

1 **Divergent Behavior Amid Convergent Evolution: A Case of Four Desert Rodents Learning**
2 **to Respond to Known and Novel Vipers**

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ABSTRACT

Desert communities world-wide are used as natural laboratories for the study of convergent evolution, yet inferences drawn from such studies are necessarily indirect. Here, we brought desert organisms together (rodents and vipers) from two deserts (Mojave and Negev). Both predators and prey in the Mojave have adaptations that give them competitive advantage compared to their middle-eastern counterparts. Heteromyid rodents, kangaroo rats and pocket mice, have fur-lined cheek pouches that allow the rodents to carry larger loads under predation risk compared to gerbilline rodents. Sidewinder rattlesnakes have heat-sensing pits, allowing them to hunt better on moonless nights when their Negev sidewinding counterpart, the Saharan horned vipers, are visually impaired. In behavioral-assays, we used giving-up density (GUD) to gauge how each species of rodent perceived risk posed by known and novel snakes. We repeated this for the same set of rodents at first encounter and again two months later following intensive “natural” exposure to both snake species. Pre-exposure, all rodents identified their evolutionarily familiar snake as a greater risk than the novel one. However, post-exposure all identified the heat-sensing sidewinder rattlesnake as a greater risk. The heteromyids were more likely to avoid encounters with, and discern the behavioral difference among, snakes than their gerbilline counterparts.

33 **Introduction**

34 Deserts, and desert rodents in particular, provide a model system for studying parallel and
35 convergent evolution. Deserts around the world form at least five evolutionarily independent
36 laboratories of adaptation, ecology, and evolution [1–6]. Shared environmental conditions of
37 temperature, precipitation, and aridity force evolutionary processes in a manner that results in
38 similar adaptations in species that fill similar ecological roles. Not only do species converge, but
39 communities may too [7–10]. A good example of this can be studied in desert dunes of the
40 Mojave and of the Negev deserts. In both of these systems we find an array of plants that drop
41 their seeds onto the sand (creating a seed bank); a variety of rodent species feed on these seeds
42 [11–13]; and medium-sized sidewinding vipers feed on the rodents [14,15].

43 The Mojave and Negev deserts of North America and the Middle East, respectively,
44 possess rodents with similar ecologies [5,7,13,16,17]. These rodents are nocturnal, semi-
45 fossorial, seed-eating, and seed caching. However, the heteromyid rodents of the Mojave may
46 have a constraint breaking adaptation compared to their convergent counterparts in the Negev,
47 the gerbilline rodents. A constraint-breaking adaptation is a game-changing evolutionary
48 adaptation that alters, relaxes or eliminates tradeoffs and confers a competitive advantage to its
49 holder over those lacking the trait as defined by Rosenzweig and McCord [18]. The heteromyids
50 have external fur lined cheek pouches that allow them to stow large quantities of food (in good
51 dry conditions) before having to return to a burrow for caching [11]. In contrast, the gerbilline
52 rodents carry their grain in their mouths, logically requiring more trips to collect the same
53 quantity of grain and thus increasing exposure to predators.

54 Similar to the rodents, rattlesnakes from North America and horned vipers from the
55 Middle East provide a textbook example of convergence [19]. Despite being separated by 18

56 million years from their most recent common ancestor [20], each has evolved the same
57 locomotion method, similar coloration patterns, and a similar adaptation of scales over the eye
58 ridge, protruding as horns. However, the North American sidewinder belongs to the evolutionary
59 lineage of pit-vipers, a lineage that evolved infra-red heat sensing pits. The pit-vipers provide
60 another example of a constraint breaking adaptation compared with Saharan horned vipers. The
61 heat-sensing pits enable the sidewinder to be active on dark nights with no ambient moonlight.
62 The pits also enable safer, more precise strikes at warmer, more vulnerable locations in their
63 endothermic prey [21].

64 We report here an intercontinental comparison for how two species of Mojave Desert
65 rodents and two species of Negev Desert rodents respond to their evolutionarily and ecologically
66 familiar versus novel snakes. We ask three questions: (1) Do gerbils and heteromyids assess risk
67 from snakes in a similar manner? That is, do they make the same choices when facing snakes
68 with and without heat-sensing pits? (2) Do both sets of rodents assess risk from novel predators
69 as equal to that of evolutionarily familiar ones? (3) Does a prolonged (two-month) exposure to
70 both snakes (in a larger and more realistic setting) diminish the perceived risk of predation from
71 horned vipers, compared with heat-sensing pit-vipers? If so, do both sets of rodents reach the
72 same conclusion, i.e. exhibit the same behavioral response?

73 **METHODS**

74 *Study Species*

75 We brought together one large and one small coexisting desert rodent from each
76 continent, two common gerbils from the Negev Desert of Israel and a kangaroo rat and a pocket
77 mouse from the deserts of the southwestern United States, to a common and controlled setting in
78 the Negev Desert. The Negev Desert gerbils include the greater Egyptian gerbil [GP] (*Gerbillus*

79 *pyramidum*), 40 g, and Allenby's gerbil [GA] (*Gerbillus andersoni allenbyi*), 30 g [22]. The
80 North American Desert rodents include Merriam's kangaroo rat [DM] (*Dipodomys merriami*), 45
81 g [23], and the desert pocket mouse [CP] (*Chaetodipus penicillatus*), 22 g [24]. All are nocturnal
82 desert granivores commonly found on sandy substrates such as sand dunes. All four rodents have
83 adaptations to reduce the risk of predation, including saltatorial locomotion for enhanced escape
84 abilities and auditory adaptations to increase hearing acuity. These adaptations are especially
85 well developed in the kangaroo rats [4,25].

86 We brought wild-caught vipers, trapped at locations where they would come in contact
87 with wild populations of the above-mentioned rodents, to the same facility. We caught
88 sidewinder rattlesnakes (*Crotalus cerastes*), 35-60cm mean length, from the Mojave Desert [26]
89 and Saharan horned vipers (*Cerastes cerastes*), 30-60cm mean length, from the Negev Desert
90 [15]. Both snakes side-wind, borrow in the sand (usually under bushes) and feed on a variety of
91 rodents and lizards [14,15].

92 Animal collection was done respectively in the Mojave and Negev Deserts. The
93 heteromyids were predominantly trapped in the Parker Dunes area (N 34°9'7.969", W
94 114°7'34.245") and supplemented by individuals from the San Bernardino (AZ) area (N
95 31°23'22.082", W 109°11' 22.851"). The sidewinders were collected in the Avra Valley
96 alongside country roads (N 32°24'49.335", W 111°29'38.138"). The gerbils in Israel were
97 collected in the Mashabim Dunes (N 31°0'14.531", E 34°44'47.31") and the horned vipers on
98 the border between Israel and Egypt at Be'er Milka (N 30°57'4.609", E 34°23'10.821").

99 *Experimental Design*

100 We used an "interview" approach [27–29] to measure the response of each rodent species
101 to the risks posed by the two snake species. We measured the response prior to exposure of the

102 rodents to the novel viper species and following a two-month exposure to both snake species in
103 an semi-natural arena (described in Bleicher 2014; Bleicher et al. 2016). We assessed the
104 response of each species to the vipers using a metric borrowed from foraging theory, the giving-
105 up density (GUD; Brown 1988). The GUD is the amount of food a forager leaves behind
106 untouched in a resource patch to measure foraging efficiencies and costs. Most relevant for our
107 purposes is that these costs include those arising from the perceived risk of predation. Hence the
108 forager will leave a lower GUD when it perceives lower risk [31].

109 The experiments were conducted in a light-controlled room at Ben Gurion University of
110 the Negev's Blaustein Institutes for Desert Research, at Midreshed Ben Gurion, Israel (N
111 30°51'17.401", E 34°47'6.637"). We erected a total of eight, 3-compartment (henceforth room)
112 behavioral-assay systems (henceforth system), which we call interview chambers (*SI*). We called
113 them interview chambers as they allow the researchers to question an individual animal and
114 allow the animal to rate how it perceives treatments in relation to each other. With repeated
115 measures it allows the researchers to obtain how each individual changed its perception of the
116 controlled treatments, *i.e.* its opinion, after a manipulation.

117 Each system consisted of a circular nest-box attached to three 80 x 40 x 40 cm test-
118 rooms. Each room was connected to the nest-box with a 30 cm PVC tube to allow rodents free
119 movement between the nest-box to any room. Each room was large enough to contain a small
120 cage and a 38 x 28 x 8 cm foraging tray (Sup. Appendix 1). Each foraging tray was set with 2
121 liters of sand and 1.5g of millet. For each system during a trial, the cage in one compartment
122 contained a sidewinder rattlesnake, the cage in the second contained a horned viper, and the cage
123 in the third was empty. In order to avoid the possibility of directional bias, we randomized the

124 positions of treatment-rooms (henceforth treatment) to different cardinal directions in each
125 system.

126 between dusk and dawn we conducted a maximum of five, 2-hour tests (henceforth
127 round), in which a single rodent was placed in the nest-box and was allowed to forage in the
128 system. This allowed sufficient time for rodents to move among compartments and forage in
129 trays under the different treatments. Each rodent was run at random times each night to nullify
130 the preferred activity periods of the rodents. The rodents weren't fed prior to the experiment
131 adding incentive to forage when in the chambers. Following the experiment, animals were
132 returned to their holding cages and fed 3 grams of millet and a mealworm (*Tenebrio molitor*) to
133 offset stress related calorie loss. Following each test, each of the foraging trays was sieved and
134 the remaining millet removed and weighed to obtain the GUD. The systems were reset after each
135 rodent was tested with fresh millet and the next rodent introduced for the following round.

136 Each individual rodent was tested for two nights pre-exposure and an additional two nights post-
137 exposure, with a night between runs to avoid possibly over-stressing the animals. The exposure
138 periods are two-month experiments in which the rodents cohabitated in a semi natural arena
139 (aviary dimensions 17 x 34 m) with uncaged snakes of both species (3 of each species) allowing
140 them to learn the differences in behavior of the predators. In addition, by flying an owl in the
141 aviary on half the nights, we compared how the risk from snakes compares to the risk from owls
142 (*cf.* Bleicher 2014). Our aviary provides a system where the rodent enjoy ideal free distribution
143 through special gates within the arena, but predators are limited in movement by the same gates.
144 Using RFID tags implanted subcutaneously in the rodents, and loggers under food patches we
145 are certain the majority of rodents experienced encounters with both snake species. We pre-
146 {post-} interviewed 51 {19} GAs, 29 {9} GPs, 36 {11} CPs, and 33 {10} DMs. Each surviving

147 individual was interviewed twice pre-exposure and twice post-exposure. All animals used were
148 male and of sexual reproductive age, to comply with importation regulations. The experiments
149 were run pre-exposure {post-exposure} on 3-26/5/2011 {3-9/8/2011}, 2-5/7/2012 {20-
150 22/9/2012}, 6-11/7/2012 {8-10/11/2012} and 27-29/5/2013 {30/7/2013-2/8/2013} for GA, CP,
151 DM and GP respectively.

152 *Data Analyses*

153 We used four different methods to determine how the rodents perceive risk posed by the
154 different snakes. First, we ran a Friedman's test of concordance, comparing the way in which
155 each rodent ranked the different snake species. The highest GUD received a rank of 1 and the
156 lowest a rank of 3. We repeated the analysis on data for each individual pre- [post-] exposure.

157 To specifically address the low variation in GUDs in the pocket mice, we assessed
158 activity patterns by running a log-linear tabulation analysis (multi way contingency table) on the
159 proportion of foraged to unforaged trays. For each small mammal we compared the proportion
160 of trays foraged based on snake treatment and experimental sequence (pre- and post- exposure)

161 Last, we averaged the GUD for each individual per snake treatment, resulting in one
162 value for at each test sequence. We then ran in Systat13© a series of generalized linear models
163 (GLM) using the mean GUD as the dependent variable. The first GLM used three independent
164 variables; rodent species, (snake) treatments, and sequence. In addition, all two and three-way
165 interactions between these variables were included. We did not use the full data set, but lowered
166 the "noise" in the data by using the mean values. This normalization means that each individual
167 provides two datapoints, one prior and one post exposure (too low for a meaningful comparison
168 on the individual level). To increase the explanatory power for each species, we ran a GLM for

169 each species individually as well. For the single species GLMs, we tested the independent
170 variables: snake treatment and sequence (and the two-way interaction). Post-hoc pairwise
171 comparisons were performed using Tukey's Honestly Significant Differences (THSD) tests for
172 variables that significantly affected variance. This analysis addresses a population-wise (or
173 species-wise in this case) comparison for the broader differences and not in-population variation.
174 We knowingly and purposefully removed individual ID for these reasons.

175 Last, we ran a random-forest Bayesian decision tree analysis in Statsoft Statistica©. This
176 analysis best described as a categorical principal component analysis describes the importance of
177 each variable, and category within each variable, in explaining the distribution of points of a
178 dependent variable. Here we tested how the rodent's GUD were distributed based on the species,
179 the snake-treatment and the sequence of the measurement.

180 RESULTS

181 At first encounter, all the species ranked the snakes similarly (Friedman's test of
182 concordance $X^2 = 6.5$, 2 df, $p = 0.039$, and $W = 0.813$), with lowest GUDs for the snakeless-
183 control, higher GUDs for the evolutionarily novel snake, and still higher GUDs for the
184 evolutionarily familiar snake. All rodent species perceived both snakes as threats ($p = 0.003$,
185 0.012 for known and sidewinders and horned vipers compared to control; Fig 1).

186 FIGURE 1

187 Desert pocket mice showed increased GUDs in response to snake presence but did not
188 distinguish between snake species in the magnitude of their GUDs. The remaining three rodents
189 responded with 100% concordance, showing highest GUDs in response to their familiar snake,
190 intermediate GUDs to the novel snake, and the lowest GUD when the cage contained no snake

191 (S2). The non-significant difference between snakes in GP pre-exposure did not alter this
192 finding. Post-exposure, the rodents showed complete concordance according to snake species:
193 they all foraged least in the presence of the rattlesnake. ($X_r^2 = 6.5$, 2 df, $p = 0.039$, and $W = 0.813$).

194 TABLE 1

195 Assessing the activity of each species of rodent, using proportion of patches of this
196 treatment in which foraging activity took place, similar patterns emerge. We found that the
197 species each exhibited different activity preferences (Table 1A). None of the rodents foraged a
198 greater proportion of trays before the snake exposure than after. However, for all four rodents the
199 exposure changed the willingness to forage in difference snake treatments (Tables 1 B-E). Pre-
200 exposure, three species were active in more compartments with the novel snake than with the
201 evolutionarily familiar one (Fig 2 A). Contrarily, GP investigated more compartments with the
202 familiar snakes than novel snakes, and DM foraged in more compartments with novel snakes
203 than in snake-less compartments. Post-exposure, all rodents foraged most in the snake-free-
204 control over the snake treatments (Fig 2 B). Three of the four species foraged least in the
205 compartment with sidewinder rattlesnakes. The GAs, foraged in more horned viper treatments
206 than near sidewinders. GA's activity pattern did not vary between pre- and post-exposure
207 interviews.

208 FIGURE 2

209 TABLE 2

210 The GLM combining all four species showed that each species foraged differently in the
211 interview chambers (Table 2). The heteromyids foraged less than the gerbils. The pocket mice
212 (CP), and kangaroo rats (DM) foraged to a mean GUDs (\pm SE) of $1.34 \pm 0.019g$ and $1.32 \pm 0.019g$,

213 respectively. Allenby's gerbils (GA) and the Egyptian gerbils (GP) foraged to mean GUD of
214 1.24 ± 0.02 g and 1.29 ± 0.027 g, respectively. In response to the snake treatments, the rodents
215 overall foraged least in the presence of the rattlesnake, and most in the control treatment (Fig 3,
216 Sup. Appendix 2). Post-hoc pairwise comparison (THSD) found a significant difference
217 between, the control and horned viper ($p=0.009$), the control and sidewinder ($p<0.001$), and
218 control and between the horned viper and sidewinder ($p=0.006$). After two months of exposure,
219 all four species exhibited a similar trend of decreased foraging in the presence of the sidewinder
220 rattlesnake (Fig 3) as shown in each of the single species models (Table 2).

221 FIGURE 3

222 The random forest analysis resulted in a model with mid-range risk-estimates (\pm SE) of
223 0.09 ± 0.02 and 0.11 ± 0.03 for the training and model respectively. The model confirmed strong
224 species and snake treatment effects (importance of 0.993 and 1.0 out of 1.0 respectively) and
225 suggested lower importance of 0.326 for the sequence. These values explain the rate of decisions
226 each variable affected. This analysis unexpectedly separated GA from the other species at the
227 first split (Fig 4; Supplement 3). The higher a split (further left) the stronger greater the accuracy
228 of that split, thus more credible. For the GAs the difference between the control and snakes was
229 critical, and the model suggests that the novel pit viper was assessed as slightly riskier post
230 exposure. The GUDs reflect the change in perception with means of 1.27 ± 0.06 g and 1.29 ± 0.06
231 g pre- and post- exposure respectively.

232 FIGURE 4

233 The difference in variance between the GUDs in the control for all three other species
234 (CP, DM & GP) was too small for the model to predict divergence between them. However, in

235 the response to the snakes a clear divergence between CP and the larger rodents was found. The
236 Pocket mice initially foraged less near the novel snake, but post exposure avoided both snakes
237 equally. The model does not predict change in the larger rodents assessment of risk from the
238 snakes after exposure, but clumps these points together to set aside the sidewinder as greater risk
239 for both. The mean GUD for both species combined in the presence of the horned vipers was
240 1.3 ± 0.05 g. The difference between the response to each snake type was larger in the kangaroo
241 rats (DM), with a GUD of 1.45 ± 0.03 g in the presence of the sidewinders, than in the gerbils
242 (GP), with respective GUDs of 1.34 ± 0.08 g.

243 DISCUSSION

244 All rodents began by assessing the snake with which they share evolutionary history as an
245 equal or greater threat to the novel snake. However after two months of interacting with uncaged
246 sidewinders and horned vipers, all four rodents ranked the heat-sensing sidewinder as the greater
247 threat. We chose to structure this discussion according to three major comparisons: two
248 intracontinental comparisons (within families) and one intercontinental comparison between the
249 gerbils and heteromyids.

250 *Heteromyids*

251 Pocket mice and kangaroo rats provide examples of opposite strategies in managing risk
252 from snakes (as shown here), and other predators such as owls [28,32]. Why the stark difference?
253 We do not believe it has to do solely with size, but in variation in anti-predator adaptations. The
254 first reason behind this speculation is a number of studies investigating microhabitat selection in
255 the kangaroo rats and pocket mice of different species [33–35]. In those studies, the kangaroo
256 rats would use both bush and open microhabitat whilst pocket mice were particular to the bush.
257 The interpretation these studies gave are based in both locomotion and signaling resulting from

258 the kangaroo rats' bipedal agility. On the opposite side the evolutionary strength of the pocket
259 mice is attributed to torpor which they apply to minimize risk and survive harsh weather events.
260 In addition, the kangaroo rats are able to ward off snakes using warning signals, foot drumming
261 and kicking sand in the face of their predators [25,36]. In facing a striking snake, they are
262 capable of hopping backwards [37–39] and to heights exceeding 2 m [40]. In contrast, the pocket
263 mice remain bush-bound, and avoid predators by climbing into dense vegetation and are
264 presumed to apply a torpor mechanism to reduce dependency on the foraging when risk levels
265 are too high [33,35].

266 In the interview chambers, differences among the species were well represented. The
267 pocket mice avoided risk where possible, leaving high GUDs near snakes, affected by the 70-
268 80% of rooms unforaged. The avoidance of the snakes was strongly offset by significantly lower
269 GUD and high activity in the snake-free control rooms. Meanwhile, the kangaroo rats exhibited
270 an inquisitive nature seen by the high proportion of foraged rooms. The genus *Dipodomys*
271 (kangaroo rats) has morphological adaptation that allow them to both located predators and avoid
272 their attack. Inflated auditory bullae allow the kangaroo rats to hear predators, such as owls,
273 approaching from a large distance [34,41,42]. The kangaroo rat's powerful hind-legs allow them
274 to hop out of harm's way to heights above one meter and are able to change the direction of
275 movement using tail flicks while in the air [37]. Thanks to their morphological adaptations,
276 kangaroo rats are able of greater risk-taking than the pocket mice [43]. This risk-taking behavior,
277 verging on being dare-devils, is best exhibited by the increased resource use and patch activity in
278 the treatment with the novel snake (greater than the control). These strong differences in anti-
279 predator adaptations, both behavioral and physical, are likely the evolutionary mechanism that
280 allows for these species to coexist in the great basin deserts.

281 *Gerbils*

282 The competition between GA and GP is a major model system for the study of the roles of
283 competition, predation risk and parasitism in community structure. It the behavioral differences
284 between these gerbils that allow them to coexist. They differ in habitat preference [44–46], in the
285 time of night they are active [47,48], in the way they respond to different types of predators
286 (snakes, owls) [49–52] and in the way they respond to inter- and intra-specific competition [53–
287 55]. Surprisingly, despite those well documented behavioral differences, we found the species
288 responded to the snakes in remarkably similar patterns.

289 Why did we find such similar patterns? The most likely explanation is that our systems
290 were devoid of environmental heterogeneity. During the exposure period, we found species-
291 specific—spatially explicit—responses to the distribution of risk posed by each snake and in
292 combination with barn owls [28,30,32,56]. However, in the enclosed systems, where individual
293 gerbils forage without competition, the response of both species to the risk of predations is
294 similar.

295 This experiment revealed that the gerbils were attentive to the type of predation-risk
296 present and their response to that risk is relatively plastic. Pre-exposure, both gerbils recognized
297 the novel sidewinder, as a risk (higher GUDs than the control) but not as great a risk as the
298 known horned viper. The change in perceived risk towards the novel sidewinder suggests the
299 gerbils gained information about the new predator. Post-exposure, the mean GUDs being similar
300 for both snake species, suggests the gerbils were able to learn, in the minimum, that these new
301 predators are snakes. Despite both having some changes in their response the GAs exhibit a
302 stronger tendency to adapt to the novel risk (based on the random-forest), not surprising for a
303 species that is known for balancing the risk from predators with stronger competitors, *a.k.a* a

304 crumb picking foraging strategy. The GA's are known to assess GP (and *Gerbillus gerbillus*)
305 activity and shift their foraging patterns to exploit patches more thoroughly when these dominant
306 species are around [47,48].

307 Another possible explanation is delayed response to stimulus. In neurological studies
308 delayed response to a novel threat is commonly studied in contexts of neophobia and classical
309 conditioning. In these types of studies lab mice, rats and rabbits are taught to recognize a novel
310 object, sound, or image as a predation-cue [57,58]. Intrinsically, most rodents fear novel objects,
311 but do not innately respond to them to the extent of the danger that they “actually” pose. In many
312 cases, they remain naïve to the proper response to these novel threats [59,60]. Despite being
313 naïve to the dangers of the sidewinder rattlesnake at the start of the experiments, both gerbils
314 quickly learned to respond to the snakes and both rank them as a risk. In out measurements in the
315 aviary they both ranked snakes as a lower risk than (lower GUDs) than owls [28,30,32]. The
316 results of the comparison between the gerbils highlight the importance of competition to species
317 that have less spatial segregation than the North American heteromyids [44,47].

318 *Intercontinental Wide Consequences*

319 During the pre-exposure interviews all rodents feared their evolutionarily familiar snake
320 equally or more than the novel one. In particular, gerbils showed higher GUDs in response to
321 greater Saharan horned vipers, and the heteromyids showed higher GUDs in response to the
322 sidewinder rattlesnake. This coincides with the snake species that each species evolved with.
323 However, this may also reflect the predator to which each of the rodents has individually been
324 exposed to previously since all animals in these experiments were wild-caught. Overall, the
325 gerbelline species were willing to take more risk investigating the predators, while the
326 heteromyids preferred to avoid both species. This reluctance to take risk in the heteromyids,

327 suggests an overall greater “respect” to risk posed by snakes, possibly due to their evolution
328 alongside snakes that have heat-sensing capabilities [32].

329 All four rodents, showed an ability to varying extent, to differentiate between the snake
330 species and to categorize the heat-sensing sidewinder as a greater threat post-exposure. This
331 could be attributed to two explanations. First, the rodents may have learned to identify the musk
332 produced by each species, as kangaroo rats are known to do [36]. Second, given the dark
333 conditions, aimed to highlight the difference between the snakes, the rodents may have been
334 responding most strongly to the sidewinders as they were more active in their cages.

335 The fur-lined cheek pouches, hypothesized to give the heteromyids an advantage in
336 maximizing harvest, under similar risk conditions, did not appear to function in such a manner in
337 the presence of the snakes [32]. The greater sensitivity of heteromyids to the interaction with the
338 snakes meant that despite having the ability to forage quickly in the presence of the predators,
339 the heteromyids simply avoided these patches resulting in higher giving up densities than their
340 gerbilline counterparts.

341 Perhaps the most interesting aspect of this comparison was the broader examination of
342 the convergence of the two deserts’ rodent and predator communities. Despite the physical and
343 dietary similarities, we found a large number of key differences in the way our four species
344 strategized in response to snake predators. Our experiment shows a tendency of North American
345 species to focus on predation risk while the gerbil responses to the caged snakes were more
346 plastic, likely suggesting other elements come to play in addition to snakes in that system. Why
347 are the heteromyids more sensitive to the risk posed by snakes? The only likely explanation is
348 the one that made us choose these systems for comparison, *i.e.* the evolution along-side predators
349 with a lethal weapon—the heat sensing pits. While sidewinders were the clear choice in terms of

350 physical convergence with the horned vipers, they are only one of 13 species of rattlesnakes that
351 call the Great Basin deserts home, and all possess the infra-red sensory ability [61]. In
352 comparison, there are only five vipers in the Negev and the Sahara, and they all are blind on
353 moonless nights [62]. The high diversity of lethal predators in North America suggests the
354 pressure to manage the risk from snakes has been a lot more important in the evolution of
355 heteromyids. From that importance stems their sensitivity and acuity to the presence and activity
356 patterns of the snakes they encounter.

357 To conclude we can recapitulate the answers we found to each of our study questions. (1)
358 Middle Eastern gerbils responded less to predation risk posed by snakes than their North
359 American convergent counterparts, kangaroo rats and pocket mice. (2) At first encounter, both
360 kangaroo rats and gerbils recognized the novel snake as a lesser (or equal) risk to that of their
361 familiar snakes. Pocket mice avoided both snakes equally. (3) Post-exposure, gerbils and pocket
362 mice assessed both snake species as similarly dangerous. However, kangaroo rats rank the novel,
363 horned viper as a lesser threat than the known heat-sensing sidewinder.

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527 **Table 1.** Log-Linear Analyses for all species combined (A) and each species separately (B-E)

Var 1	Var 2	G2	Df	P
Table 1A Log-Linear Analysis Combining All Small Mammals				
Species		9.46	3	0.024
Snake Treatment		40.28	2	<0.001
Snake Treatment	Species	80.76	17	<0.001
Species	(Snake Treatment)	32.48	9	0.002
Table 1B. Log-Linear Analysis for Pocket Mice (<i>C. penicillatus</i>)				
Snake Treatment		31.4	2	<0.001
Sequence		0.02	1	0.888
Snake Treatment	(Sequence)	33.22	4	<0.001
Table 1B. Log-Linear Analysis for Kangaroo Rats (<i>D. merriami</i>)				
Snake Treatment		16.58	2	0.003
Sequence		0.02	1	0.99
Snake Treatment	(Sequence)	19.72	4	0.001
Table 1C. Log-Linear Analysis for Allenby's Gerbils (<i>G.a. allenbyi</i>)				
Snake Treatment		18	2	0.001
Sequence		0	1	1
Snake Treatment	(Sequence)	18.9	4	0.001
Table 1D. Log-Linear Analysis for Greater Egyptian Gerbils (<i>G. pyramidum</i>)				
Snake Treatment		5.34	2	0.07
Sequence		0.02	1	0.99
Snake Treatment	(Sequence)	11.6	4	0.021

528 Variables: Species (GA, GP, CP, DM), Snake Treatment (Horned-Viper, Sidewinder, Control), Sequence
 529 (Pre-, Post-Exposure)

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532 Table 2. ANOVA Tables for General Linear Models for all species combined (A) and each species
533 separately (B-E)

Var.1	Var.2	Var.3	Type III SS	df	Mean Squares	F-Ratio	p-Value
Table 2A. ANOVA Table for all four species N=582, Multiple R²=0.346							
Species			0.591	3	0.197	2.741	0.043
Sequence			0.007	1	0.007	0.091	0.762
Snake Treatment			1.967	2	0.984	13.691	<0.001
Species	* Sequence		0.165	3	0.055	0.766	0.513
Snake Treatment	* Sequence		0.793	2	0.397	5.52	0.004
Species	*Snake Treatment		0.973	6	0.162	2.256	0.037
Snake Treatment	* Sequence	*Species	0.305	6	0.051	0.708	0.643
Error			40.093	558	0.072		
Table 2B. ANOVA table for Desert Pocket Mouse (<i>C. penicillatus</i>) N=141, Multiple R²=0.324							
Sequence			0.001	1	0.001	0.03	0.863
Snake Treatment			0.584	2	0.292	6.16	0.003
Snake Treatment	* Sequence		0.026	2	0.013	0.272	0.762
Error			6.404	135	0.047		
Table 2C. ANOVA table for Allenby's gerbil (<i>G. andersoni allenbyi</i>) N=210, Multiple R²=.225							
Sequence			0.018	1	0.018	0.164	0.686
Snake Treatment			0.719	2	0.359	3.276	0.04
Snake Treatment	* Sequence		0.242	2	0.121	1.102	0.334
Error			22.383	204	0.11		
Table 2D. ANOVA table for Greater Egyptian Gerbil (<i>G. pyramidum</i>) N=104, Multiple R²=.460							
Sequence			0.008	1	0.008	0.146	0.703
Snake Treatment			0.79	2	0.395	6.926	0.002
Snake Treatment	* Sequence		0.695	2	0.347	6.091	0.003
Error			5.476	96	0.057		
Table 2E. ANOVA table for Merriam's Kangaroo Rat (<i>D merriami</i>) N=129, Multiple R²=.406							
Sequence			0.138	1	0.138	2.912	0.09
Snake Treatment			0.891	2	0.446	9.4	<0.001
Snake Treatment	* Sequence		0.162	2	0.081	1.709	0.185
Error			5.83	123	0.047		

534 Variables: Species (GA, GP, CP, DM), Snake Treatment (Horned-Viper, Sidewinder, Control), Sequence
535 (Pre-, Post-Exposure)

536

537 **Figure Legends**

538 **Fig 1.** Giving-up densities (GUDs) \pm SE combined for all four rodent species pre- and post-
539 exposure.

540 **Fig 2.** Cumulative proportion (active/total per treatment) of active foraging trays pre- (A) and
541 post-exposure (B). “N” represents the novel snake treatment for each species. Black, gray and
542 white bars represent sidewinder rattlesnakes, Saharan horned vipers and snake-less treatments
543 respectively.

544 **Fig 3.** Perception of risk of familiar and novel snakes, in pre- and post-exposure interviews, as
545 reflected by giving-up densities (GUDs) \pm SE. Each frame subfigure depicts the response of one
546 species: (A) DM, (B) CP, (C) GA and (D) GP. The rodents were exposed to Saharan horned
547 vipers from the Negev and sidewinder rattlesnakes from the Mojave. In each frame the diagonal
548 striped bar reflects the snake that is evolutionarily novel, the gray bar is the known snake and the
549 white bar is the snake-less control.

550 **Fig 4.** Random-Forest Decision-Tree with GUD as the dependent variable and species, snake-
551 treatment and sequence as the independent variables. The figure is read from left to right with
552 greater value to the initial nodes (left) than to final nodes marked with a bold outline.

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