

The effects of exposure to predators on personality and plasticity

running title: Predator Exposure Effects on Behavior

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Abstract

Past experiences are known to affect average behavior but effects on “animal personality”, and plasticity are less well studied. To determine whether experience with predators influences these aspects, we compared the behavior of *Gryllobates sigillatus* before and after exposure to live predators. We found that emergence from shelter and distance moved during open-field trials (activity) changed after exposure, with individuals becoming less likely to emerge from shelters but more active when deprived of shelter. We also found that plasticity in activity increased after exposure to predators and some indications that differences among individuals (i.e. “personality”) in emergence from shelter and the amount of an arena investigated increased after exposure. Our results demonstrate that experience with predators affects not only the average behavior of individuals but also how individuals differ from each other—and their own prior behavior—even when all individuals have the same experiences.

Key Words: predator exposure, within- individual variation, between individual variation, repeatability, latency, open field

1 **Introduction**

2 'Animal personality' has been defined as repeatable among individual variation in behavior
3 (Dall et al. 2004). This can informally be thought of as differences amongst individuals in
4 their average behaviors (for formal statistical definitions see Dingemanse and
5 Dochtermann 2013). These repeatable behavioural differences have important ecological
6 and evolutionary implications (reviewed by Wolf and Weissing 2012). Personality
7 variation has also been found to broadly correlate with fitness (Smith and Blumstein 2008)
8 and to be underpinned by genetic variation (Dochtermann et al. 2015).

9 Repeating behavioral variation has been observed across species (Gosling 2001,
10 Bell et al. 2009) but most research has focused on vertebrates (Bell et al. 2009), a pervasive
11 and pernicious problem in the study of behavior (Rosenthal et al. 2017). Eusocial insects
12 are an exception and their behavioral variation has been well described. Eusocial insects
13 exhibit high behavioral variation due to complex caste organization, and can vary within
14 and among colonies effect of group living on behavioral traits and hypothesizes that
15 mixtures of behavioral types in a colony has shaped the evolution of division of labor (Jandt
16 et al. 2014). The long-standing focus on birds and mammals (Rosenthal et al. 2017) in the
17 study of behavior is potentially misleading as to how the majority of animals behave. For
18 example, many invertebrates exhibit a wide range of life history events not seen in more
19 well-studied taxa, with correspondingly unique behaviors. The dramatic physiological and
20 morphological rearrangement accompanying metamorphosis may also lead to a
21 rearrangement of behavior. Indeed, repeatability across even just hemimetabolous
22 metamorphosis differs by sex in crickets (*Gryllus integer*; (Hedrick and Kortet 2012)).
23 Consequently, invertebrate personality research is necessary to determine the generality of
24 mechanisms proposed to underpin personality variation.

25 As is now well recognized, the among-individual variation that characterizes
26 personality is not mutually exclusive of the expression of behavioral plasticity. The
27 compatibility of the two is perhaps most clear when an evolutionary reaction norm
28 approach is adopted (Dingemanse et al. 2010) but can also be apparent with both more

29 classic approaches to studying plasticity and by examining how variation *not* explained by
30 among-individual differences changes with experience or time. As detailed by Westneat et
31 al. (2015) variation unexplained by statistical models, including those used to estimate
32 among-individual variation in studies of personality, represents plastic variation (and
33 measurement error) and this is often a considerable amount of the biologically relevant
34 variation in behaviors (see also Lynch and Walsh 1998, Whitman and Agrawal 2009, Bernal
35 and Dochtermann 2019). For example, in crickets (*Acheta domesticus*) manipulation of diet
36 during development affected plasticity/within-individual variation despite no clear effects
37 on either average behaviors or among-individual variation in personality (Royauté and
38 Dochtermann 2017, Royauté et al. 2019).

39 One particularly important potential contributor to personality and plasticity is
40 predation risk and exposure to predators. Animals assess risks in their environment and
41 this assessment influences decision making to optimize fitness (Lima and Dill 1990).
42 Predation risk has been documented to shape all attributes of behavior: means, variances,
43 and correlations. Firstly, mean behavioral responses have been shown to be affected by
44 predator exposure. For example, in stickleback fishes an individual's behavior while under
45 high risk of predation is shy and less active (Furtbauer et al. 2015). Secondly, long-term
46 levels of variable predator exposure lead to the evolution of increased plasticity response
47 in zooplankton, showing how behavioral variability may be influenced on an evolutionary
48 level by predation risk (Cousyn et al. 2001). Thirdly, correlations between behaviors have
49 been documented to change due to exposure to predators or predation risk. For example,
50 predation strengthens behavioral correlation in stickleback as a result of both selection
51 (bold individuals were more likely to be preyed upon) and plasticity (shift of behavior to be
52 unaggressive; Bell and Sih 2007). Similarly, populations from environments with strong
53 predatory pressure have been seen to have different personalities when compared to
54 populations from safe environments (Bell 2005, Dingemanse and Reale 2005, Dingemanse
55 et al. 2007). In contrast, Madagascar hissing cockroaches with a bold-active behavioral
56 syndrome responded to repeated predator exposure with a shift in boldness independent
57 of activity (McDermott et al. 2014) and a correlation between behavioral composition

58 (proportion of bold spiders) and foraging aggressiveness in social jumping spider colonies
59 was eliminated after exposure to predators (Wright et al. 2017).

60 Here we examined the effects of predator exposure on personality and plasticity in
61 the banded cricket, *Gryllobes sigillatus*. We specifically sought to determine if mean
62 behaviors change after exposure to predators and whether among-individual variation (i.e.
63 personality) and within-individual variability (i.e. plasticity) are influenced by predator
64 exposure.

65 **Methods**

66 Forty adult female *Gryllobes sigillatus* were obtained from an outbred line originally
67 collected in New Mexico (the total number of behavioral assays varied due to mortality
68 during predator exposure). Crickets were independently housed in a 0.71-liter container
69 with shelter, ad libitum food (commercially purchased chicken feed), and water. Crickets
70 were housed under a 12:12h light/dark photoperiod. All testing took place during August
71 2018.

72 Individual behavior was assessed in both latency trials and open field tests
73 conducted at the beginning of the experiment and repeated after individuals were exposed
74 to active predators. Both latency and open field trials were conducted three times before
75 exposure to predators and three times after. Post-exposure behavioral assays were started
76 24 hours after predator exposure and repeated twice at subsequent 24-hour intervals. For
77 each behavioral test, crickets were selected at random and assigned to groups of four
78 individuals (the testing apparatus was designed to conduct four simultaneous trials).
79 Temperature, time, and date of each test were recorded at the start of trials.

80 *Latency Behavioral Assay*

81 Crickets were randomly selected and placed into a 12 cm cylindrical shelter in the
82 center of a 30 cm × 30cm testing arena. After a 2-minute habituation period, one end of the
83 tube was removed and the cricket was allowed to freely emerge and move about the arena.
84 Similar methods have been used previously to measure boldness in crickets (Hedrick
85 2000). Trials were recorded to accurately measure the time required for the cricket to
86 emerge from the tube. If after 6 minutes the cricket had not emerged the trial was ended. At

87 the end of the test, individuals were captured, their mass recorded, and were returned to
88 housing containers. Video recordings were analyzed using VLC media player to determined
89 amount of time until full body emergence (max 320 seconds).

90 *Open Field Behavioral Assay*

91 Crickets were placed in the lower right corner of a 30cm × 30cm arena. After a 30 second
92 habituation period, cups were removed and subjects were allowed to move freely in the
93 testing arena for 3 minutes 40 seconds. Trials were recorded and analyzed using
94 Ethovision (Noldus Information Technology, Wageningen, The Netherlands). Each arena
95 was split into 32 unique zones (Figure S1). Measurements recorded were total distance
96 moved and number of unique zones entered. At the end of the test, individuals were
97 captured, mass was recorded, and individuals returned to their housing containers. Arenas
98 were cleaned with 70% ethanol between tests.

99 *Predator Exposure*

100 Crickets were randomly selected for the order of predator exposure. An individual cricket
101 was trapped using a plastic cup and placed in the center of a 30 cm × 30 cm arena. All
102 cricket handling was conducted in the same manner as for the Open Field Behavioral Assay.

103 Four juvenile leopard geckos (*Eublepharis macularius*) were used throughout the
104 duration of the experiment, removed from individual housing, and placed under a
105 cardboard cup in the same arena as were the crickets. After a 30 second habituation period,
106 leopard geckos were released from the cups. Immediately afterwards, test subjects were
107 released from their cups. Predator exposure experiment lasted 10 minutes or until the
108 subject experienced an attack by the gecko. Attacks were defined as a missed strike, a
109 strike that injured the cricket, or a successful strike. At the end of the test, individual
110 crickets were captured, had their mass recorded, and returned to housing containers. The
111 exposure arena was cleaned with 70% ethanol between all tests to eliminate any social or
112 predator cues left in the arena. All geckos were housed and cared for according to NDSU
113 IACUC Protocol A17027 and the guidelines described by the Animal Behavior Society
114 (2012).

115 We did not include a control treatment because the arenas used for predator
116 exposure were the same arenas which had previously been used for the pre-exposure open
117 field behavioral assays. Consequently, each cricket's pre-exposure trials act as procedural
118 controls as the only difference pre- and post-exposure was exposure to the leopard geckos.
119 Subsequent analyses can therefore be considered analogous to a paired t-test.

120 *Statistical Methods*

121 To assess the effect of exposure to predators on behavioral means and variances we
122 analyzed the behavioral data using linear mixed effects models (Dingemanse and
123 Dochtermann 2013). Specifically, we fit models wherein exposure (pre or post),
124 temperature (Celsius, mean centered), and mass (grams, mean centered) were included as
125 fixed effects and individual was fit as a random effect.

126 To separately tease apart whether exposure to predators affected among- or within-
127 individual variances (or both) we fit four distinct models with each variance differentially
128 modeled. Following Royauté et al. (2019), we fit (i) a model where among- and within-
129 individual variances were the same before and after exposure, (ii) a model where among-
130 individual variances differed before and after exposure but within-individual variances
131 remained the same, (iii) a model where within-individual variances differed but among-
132 individual variances did not change, and (iv) a model where both among- and within-
133 individual variances differed before and after exposure. The four models were compared
134 using Deviance Information Criterion scores (DIC) to determine which model structure
135 best fit the data. An alternative approach to this "character state" analysis would be using a
136 random regression approach where the pre and post exposure periods are treated as an
137 environmental gradient over which a reaction norm is expressed. We did not use such an
138 approach here because for the two environment case, the character state and reaction
139 norm approaches are mathematically equivalent. The reaction norm approach would also
140 have made the interpretation of differences in among- and within-individual variances
141 more difficult.

142 "Significance" of a fixed effect was determined based on the probability that an
143 estimate was greater or less than zero (whichever was smaller). DIC scores were compared

144 to each other, with particular inferential credence given to models with substantially lower
145 scores than others. DIC scores are evaluated in a relative manner without the concrete
146 cutoff criteria used with p-values. Instead, we interpreted a DIC difference between the
147 best fit model and a competitor (i.e. Δ DIC) of 5 or greater as a substantial reduction of
148 explanatory power. A Δ DIC of 10 or greater suggests a model is of little inferential utility
149 (Barnett et al. 2010).

150 All models were fit using the `MCMCglmm` library (Hadfield 2010) in the R
151 programming environment. Models were fit using parameter expanded priors and fit for
152 2.6×10^6 iterations with a burn-in of 6×10^5 iterations and a 2000 iteration thinning
153 interval. This combination of priors and chain length maintained high levels of mixing and
154 low levels of autocorrelation (variance component autocorrelations were all less than 0.06
155 even for Poisson distributed behaviors). Distance moved was fit as Gaussian distributed
156 while unique zones visited and emergence (no or yes) were fit, respectively, as Poisson and
157 Binary distributed. From these models we also estimated the behavioral variance explained
158 due to fixed effects and estimated adjusted repeatabilities following Nakagawa and
159 Schielzeth (2010) & (2013).

160 We were not able to fit multivariate models due to the mixture of error
161 distributions: multivariate models failed to properly converge despite doing so for
162 univariate models. This prevented us from assessing the effects of exposure to predators
163 on behavioral syndromes despite that originally being one question of interest.

164 **Results**

165 Prior to exposure, mean distance traveled during the open field trials was 220.43 cm, mean
166 number of unique zones visited 15.51, and mean latency to emerge was 164.10 seconds.
167 Post-exposure mean distance moved was 305.49 cm, mean number of unique zones visited
168 15.95, and mean latency to emerge 245.02 seconds. Activity in the open field and
169 emergence from shelter significantly differed pre to post exposure ($p = 0.034$ & 0.006
170 respectively; Figure 1, Table 1). Unique Zones visited were not significantly different pre to
171 post exposure (Figure 1B, Table 1). Mass significantly affected activity ($p = 0.03$) and UZ (p

172 = 0.03), but not emergence ($p = 0.956$). Temperature did not have a significant interaction
173 with exposure conditions on any behavioral responses (Table 1).

174 The influence of predator exposure on among-individual and within-individual
175 variances of behavioral response varied by behavior (Table 2). For activity, the top model
176 suggested that within-individual variation, but not among-individual variation, differed
177 following exposure to predators (Table 2). For UZ, the top model included differences in
178 among-individual variances but no one model could be distinguished from the rest (Table
179 2). Similarly, for emergence, the top model included a change in among-individual variance
180 following exposure but a similarly weighted model suggested no change in variances
181 (Table 2).

182 These model comparison conclusions about differences in variances pre- and post-
183 exposure are reflected in changes in both the magnitude of variances and in the
184 magnitudes of repeatabilities (τ ; Table 3). Most notably, the repeatability of emergence
185 drastically increased following exposure—from 0.13 to 0.59. This was driven by an
186 increase in the among-individual variance following exposure (Table 3), a finding
187 consistent with the top model examining changes in variances. Recall, however, that this
188 top model could not be clearly distinguished from others (Table 2). In contrast, based on
189 model comparison results and estimate uncertainties, an increase in repeatability of
190 activity following exposure was driven by a substantial decrease in within-individual
191 variances.

192 **Discussion**

193 Comparing pre- and post-predator exposure behavior, we found a shift in both mean
194 behaviors and individual variances. Notably, after predator exposure, activity significantly
195 increased and emergence significantly decreased in *Gryllodes sigillatus* (Table 1, Figure 1A).
196 Biologically, increased activity can be used as an anti-predator response (Jones and Godin
197 2009, Wilson et al. 2010) and crickets are known to respond by increasing activity in
198 response to some spider predators (Binz et al. 2014). Similarly, in grasshoppers,
199 individuals respond to predators with active hunting strategy (as is the case for leopard
200 geckos) by increasing their activity (Miller et al. 2014). In this study, subjects potentially

201 increased activity after predator exposure as a general response to avoid capture by
202 predators. Similarly, delaying emergence (Figure 1C) is often considered a measure of
203 cautiousness, or the inverse of boldness (Hedrick and Kortet 2012). Consequently, the
204 decreased probability of emergence following exposure is perhaps an anti-predator
205 response in which crickets avoid leaving safety when there exists a known predator threat.

206 Interestingly, exposure to predators did not affect behavioral variation in the same
207 direction across behaviors. Plasticity, or within-individual variation, differed pre- and post-
208 exposure for the distance moved (Table 2) and was greater after exposure (Table 3).
209 Therefore, individuals become more plastic in their behavior after exposure to predators.
210 This also creates the possibility for increased individual differences in behavioral
211 responses to predator interaction with some individuals moving erratically and others not
212 at all as an anti-predator tactic. Predator-exposure coping mechanisms are therefore
213 potentially individual specific and successful tactics can lead to evolutionary changes.
214 Unfortunately, assessing this possibility is not possible with the current data, requiring the
215 use of data-hungry approaches (such methods are described in Cleasby et al. 2015).

216 Among-individual variance also potentially differed pre- and post- exposure for
217 emergence (Table 2), being greater after exposure (Table 3). While there was mixed
218 support for this conclusion, it suggests that individuals may become more fixed in their
219 differences from each other in whether they emerge or not after exposure. Further,
220 repeatability of the behavior increased substantially despite an absence of clear specific
221 differences in among- or within-individual variances. These results suggest an increased
222 conformity to an individual's behavioral type after exposure, i.e. anti-predator tactics are
223 individual specific. Importantly this also shows that the behavior of individuals continues
224 to differ—and possibly increases—even when presented with the same experiences. This
225 could suggest the emergence of new behavioral tendencies: if individuals randomly emerge
226 from shelter under conditions without pressure, new individually specific latency
227 personalities may effectively canalize after life experiences. This possibility is consistent
228 with Bayesian updating models of development (Stamps et al. 2018) but, due to the
229 ambiguous results regarding emergence here, future work should further investigate this
230 possibility in crickets.

231 Previous research has similarly shown that predator exposure changes average
232 anti-predator responses from subjects, with putative effects on survival probabilities. For
233 example, predator-naïve mammals exposed to predators under controlled conditions
234 showed changes in behavior including increased wariness and greater flight initiation
235 distances (West et al. 2018). Second-hand fear cues, bedding material used by predator-
236 exposed voles, lead to increased litter sizes and sex based behavioral changes in regard to
237 the bedding (Haapakoski et al. 2018). Such results show a population level effect on
238 individuals who have not been directly exposure to a predator. In contrast, the results of
239 our study suggest that patterns of behavioral change rely on individual specific anti-
240 predator responses and a combination of changes in average behavior and in variances.
241 This result has important implications for our understanding of the interaction between
242 selection and personality. For example, in crabs (*Panopeus berbstii*), individual specific
243 behavioral responses interacted with predator type to affect survival (Belgrad and Griffen
244 2016).

245 Animals constantly assess risks in their environment and use this information to
246 guide decision making (Lima and Dill 1990), with personality having been shown to affect
247 survival rates in response to predation threat (Santos et al. 2015). The results of this study
248 show that *Gryllodes sigillatus* likewise use information from predator experience to shape
249 behavior. Comparing pre- and post-exposure behavioral assays, we demonstrated a shift in
250 mean behaviors and in how individuals differ from each other (variances). Thus, exposure
251 to predators can change among-individual differences—personality—and plasticity.

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360 Tables & Figures

361 Figure Legends

362 Figure 1: Differences in average behavioral response pre- and post-exposure to a predator.

363 (A) Activity, estimated as distance traveled in the open field, significantly increased
364 following exposure ($P_{mcmc} = 0.034$). (B) The number of unique zones visited did not
365 significantly change in response to predator exposure. (C) Probability of emergence
366 significantly decreased following exposure ($P_{mcmc} = 0.006$).

367 Figure S1: Schematic of the open-field arena.

368 Table 1. Summary of fixed effect estimates on behavioral responses, values are posterior
 369 means. Results are from Bayesian analyses fit using the `MCMCglmm` package in R. Fixed
 370 effect structure was the same for each of the three behavioral responses: Pre-exposure was
 371 fit as the intercept against which the estimate for post-exposure was contrasted (i.e. the
 372 estimate for Post-exposure would be the sum of the pre- and post-exposure estimates). The
 373 effects temperature (Celsius, mean centered) and mass (g, mean centered) were also
 374 estimated for post-exposure, with pre-exposure then contrasted (i.e. exposure ×
 375 temperature and exposure × mass interactions). Activity was fit using a linear mixed-
 376 effects model while the unique zones visited and whether an individual emerged from
 377 shelter were fit with generalized linear mixed-effects models as Poisson distributed and as
 378 a categorical (binary) outcome respectively. Random effects structure was as in the best
 379 fitting model (Table 2). P_{mcmc} for a factor is estimated based on the number of posterior
 380 estimates that did not exclude 0.

	Estimate*	lower 95% CI	upper 95% CI	p_{mcmc}
Activity (Gaussian)				
Intercept (pre)	216.46	171.51	261.90	
vs. post	70.99	6.34	139.33	0.034
Temperature (pre)	-15.83	-74.99	52.77	0.63
vs. post	-18.04	-137.39	96.75	0.76
Mass (pre)	-707.00	-1312.21	-40.30	0.03
vs. post	867.37	-89.18	1911.61	0.09
Unique Zones (Poisson)				
Intercept (pre)	2.33	2.08	2.62	
vs. post	0.06	-0.33	0.46	0.76
Temperature (pre)	-0.003	-0.36	0.34	1
vs. post	-0.009	-0.57	0.59	0.98
Mass (pre)	-4.18	-7.50	-0.19	0.03
vs. post	5.33	0.06	10.90	0.06
Emergence (binary)				
Intercept (pre)	121.43	55.64	192.37	
vs. post	-171.90	-311.39	-32.46	0.006
Temperature (pre)	-22.69	-107.35	74.22	0.579
vs. post	33.76	-125.29	195.48	0.668
Mass (pre)	-32.53	-798.40	836.25	0.956
vs. post	-295.41	-2371.10	1345.00	0.726

381 *coefficients for mass are estimated in terms of grams. Crickets ranged in mass from 0.195
382 – 0.474 grams

383

Table 2. Results from model comparisons evaluating the fit of models in which either, or neither, among-individual (V_i) and within-individual variances (V_w) of behavioral responses differ before and after exposure to predators. Models were compared based on Deviance Information Criteria scores (DIC) and the difference in DIC between the best fitting model, i.e. the model with the lowest DIC score (in bold), and each other model (Δ DIC). Models within 2 Δ DIC values do not substantively differ in fit and are indicated by italicization.

Model	Variance comparison	Activity		Unique zones		Emergence	
		DIC	Δ DIC	DIC	Δ DIC	DIC	Δ DIC
Model 1	$V_i = \& V_w =$	3087.76	8.98	<i>1397.15</i>	<i>0.26</i>	<i>5.46</i>	<i>0.32</i>
Model 2	$V_i \neq \& V_w =$	3085.42	6.64	1396.89	0	5.14	0
Model 3	$V_i = \& V_w \neq$	3078.78	0	<i>1397.19</i>	<i>0.3</i>	14.52	9.38
Model 4	$V_i \neq \& V_w \neq$	3084.37	5.59	<i>1397.11</i>	<i>0.22</i>	7.39	2.25

Table 3. Among-individual variances (V_i) and within-individual variances (V_w) for each of the three behavioral responses, estimated separately pre- and post-exposure. Also reported is the amount of variation explained by fixed effects (V_F) and the unadjusted repeatability (τ).

	V_i (CI)	$V_w + \text{DSV}^*$ (CI)	V_F (CI)	τ^{**} (CI)
Activity				
Pre-exposure	4259 [1 : 12932]	25770 [20618 : 37871]	3334 [699 : 7971]	0.14 [0 : 0.31]
Post-exposure	15155 [0 : 33054]	47689 [35750 : 68101]		0.20 [0 : 0.41]
Unique zones				
Pre-exposure	0.28 [0 : 0.58]	0.60 [0.48 : 1.04]	0.05 [0.01 : 0.12]	0.24 [0 : 0.47]
Post-exposure	0.22 [0 : 0.61]	0.92 [0.68 : 1.50]		0 [0 : 0.38]
Emergence				
Pre-exposure	128 [0 : 20079]	16744 [678 : 49224]	3056 [494 : 19387]	0 [0 : 0.42]
Post-exposure	14879 [638 : 104923]	1913 [54 : 39224]		0.65 [0.33 : 0.86]

*DSV: Distribution specific variance. Calculated following Nakagawa and Schielzeth (2010): for Poisson distributed data (Unique zones), calculated as $\ln\left(\frac{1}{e^{\beta_0}} + 1\right)$; for binary data, calculated as: $\frac{\pi^2}{3}$

** τ : unadjusted repeatability. Calculated following Nakagawa and Schielzeth (2010) as: $\frac{V_i}{V_i + V_f + V_w}$; includes DSV.

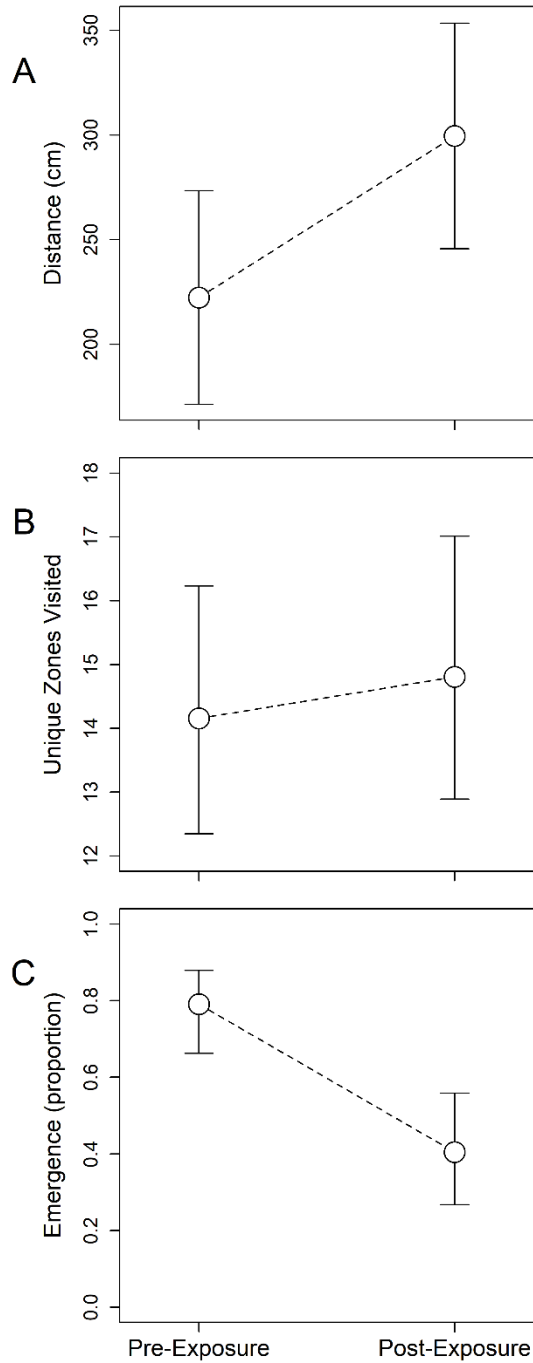


Figure 1: Differences in average behavioral response pre- and post-exposure to a predator. Points are the posterior modal estimates and error bars show the 95% highest probability density intervals. (A) Activity, estimated as distance traveled in the open field, significantly increased following exposure ($P_{mcmc} = 0.034$). (B) The number of unique zones visited did not significantly change in response to predator exposure. (C) Probability of emergence significantly decreased following exposure ($P_{mcmc} = 0.006$).

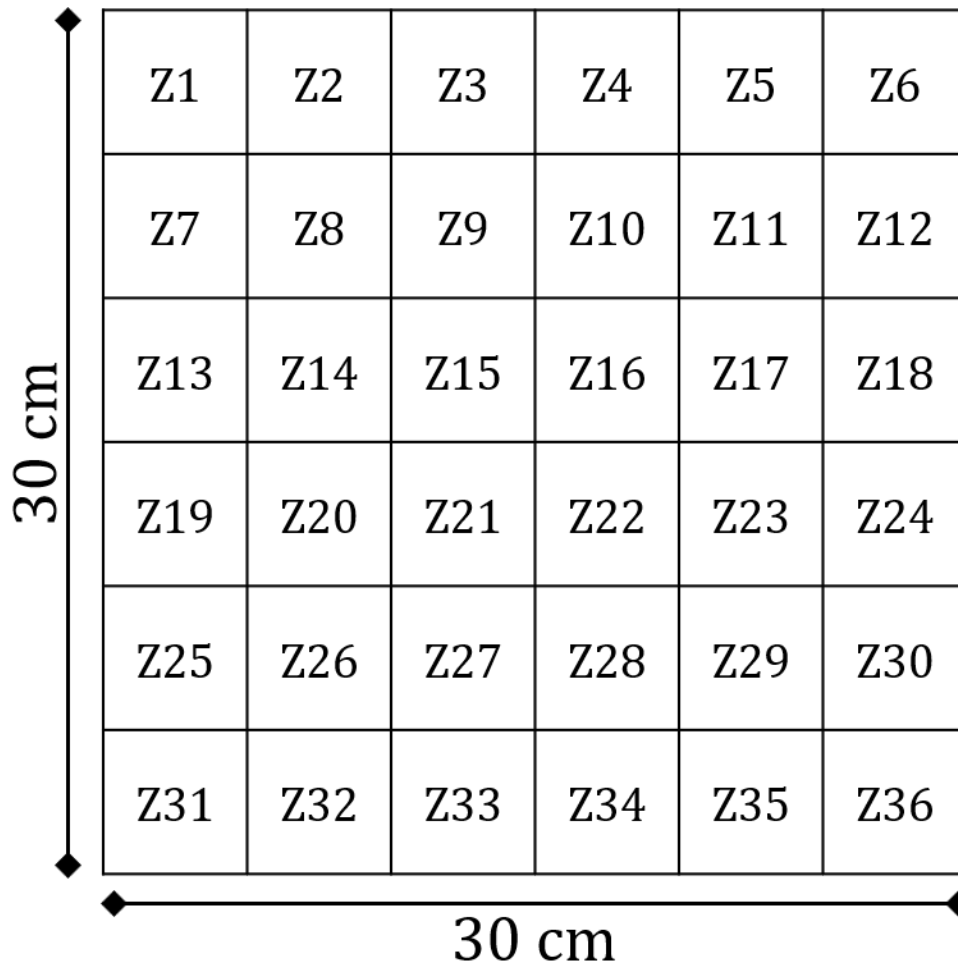


Figure S1: Schematic of the open-field arena.