

## Original Article

# Food limitation leads to risky decision making and to tradeoffs with oviposition

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A growing body of research over the past decade indicates that interindividual variation in behavior can result from a variety of factors. Two important sources of this variation are behavioral plasticity (adaptive variation in behavior) and behavioral type (i.e., an individual with consistent behavioral differences across one or more situations). Although oviposition-site selection (OS) is widespread and affects both parents and offspring, it has been overlooked in the context of the behavioral type. Thus, we used the Texas field cricket (*Gryllus texensis*) to determine if OS could be integrated into the behavioral type paradigm and if a relevant environmental variable (food limitation) influences behavioral type. We found that behavioral type was consistent across contexts because individuals exhibiting riskier (bolder) behavior in a novel environment also exhibited riskier behavior during oviposition. Also, individuals traded off safety with food availability during oviposition—that is, fasted crickets were more likely to choose food over safety (shelter) when making an oviposition decision. Last, relative to fed crickets, those that were fasted oviposited fewer eggs during overnight trials in which food was available. By integrating a behavior tightly linked to multigenerational fitness with an established behavioral assay (behavior to novel stimuli), we show that behavioral type can be both consistent across contexts and plastic in response to a ubiquitous environmental factor (food limitation).

**Key words:** behavioral syndrome, behavioral type, cricket, parental care, predation, reproduction.

## INTRODUCTION

Behavior strongly influences traits linked to animal fitness, including survival, reproduction, and energy balance (Brown 1988; reviewed in Smith and Blumstein 2008). Interindividual variation in behavior was traditionally viewed as nonadaptive “noise” around an adaptive mean (Wilson 1998). However, a growing body of research over the past decade indicates that interindividual differences result from behavioral plasticity (adaptive variation in behavior), behavioral types (individuals with consistent behavioral differences across one or more situations), or both (Sih et al. 2004; Bell 2007; Smith and Blumstein 2008; Dall et al. 2012). For example, a “bold” behavioral type may confer a fitness advantage in one environment or situation, whereas a “shy” type is advantageous in another environment or situation—thus, both types persist in variable environments (Réale and Festa-Bianchet 2003; Dingemanse et al. 2004; Sih et al. 2004). Further, examining behavioral type in different functional behavioral categories (“contexts”) and under different conditions (“situations”) can account for environmental effects and can validate the reliability of behavioral type assessments (Sih et al. 2004).

Despite the relative rigidity of behavioral type, individuals typically exhibit some amount of behavioral plasticity, which allows individuals to adapt their behavior to varying environments (Sih 1992; Dewitt et al. 1998; Sih et al. 2004; Tremmel and Müller 2013). Predation and food availability are key environmental forces that vary across temporal and spatial scales (reviewed in Brown 1988). Predation affects the behavior and fitness of animals (Lima 1998; Preisser et al. 2005; Cressler et al. 2010), and predation pressure can select for behavioral types (Bell 2005; Dingemanse et al. 2007; Luttbeg and Sih 2010; but see Pruitt et al. 2010). Food availability can also affect behaviors linked to fitness, including reproductive behaviors (Kim et al. 2008; Smith et al. 2013), foraging activity (Sogard and Olla 1996; Metcalfe et al. 1999), and activity in an open field (Heiderstadt et al. 2000). In addition to their individual effects, predation and food availability can interact to influence behavior (Brown and Kotler 2004), which can result in a foraging-survival tradeoff. For example, if predation is high, food-limited individuals must balance the benefits of increased behavioral (foraging) activity (e.g., increased energy intake) with its costs (e.g., increased risk of predation) (*sensu* the “marginal value theorem”; Charnov 1976; Brown 1988; Brown and Kotler 2004).

We used manipulative approaches to explore related tradeoffs using the behavioral type paradigm in the Texas field cricket (*Gryllus texensis*). We examined variation in behavioral type in

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different contexts (behavior in a novel environment and oviposition behavior) and situations (fed or fasted) to address 3 hypotheses related to environment-induced tradeoffs mediated by behavior. First, behavioral type is consistent across contexts. We predict that a cricket exhibiting relatively risky (bold) behavior in a novel environment will also exhibit relatively risky behavior during oviposition-site selection (OS). Many animals, including insects, exhibit OS (reviewed in Royle et al. 2012). It can profoundly affect offspring fitness, (and hence the fitness of parents) yet has been overlooked in the context of behavioral type. Second, individuals tradeoff safety with food availability during OS. Therefore, we predict that fasted crickets will be relatively more likely to choose food over safety (shelter) when making an oviposition decision. Third, fasting influences oviposition. We predict that relative to fed crickets, those that are fasted will oviposit fewer eggs during overnight trials in which food is available. By integrating a behavior tightly linked to multigenerational fitness (OS) with an established behavioral assay (behavior to novel stimuli: Boissy 1995; Hedrick 2000; reviewed in Smith and Blumstein 2008), we provide new insight into the independent and interactive effects of predation risk and food availability on behavioral type.

## MATERIALS AND METHODS

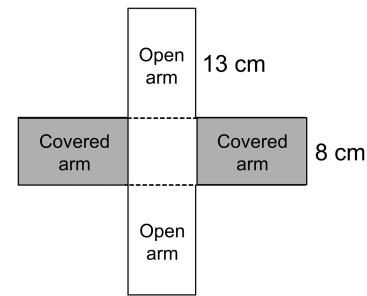
### Study animals and feeding treatments

We used long-winged adult *G. texensis* that were part of a long-term (>12 generations), predator-free colony, which has been described previously (Adamo and Lovett 2011). Initially, we held nymphs in large 166L plastic containers with approximately a few hundred nymphs per container. We supplied nymphs with abundant food, water, and egg carton shelters. Once crickets became adult, we transferred them to large, mixed sex containers (72 × 37 × 34 cm) with approximately 20–60 adults per container. This species is omnivorous and forages intermittently. Briefly, we supplied all crickets with water ad libitum and housed crickets in a room maintained at 26 ± 1 °C and a 12:12 light:dark cycle. All studies were approved by the Animal Care Committee of Dalhousie University (#I9-026) and are in accordance with the Canadian Council on Animal Care.

We used 2 behavioral trials on *G. texensis* over a 22-h period to characterize 1) the effects of food limitation on behavior in a novel environment and 2) the effects of food limitation and predation risk on OS (see below). We isolated female crickets 10–15 days post-adult molt from group housing in the colony because *G. texensis* have typically mated at least once by 10 days post-adult molt (Solymar and Cade 1990; Adamo SA, unpublished data). We individually housed crickets for 3 days in transparent plastic containers (18 × 14.5 × 9 cm). During this isolation period, we created 2 feeding treatments: “fed” crickets were supplied with food (cat food pellets) ad libitum and “fasted” crickets were not supplied with any food.

### Trial 1: Behavior in a novel environment

After 3 days of isolation, we used a “plus maze” arena to characterize crickets’ behavior in a novel environment between 11:00 and 13:00 (Figure 1). The arena was 6.5 cm high, 34 cm long, and constructed of black acrylic. It consisted of an open center region (8 × 8 cm), 2 covered (sheltered) arms, and 2 open (nonsheltered) arms. We carefully transferred each cricket from its individual container into a translucent cup (height and diameter of base: 7 cm). We then capped the cup with a sheet of black cardboard before gently inverting the cup and placing it on the floor of the center



**Figure 1**

Top-view schematic of the plus maze arena used in Trial 1: Behavior in a novel environment. Each cricket began a given trial in the center of the arena, and its behavior was monitored for 10 min. Detailed information can be found in Materials and Methods.

of the arena. Next, we carefully removed the black cardboard from the rim of the cup. After 1 min, we gently raised the cup to expose the cricket to a novel environment (i.e., the “plus maze” arena).

For 10 min, we characterized 3 behaviors associated with the bold–shy continuum or behavioral activity that were previously shown to be repeatable in *G. texensis* (Adamo et al. Forthcoming). First, we measured “freeze time,” which is the duration of time between a cricket’s exposure to the novel environment (i.e., the raising of the cup) and any motion by a cricket (e.g., walking, antennal movement, or grooming). Freezing is a stereotypic anti-detection response associated with predation avoidance across taxa (Chelini et al. 2009; reviewed in Stynoski and Noble 2012). Second, we measured the number of times each cricket entered/exited a covered arm (“covered arm exploration”). Crickets should seek the arena’s covered arms to reduce their risk of predation—thus, individuals that entered and exited multiple covered arms were presumably bolder (less risk averse) than those that simply stayed within a single covered arm during the 10-min trial period. Third, we measured the proportion of time each cricket spent locomoting (“locomotion”) as a proxy for behavioral activity. After each trial, we cleaned the arena with 70% ethanol and returned each cricket to its individual container. We weighed each cricket between 14:00 and 15:00 before OS trials (see below).

### Trial 2: OS

We used a cylindrical arena that has previously been described (Stahlschmidt and Adamo 2013) to measure OS in *G. texensis* after “plus maze” trials (see above). Briefly, the arena (height: 30.5 cm; diameter: 24 cm) had several ports for cotton-filled water bottles (height: 6.2 cm; width: 2.4 cm) that served as oviposition sites. We conducted all trials overnight and into the next morning between 17:00 on the first day until 9:00 the second day (16 h in total). At each trial’s conclusion, we counted the number of eggs laid in each oviposition site (2 sites per cricket) to determine OS. To reduce the scent of previous crickets, we lined the floor of each arena with clean white paper and wiped the inside surface of each arena with 70% ethanol prior to each trial.

In front of each oviposition site, we placed a small disposable weigh boat. We randomly filled one of these 2 weigh boats with approximately 0.27 g of ground cat food (equivalent to 1 cat food pellet), whereas the other weigh boat was left empty. Thus, only one oviposition site was adjacent to food. We also placed a shelter over one of the 2 oviposition sites. Each shelter had 2 ports that allowed crickets access to the water bottle and to leave/enter the shelter. The shelters were opaque plastic and in the shape of

a truncated cone (height and diameter of base: 7 cm). Crickets are thigmotactic and prefer sheltered areas over nonsheltered areas likely due to higher rates of predation in nonsheltered areas (Sakaluk and Belwood 1984; Hedrick and Dill 1993; Csada and Neudorf 1995; Hedrick 2000; Stahlschmidt and Adamo 2013). Thus, we created one oviposition site with low predation risk by providing shelter, and we created another site with high predation risk by not providing shelter. Together, this design produced 2 shelter treatment groups: “Food sheltered” was an ideal scenario (an oviposition site where food was sheltered), whereas “Food not sheltered” was a nonideal scenario (where crickets were forced to choose between an oviposition site with food but not shelter and a site with shelter but not food).

## Statistical analyses

We performed all analyses with SPSS (version 19, IBM Corp.), and we determined 2-tailed significance at  $\alpha < 0.05$ . All data met the assumptions of parametric statistics, were transformed as necessary, or were analyzed using nonparametric tests (see below).

We used principal components analysis (PCA) to generate an index of behavioral type in a novel environment using “freeze time,” “covered arm exploration,” and “locomotion” as initial variables. For subsequent analyses, we included the only principal component (PC) with an eigenvalue  $> 1$  (accounting for 59% of the variance), which loaded negatively onto “freeze time” (−0.36) and positively onto “covered arm exploration” (0.89) and “locomotion” (0.92)—that is, a relatively high PC score reflected less freeze time and more exploration and activity. Thus, we herein refer to this PC as “plus maze boldness.”

We also used PCA to generate an index of behavioral type that integrated behavior in the plus maze and during oviposition. We included “freeze time,” “covered arm exploration,” “locomotion,” and the proportion of eggs laid in the sheltered oviposition site as initial variables. For subsequent analyses, we included the only PC with an eigenvalue  $> 1$ , which accounted for 47% of the variance. Behavior in the plus maze and during oviposition was correlated because this PC loaded negatively onto “freeze time” (−0.37) and the proportion of eggs laid in the sheltered oviposition site (−0.20) and positively onto “covered arm exploration” (0.89) and “locomotion” (0.92)—that is, a relatively high PC score reflected less freeze time and relatively fewer eggs laid in the sheltered oviposition site, and more exploration and activity. Thus, we herein refer to this PC as “integrated boldness.”

To determine the effects of food limitation on behavior type, we used a log-rank test (Mann–Whitney  $U$  test) to compare the boldness indices (plus maze boldness and integrated boldness) of fed and fasted crickets because data were not normally distributed. To examine a tradeoff between shelter and feeding status during oviposition, we used a mixed model with the number of eggs laid in the sheltered oviposition site as the dependent variable, feeding status and shelter treatment as fixed effects, individual ID as a random effect, and the total number of eggs laid and femur length (a proxy for body size) as covariates. To examine a tradeoff between feeding and oviposition, we used a linear mixed model with the total number of eggs laid as the dependent variable, feeding treatment and shelter treatment as fixed effects, individual ID as a random effect, and femur length as a covariate. To determine whether food limitation affected behavioral consistency, we used the Fisher  $R$ -to- $\zeta$  transformation to compare the correlation coefficient between “plus maze boldness” and the proportion of eggs laid in the sheltered oviposition site of fed and fasted crickets.

## RESULTS

### Trial 1: Behavior in a novel environment

Fasted crickets ( $n = 28$ ) had a higher plus maze boldness than fed crickets ( $n = 29$ ) ( $U = 277$ ,  $\zeta = 2.07$ ,  $P = 0.039$ )—that is, fasted crickets tended to be relatively exploratory and active in a novel environment.

### Trial 2: OS

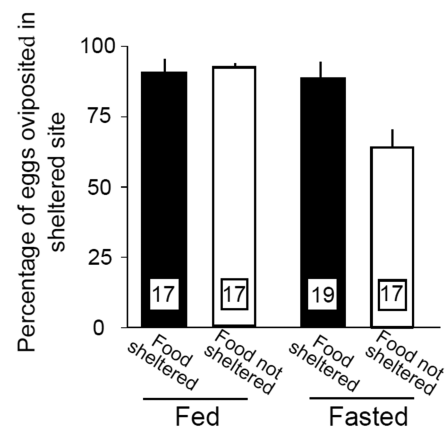
The relative number of eggs that females laid at the sheltered oviposition site was affected by feeding treatment ( $F_{1,64} = 6.61$ ,  $P = 0.012$ ) and a feeding  $\times$  shelter treatment interaction ( $F_{1,64} = 5.38$ ,  $P = 0.024$ ), but not by shelter treatment alone ( $F_{1,64} = 2.41$ ,  $P = 0.13$ ) or femur length ( $F_{1,64} = 3.21$ ,  $P = 0.078$ ) (Figure 2). The total number of eggs that females laid was affected by feeding treatment ( $F_{1,65} = 18.7$ ,  $P < 0.001$ ) and a feeding  $\times$  shelter treatment interaction ( $F_{1,65} = 5.43$ ,  $P = 0.023$ ), but not by shelter treatment alone ( $F_{1,65} = 1.69$ ,  $P = 0.20$ ) or femur length ( $F_{1,65} = 2.59$ ,  $P = 0.11$ ) (Figure 3). Thus, fasted crickets laid significantly fewer eggs than fed crickets during the trial (Figure 3).

### Effect of fasting on integrated boldness and behavioral consistency

Fasted crickets ( $n = 24$ ) had a higher integrated boldness than fed crickets ( $n = 23$ ) ( $U = 154$ ,  $\zeta = 2.59$ ,  $P = 0.010$ ). In other words, fasted crickets tended to be relatively exploratory and active in a novel environment, and they tended to lay relatively fewer eggs in the sheltered oviposition site. We found no difference in behavioral consistency between crickets in the fed and fasted treatment groups ( $\zeta = -1.34$ ,  $P = 0.18$ ).

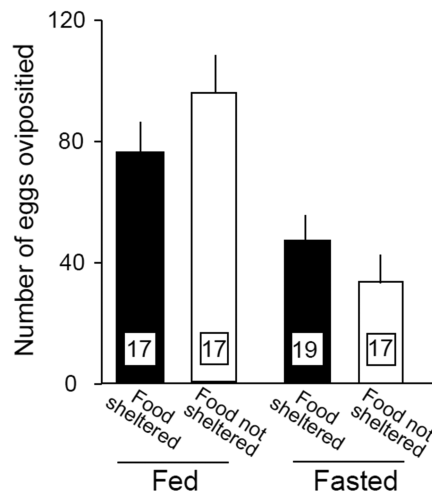
## DISCUSSION

Our first hypothesis that behavioral type was consistent across contexts was supported because fasted crickets exhibited bolder or riskier behavior in a novel environment and when ovipositing. A related field cricket (*Gryllus integer*) similarly exhibits behavior type consistency across contexts (activity in a novel environment



**Figure 2**

Effects of feeding status (fed or fasted) and shelter status (food sheltered or not sheltered) on the percentage of eggs oviposited at sheltered oviposition sites by *Gryllus texensis* during 16-h trials. Sample sizes are displayed on each bar, and values are displayed as mean  $\pm$  standard error of the mean. Significant effects: feeding status and feeding status  $\times$  shelter status interaction.



**Figure 3**

Effects of feeding status (fed or fasted) and shelter status (food sheltered or not sheltered) on the number of eggs oviposited by *Gryllus texensis* during 16-h trials. Sample sizes are displayed on each bar, and values are displayed as mean  $\pm$  standard error of the mean. Significant effects: feeding status and feeding status  $\times$  shelter status interaction.

and aggressive behavior) (Kortet and Hedrick 2007). However, to our knowledge, we are the first to demonstrate that oviposition decisions can be integrated into the behavioral type paradigm. Traditional metrics of behavioral type, such as exploratory behavior and aggression, influence survival and/or reproductive success across taxa (Smith and Blumstein 2008). However, OS is a widespread trait that entails benefits and costs to mothers (e.g., increased reproductive success and susceptibility to predation, respectively) and that affects offspring (e.g., variation in hatching success and hatchling size: Stahlschmidt and Adamo 2013). Thus, we argue for the continued incorporation of OS into the behavioral type paradigm. For example, future research could investigate how rigid or plastic OS is by measuring its repeatability in different situations.

Fasted crickets were more likely to choose food over shelter when making an oviposition decision (Figure 2) in support of our second hypothesis that individuals tradeoff safety with food availability during oviposition. Fed crickets overwhelmingly chose to oviposit in sheltered sites with no food (95% of each female's eggs on average) over non-sheltered sites with food (Figure 2). However, fasted crickets adopted a riskier oviposition strategy that included ovipositing relatively more in sites with food that lacked shelter (Figure 2), presumably due to increased food motivation as is the case in other animals (reviewed in Lima and Dill 1990). Crickets are at the bottom of the food chain and are eaten by a large variety of predators that can appear at any time (Hedrick 2000). Consequently, there should be heavy selection against crickets remaining in an exposed position, and even lab-reared crickets tend to stay in shelter unless actively foraging or searching for mates (Sakaluk and Belwood 1984; Hedrick and Dill 1993; Csada and Neudorf 1995; Hedrick 2000; Stahlschmidt and Adamo 2013). We found that fasted crickets were also bolder or less risk averse in a novel environment—presumably, this increase in exploratory behavior was due to increased foraging effort. Thus, future efforts should continue to focus on linking boldness with predator avoidance (e.g., Niemela, DiRienzo, et al. 2012; Adamo et al. Forthcoming) to better understand the costs and benefits of behavioral type.

In support of our third hypothesis that fasting influences oviposition, fasted *G. texensis* oviposited fewer eggs during trials relative to

fed crickets (Figure 3). Reduced oviposition was likely not due to fasted females having fewer eggs available to oviposit because *G. texensis* eggs take about 6 days to produce (Shoemaker and Adamo 2007). Therefore, the number of stored eggs should have been minimally affected by the brief period (3 days) of food limitation in this study. Rather, oviposition in *G. texensis* may be constrained by time because females produce more eggs than they oviposit (Adamo, unpublished data) similar to other insects (Diaz-Fleischer and Aluja 2003; Xu et al. 2012). Egg laying is time intensive in field crickets (ca. 1 min per egg: Sugawara and Loher 1986). Thus, the time a fasted female spent feeding may reduce the amount of time available for ovipositing. Although reproduction-foraging tradeoffs are widespread—from insects (Scheirs and De Bruyn 2002) to reptiles (reviewed in Stahlschmidt and DeNardo 2011)—we show that meeting foraging needs may contribute to a reduction in oviposition of more than 50% in the short term (Figure 3). Yet, recent work in *G. texensis* demonstrates that short-term food deprivation (4 days) leads to reduced oviposition rate even in the absence of food presentation—that is, when a reproduction-foraging tradeoff is not possible (Stahlschmidt ZR, Adamo SA, unpublished data). Thus, food availability and/or body condition may influence oviposition rate. Reduced food availability and, as a result, reduced body condition may downregulate insulin or insulin-like signaling pathways that regulate several traits in other invertebrates, including reproduction, growth, and feeding (Riehle et al. 2002; Nassel 2012; reviewed in Van Wieldendaele et al. 2013). Future work should examine the consequences of chronic food limitation on the number and quality of offspring produced by females over their lifespan.

Together, our results demonstrate the complexity of the behavioral type paradigm. Crickets varied consistently across several contexts because individuals exhibiting riskier (bolder) behavior in a novel environment also exhibited riskier (bolder) behavior during oviposition. However, food limitation shifted these interindividual differences in behavior. Thus, in combination with other recent work (Niemela, DiRienzo, et al. 2012; Niemela, Vainikka, et al. 2012; Tremmel and Müller 2013), we demonstrate that environmental conditions may significantly influence behavioral types or “personality” in insects. We encourage others to continue to use factorial manipulations and to integrate OS (a behavior tightly linked to multigenerational fitness) when investigating the causes and consequences of behavioral types. In particular, future work could address the interactive effects of ontogenetic factors (e.g., predator exposure and social experience: Niemela, Vainikka, et al. 2012) on behavioral type.

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