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Predator-driven natural selection on risk-taking behavior in anole lizards

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1 **Title: Predator-driven natural selection on risk-taking behavior in anole**
2 **lizards**

3

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16

17 **One sentence summary:** “Natural selection on behavior”

18 **Abstract**

19 Biologists have long debated behavior's role in evolution, yet understanding its role as
20 a driver of adaptation is hampered by the scarcity of experimental studies of natural
21 selection on behavior in nature. After showing that individual *Anolis sagrei* lizards vary
22 consistently in risk-taking behaviors, we experimentally established populations onto
23 eight small islands either with, or without, *Leiocephalus carinatus*, a major ground
24 predator. Selection predictably favors different risk-taking behaviors under different
25 treatments: exploratory behavior is favored in the absence of predators whereas
26 avoidance of the ground is favored in their presence. On predator islands, the selection on
27 behavior is stronger than selection on morphology, whereas the opposite holds on islands
28 without predators. Our field experiment demonstrates that selection can shape behavioral
29 traits, paving the way to adaptation to varying environmental contexts.

30 Understanding the role of behavior in adaptation of animals to new environmental
31 circumstances remains a major challenge in biology. Research has long addressed the
32 debate about whether behavior spurs or impedes evolution (1–3) on phenotypic
33 dimensions such as morphology (4, 5) or physiology (6). In order to unravel the process
34 by which behavior shapes adaptation, we must examine how natural selection operates
35 among individuals in a population (7, 8). Recent growth in the study of inter-individual
36 variation in behavior (9–11) has revealed that behavior often varies consistently among
37 individuals within a population (12), and recent studies have also suggested this variation
38 has fitness consequences (13–16). These observations set the stage to investigate the
39 hypothesis that natural selection on inter-individual variation in behavior could drive
40 different ecological and evolutionary trajectories for populations under different selective
41 regimes (7, 8, 17–20). Assessing a hypothesis like this under natural conditions requires
42 controlled experiments in which natural selection is quantified under contrasting selective
43 regimes generated by manipulating well-known selective pressures (21). Here we used
44 small Caribbean islands as replicates to test directly whether and how natural selection
45 operates on lizards with different behaviors and morphologies under different selective
46 regimes.

47

48 We conducted this experiment on a well-studied predator-prey system involving the
49 small lizard *Anolis sagrei* – commonly found on or near the ground (22, 23) – and its
50 ground-dwelling predator, the larger lizard *Leiocephalus carinatus* (24) (Fig. 1A). We
51 focused on individual variation in two behaviors of *A. sagrei* (Fig. 1B) that are
52 consistently repeatable across time and in different contexts within individuals of this
53 species (25, see repeatability scores from this study in Table S1). Specifically, the
54 rapidity of individuals to explore new and potentially dangerous environments and the
55 time individuals spend on the ground and thereby potentially exposed to ground-dwelling
56 predators (26). The ecological relevance of these risk-taking behaviors in *A. sagrei* is
57 illustrated by a simple cost-benefit tradeoff (27, 28). *A. sagrei* individuals more willing to
58 explore new environments should survive better in the absence of significant predation
59 pressures (17) because they are more likely to obtain resources. In contrast, *A. sagrei*
60 individuals that spend more time exposed on the ground are more vulnerable to ground

61 predators as compared with individuals that spend less time exposed on the ground (22,
62 25, 29). Previous studies have reported differences in habitat use and modulation of
63 social signals in *A. sagrei* populations in the presence or absence of *L. carinatus* (30, 31),
64 leading us to hypothesize that variation in risk-taking behavior might be adaptive.

65

66 To experimentally examine natural selection on these risk-taking behaviors under natural
67 conditions, we translocated 274 adult *A. sagrei* individuals onto eight small islands in the
68 Bahamas (Fig. S2). Lizards were captured from source islands in the study area that
69 generally have higher vegetation and host more complex biological communities (32)
70 than our experimental islands, which have scrubbiest, shorter vegetation and do not
71 support resident populations of any known lizard predator (see Table S2A).

72

73 Before translocation, we used outdoor laboratory behavioral assays following (25, see
74 details in 26) to characterize inter-individual variation in two behaviors known to
75 consistently vary among individuals (25, see also Table S1). After being exposed to the
76 presence of a *L. carinatus* (position 1 in Fig. 1B), ‘time to initiation of exploration in a
77 new environment’ was defined as the amount of time until the lizard started exploring the
78 experimental cage by poking its head out of the wooden refuge (position 2 in Fig. 1B).
79 ‘Time exposed on the ground’ corresponded to the interval of time during which the
80 lizard was out of the refuge (position 3 in Fig. 1B) until it climbed on the perch or hid
81 underneath the rocks (position 4 in Fig. 1B). Each lizard was X-rayed (Fig. 1C) and
82 individually tagged before translocation onto experimental islands. We randomly
83 assigned individuals to islands. Each island received lizards in proportion to its vegetated
84 area, which was determined conducting vegetation transects following (32)(see details in
85 26). A week later, we added *L. carinatus* on four randomly selected islands, while the
86 other four islands remained as predator-free controls. Four months later, we re-captured
87 lizards on each of the experimental islands and identified surviving adult lizards from
88 their individually unique sub-cutaneous tags.

89

90 Based on re-capture data, we found that survival was lower on predator islands as
91 compared to predator-free islands (mixed-effects model including island ID as a random

92 factor and modeled following the Binomial Distribution; $p < 0.001$; Fig. S3A). We also
93 observed that *A. sagrei* from predator islands used the ground less frequently (16.9 % of
94 observations) than those from predator-free islands (41.4 % of observations), and mean
95 perch height was over twice as high on predator islands (33.9 cm) compared to predator-
96 free islands (14.4 cm) ($t = -4.9$, $df = 102.5$, $p < 0.001$; Fig. S3B).

97

98 Because *A. sagrei* is a sexually dimorphic species in which males and females differ in
99 both morphology and behavior (23, 33; see also Fig. S8-S10), we hypothesized that
100 natural selection on inter-individual variation in behavior could operate differently
101 between sexes under different environmental conditions. On predator-free islands, natural
102 selection favored females that took less time to initiation of exploration in the
103 experimental trials conducted before release (Fig. 2), a pattern not observed on predator
104 islands (Fig. 2). On predator islands, females that spent less time exposed on the ground
105 had a greater chance of survival (Fig. 2). Behavior was not a significant predictor of
106 survival for males (Fig. S3A). Whether or not *A. sagrei* were initially captured from
107 islands with *L. carinatus* present did not significantly affect their chances of survival
108 during the experiment (Table S3).

109

110 That we only found significant selection on time spent on the ground on predator islands
111 for females, but not males, suggests a greater effect from predatory lizards on females
112 compared to males. In support of this possibility, female mortality was higher on predator
113 islands as compared to predator-free ones ($X^2 = 9.7$, $p = 0.002$), whereas for males there
114 was no difference ($X^2 = 2.9$, $p = 0.086$; Fig. 3A). In addition, on predator islands, use of
115 the ground was also lower in females than in males (11.9 % vs. 22.9 % respectively; $X^2 =$
116 41.9, $p < 0.001$; Fig. 3B). Because *A. sagrei* feeds primarily on the ground (23), the
117 observed patterns of ground use suggest that females could be having more difficulties
118 obtaining food resources on the predator islands. Indeed, four months after experimental
119 translocation, females were in poorer body condition on predator islands than on
120 predator-free islands ($p < 0.001$), a pattern not observed in males ($p = 0.68$) (Fig. S3).
121 Together, these results suggest that differences in habitat use between sexes influence
122 natural selection on behavioral traits.

123

124 A long-standing debate in evolutionary biology concerns the association between
125 behavioral and morphological evolution (1, 2, 34). Our study design allowed us to
126 investigate whether selection on morphological traits occurs simultaneously with
127 selection on behavioral traits and to assess if selection on both phenotypic dimensions
128 was correlated. Specifically, we tested a well-established morphological pattern in *Anolis*
129 lizards: that the use of the ground or other broad surfaces favors longer limbs, which
130 provide greater sprinting abilities (reviewed in (23)). We found that females with longer
131 hindlimbs relative to their body size survived better than shorter-limbed individuals on
132 predator-free islands ($p = 0.002$; Table 1; Fig. S6). This is consistent with our observation
133 that females used the ground more often on predator-free islands than on predator islands
134 (Figure 3b). On predator islands, relative hindlimb length did not affect survival ($p =$
135 0.26 ; Fig. S6). We did not find selection on the relative hindlimb length for males ($p >$
136 0.80) in either experimental treatment. In addition, we found that smaller females
137 survived better on predator islands than larger individuals ($p = 0.013$; Table 1). Finally,
138 selection on behavior and morphology was not correlated. For females from predator-free
139 islands, selection for longer hindlimbs was independent of selection for increased
140 exploratory behavior (shown by the lack of a significant interaction term in mixed models
141 shown in Table 1). On predator islands, selection for smaller females was also
142 independent of selection favoring individuals that spent less time exposed on the ground
143 (Table 1). Overall, these results indicate that natural selection on behavior can occur
144 simultaneously and independently with selection on morphology.

145

146 Given that selection operated on both morphology and behavior, we asked which of these
147 factors explained a higher proportion of the variation in mortality in females (no
148 significant factors were detected in males). An analysis of the proportion of variation in
149 mortality explained by behavior versus morphology (26) revealed that, on predator-free
150 islands, selection on hindlimb length explained 19.1% of the variation in mortality,
151 whereas selection for more exploratory females accounted for 13.9%. Conversely, on
152 predator islands, the proportion of variance in mortality explained by time exposed on the
153 ground was 22.5%, whereas body size (SVL) accounted for 9.8%. These findings suggest

154 that although both behavior and morphology can simultaneously contribute to adaptation,
155 their importance is context dependent, varying under different selective regimes.

156
157 Although behavior largely defines how animals interact with the environment, the
158 evolutionary consequences of inter-individual variation in behavior remain largely
159 unknown (7, 8). Our replicated field study provides evidence that natural selection
160 operates differently on inter-individual variation in behavior under different,
161 experimentally manipulated selective pressures. Moreover, our results indicate that
162 differences in habitat use between sexes likely influence the strength of natural selection
163 on behavioral traits. By showing that selection can simultaneously and independently
164 operate on behavior and morphology, we demonstrate that rapid environmental changes
165 can shape different phenotypic dimensions at the same time; the evolutionary outcome of
166 such selection will depend on the genetic basis of these traits and the extent to which they
167 are correlated. Our results thus underscore the need to explicitly integrate inter-individual
168 variation in behavior as a relevant phenotypic dimension in studies of adaptation (7, 8,
169 35). In fact, we show that under increased predation pressure, behavior is a more
170 important factor explaining survival than the morphological traits that have been the
171 subject of previous investigation (22)—the extent to which these results will be general
172 across species remains to be discovered. Our results demonstrate that consistent
173 behavioral variation among individuals can be an important focus of selection when
174 populations experience novel environmental conditions, an increasingly common
175 situation in the current context of global change.

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228 **Figure legends and Tables:**

229

230 **Figure 1 | Assessment of risk-taking behavior and morphological characterization of *A.***

231 *sagrei* individuals. **A**, *Anolis sagrei* (left) and *Leiocephalus carinatus* (right) photographed on
232 the experimental islands. **B**, Experimental assessment of behavioral traits (26). Following (25), *A.*
233 *sagrei* were gently placed into a wooden refuge inside a butterfly cage. During a three-minute
234 habituation period, we placed a clear plastic cage that contained a live adult curly-tailed lizard
235 between the refuge and a natural perch. Then, we remotely opened the door of the refuge and the
236 *A. sagrei* was able to see the predator for five minutes (1). At the end of this period, we closed the
237 door of the refuge and removed the plastic container with the curly-tailed lizard from the
238 experimental cage. After another five-minute habituation period we again opened the refuge
239 cover and measured the ‘time to initiation of exploration in a new environment’ (2) -defined as
240 the time interval between the time we opened the refuge cover and the time when the lizard
241 started exploring the experimental cage by poking its head out of the refuge. We defined ‘time
242 exposed on the ground’ as the interval between the ‘exposed time start’ (3), defined as the time
243 when the experimental lizard went out of the refuge (i.e. all its body, excluding the tail), and the
244 ‘exposed time end’ (4), the time the lizard either climbed the perch or hid underneath the rocks.
245 Further details are provided in the Methods section. **C**, Example of an X-ray image from which
246 we measured the morphological traits in this study (i.e. SVL and hindlimb length).

247

248 **Figure 2 | Effects of time to initiation of exploration in a new environment (A) and time**
249 **exposed on the ground (B) for the survival of female *A. sagrei* on predator-free vs. predator**
250 **islands. Solid lines represent the fitted model logistic regression and dashed lines represent the**
251 **95% confidence intervals. Results pooling both sexes can be found in Table S4.**

252

253 **Figure 3 | Comparison of survival frequencies and habitat use between sexes and**
254 **experimental treatments. A**, The proportion of females surviving was higher on predator-free
255 islands as compared with predator islands, but this difference was marginally non-significant for
256 males. Error bars indicate +/- (SEM). **B**, Both sexes used the ground less on predator islands, but
257 this difference was greater for females than for males.

Females					
Predator-free islands					
(n = 63)					
		Estimate	SE	z	p-value
	(Intercept)	2.82	1.05	2.7	0.007
Random effects					
	Island	0.18	0.423	0.43	0.669
Fixed effects					
	Time to initiation of exploration	-1.03	0.4	-2.55	0.011
	Relative hindlimb length	48.7	15.78	3.08	0.002
Predator islands					
(n = 68)					
		Estimate	SE	z	p-value
	(Intercept)	14.68	5.55	2.65	0.008
Random effects					
	Island	0	0	0	1
Fixed effects					
	Exposed time on ground	-1.27	0.61	-2.1	0.035
	Body size (SVL)	-0.34	0.14	-2.48	0.013

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273 collected the data. O.L. analyzed the data. All authors extensively discussed results and
274 contributed to manuscript preparation. **Competing interests:** The authors declare no competing
275 interests. **Data and materials availability:** Data are available from the Dryad Digital Repository.
276
277 **Supplementary Materials**
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282 References (36-43)