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Aggression and Mating Behavior in Wild and Captive Populations of the House Cricket, *Acheta domesticus*

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Abstract Animals in captivity experience drastically different selective pressures than their wild counterparts. This can cause evolutionary divergence in behavior between captive and wild populations. While most research on evolution under captivity has focused on vertebrates, we expect similar behavioral changes in insects that live and breed in commercial facilities. Using the common house cricket, *Acheta domesticus*, we tested how crickets reared in captivity for many generations differed from wild-caught counterparts in two aspects of social behavior: male aggression and female responsiveness to male calling song. *Acheta domesticus* is an important model organism for behavioral research and are often reared in dense, commercial facilities with ad-libitum access to food and no risk of mortality from predators— very different conditions from the wild. We predicted that commercially-derived males would exhibit less intrasexual aggression due to selection from living in dense conditions. We predicted that commercially-derived females would be less responsive to male calling song because they are more likely to encounter many males at random. Instead, we found that commercially-derived males were more aggressive than wild ones, and that commercially-derived and wild females did not differ in responsiveness to calling song. Insects serve as model systems for a great deal of research in evolutionary and behavioral biology. If these animals are evolving in captivity, they may not provide an accurate representation of the natural phenomena we aim to understand.

Keywords Male aggression · Phonotaxis · Captivity · Model systems · Cricket behavior

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Introduction

Animals living and breeding in captivity often experience dramatically different conditions than their wild counterparts. As a result, selection can act differently on animals in captivity, which can lead to evolutionary divergence between captive and wild populations. Some animals can evolve adaptations to captive conditions in as little as one or two generations (Frankham 2008; Christie et al. 2016), In Oldfield mice, *Peromyscus polionotus subgriseus*, cranial shape and size significantly differs between captive and wild populations, and these differences became more pronounced as the number of generations in captivity increased (McPhee 2004). A similar phenomenon has been observed in some mammals, like wild African lions and black-footed ferrets, where differences in the musculature around the jaw and mouth were linked to drastic dietary changes as a result of living and breeding in captivity for several generations (Zuccarelli 2004; Antonellie et al. 2016).

Our current understanding of evolution in captivity has largely been shaped by research on

vertebrates (McPhee 2004; Zuccarelli 2004; O'Regan and Kitchener 2005; Bello-Hellegouarch et al. 2013; Antonellie et al. 2016; Kapoor et al. 2016; Turner et al. 2016). How animals, particularly those housed in zoos and fisheries, adapt to life in captivity has been of great interest because of the implications for the success of conservation and wildlife management programs (Christie et al. 2014; Attard et al. 2016; Mucha and Komen 2016; Courtney Jones and Byrne 2017; Lawrence et al. 2017; Bordeleau et al. 2018; Duong and Scribner 2018; Liu et al. 2018). Similar morphological and behavioral changes may occur in invertebrates, such as insects, when they live and breed in captivity over multiple generations. Insects can rapidly evolve, owing to short generation times, fast rates of reproduction, and high fecundity (Bertin et al. 2017; Hoffmann and Ross 2018). This suggests that living in a captive environment can have immediate and lasting effects on insect behavior. Not only is this important in a wildlife management context, as captive-breed-and-release programs have recently been implemented for endangered species like Monarch butterflies (Oberhauser et al. 2015), but many insects are used as model systems in basic scientific research as well. For example, drosophilid flies have been used as an effective model organism in genetics research for nearly a century (Hales et al. 2015) and many species of crickets and katydids are central to behavioral research (Horch et al. 2017). Yet, these model organisms are often kept in laboratories where conditions — like temperature, food type and availability, risk of predation, and population density — differ from what they experience in the wild. The extent to which a history of captivity affects insect behavior has not been fully investigated.

The common house cricket, *Acheta domesticus*, is an ideal system for examining the influence of captivity on social behaviors like mate choice and aggression. Although *A. domesticus* are common in the wild, these crickets have also been kept in captivity for many decades. Likely beginning in the mid-1900s, *A. domesticus* has been used as a standard feeder insect for the pet industry and is a model system for studying animal social behaviors, particularly male-male aggression (Hack 1997; Nelson and Nolen 1997; Buena and Walker 2008; Killian and Allen 2008) and female mate choice (Gray 1997; Nelson and Nolen 1997; Mautz and Sakaluk 2008; Stoffer and Walker 2012). Most *A. domesticus* used in scientific research are purchased from biological research suppliers or pet feeder companies where they are often reared and stored in high density containers with ad-libitum access to food and no risk of mortality from predators — very different conditions from that experienced by their wild counterparts.

In this study, we tested how spending many generations in captivity affects two aspects of social behavior: male aggression and female phonotaxis (i.e. responsiveness to male calling song). We used F1 crickets from a wild population of *A. domesticus* collected from California, and a captive population ordered from Fluker's Farm to examine whether captive crickets have evolved differences as a result of living and breeding in a commercial facility. With respect to aggression, while some animals become more aggressive in high density environments, a number of studies on insects, particularly crickets, show that individuals reared in isolation are more aggressive than individuals reared in groups (Alexander 1961; Iba et al. 1995; Funato et al. 2011; Stevenson and Rillich 2013). Therefore, we predicted that commercially-derived *A. domesticus* would show less intrasexual aggression than males derived from a wild population, because captive males should have evolved a tolerance for interacting with conspecifics in a high density environment. Captivity might also affect female responsiveness to male song (i.e. phonotaxis behavior). This is important because in dense environments, like commercial facilities, females may have difficulty discriminating among many calling males, which can weaken female mate choice (Gerhardt and Huber 2002; Gerhardt and Bee 2006; Bee and Micheyl 2008; Wiley 2013, 2015). In high density environments, as is common in commercial facilities and other captive settings, male and female crickets may frequently come into contact, often by accident. However, in low density environments, like in the wild, it is likely that encounter rates are driven by female responsiveness toward calling males (Alexander 1961). Therefore, we predicted that despite being reared in a common garden environment, females derived from the wild would be more responsive to male calling song compared to females derived from a commercial facility.

Methods

Study Organism

For our captive crickets, we obtained juvenile *Acheta domesticus* from Fluker's Cricket Farm in Louisiana (USA) and reared them in the laboratory at the University of Minnesota. These crickets have spent approximately 105 generations in captivity (correspondence with Fluker's Cricket Farm). Adult crickets are generally stored at approximately 8000–10,000 individuals per bin, wherein each bin has 4 dividers. Each divider measures approximately 25,000 sq. cm, for a total of 100,000 sq. cm per bin (correspondence with Fluker's Cricket Farm). We allowed these crickets to mate and lay eggs, then used the resulting F1 offspring in our study. For our wild crickets, we captured female *A. domesticus* from Corn Spring, Riverside County, California near a BLM campsite (33.929, −117.506), which have been in the wild for at least 10 years (personal communication, David Gray, California State University, Northridge). We allowed these females to lay eggs, and reared the F1 offspring in the laboratory at the University of Minnesota.

We reared captive and wild crickets in separate 15-L plastic containers containing egg carton for shelter. Throughout rearing crickets had ad-libitum access to water and food. All containers were housed at room temperature with a 12-h photo-reversed light/dark cycle. Each 15-L container had a footprint of 1428 sq. cm and housed approximately 30 individuals in each container. This is approximately 4-5x less dense than the commercial rearing conditions at Fluker's Cricket Farm. We housed male and female juvenile crickets together until the final eclosion to adulthood. Upon eclosion, we removed males and isolated them in individual, 118-mL cups. We removed females from the population upon eclosion, but did not isolate them in separate containers. Instead adult females were housed together in 15-L plastic containers. To avoid age-related variation in behavior, we tested male intraspecific aggression at 5–10 days post-eclosion and we tested female phonotaxis at 6–9 days post-eclosion. We conducted all trials during the dark cycle of the 12-h photo-reversed light-dark cycle, which corresponds to the crickets active period between 9:00 and 21:00 h. Both aggression and phonotaxis trials were conducted in an anechoic chamber at 23–26 °C under red light using a single 13-watt light bulb. The red light was placed high enough above the testing arenas, so as to illuminate the entire arena in which the crickets were being observed.

Male Aggression

We assessed male behavior by conducting one aggression trial per individual in an anechoic chamber under red light. We performed a total of 80 aggression trials (40 trials per population) on 160 males in total. Trials were performed in a 155-cm-long by 34-cm-wide by 31-cm deep arena.

At 5–10 days post-eclosion, we recorded the mass of each male to the nearest 0.001 g. We then paired males who differed in mass by no more than 25% to ensure that size differences between males did not affect the intensity or outcome of aggressive interactions (Brown et al. 2006). Pairs consisted of males from the same population such that wild males were paired together, while captive males were paired together. To keep track of each individual's behavior throughout the trial, we gave one individual of each pair a small dot on its pronotum using a metallic sharpie. Both males were handled similarly prior to the start of the trial to avoid any effect handling may have on aggression. At the beginning of each trial, both males of a pair were placed equidistant from each other and from the ends of the rectangular testing arena. We placed a plastic container 11-cm in diameter over each male and allowed them to acclimate in the arena for 5 min. After the 5-min acclimation period, we lifted the plastic containers covering each male, and began recording behavioral data for each male. One individual watched and recorded the behaviors of each male.

Although, *A. domesticus* can perform a number of different behaviors during agnostic interactions, the actual fighting behavior can be characterized as an escalating contest with a stereotypical sequence of behaviors that can be used to determine the outcome of fights (Alexander 1961; Savage et al. 2005; Brown et al. 2006). Lower levels of aggression are indicated by antennal fencing and are followed by a series of more aggressive and energetically expensive behaviors like mandible flaring and grappling (Hack 1997).

Throughout the trial, we scored 8 behaviors: withdraw (score: 0); antennal fencing (score: 1); kick (score: 2); mandible flaring, chasing, biting, aggressive singing (score: 3); grapple (score: 4). Each male was given a total aggression score measured as the sum of the frequency times the score of each behavior following

Adamo and Hoy (1995). For example, an individual who kicked once, chased twice, and grappled three times, would have a total aggression score of 20. Because total aggression scores can arise from a number of different behaviors, we also calculated the average proportion of each population's total aggression scores that was due to each of the 8 behaviors recorded as the sum score for each behavior divided by the total aggression score. For example, a population with an average aggression score of 20, might have 1/20th of their score to attributed to kicking, 6/20ths to chasing, and 12/20ths to grappling. This population would be considered more aggressive, compared with an population who received the same total aggression score, but had a higher proportion attributed to antennal fencing or kicking.

Lastly, we measured the total time spent fighting as the first aggressive behavior to the final retreat, wherein a winner was established as the individual rushing toward the other, and the loser was established to be the individual who retreated. We stopped recording aggressive behaviors at 10 min if dominance had not been established by one of the males in the arena. We recorded this fight as a draw (i.e. no winner and no loser had been established).

Phonotaxis Trials

We assessed female mating behavior by conducting one phonotaxis trial per individual in an anechoic chamber under red light. We performed a total of 124 phonotaxis trials (62 trials with captive females and 62 trials with wild females), in a 155-cm-long by 34-cm-wide by 31-cm deep arena. To avoid age-related variation in behavior, we tested females 6–9 days post-eclosion. We approximated the intensity of calling song that females typically experience, by maintaining the playback intensity at 60 dB from the release point.

At the beginning of each trial, we positioned a single female approximately 100-cm from the playback speaker. We placed a plastic container 11-cm in diameter over the female cricket and allowed her to acclimate in the testing arena for 2 min. After the 2-min acclimation period, we began playback of the conspecific calling song and lifted the container, allowing the female cricket to freely move around the testing arena. To construct the calling song used in our playback experiments, we averaged the song characteristics (i.e. chirp duration, interchirp interval, interpulse interval, song duration) of wild *A. domesticus* males using the software package *Raven* v.1.2 (Cornell Lab of Ornithology, Ithaca, NY, USA). We calibrated the sound pressure level for each trial to be roughly 65 dB from the release point inside the testing arena.

Immediately after releasing a female, we began a 5-min observation period following (Bailey and Zuk 2008). Females were undisturbed throughout this 5-min observation period, during which we recorded two measurements of female choice: (1) whether a female responded positively by moving toward and settling near the playback speaker, or negatively by moving away from and settling opposite the playback speaker; and (2) the amount of time that females took to travel to and settle near the playback speaker. If females settled less than 1-cm from the playback speaker, the trial ended. If the female did not settle within 1-cm of the playback speaker, after 5 min we recorded the final distance that she settled instead.

Data Analysis

We performed all analyses in *JMP Pro* 14.2.0 using a significance level of 0.05. We did not use age as a covariate in any of our models, because it had no significant effect on any response variables associated with male aggression or female phonotaxis.

Male Aggressive Behavior

We began by examining the effect of population (captive vs. wild) on aggression. We used total aggression score as our dependent variable and population as the fixed effect ($n = 80$ captive and 80 wild; $N = 160$ males in total). Because the response variable did not follow a normal distribution (Shapiro-Wilk goodness-of-fit, $p < 0.0001$) and could not be correct by applying a transformation, we used a Mann-Whitney U non-parametric test of medians.

We also performed a series of Mann-Whitney U non-parametric test of medians to examine the effect of population on the proportion of total aggression scores that was due to each of the 8 recorded behaviors. We used the frequency of each aggressive behavior as the dependent variables and population as the fixed effect in each of the models ($n = 75$ captive and 74 wild; $N = 149$ males in total). Because we conducted multiple tests on the same data from the same trials, we used the False Discovery Rate (FDR; Benjamini and Hochberg

1995) add-in for JMP to control for family-wise, type-I error rates.

Female Phonotaxis Behavior

We began by examining the effect of population (captive vs. wild) on response type (positive vs. negative) by using a contingency analysis with response type as our dependent variable and population as our independent variable ($n = 64$ captive and 60 wild; $N = 124$ females in total).

For latency to positively respond to the playback speaker, we used a Mann-Whitney U non-parametric test of medians to examine the effect of population, because the response variable was not normally distributed (Shapiro-Wilk goodness-of-fit, $p = 0.02$). We used response time (in seconds) as the dependent variable and population as the independent variable ($n = 47$ captive and 50 wild; $N = 97$ females in total).

To examine the effect of population on distance settled when females responded negatively to the playback speaker we performed a Mann-Whitney U non-parametric test of medians with settling distance (in centimeters) as the dependent variable and population as the independent variable ($n = 17$ captive and 10 wild; $N = 27$ females in total).

Results

Male Aggressive Behavior

We found a significant effect of population on total aggression such that males derived from a captive population had 1.5 times higher aggression scores on average compared with males derived from a wild population ($X^2_1 = 24.4$; $p < 0.0001$). Captive males had a median total aggression score of 18.5, while wild males had a median total aggression score of 8 (Fig. 1).

With regard to the proportion of the total aggression score that is attributed to each of the 8 recorded behaviors, males significantly differed in the amount of: antennal fencing ($X^2_1 = 10.8$; $p = 0.002$); mandible flaring ($X^2_1 = 15.6$; $p = 0.0007$); aggressive chirping ($X^2_1 = 7.17$; $p = 0.01$); and grappling ($X^2_1 = 11.6$; p = 0.002).

Antennal fencing accounted 37% of their total aggression score for wild males, while this behavior accounted for just 20% of the aggression score for captive males. Domestic males had a much higher

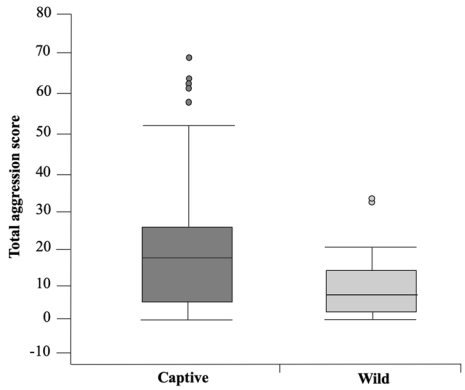

Fig. 1 Total aggression scores for males based on a measure of eight stereotyped behaviors. Captive male aggression is represented by dark grey on the left. Wild male aggression scores are represented in light grey on the right

frequency of mandible flaring, aggressive chirping, and grappling. Mandible flaring and grappling accounted for 7% of total aggression scores for domestic males and aggressive chirping accounted for 50%. For wild males, mandible flaring and grappling accounted for just 2% each, and aggressive chirping made up 35% of their total aggression scores (Fig. 2). Kicking ($X^2_1 = 0.279$; $p = 0.60$), chasing ($X^2_1 = 0.680$; $p = 0.48$), and biting ($X^2_1 = 2.50$; $p = 0.16$) accounted for the remainder of the total aggression scores, but with no significant differences between the two populations.

Female Phonotaxis Behavior

We found no difference between captive and wild females in their response type (positive vs. negative: Pearson $X^2_1 = 1.78$; $p = 0.18$). Both captive and wild females responded positively to the playback speaker more often than they responded negatively. On average, captive females responded positively in 73.4% of the trials and wild females responded positively in 83.3% of the trials (Fig. 3a). Captive and wild females also did not significantly differ in their latency to respond to the playback speaker ($X^2_1 = 0.120$; $p = 0.73$). Captive females had a median response time of 132 s, while wild females had a median response time of 111 s (Fig. 3b).

Finally, we found no difference between captive and wild crickets in the distance settled when females responded negatively to the playback speaker ($X^2_1 = 1.98$; p = 0.16). On average, captive females settled

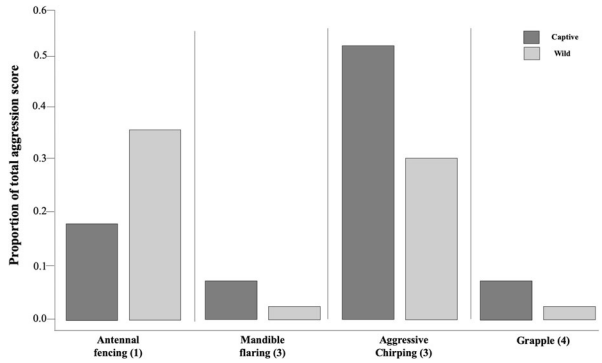

Fig. 2 Proportion of the total aggression score due to each highlighted aggressive behavior. Captive and wild populations differed significantly in the proportion of the total aggression score due to each highlighted behavior above. Aggression value of each of these behaviors is shown in parentheses

about 76.8± 8.4 cm from the playback speaker when responding negatively, and wild females settled about 69.0± 11.0 cm from the playback speaker.

Discussion

We found differences between commercially-derived and wild crickets with regard to male aggression, but not female phonotaxis. We found support for our hypothesis that there are evolved differences in male aggression between commercially-derived and wild *A. domesticus*; however, these differences were not what we predicted. Many studies on crickets show that males kept in isolation are more aggressive upon encountering conspecifics (Alexander 1961; Iba et al. 1995; Funato et al. 2011; Stevenson and Rillich 2013). Further, animals living with abundant resources, like ad-libitum access to food and shelter, as is common with commercial facilities, are expected to exhibit less intraspecific aggression. Therefore, we predicted that males from the wild would be more aggressive than captive males. Instead, we found that males from a commercial facility were more aggressive than wild males. One explanation is that the increase in population density in captivity caused an increase in intraspecific aggression. At high population densities, as is common in commercial facilities, males sometimes perceive an increase in competition, and will increase their intraspecific aggression to better monopolize females (Wedell et al. 2002). Interestingly, captive males did not show an increase in all aggressive behaviors. Captive males engaged in more intense aggressive

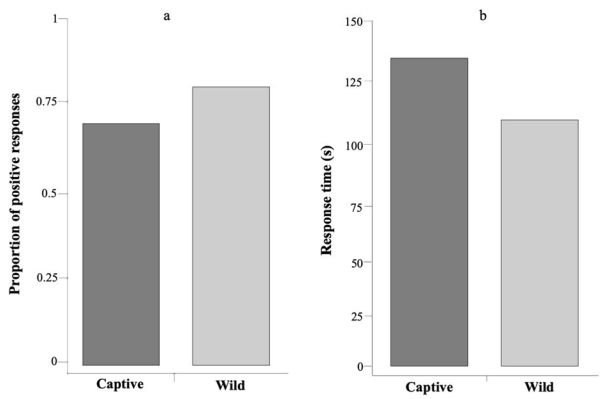

Fig. 3 Proportion of females responding positively by moving toward and touching the playback speaker broadcasting male calling on the left (**a**). The amount of time it took females to respond positively by moving toward and touching the playback speaker on the right (**b**)

behaviors like mandible flaring, aggressive chirping, and grappling; while wild males engaged in more antennal fencing. The lower intensity behaviors like kicking, chasing, and biting did not differ between the two populations— suggesting that perhaps males have evolved to be more aggressive in captivity.

With regard to mating behavior, we hypothesized that wild females would be more phonotactic than captive females. This is because females are less likely to encounter males at random in the wild, and therefore, encounter rates are most likely driven by female responsiveness toward calling males (Alexander 1961). In addition, theory predicts that when mates are readily available, as is common in more dense environments like commerical facilities, females will adjust their mate choice behaviors to reflect the reduced search costs, and can afford to be more selective about their mates (Kokko and Rankin 2006). Other factors, like predation risk and food availability, which can differ significantly between captive and wild environments, often affect female mate choice as well (Travers and Sih 1991; Ortigosa and Rowe 2002; Moskalik and Uetz 2011; Scharf 2016; Gilad et al. 2018). For example, female *Gryllus integer* typically prefer long-bout male calls, but when prediation risk is high, females will instead mate with males producing the less conspicious, short-bout calls (Hedrick and Dill 1993). We did not find support for our hypothesis that there are evolved differences in female mating behavior in response to captivity. Instead, we found that female *A. domesticus* exhibit similar responses to a calling song playback regardless of their population of origin. Females exhibited no difference in response type (positive vs. negative) and a post-hoc analysis revealed that we would need a sample size of over 250 females per population to reach 80% power. Therefore, it is unlikely that populations differ in response type in our current study. One explanation for why there were no difference between the populations is that females exhibit a high degree of plasticity in response to their immediate rearing environment, rather than evolving different mating behaviors under each set of environmental conditions. To test this, we would need to obtain adult females from the the wild and captivity and test their responses to male song. Conversely, we could conduct a reciprocal transplant experiment in which females from the wild are reared in captivity and females from captivity are reared in the wild. If female phonotaxis is indeed plastic, then their responses should differ if they are kept in different enviornments throughout development.

An important caveat to our study is that we tested for behavioral differences in only one captive and one wild population of *A. domesticus*. It is possible that the differences we found in male aggression are simply due to drift, neutral evolution, or founder effects. For instance, the wild founders of the Fluker's Farm crickets may have been genetically distinct and exhibit differences in aggression from our wild California population due to natural variation among populations. Another possibility is that the captive cricket population from Fluker's Farm lacks genetic diversity after many years without any migration — it is not clear whether this captive population is supplemented with crickets from other sources in order to maintain genetic variation. It is critical for more studies to investigate behavioral differences between multiple captive and wild populations to draw firm conclusions. However, our results are still important as they provide one of the first windows into how selection on insect may operate differently in captivity and in the wild.

There are a nunber of important reasons to examine how insects may be adapting to life in captivity. Understanding the evolved differences between commerically-derived and wild populations may allow us to adjust our conservation and wildlife management practices to better achieve the intended goals of halting species decline. Following the decline of Monarch butterfly populations across the US, some people began obtaining commerically-reared butterflies and releasing them into the wild, with the goal of supplementing local populations (Brower et al. 1995; Oberhauser et al. 2015). But many biologists caution against this practice (Brower et al. 1995; Altizer and Oberhauser 1999; Bradley and Altizer 2005; Lindsey et al. 2009). Monarchs kept in captivity for many generations are significantly smaller and less likely to be recovered in the Mexican overwintering grounds than their wild counterparts (Steff 2015). Smaller Monarchs live shorter lives as adults and smaller females are less fecund (Altizer and Oberhauser 1999). Further, commerical and mass-rearing environments can cause excess disease spread, and for may animals like Monarchs, parasites can hinder critical survival

behaviors, like migration (Altizer and Oberhauser 1999; Altizer and de Roode 2010; Boppré and Vane-Wright 2012). A similar trend in bumblebees has been implicated in the decline of four native, wild populations- *Bombus terricola*, *B. affinis*, *B. franklini*, and *B. occidentalis* (Cameron et al. 2011; Goulson and Hughes 2015). This suggests that there may be evolutionary changes happening in captivity. Without fully understanding how insects in captivity differ from insects in the wild, we may not be achieving the intended goals of our conservation and wildlife management programs, and we way be harming wild populations in the process.

If insect behavior is evolving in captive environments, like commerical facilities and research laboratories, this can cause scientists to over- or underestimate the effects of behaviors such as female choice and male aggression on the evolution of insect mating systems. For example, drosophilid flies have been used as model systems in sexual selection and sexual conflict research for many decades. A 2014 survey of the literature on sexual selection in insects revealed that *Drosophila melanogaster* were used in more than one-quarter of sexual conflict research over the past few decades (Zuk et al. 2014). Yet, *Drosophila* are studied in nearly 1800 labs (Hales et al. 2015) and the extent to which they have undergone selection as a result of being kept in captivity has not been fully elucidated. Model systems are important for advancing our knowledge about biological phenomena. However, we often do not examine whether these models are providing the most accurate representation of the natural world, because the extent to which animals have undergone selection in the laboratory has not been fully elucidated, and this may have unintentional consequences for the conclusions we draw from our work. One of the benefits of laboratory experiments is the ability to "simplify nature so that it can be more easily understood" (Jessup et al. 2004). Nonetheless, distinguishing between wild and captive populations is a useful reminder to consider the strengths and weaknesses of different modeling approaches, particularly in evaluating the scope of our results (Winther et al. 2015).

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Data Availability The raw data for this study can be found in the Mendeley Data repository (https://doi.org/10.17632/mhnvkd54cx.1).

Compliance with Ethical Standards

Conflict of Interest The authors declare that they have no conflicts of interest.

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