

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

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13

14 **Abstract**

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

31

32 **Key Words: Biological invasions, Common-garden experiments, Constraint-breaking**  
33 **adaptations, Prey naiveté, Predator-prey foraging games, Vipers.**

34 **Introduction**

35           Prey species worldwide face novel predators as humans, intentionally and accidentally,  
36 move species around and create biological invasions. Such biological invasions invite  
37 frameworks for studying prey naiveté in response to invasive predators. Investigations of prey  
38 naiveté have included prey communities in aquatic systems (e.g., Gozlan *et al.* 2010, Francis  
39 2011), and prey on islands (e.g., Karl and Best 1982, Veitch and Clout 2002) as compared to  
40 prey in terrestrial systems (Cox and Lima 2006). For terrestrial systems, researchers have  
41 identified the behavioral components that lead to naïve and highly vulnerable prey. Can the prey  
42 recognize the predator as a threat, can it accurately assess the risk, and does the prey have the  
43 ability to respond properly (Banks and Dickman 2007)? Modelers, too, have picked up the  
44 challenge, explaining the conditions by which predators can invade a community, and the  
45 resulting evolutionary changes that might occur following successful invasions (Sih *et al.* 2010,  
46 Pintor *et al.* 2011).

47       Here, we address whether prey respond differently to a familiar predator than to a novel and  
48 putatively more effective one. We introduced a population of wild-caught gerbils into a semi-  
49 natural arena (vivarium) and exposed them to various predators, a sort of “common garden”  
50 experiment. Specifically, we compared the gerbils’ responses to a familiar viper (the Saharan  
51 horned viper; *Cerastes cerastes*) and to a novel, but otherwise highly convergent pit-viper (the  
52 sidewinder rattlesnake *Crotalus cerastes*) from the Mojave Desert. Pit-vipers use infra-red  
53 sensing pits to hunt, providing a constraint-breaking adaptation (Rosenzweig and McCord 1991,  
54 Vincent and Brown 2005) that should give them a competitive advantage over their native  
55 counterparts. Absence of difference in response between snakes could simply mean that the  
56 gerbils are inflexible in reaction to predators. Therefore, we also exposed the gerbils to

57 qualitatively different, but familiar predators such as the terrestrial red fox (*Vulpes vulpes*) and  
58 the aerial barn owl (*Tyto alba*). A difference between foxes and owls would demonstrate that the  
59 gerbils are flexible in their risk management and that any absence of difference between snakes  
60 documents equal risk perception.

61 Allenby's gerbil (*Gerbillus andersoni allenbyi*) for over 30 years has provided a model  
62 organism for the study of community dynamics (*e.g.* Abramsky and Rosenzweig 1984,  
63 Khokhlova et al. 2004, and more) and specifically responses to predation risk. The gerbils have  
64 been shown to respond to owls by favoring the bush microhabitat and nights with new moon  
65 (Kotler *et al.* 1992). In response to snakes, gerbils favor the open microhabitat and dark nights.  
66 Presumably, this is because snakes ambush more frequently from near and under bushes, and  
67 the snakes benefit from the vision afforded by moonlight (Kotler et al. 1993). Given the  
68 extensive knowledge of the relevant ecology and natural history of these populations, studying  
69 gerbils provides an advantageous platform for examining prey responses to an invasive  
70 predator.

71 As our framework for investigating the effect of a novel predator on the gerbils, we  
72 consider the three levels of naiveté suggested by Banks and Dickman (2007): 1) Do the gerbils  
73 perceive the novel predator as a threat? 2) Do they respond differently to the novel snake than  
74 they do to the snake species with which they have evolved? 3) Do the gerbils adjust their normal  
75 pattern of moonlight avoidance to accommodate the infra-red "vision" of the pit-viper? In  
76 addition, we asked: 4) how do the gerbils rank their perceived risk from the pit-viper and horned-  
77 viper in relation to other familiar predators such as the barn owl and red fox?

## 78 **Methods**

79 Fifty Allenby's gerbils (*Gerbillus andersoni allenbyi*) were trapped in the winter and  
80 spring of 2010 at the Ashalim Dunes and the Be'er Milka Dunes (Latitude 30.910132° N,  
81 Longitude 34.388752° E), Negev Desert, Israel. Eight adult male Saharan horned vipers  
82 (*Cerastes cerastes*) were collected at the Be'er Milka dunes, and maintained in the laboratory. In  
83 May of 2009, eight sidewinder rattlesnakes (*Crotalus cerastes*) were captured from the Parker  
84 Dunes (Latitude 34.121859° N, Longitude -114.237900° W) and Mohawk Dunes (Latitude  
85 32.592925° N, Longitude -113.889084° W) of southwestern Arizona, USA, and imported to  
86 Israel.

87 Experiments were run in a large outdoor vivarium at the Blaustein Institutes for Desert  
88 Research in Sede Boker, Israel from June 1<sup>st</sup> to July 29<sup>th</sup>, 2011. The vivarium (17 x 34 x 4.5 m)  
89 is rodent, snake, owl, and fox proof. One-meter tall galvanized steel walls with concrete bases  
90 extend 1 m into the ground (Figure 1). In addition, the walls continue to a height of 4.5 m with  
91 chicken wire mesh (1.5 cm diameter). The entire vivarium is roofed with chicken wire to contain  
92 owls. We divided the vivarium into 4 equal-sized quadrants using hardware cloth or galvanized  
93 steel fences running perpendicularly from the middle of both the long and short axes. A chicken  
94 wire wall rising to the ceiling along the center divider prevented the movement of foxes and owls  
95 from one side to the other (restricting these predators to the western half of the vivarium). The  
96 quadrants were connected with one snake-proof gate between northeastern/northwestern and  
97 southeastern/southwestern quadrants and two gates between northeastern/southeastern and  
98 northwestern/southwestern quadrants. These gates allowed for the movement of gerbils among  
99 quadrants, while restricting the movement of snakes.

100 Three quadrants of the vivarium contained two each and one remained snake-free. The  
101 southwestern quadrant had one individual of each snake species snakes (BOTH), the

102 northwestern quadrant was empty of snakes (NONE), the northeastern quadrant housed two  
103 Saharan horned vipers (HV), and the southeastern quadrant housed two pit-vipers (PV). Each  
104 quadrant contained a grid of 18 low-lying trellises (18 cm tall) topped by cut brush to simulate  
105 shrubs. Gerbils foraged in artificial food patches consisting of a 28 x 38 x 8 cm tray filled with 3  
106 l of sifted sand into which we mixed 3 g of millet seeds. Twelve food patches per quadrant were  
107 set out nightly (total of 48), of which six were in the open microhabitat adjacent to a trellis and  
108 six were placed under trellises in the bush microhabitat. Data were collected for six nights during  
109 each of the four moon phases over a period of two lunar months. For each collection period  
110 (moon phase), we also exposed the gerbil population in the vivarium to the presence of a barn  
111 owl (two nights), a red fox (two nights), or no additional predators above and beyond the snakes  
112 (two nights). The night-to-night order of the additional predator treatments were randomized  
113 within each 6-night moon phase with the constraint of avoiding two consecutive nights of the  
114 same predator addition treatment.

115         The gerbils were injected subcutaneously with uniquely numbered radio-frequency-  
116 identification PIT tags. The tags allowed identification of individuals and quantification of  
117 predation events based on feces and owl spit pellets that contained tags. For the experiment, we  
118 began by releasing six gerbils into each quadrant; thereafter, they were free to move among  
119 quadrants. Gerbils were given three nights to acclimate. When a tag was found in predator fecal  
120 matter or owl spit pellets, another gerbil was released into the quadrant where the individual  
121 gerbil was last recorded. We delayed the release of replacement gerbils until the end of a six-  
122 night moon phase. Thus, newly introduced animals had a night or two to acclimate before the  
123 next 6-night round of data collection. Following each night of the experiment, we sifted the sand  
124 from each tray to remove the remaining seeds and took the seeds to the laboratory for cleaning of

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

129 We estimated gerbil activity by tabulating the number of foraged versus unforaged trays  
130 for all combinations of snake treatment (4 quadrants), additional predators (owl, fox, and no  
131 added predator), moon phase (new, full, waning and waxing), and microhabitat (bush and open),  
132 to yield a multi-way contingency table. We used this multi-way contingency table to perform a  
133 log-linear analysis that examined direct and interactive effects of predation risk (snake  
134 treatments, additional predators), moon phase, and microhabitat on the number of trays foraged.

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

## 144 **Results**

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

#### 148 *Fatalities*

149 In the two months of the experiment, 11 gerbils were depredated, a small number to draw  
150 conclusions from. Feces, spit pellets, and PIT tags within them provided direct evidence of  
151 predation events. In total, owls were responsible for 3 fatalities, foxes for 4, horned vipers for 1,  
152 and pit-vipers for 1. In addition, there was one more fatality from snakes for which we could not  
153 assign species, and one from the other predators that we could not assign to either foxes or owls.

#### 154 *Activity*

155 Over the 8 moon phases of data collection (48 nights in total), 29% of the trays were left un-  
156 foraged (351 of 1200). The distribution of foraging activity was significantly affected by the  
157 predation risk treatments of snakes, additional predators (owl and fox), and the environmental  
158 factor of moon phase (Table 1).

#### 159 *Snake treatments--*

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

#### 164 *Additional predators--*

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

### 172 *Patch Use*

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

### 176 *Snake Treatments--*

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

183 Gerbils were expected to choose open microhabitat patches in areas with snakes, and the  
184 GUDs confirmed this. The gerbils foraged to a mean GUD of  $2.05 \pm 0.05$ g standard error in open  
185 microhabitat trays and to a mean GUD of  $2.14 \pm 0.05$ g in the bush. Similarly, given that the  
186 gerbils evolved with vipers that are “blind” on dark nights, we expected their foraging to be more

187 thorough (lower GUDs) during the new moon phase. Indeed, the gerbils foraged to a mean GUD  
188 of  $2.02 \pm 0.05$ g on the new moon as compared with  $2.18 \pm 0.05$ g during the full moon.

189 Giving-up densities depended on an interaction between the snake treatments and  
190 microhabitat as well as an interaction between the snake treatments and moon phase (Appendix  
191 D). In regards to the snake x microhabitat interaction, here was a strong difference in response to  
192 the open and the bush microhabitats, but only in the single-snake species treatments (both THSD  
193 p-values  $< 0.001$ ). In regards to the snake x moon phase interaction, the presence of both the  
194 familiar horned vipers and novel pit-vipers, the gerbils foraged less (had higher GUDs) in the  
195 bush microhabitat than in the open microhabitat (Figure 3)

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

### 203 *Additional Predators--*

204 The additional predators caused gerbils to reduce their patch use. Mean GUDs increased  
205 from  $1.72 \pm 0.05$ g during control nights, to  $2.08 \pm 0.06$ g and  $2.4 \pm 0.06$ g during nights with an owl  
206 or fox present, respectively (Figure 4B). Giving-up densities depended on a significant three-way  
207 interaction among the snake treatments, the additional predators, and moon phase (THSD p-  
208 value  $< 0.001$ ). This interaction can be attributed to divergent effects between the inaccessible (to

209 the fox and owls) northeastern/southeastern quadrants and the accessible  
210 northwestern/southwestern quadrants of the vivarium (Figure 4B). Even when indirect, the  
211 presence of either the foxes or owls in the northwestern/southwestern half resulted in  
212 equivalently higher GUDs in the northeastern/southeastern quadrants. With direct contact with  
213 the predators in the northwestern/southwestern half, the difference in response to the predators  
214 was more pronounced.

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

218 (1) Within the quadrant housing both snake species (BOTH), on owl nights, the GUDs were  
219 significantly higher during the full moon phase than during the new moon phase (THSD p value  
220  $<0.001$ ). (2) In the same quadrant (BOTH), during nights with the fox, gerbils did not forage  
221 during nights of the full moon, but did forage briefly during the new moon (the mean GUD  
222 decreased to  $2.59 \pm 0.1$  g). (3) In the presence of the novel pit-vipers (PV), during nights of the full  
223 moon, the effect of the owl (indirect) was as high as that of the fox. However, on dark nights of  
224 the new moon, the effect of the owl was similar to the control.

225 ***Month --***

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

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

## 235 **Discussion**

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

240 The gerbils responded by increasing activity during the new moon in the presence of either  
241 snake species. This is the most effective response to the snakes with which they evolved (horned  
242 vipers), whose activity and lethality is restricted by moonlight. But it may not be the best  
243 response to rattlesnakes (pit-vipers) that can “see” in the dark. Our results suggest, then, that the  
244 gerbils recognized the novel pit-vipers as a risk, but one that is not much different from that  
245 posed by their familiar horned viper. Gerbils did not avoid dark nights with the pit-viper as  
246 might be expected based on Bouskila’s (1995) work with Heteromyid rodents and rattlesnakes  
247 under natural conditions in California. There, the North American rodents also favored the open  
248 over the bush microhabitat. But they favored moonlit nights, presumably because of the  
249 advantage on dark nights afforded to the rattlesnakes from their infra-red vision.

250 The gerbils exhibited behavioral patterns consistent with prior research showing a lower  
251 perceived risk of predation from snakes than from owls and foxes (Kotler *et al.* 1992). As seen  
252 previously (Kotler *et al.* 1993, Bouskila 1995), the gerbils in our experiment treated the open

253 microhabitat as safer than the bush when snakes were present (lower GUDs in the open than  
254 bush). Gerbils reversed their assessment of microhabitat when owls or foxes were present along  
255 with the snakes. GUDs were lower under bushes than in the open with owls and foxes. Although  
256 snakes and owls are known to facilitate each other (Kotler et al. 1992, Embar et al. 2014), and  
257 although snakes make the bush microhabitat more dangerous and owls make the open more  
258 dangerous, overall higher GUDs in the open when both are present suggests that gerbils treat  
259 owls as the greater danger.

260 ***Recognizing that the novel predator is indeed a predator (Level one of naiveté)***

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

270 ***Ability to properly assess risk posed by the novel predator (Level two of naiveté).***

271 Did the gerbils adjust their fear responses appropriately for the aptitudes of the novel  
272 sidewinder rattlesnake? Our data provide only an equivocal answer, as it was difficult to know  
273 the actual mortality risk imposed by the two types of snakes in the absence of fear responses. In  
274 our experiment, using GUDs, we asked whether the gerbils modulate their perceptions of risk in

275 response to environmental factors such as microhabitat, moon phase, and snake species. We  
276 addressed the gerbils' perception of snake lethality by analyzing their response to moon phase  
277 and microhabitat. Regardless of the snake species the gerbils responded to the snakes by  
278 preferring the open microhabitat (Figure 3). However, in the presence of other predators, the  
279 bush microhabitat was preferred. If gerbils learned that their pit-viper predators were more  
280 dangerous in darkness than horned vipers due to the former's infra-red vision, then they should  
281 have shown greater GUDs during the new moon nights than during the full moon nights. Also,  
282 their response to the new moon should have intensified over time. These did not happen.  
283 Rather, gerbils increased foraging activity in the presence of the pit-vipers at new moon. The  
284 gerbils did adjust their response to the novel snake following prolonged exposure, but opposite to  
285 expectation. The gerbils actually lowered their fear of the novel snake at new moon in the  
286 second month of the experiment (Figure 5). The gerbils' increasingly relaxed assessment of the  
287 pit-viper at new moon, however, did not result in any obviously increased mortality.

288 The greater fear response of the gerbils to owls and foxes compared to snakes seemed  
289 merited. The foxes and owls captured more gerbils than did the two snake species combined.  
290 This is an even more extreme result considering that just a single owl (or single fox) was present  
291 on only one-third of the nights. Conversely, gerbils were exposed to individuals of six snakes (3  
292 of each species) every night of the experiment.

293 More so than the density of predators (both familiar and novel) in the environment, prey may  
294 respond most to their activity level. For example, minnows respond to increased strength of  
295 predator scent (Gilliam and Fraser 1987), and wall lizards are perplexed by a combination of  
296 searching predators and burrows smelling of snakes (Amo *et al.* 2004). Even insects avoid  
297 individuals of the same species when there are greater chances of cannibalistic behavior

298 (Crumrine 2010). Carthey and Banks (2014) suggested that most naïve prey species can, and do,  
299 respond to general risk, even in the absence of direct interactions. In our experiment, snake  
300 activity, as measured by the density of snake-tracks, was found to be greater under the bushes  
301 than in the open for both snake species (Embar *et al.* 2014), and gerbils avoid this microhabitat  
302 in the presence of snakes.

303 *Even with adjustments, the prey are still highly vulnerable to the risk posed by the novel*  
304 *predator (Level three of Naiveté)*

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

315 In contrast to the relatively low impact of novel snakes in our experiments, Australia  
316 provides many examples of novel, invasive predators causing extensive community disruption  
317 (Letnic *et al.* 2011, Heavener *et al.* 2014, Doherty *et al.* 2015). There, the dominant examples  
318 are often invasive mesopredators to which the prey may have at least a limited ability to respond.  
319 Several experiments document that kangaroos, possums, and other genera of native wildlife have  
320 learned to recognize fox and coyote urine despite distinct evolutionary histories (Parsons *et al.*

2005, Carthey and 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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407 **Figure Legends**

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

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

423

424

425 **Figure Legends (Continued)**

426 **Figure 3.** Patch use reflected by GUDs according to snake treatment and microhabitat. The  
427 gerbils showed preference for the open microhabitat in contact with the snakes, with the  
428 exception of the quadrant with both snakes, likely a result of direct interactions with owls and  
429 foxes in that quadrant that did not occur by experimental design in the quadrants with the single  
430 snake species. Notice that the difference between direct and indirect exposure is larger in activity  
431 levels (Figure 2C). GUDs reflect the means of foragers' exploitation of both safe and risky  
432 patches. Therefore, the exploitation of safe stations to a lower GUD averaged with the unforaged  
433 stations results in an overall smaller difference between safe and risky environments than  
434 reflected in activity patterns. The error bars reflect the standard error of the mean.

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

440 **Figure 5.** Patch use as reflected by GUDs according to month: (A) significant decrease in  
441 perceived risk (reduction of GUD) with prolonged exposure, predominantly in the interaction  
442 between the novel pit-viper and the dark nights of the moon, (B) increased respect towards the  
443 owls (increase in GUDs) compared with a loss of respect towards the fox (decrease in GUDs).  
444 The error bars reflect the one standard error of from the mean.

445