision. Does this history affect their ability to assess and respond to a snake that has this ability? As a test, we exposed gerbils to risk of predation from various predators, including snakes, owls, and foxes. The snakes included the Saharan horned viper (*Cerastes cerastes*) and the sidewinder rattlesnake (*Crotalus cerastes*). The former snake lacks sensory pits and shares a common evolutionary history with the gerbil. The latter snake, while convergent evolutionarily on the horned viper, has sensory pits and no prior history with the gerbil. The gerbils exploited depletable resource patches similarly, regardless of snake species and moon phase. While the gerbils did not respond to the novel snake as a greater threat than their familiar horned viper, the gerbils were cognizant that the novel predator was a threat. In response to both snakes, giving-up densities (GUDs; the amount of food left in a resource patch following exploitation) of the gerbils were higher in the bush than open microhabitat. In response to moonlight, GUDs were higher on full than on the new moon. Based on GUDs, the gerbils responded most to the risk of predation from the red fox, least from the two snake species, and intermediate for the barn owl.

Keywords: biological invasions; common-garden experiments; constraint-breaking adaptations; prey naiveté; predator–prey foraging games; vipers

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Introduction

Prey species worldwide face novel predators as humans, intentionally and unintentionally, move species around and create biological invasions. Such biological invasions invite frameworks for studying prey naiveté in response to invasive predators. Investigations of prey naiveté have included prey communities in aquatic systems (e.g., Gozlan et al. 2010; Francis 2011), and prey on islands (e.g., Karl & Best 1982; Veitch & Clout 2002) as compared to prey in terrestrial systems (Cox & Lima 2006). For terrestrial systems, researchers have identified the behavioral components that lead to naïve and highly vulnerable prey. Can the prey recognize the predator as a threat, can it accurately assess the risk, and does the prey have the ability to respond properly (Banks & Dickman 2007)? Modelers too, have picked up the challenge, explaining the conditions by which predators can invade a community, and the resulting evolutionary changes that might occur following successful invasions (Sih et al. 2010; Pintor et al. 2011).

Here, we address whether prey responds differently to a familiar predator than to a novel and putatively more effective one. We introduced a population of wild-caught gerbils into a semi-natural arena (vivarium) and exposed them to various predators, a sort of "common-garden" experiment. Specifically, we compared the gerbils' responses to a familiar viper (the Saharan horned viper; *Cerastes cerastes*) and to a novel but otherwise highly convergent pit-viper (the sidewinder rattlesnake *Crotalus cerastes*) from the Mojave Desert. Pit-vipers use infra-red sensing pits to hunt, providing a constraint-breaking adaptation (Rosenzweig & McCord 1991; Vincent & Brown 2005) that should give them a competitive advantage over their native counterparts. Absence of difference in response between snakes could simply mean that the gerbils are inflexible in reaction to predators. Therefore, we also exposed the gerbils to qualitatively different, but familiar predators such as the terrestrial red fox (*Vulpes vulpes*) and the aerial barn owl (*Tyto alba*). A difference between foxes and owls, or with foxes and owls, would demonstrate that the gerbils are flexible in their risk management and that any absence of difference between snakes documents equal risk perception.

Allenby's gerbil (*Gerbillus andersoni allenbyi*) over 30 years has provided a model organism for the study of community dynamics (e.g., Abramsky & Rosenzweig 1984; Khokhlova et al. 2004, and more) and specifically response to predation risk. The gerbils have been shown to respond to owls by favoring the bush microhabitat and nights with new moon (Kotler et al. 1992). In response to snakes, gerbils favor the open microhabitat and dark nights. Presumably because snakes ambush more frequently from near and under bushes, and the snakes benefit from the vision afforded by moonlight (Kotler et al. 1993). Given an extensive knowledge of the relevant

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natural history of these populations, studying gerbils provides an advantageous platform examining prey responses to an invasive predator. Bouskila (1995), in working with kangaroo rats and pit-vipers at a Mojave Desert site, found that North American rodents also favored the open over the bush microhabitat. They also favored moonlit nights, presumably because of the advantage afforded to the snakes in darkness by using infra-red vision.

As our framework for investigating the effect of a novel predator on the gerbils, we consider the three levels of naiveté suggested by Banks and Dickman (2007): (1) do the gerbils perceive the novel predator as a threat? (2) Do they respond differently to the novel snake than they do to the snake species with which they have evolved? (3) Do the gerbils adjust their normal pattern of moonlight avoidance to accommodate the infra-red "vision" of the pit-viper? In addition, we asked: how do the gerbils rank their perceived risk from the pit-viper and horned viper in relation to other familiar predators such as the barn owl and red fox?

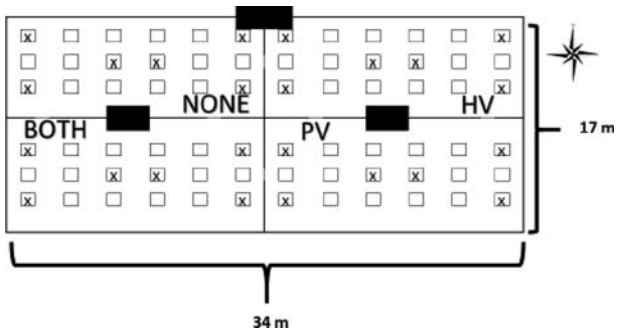

Figure 1. Vivarium layout where the snake treatments were (HV) two horned vipers, (PV) two pit-vipers, i.e., sidewinder rattlesnakes, (NONE) no snakes, and (BOTH) one snake of each species. Within the six days of a moon phase, the owl, fox, or no additional predator treatments were added in a randomized order of two nights each. Owls and foxes could only access the *Y* and *Z* quadrants. The squares with an (x) represent inactive trellises while empty squares signify the location of collection trays where the microhabitat (under the trellis for bush or by the trellis for open) was changed every two weeks. Black spaces refer to the location of human gates crossing between sections, whereas, the thin line along interior divisions refers to the location of rodent "S" shaped gates that restrict the movement of snakes across quadrants.

Methods

Fifty Allenby's gerbils (*G. andersoni allenbyi*) were trapped in the winter and spring of 2010 at the Ashalim Dunes and the Be'er Milka Dunes (latitude 30.910132; longitude 34.388752), Negev Desert, Israel. Eight adult male Saharan horned vipers (*C. cerastes*) were collected at the Be'er Milka dunes, and maintained in the laboratory. In May of 2009, eight sidewinder rattlesnakes (*C. cerastes*) were captured from the Parker Dunes (latitude 34.121859; longitude −114.237900) and Mohawk Dunes (latitude 32.592925; longitude −113.889084) of southwestern Arizona, USA, and imported to Israel.

Experiments were run in a large outdoor vivarium at the Blaustein Institutes for Desert Research in Sede Boker, Israel from 1 June 2011 to 29 July 2011. The vivarium (17 × 34 × 4.5 m) is rodent, snake, owl, and fox proof. One meter tall galvanized steel walls with concrete bases extend 1 m into the ground (Figure 1). In addition, the walls continue to a height of 4.5 m with chicken wire mesh (1.5 cm diameter). The entire vivarium is roofed with chicken wire to contain owls. We divided the vivarium into four equal-sized quadrants using hardware cloth or galvanized steel fences running perpendicularly from the middle of both the long and short axes. A chicken wire wall rising to the ceiling along the center divider prevented the movement of foxes and owls from one side to the other (restricting these predators to the western half of the vivarium). The quadrants were connected with two snake-proof gates between north and south quadrants and one gate between east and west quadrants. These gates allowed for the movement of gerbils among quadrants, while restricting the movement of snakes.

Three quadrants of the vivarium contained two each and one remained snake-free. The northwestern quadrant had one individual of each snake species snakes (BOTH), the southwestern quadrant was empty of snakes (NONE), the northeastern quadrant housed two Saharan horned vipers (HV), and the southeastern quadrant housed two pit-vipers (PV). Each quadrant contained a grid of 18 low-lying trellises (18 cm tall) topped by cut brush to simulate shrubs. Gerbils foraged in artificial food patches consisting of a 28 × 38 × 8 cm tray filled with 3 l of sifted sand into which we mixed 3 g of millet seeds. Twelve food patches per quadrant were set out nightly (total of 48), of which six were in the open microhabitat adjacent to a trellis and six were placed under trellises as the bush microhabitat. Data were collected for six days during each of the four moon phases, over a period of two lunar months. For each collection period (moon phase), we also exposed the gerbil population in the vivarium to the presence of a barn owl (two nights), a red fox (two nights), or no additional predators above and beyond the snakes (two nights). The night-to-night orders of the additional predator treatments were randomized within each six-day moon phase with the constraint of avoiding two consecutive nights of the same predator addition treatment.

The gerbils were injected subcutaneously with radio-frequency-identification PIT (passive integrated transponder) tags. The tags allowed identification of individuals and quantification of predation events based on feces and owl spit pellets that contained tags. For the experiment, we began by releasing six gerbils into each quadrant; thereafter, they were free to move among quadrants. Gerbils were given three nights to acclimate. When a tag was found in predator fecal matter or owl spit pellets, another gerbil was released into the quadrant where the individual gerbil was last recorded. We delayed the release of replacement gerbils until the end of a six-day moon phase. Thus, newly introduced animals had a day or two to acclimate before the next six-day round of data collection. Following each night of the experiment, we sifted the sand from each tray to remove the remaining seeds and took the seeds to the laboratory for cleaning of husks and

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debris. We then weighed the remaining seeds to the nearest 1/100th of a gram to measure the gerbils' giving-up densities (GUDs) for the tray (the amount of resources left behind in a resource patch following exploitation; Brown 1988). Gerbil activity was recorded daily by marking whether trays were foraged or not.

We estimated gerbil activity by tabulating the number of foraged versus unforaged trays for all combinations of snake treatment (four quadrants), additional predators (owl, fox, and no added predator), moon phase (new, full, waning, and waxing), and microhabitat (bush and open), to yield a multi-way contingency table. We used this multi-way contingency table to perform a log-linear analysis that examined direct and interactive effects of predation risk (snake treatments, additional predators), moon phase, and microhabitat on the number of trays foraged.

We then analyzed patch use using GUDs. To control for possible pseudo-replication among trays and within a quadrant, we averaged the GUDs in each microhabitat within each quadrant for each collection day to form the dependent variable. This provided eight GUD means per night (2 microhabitats × 4 quadrants). For these means, we included both food patches, and foraged and unforaged trays, using 3 g as the GUD for unforaged trays. A general linear model was used to evaluate whether the GUDs varied with predation risk (snake treatments, additional predators), moon phase, microhabitat, month, and their two and three-way interactions. We tested for differences within factors and interactions using post-hoc Tukey's Honestly Significant Difference Test (THSD).

Results

We present results in three subsections. The first represents the consumptive effects of the predators; the second considers activity in terms of number of foraged trays; the third considers the GUDs as a measure of patch use and risk assessment.

Fatalities

In the two months of the experiment, 11 gerbils were depredated, a marginal number from which to draw conclusions. Feces, spit pellets, and PIT tags within them provided direct evidence of predation events. In total, owls were responsible for three fatalities, foxes for four, horned vipers for one, and pit-vipers for one. In addition, there was one more fatality from snakes for which we could not assign species, and one from the other predators that we could not assign to either foxes or owls.

Activity

Over the eight moon phases of data collection (48 nights in total), 29% of the trays were left unforaged (351 of 1200). The distribution of foraging activity was significantly affected by the predation risk treatments of snakes, additional predators (owl and fox), and the environmental factor of moon phase (Table 1).

Table 1. Log-linear analysis for interactions of snake treatment (representing quadrant as well), additional predators, moon phase, and microhabitat. All interactions are measured by the proportion of foraged to unforaged trays.

Var1	Var2	*G*	df	*p*-value
Additional predators		11.485	2	0.003
Snake		42.521	3	<0.001
Microhabitat		0.782	1	0.377
Moon phase		14.158	1	<0.001
Snake	x Additional predators	44.722	6	<0.001
Microhabitat	x Additional predators	0.039	2	0.981
Moon phase	x Additional predators	6.961	2	0.031
Microhabitat	x Snake	1.968	3	0.579
Moon phase	x Snake	7.669	3	0.053
Moon phase	x Microhabitat	0.001	1	0.98

Snake treatments

The gerbils responded to predation risk. They were more active in the quadrant with the novel pit-vipers than in the quadrant with the endemic horned vipers (Figure 2(A)). The gerbils foraged more trays on dark nights associated with the new moon than on moonlit nights around the full moon (Figure 2(B)).

Additional predators

Owls and foxes had dramatic effects on foraging in the quadrants directly affected by them and a spillover effect on the two quadrants inaccessible to them. We found significant interactions between the additional predators and snake treatments (Table 1). On the eastern half of the vivarium (inaccessible to the fox and owls; HV and PV), the gerbils were significantly more active than in the western half (NONE, BOTH; Figure 2(C)). The effect of the additional predators was greatest during fox nights followed by owl nights. The highest gerbil foraging activity levels were observed during control nights (Figure 2(D)).

Patch use

Gerbil foraging within patches, measured as GUDs, was significantly affected by the predation risk treatments of snakes, additional predators (owl and fox), moonlight (expressed by the moon phase), and microhabitat (Appendix).

Snake treatments

The gerbils foraged more in the presence of the novel pit-viper than in the presence of the endemic horned viper (Figure 3). Paradoxically, the combined effect of both snakes resulted in higher GUDs than the control. However, we refrain from making comparison of this treatment to each of the snake species alone because the gerbils in the quadrant with both snake species also experienced foxes and owls directly. The gerbils in the horned viper quadrant and the pit-viper quadrant did not.

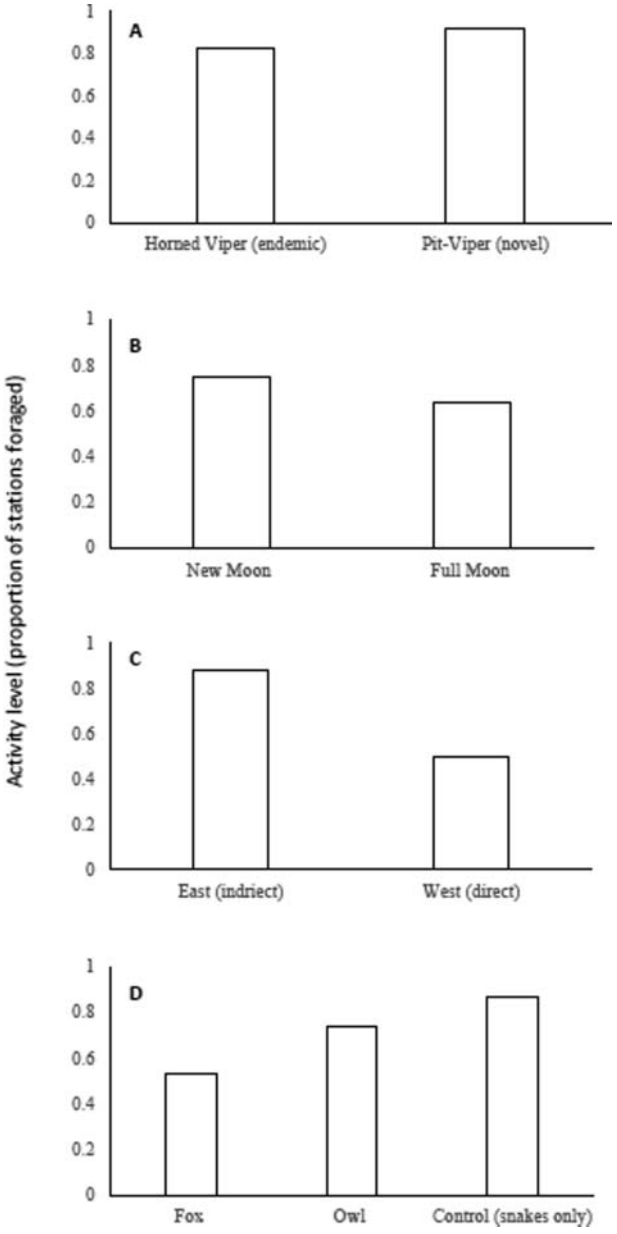

Figure 2. Cumulative foraging activity as reflected by the percent of foraged stations showing: (A) lower activity in the quadrants with the endemic than the novel snakes, (B) lower activity on nights of the full moon than the new moon, (C) much lower activity in direct contact with the additional predators, and (D) the impact of the different types of predators (foxes and snakes, owls and snakes, and snakes alone).

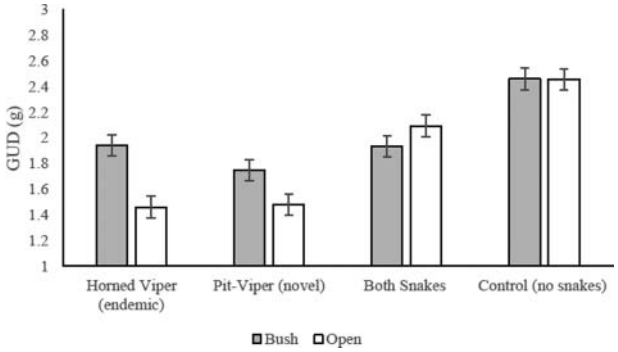

Figure 3. Patch use reflected by GUDs as collected in each of the snake treatment quadrants in trays laid in bush and open microhabitat. The gerbils showed preference for the open microhabitat in contact with the snakes with exception of the quadrant with both snakes, likely a result of direct interaction with owls and foxes in that quadrant absent from the quadrants with the single-snake species. Notice that the difference between direct and indirect exposure is larger in activity levels (Figure 2(C)). GUDs reflect the mean of foragers' exploitation of both safe and risky patches. Therefore, the exploitation of safe stations to a lower GUD averaged with the unforaged station results in an overall higher mean. Meanwhile, the count of active stations remains much lower. The error bars reflect one standard error from the mean.

Gerbils were expected to choose open microhabitat patches in areas with snakes, and the GUDs confirmed this. The gerbils foraged to a mean GUD of 2.05 ± 0.05 g standard error in open habitat trays and to a mean GUD of 2.14 ± 0.05 g in the bush. Similarly, given that the gerbils evolved with vipers that are "blind" on dark nights, we expected their foraging to be more thorough (lower GUDs) during the new moon phase. Indeed, the gerbils foraged to a mean GUD of 2.02 ± 0.05 g on the new moon as compared with 2.18 ± 0.05 g during the full moon.

GUDs depended on a significant interaction between the snake treatments and microhabitat as well as between the snake treatments and moon phase (Appendix). There was a strong difference in response to the open and the bush microhabitats, but only in the single-snake species treatments (both THSD p-values < 0.001). In the presence of both familiar horned vipers and novel pit-vipers, the gerbils foraged less (had higher GUDs) in the bush microhabitat than in the open microhabitat (Figure 3).

GUDs also depended on an interaction between the snake treatments with moon phase (THSD p-value < 0.001, Figure 4(A)). In the quadrants with pit-vipers (PV) and with both snakes (BOTH), GUDs were higher during full moon than during the new moon. In the presence of both snakes, mean GUDs declined from 2.68 ± 0.06 g during the nights of the full moon to 2.25 ± 0.08 g during the nights of the new moon. Comparably, in the presence of the pit-vipers, the GUDs decreased from 1.75 ± 0.08 g on the nights of the full moon to 1.55 ± 0.09 g on the nights of the new moon.

Additional predators

The additional predators caused gerbils to reduce their patch use. Mean GUDs increased from 1.72 ± 0.05 g during control nights, to 2.08 ± 0.06 g and 2.4 ± 0.06 g during nights with an owl or fox present, respectively (Figure 4(B)). GUDs depended on a significant three-way interaction among the snake treatments, the additional predators, and moon phase (THSD p-value < 0.001). This interaction can be attributed to divergent effects between the inaccessible (to the fox and owls) eastern quadrants and the accessible western quadrants of the vivarium (Figure 4(B)). Even when indirect, the presence of either the foxes or owls in the western half resulted in equivalently higher GUDs in the eastern quadrants. With direct

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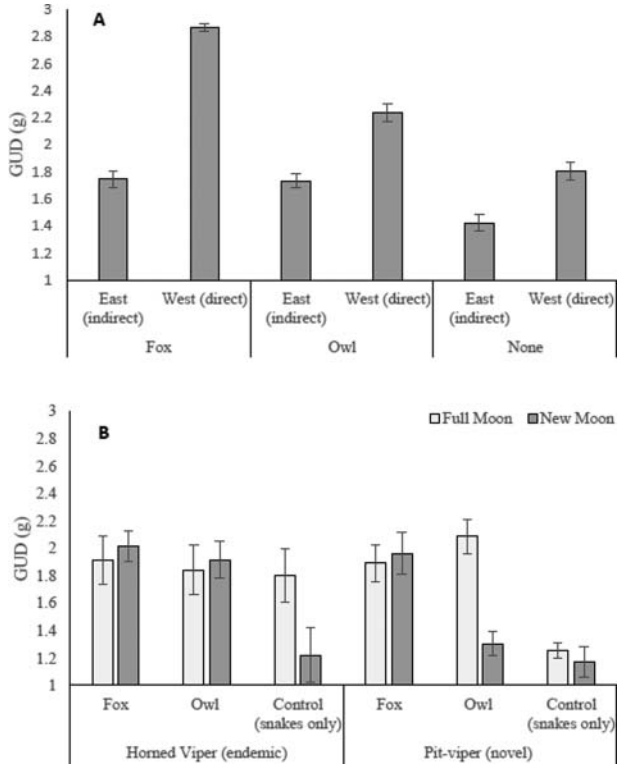

Figure 4. Patch use reflected by GUDs in concordance with additional predator treatments showing: (A) a decrease in perceived risk from owls combined with the novel pit-viper on the dark nights of the new moon and (B) the impact of direct exposure to the predators compared with the indirect effect across physical boundaries. The error bars reflect one standard error from the mean.

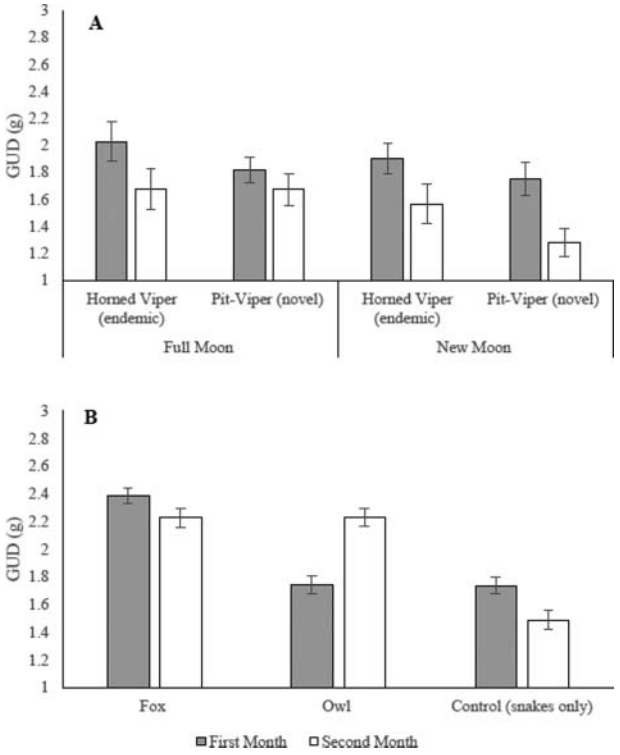

Figure 5. Change in patch use as reflected by GUDs from the first to the second month of the experiment: (A) significant decrease in perceived risk with prolonged exposure, predominantly in the interaction between the novel pit-viper and the dark nights of the moon; (B) increased respect towards the owls compared with a loss of respect towards the fox. The error bars reflect one standard error from the mean.

contact with the predators, in the western half, the difference in response to the predators was more pronounced.

The three-way interaction (additional predators × snake treatments × moon phase) resulted in several significant pairwise comparisons (Figure 4(A)). However, we wish to highlight only those results that increase our understanding of prey naiveté towards the novel snakes.

(1) Within the quadrant housing both snake species (BOTH), on owl nights, the GUDs were significantly higher during the full moon phase than during the new moon phase (THSD p-value < 0.001). (2) In the same quadrant (BOTH), during nights with the fox, gerbils did not forage during nights of the full moon, but did forage briefly during the new moon (the mean GUD decreased to 2.59 ± 0.1 g). (3) In the presence of the novel pit-vipers (PV), during nights of the full moon, the effect of the owl (indirect) was as high as that of the fox. However, on dark nights of the new moon, the effect of the owl was similar to the control.

Month

Logically, the longer the gerbils spend in the presence of a predator the better should be their assessment of the various predator treatments. If the perceived risk increases, so will the GUDs. Likewise, if the foragers "lose respect" for the predators, the GUDs will decrease. Two major changes between the first and second month of the experiment were consistent with such a change in risk perception.

(1) The respect for the novel pit-viper, as measured by GUDs, decreased from the first to the second month, especially during the new moon. (2) The gerbils altered their response towards both the owl and the fox (THSD p-values < 0.001). With increased exposure to additional predators, gerbils became less fearful of foxes but more fearful of owls (Figure 5(B)).

Discussion

Gerbils rapidly learned to treat the risk from the novel rattlesnake as that typically posed by a snake such as the horned viper. However, the combination of environmental conditions and additional predators showed that within the two months of the experiment, the gerbils remained largely naïve or unresponsive to the heat sensing capabilities of the rattlesnakes.

The gerbils responded by increasing activity during the new moon in the presence of either snake species. This is the most effective response to the snakes with which they share an evolutionary history (horned vipers), whose activity and lethality is restricted by moonlight. However, it may not be the best response to rattlesnakes (pit-vipers) that can "see" in the dark. Then, our results suggest that the gerbils recognized the novel pit-vipers as

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a risk, but one that is not much different from that posed by their familiar horned viper. Gerbils did not avoid dark nights with the pit-viper as might been expected based on Bouskila's (1995) work with Heteromyid rodents and rattlesnakes under natural conditions in California.

The gerbils exhibited behavioral patterns consistent with previous research showing a lower perceived risk of predation from snakes than from owls and foxes (Kotler et al. 1992). As seen previously (Kotler et al. 1993; Bouskila 1995), the gerbils in our experiment treated the open microhabitat as safer than the bush when snakes were present (lower GUDs in the open than bush). Gerbils reversed their assessment of microhabitat when owls or foxes were present along with the snakes. GUDs were lower under bushes than in the open with owls and foxes. Although snakes and owls are known to facilitate each other (Kotler et al. 1992; Embar et al. 2014), and although snakes make the bush microhabitat more dangerous and owls make the open more dangerous, overall higher GUDs in the open when both are present suggest that gerbils treat owls as the greater danger.

Recognizing that the novel predator is indeed a predator (level one of naiveté)

Banks and Dickman's (2007) first level of naiveté states that a naïve individual in an invaded system might not recognize the invasive predator as a predator at all. The consequence of such naiveté is usually extirpation of the naïve population. Such an outcome will usually happen too quickly for us to observe it in a timely manner. In our experiment, we found strong evidence that the gerbils responded to the novel sidewinder as a predator: they responded in similar fashions to both the familiar and exotic snake species. The gerbils' avoidance of moon light may not be the most appropriate response to the presence of pit-vipers; however, the "choices" they made proved effective in evasion of actual depredation. Just three gerbils were killed by snakes over the two months – one to two by each of the viper species.

Ability to properly assess risk posed by the novel predator (level two of naiveté)

Did the gerbils adjust their fear responses appropriately for the aptitudes of the novel sidewinder rattlesnake? Our data provide only an equivocal answer, as it was difficult to know the actual mortality risk imposed by the two types of snakes in the absence of fear responses. In our experiment, using GUDs, we asked whether the gerbils modulate their perceptions of risk in response to environmental factors such as microhabitat, moon phase, and snake species. We addressed the gerbils' perception of snake lethality by analyzing their response to moon phase. If gerbils learned that their pit-viper predators were more dangerous in darkness than horned vipers due to the former's infrared vision, then they should have shown greater GUDs in the bush than the open. Their response to the new moon should have intensified over time. This did not happen. Rather, gerbils increased foraging activity in the presence of the pit-vipers at new moon. The gerbils did adjust their response to the novel snake following prolonged exposure, but opposite to expectation. The gerbils actually lowered their fear of the novel snake at new moon in the second month of the experiment (Figure 5). The gerbils' increasingly relaxed assessment of the pit-viper at new moon, however, did not result in any obvious increased mortality.

The greater fear response of the gerbils to owls and foxes compared to snakes seemed merited. The foxes and owls captured more gerbils than did the two snake species combined. This is an even more extreme result considering that just a single owl (or single fox) was present on only one-third of the nights. Conversely, gerbils were exposed to individuals of six snakes (three of each species) every night of the experiment.

More so than the density of predators (both familiar and novel) in the environment, prey may respond most to their activity level. For example, minnows respond to increased strength of predator scent (Gilliam & Fraser 1987), and wall lizards are perplexed by a combination of searching predators and burrows smelling of snakes (Amo et al. 2004). Even insects avoid individuals of the same species when there are greater chances of cannibalistic behavior (Crumrine 2010). Carthey and Banks (2014) suggested that most naïve prey species can, and do respond, to general risk even in the absence of direct interactions. In our experiment, snake activity, as measured by the density of snake-tracks, was found to be greater under the bushes than in the open for both snake species (Embar et al. 2014), and gerbils avoid this microhabitat in the presence of snakes.

Even with adjustments, the prey is still highly vulnerable to the risk posed by the novel predator (level three of naiveté)

The gerbils responded to the risk of a novel snake as they would to any familiar snake. The relatively low GUDs suggest a similarly low perception of risk from the snakes. Other rodent species, some evolutionarily convergent on the Negev Desert gerbils, such as the kangaroo rats of the Great Basin Desert, exhibit a response to snake predation risk that decreases with time of exposure (Bleicher, Kotler, Downs, & Brown, in preparation; Randall & Boltas King 2001; Bleicher 2014), suggesting that the change in risk is not large enough to drive a large behavioral shift in the population. In our experiments, the persistent presence of the snakes confined to a relatively small space may have allowed the gerbils to keep track of each snake and make adjustments accordingly. This would explain the decline in GUDs from the first to second month.

In contrast to the relatively low impact of novel snakes in our experiments, Australia provides many examples of novel, invasive predators causing extensive community disruption (Letnic et al. 2011; Heavener et al. 2014; Doherty et al. 2015). There, the dominant examples are often invasive mesopredators to which the prey may have at least a limited ability to respond. Several experiments document that kangaroos, possums, and other genera of native

wildlife have learned to recognize fox and coyote urine despite distinct evolutionary histories (Parsons et al. 2005; Carthey & Banks 2012; Banks et al. 2014; Spencer et al. 2014). These results suggest that some cues of predators can lead to appropriate responses by prey. Still, Australian native species provide examples of type three naiveté: being "outgunned" by the novel predators. Even with an awareness of the risk, the native prey under these conditions may still be decimated by the invasive predators.

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Appendix. ANOVA table for the general linear model assessing differences in GUD ($n = 224$, $R^2 = 0.81$)

Var1	Var2	Var3	Type III SS	df	MS	*F*-ratio	*p*-value
Micro			1.22	1	1.22	7.091	0.009
Snake			23.3	3	7.766	45.12	<0.001
Moon			4.123	3	1.374	7.986	<0.001
Additional predators			12.34	2	6.166	35.83	<0.001
Month			0.056	1	0.056	0.325	0.57
Snake	x Micro		3.258	3	1.086	6.31	0.001
Moon	x Micro		0.303	3	0.101	0.588	0.624
Additional predators	x Micro		0.65	2	0.325	1.888	0.156
Month	x Micro		0.068	1	0.068	0.395	0.531
Moon	x Snake		12.51	9	1.389	8.073	<0.001
Additional predators	x Snake		6.967	6	1.161	6.748	<0.001
Month	x Snake		4.952	3	1.651	9.591	<0.001
Additional predators	x Moon		2.42	6	0.403	2.343	0.036
Month	x Moon		1.092	3	0.364	2.116	0.102
Month	x Additional predators		5.203	2	2.602	15.12	<0.001
Moon	x Snake	x Micro	1.049	9	0.117	0.677	0.728
Additional predators	x Snake	x Micro	0.169	6	0.028	0.164	0.986
Month	x Snake	x Micro	0.58	3	0.193	1.124	0.342
Additional predators	x Moon	x Snake	8.698	18	0.483	2.808	<0.001
Month	x Moon	x Snake	4.012	9	0.446	2.591	0.009
Additional predators	x Moon	x Micro	0.722	6	0.12	0.699	0.651
Month	x Additional predators	x Micro	0.476	2	0.238	1.384	0.255
Month	x Additional predators	x Micro	1.75	6	0.292	1.695	0.128
Error			19.96	116	0.172		

Abbreviations: micro – microhabitat, moon – moon phase, snake – refers to location of snake species (as arranged by spatial quadrant), additional predators – (addition of a barn owl or red fox into the eastern side of the arena), and month – the month of the experiment, SS – sum of squares, MS – mean square.

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