

Research Article

Females Prefer Bold Males; an Analysis of Boldness, Mate Choice, and Bacterial Resistance in the Field Cricket *Gryllus integer*

Raine Kortet,¹ Petri T. Niemelä,^{1,2} Anssi Vainikka,^{1,2} and Jouni Laakso³

¹Department of Biology, University of Eastern Finland, P.O. Box 111, 80101 Joensuu, Finland

²Department of Biology, University of Oulu, P.O. Box 3000, 90014 Oulu, Finland

³Department of Biosciences, University of Helsinki, P.O. Box 65, 00014 Helsinki, Finland

Address correspondence to Raine Kortet, raine.kortet@uef.fi

Received 22 May 2012; Revised 20 July 2012, Accepted 3 August 2012

Abstract Recent theory predicts that personality traits contributing to resource intake rates could reflect the individual's condition-dependent capacity to resist parasites and pathogens. Since females often prefer mates with strong immune defence, females could potentially gain fitness benefits by using male's behavioral type (BT) as one mate choice criteria. We studied if female field crickets base their mate choice on male boldness and if the boldness would predict survival under challenge to opportunist pathogen *Serratia marcescens*. In addition, we tested if three different females would prefer the same males. Boldness did not explain individual's lifespan in experimental infection. All the three females preferred one male within pair over the other male in 26.9% of the mate choice tests, but the preferred male varied between the females. Our results suggest that females show preferences for bold BTs, but that male boldness may not reflect his capacity to resist bacterial pathogens.

Keywords consistent behavior; parasite; pathogen; sexual selection

1 Introduction

During the recent years, interest in consistent, individually repeatable behaviors (i.e., personalities) and their evolutionary importance has increased in a multitude of ecological contexts [3,4,7,8,35,38,40]. Most often the fitness consequences of personalities are assessed in predator-prey context: for example, animals with a "shy" behavioral type (BT) are consistently cautious and avoid risk-taking (and may thus have high fitness in high predation environments), whereas those with a "bold" BT are consistently incautious and prone to take risks (and may thus suffer high mortality in high predation environments) [38]. However, parasitism can also affect the evolution of animal personalities by imposing both direct and trait-mediated indirect fitness costs comparable to those of predation [23,30,36,37]. In addition, the development

of an individual's BT may depend on the parasite and pathogen environment where the individual has lived or has been reared [2,23].

It was recently proposed that personality traits contributing to resource intake rates could reflect the individuals' condition-dependent capacity to resist parasites and pathogens through effects on realized resource intake rates [23]. This proposition was based on the fact that individuals that have better access to resources may afford to build and maintain stronger immune defence [34]. Moreover, since parasites have major impacts on fitness (also through behaviors), and because personality traits can affect the probability of acquiring and resisting parasites [5,13,25,45], individuals should evolve to match their investments in immune function with their personalities [2,23]. However, the idea of the association between parasite resistance and personality traits has not yet been comprehensively studied experimentally [28,29].

In the field crickets (*Gryllus spp.*), females are usually larger than males, and mount the males for copulation, which means that males cannot force females to mate [21]. Male field crickets aggressively fight for and defend territorial shelters and females [1,19,33,39]. Female field crickets are choosy and have strong individual preferences with respect to males [14,18,21,32]. Females use both male acoustic and pheromonal signals as criteria in their mate choice [10,14,21,19,39]. Also, success in male-male competition can directly influence a male's mating success [32,33,44]. Since success in intrasexual contests may demand energetic resources, female field crickets can also use a male's competitive ability as a cue to select mates with good condition. Thus, it would be beneficial for females to prefer males with certain BTs (i.e., bold and aggressive males) as mates. For example, in *G. bimaculatus*, males who were successful under simultaneous male-male competition and female choice tests sired sons that were also similarly successful [44], indicating heritable components

in personality-associated traits like aggressiveness. In *G. integer* male dominance, that is often associated with high quality, is positively coupled with boldness [22]. Therefore, it is likely that *G. integer* females could detect and prefer bold males.

In the present study, we examined if female field crickets (*G. integer*) would prefer certain male BTs (shy-bold continuum) in their mate choice, and whether the BT in general is a predictor of resistance against bacterial pathogens. We predicted that (1) the individual's resistance against bacterial disease would be dependent on BT in such a way that bold individuals would have a stronger resistance, and (2) that females would prefer male BTs that are correlated with strong resistance. To test these hypotheses, we reared crickets in a controlled environment, studied their boldness, and then conducted female choice experiments in which we also evaluated male aggressiveness. We exposed three females to a pair of males in sequential mate choice trials to additionally test if different females would prefer the same males, and whether the female preference would be assortative with respect to male BT. Finally, resistance against bacterial disease was studied (Figure 1).

2 Materials and methods

2.1 Study animals

We used laboratory reared crickets ($N = 192$) that represented the 9th–10th laboratory generation originating from a wild cricket population (Davis, CA, USA). The laboratory colonies were supplemented with the offspring of wild collected individuals around the 6th generation. Crickets were maintained at the University of Oulu, Finland, under a constant 12 h : 12 h light-dark cycle at 27 ± 1 °C with access to food and water ad libitum. All crickets were raised individually in transparent plastic containers (128 mm \times 98 mm \times 73 mm).

2.2 Personality tests

We quantified the individual boldness for all the crickets using commonly applied methods [15, 16, 22, 24]. Behavioral trials were conducted in a sound-proof, temperature-controlled dark room (27 ± 1 °C), in which the experimental setting consisted of a computer, a desk, and three experimental arenas (188 mm \times 188 mm \times 112 mm). Since *Gryllus spp.* likely cannot see long (red) wavelengths properly [6], and therefore dim red light mimics dark conditions, we used dim red light (25 W red incandescent bulb) to minimize potential disturbance by the observer. Each arena was placed in a polystyrene box with 15 mm thick walls (282 mm \times 270 mm \times 207 mm) for acoustic shielding.

At the beginning of each boldness trial, a focal cricket that had matured 7 days before was put in a clean experimental vial (100 mm high, 70 mm diameter non-transparent round plastic vial) and placed upside up in the center of the

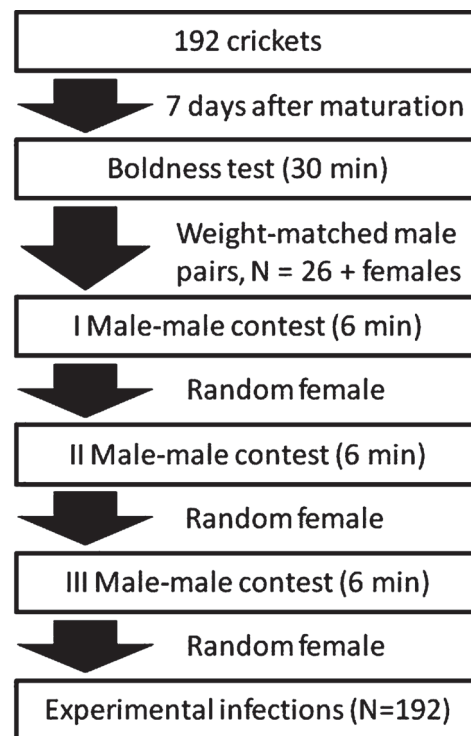


Figure 1: The experimental procedure. See more details in Section 2.

arena. The vial had a hole in the top of one side (20 mm \times 15 mm) from which the cricket could emerge during the trial but not during acclimatization. After a two-minute acclimatization period, the vial was carefully flipped to mimic a natural disturbance, and a plexiglass cover was set over the top of the arena to attenuate sounds from outside of the arena and to prevent the cricket from escaping. Each trial lasted for 30 minutes, and the latency times before emergence (i.e., the time it takes for the cricket's antenna, head, and entire body to emerge from the vial) from a shelter were recorded for each individual using custom software "AV Bio-Statistics 4.9," produced by one of the authors (AV). If the individual did not move or emerge from the vial within this time, the corresponding time was assigned the maximum value of 30 minutes (2.95% of the cases). After the trials, the crickets were weighed to the nearest 0.001 g.

Upon reaching the entrance of the vial, cricket acts cautiously, and often does not emerge from the vial until after spending a long time scanning the novel environment. Some individuals turn back upon reaching the open end of the vial, and will not emerge until they have rescanned the open end several times. Thus, the recorded variables can be defined as measures of boldness in an exploratory context. In the present work, we refer to the inverse of the measured variables (long times mean low boldness, i.e., shy individuals) using the term boldness, bearing in mind the definitions mentioned above.

2.3 Female choice and male-male aggression

Methods used in this study to test female choice, aggression, and dominance were similar to those used previously for the field crickets [22]. Three repetitive, combined aggression and female choice trials were accomplished, so that each pair of males was tested three times, each time with a different female (Figure 1). The experiments were conducted in the same sound-proof, temperature-controlled, dark experiment room as described for the boldness trials. The bottom of the round arena (height 240 mm, diameter 210 mm) was covered with sawdust and illuminated with a red filter light (25 W red incandescent bulb). After each trial, the sawdust was replaced with fresh sawdust. All the experiments were carried out between 8.00 and 13.00, 2–4 days after the boldness trial. For recognition in the trials, males were anesthetized using carbon dioxide, and marked by a small dot on the left or right side of their pronotum with enamel paint. Females were not re-used.

In a trial, experimental age- and weight-matched males (at max. 6% difference) ($N = 26$ pairs) were allowed to fight with each other in the presence of a randomly chosen female. The age of the females used was from 7 to 14 days after maturation. Based on our experiences, the longevity of the female crickets in the lab is easily up to 120 days, but their activity seems to decrease when they get older. Thus, we feel that the age of the females used in the present experiment was optimal. At the beginning of each trial, two experimental males and one female (to trigger the males to fight) were placed under separate round plastic vials (height 60 mm, diameter 38 mm) in the arena for 3 minutes to acclimatize. After removal of the vials, the male-male contest and female's mounting behavior was observed for 6 minutes. A 6-minute observation period was chosen based on the fact that *G. integer* males will establish their dominance hierarchy well during this time period [21]. The time and frequency of aggressive encounters won by each male, and the number of subsequent female mountings were recorded to a computer using the same software as described for boldness tests. Aggressive encounters included wrestling, biting, and chasing. Avoidance behaviors and retreat by one cricket after a fight were considered to be signs of submission, and thus an indication that the fight was lost. Intrasexual aggression was quantified as the frequency of fights won in six minutes and the dominant male was the one who won more fights. The female choice was based on with whom the female chose to mount with. When male got more than 50% of the copulations, female was defined to prefer the male within male-male pairs, and if the mountings were evenly distributed between males, an average value of both males was used in statistical tests for both males. Actual mating was prevented by removing the female off of the back of the male using a wooden stick after each mating attempt. Fights were counted also after copulation attempts until the end

of the experimental period. We have not noticed that interrupted copulation attempt would affect on the future aggressive encounters. Males did not show aggressive behavior towards females, and as such female choice was considered independent of male's aggressive behavior.

2.4 Experimental infections

A number of 192 crickets (102 males and 90 females) were experimentally injected either with opportunistic bacterial pathogen or sterile buffer solution in four batches ($N_1 = 61$, $N_2 = 69$, $N_3 = 40$, and $N_4 = 22$) one to three weeks after the behavioral trials. Even though we were mostly interested in males, we also infected females in order to study the relationship between boldness and bacterial resistance. The crickets were injected between the 3rd and 4th segment of abdomen either with 5 μ L of well-mixed *Serratia marcescens* bacterial suspension (approximately 1.66×10^6 live cells in sterile phosphate buffer, pH 7.4) or 5 μ L of sterile phosphate buffer control using 10 μ L Hamilton syringe [9].

The *S. marcescens* strain was obtained from American Type Culture Collection (ATCC 31880). *S. marcescens* is a gram negative broad-spectrum opportunist pathogen that commonly infects plants, nematodes, insects, fish, and mammals, including humans [11]. After the injections, cricket mortality was monitored at 30 minute intervals at 25 °C until all the individuals were dead. The injection technique bears a resemblance to the infection by pathogenic bacteria that occasionally invade insect hemocoel directly through breaches of the cuticle [43], occurring, for example, on plant spines [12]. It has been shown that injection and oral infection methods correlate positively, even though the death rate of infected organism is usually slower following oral infection [27].

2.5 Statistical methods

First, the number of behavioral variables was reduced using principal component analysis (PCA) on Ln-transformed variables antenna out, head out, and body out. Transformations were used to improve the normality of the distributions. For the analysis of consistency of female preference, male pairs were classified to the following categories per each female (male 1 was preferred, male 2 was preferred, 3 no choice occurred) according to the proportion of mountings they received per trial. The sum of these scores was calculated over all the three females, and Fleiss' kappa (that can get values 0–1) was used as a measure of consistency. Female preference for dominant males was tested using Friedman's test on the number of females preferring, not preferring and not making the choice on dominant males.

Assortativeness of female preference was analyzed by first calculating the absolute values of female's own

behavioral score (“boldness score”) obtained from PCA—preferred or non-preferred male’s behavioral score, and testing the difference of males using repeated measures (RM) ANOVA (that is suitable since the triplet design makes males dependent on each other). RM-ANOVA was used also to test if preferred and non-preferred males differed in behavioral score or in survival time in absolute sense. In RM-ANOVA the pair of winning and losing male was entered as a within-subject factor together with the number of trial (female). The biologically meaningless main effect of the number of trial was omitted from the model, as preliminary analyses showed that it was not significant.

Cox regression analysis with backward stepwise model selection procedure based on log-likelihood ratio comparison criterion was used to study the impact of experimental infections on survival. Individuals that did not die within three days were censored (i.e., assumed to survive the infection) Infection batch was entered as strata.

3 Results and discussion

3.1 Integration of different behaviors into one personality score

A percentage of 97.05% of all the studied individuals came out from the vial within 30-minute experimental time. PCA formed only one principal component “behavioral boldness score” having eigenvalue above 1. This component accounted for 91.1% of all variance in the studied behaviors: (1) the first antenna move (communality 0.92), (2) the first head move (communality 0.98), and (3) emergence from the vial (communality 0.96). These results indicate that all the studied variables were correlated with each other and indicate the same underlying personality trait: boldness. Similar patterns have been also described in recent work with the field crickets [28].

3.2 Experimental infections

All the individuals except two males infected with *S. marcescens* ($N = 98$) died within three days from infection. The final Cox-regression model ($\chi^2 = 14.23$, d.f. = 2, $P = .001$) indicated that only treatment (bacteria vs. sham-injection, $\beta = 1.13$, $P < .001$) and marginally but not significantly body mass ($\beta = -2.58$, $P = .064$) affected the survival time (significances of removed terms in the order of removal: sex: $P = .511$; boldness score: $P = .414$; development time: $P = .193$). Since infection batch did not affect the survival (when entered as the only factor, model: $\chi^2 = 1.27$, d.f. = 3, $P = .735$), we can judge that crickets were not differentially susceptible to *S. marcescens* depending on age. Additional sex-specific Cox-regression analyses revealed that body mass improved survival times in females ($\beta = -5.77$, d.f. = 1, $P = .011$), whereas in males none of the covariates body mass, boldness score or

development time explained survival under experimental infection.

Positive associations between body size and immune defence against pathogens have often been reported in insects [31,42]. It is likely that a large individual has more reserves (energy or material) to mount a higher response against invading pathogens than a smaller individual, which could explain the observed results. Immunological priming has been demonstrated in other insects (e.g., [26]). Therefore, it is also possible that larger female individuals with a larger skin area may have earlier experienced mild infection through, for example, aggressive encounters and thus elevated their immune responses, which may explain better survival against new intruders (i.e., our bacterial treatment). However, the effect was not observed in males.

3.3 Female preference

In seven out of 26 pairs, all the three females preferred one of the two males (more than 50% of all female mountings and at least one mounting). In four of these cases, all the females preferred the same male. Fleiss’ kappa indicated only slight (potential range 0–1) but statistically significant consistency for preference of certain males over all preference tests (Fleiss’ $\kappa = 0.199$, $P = .007$).

Female choice was not dependent on the male’s dominance status in his fights (Friedman’s test, $\chi^2 = 2.956$, d.f. = 2, $P = .228$). In 34.7% of the trials ($N = 75$), females mounted more often with the dominant male, in 41.3% cases, females did not make a clear choice, and in 24.0% of the cases, females preferred the subordinate male.

For those trials where females showed preference for certain males, the mean behavioral score of preferred males was lower than that of non-preferred males (RM-ANOVA, difference in boldness, Wilk’s $\lambda = 0.742$, $F_{1,21} = 7.31$, $P = .013$) (Figure 2), indicating that females preferred bold males. The interaction between trial number and preference was not significant (RM-ANOVA, boldness \times trial number, Wilk’s $\lambda = 0.787$, $F_{2,20} = 2.70$, $P = .213$).

The female choice was not assortative in relation to the male’s behavioral score, that is, there was no association between the females’ boldness and chosen male’s boldness (RM-ANOVA, difference in boldness-score, Wilk’s $\lambda = 0.904$, $F_{1,18} = 1.91$, $P = .184$). Neither was the interaction between boldness-score and the number of trial (1, 2, 3) significant (RM-ANOVA, difference in boldness \times trial number, Wilk’s $\lambda = 0.7226$, $F_{2,17} = 2.48$, $P = .114$).

Male survival time under the experimental infection did not differ between the preferred and non-preferred males (RM-ANOVA, difference in survival, Wilk’s $\lambda = 0.079$, $F_{1,19} = 1.63$, $P = .217$), nor in the interaction with the number of trials (RM-ANOVA, difference in survival \times trial number, Wilk’s $\lambda = 0.035$, $F_{2,18} = 0.323$, $P = .728$). Preferred and non-preferred males did not differ in body mass (RM-ANOVA, $P > .05$).

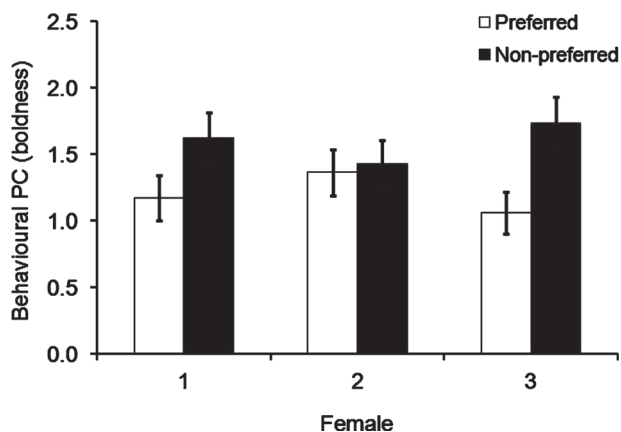


Figure 2: Female preference versus male behavioral principal component (i.e., boldness score). Three repetitive, combined aggression and female choice trials were accomplished, so that each pair of males was tested three times, each time with a different female. Numbers 1, 2, and 3 refer to these three different females. Note that lower values in boldness score indicate bold BT. The mean boldness score of preferred males was lower than that of non-preferred males (RM-ANOVA, difference in boldness, Wilk's $\lambda = 0.742$, $F_{1,21} = 7.31$, $P = .013$), indicating that females preferred bold males. According to paired t -tests, the corresponding P -values for females 1, 2, and 3 are 0.085, 0.774, and 0.009, respectively.

The present results suggest that females do mate selectively, but that their mate choice may not be based on male survival under bacterial infection. Interestingly, and according to our predictions, females seemed to prefer bold males over the cautious males. However, in the present data females did not prefer aggressive males. Previously, it has been demonstrated that in the offspring generation of wild *G. integer*, females prefer pheromones of the dominant males and that male dominance-indicating aggression and boldness are coupled together [21, 22]. Thus, in accordance with our data, it would be beneficial for females to prefer bold and aggressive males. In the present experiment, we did not study separately female preferences for male pheromones. Nevertheless, females may not rely on a single cue but instead use combination of different sexual signals to assess potential mates [10, 14, 17, 32, 33, 39, 41].

The present data were collected using crickets that had been reared in laboratory environment for nine generations, which may have affected the observed results. For example, lighting conditions and diurnal patterns of the animals differ in the laboratory when compared to the wild. In our study, the crickets were likely well adapted to the stable lighting rhythm, and our experiments were conducted between 8.00 and 13.00, which presumably decreased variation that would have been caused by possible night time activity of the

animals. In the laboratory environment, different behavioral patterns may occur compared to the wild, as demonstrated already in *G. bimaculatus* field crickets [42]. Thus, one has to be careful when expanding our results to wild animals. In the wild, *G. integer* is being predated by a wide variety of vertebrate and invertebrate predators [16], and the species is known to respond to perceived predation risk by altering its behavior to reduce risk [15, 20]. Therefore, if females prefer bold males also in the wild, they may prefer males that are either really in the high risk to become predated or males that can well compensate with their increased predation risk. Clearly, more research is needed to evaluate whether this is true.

4 Conclusion

The present results suggest that female *G. integer* field crickets show at least some level of selectivity in mating by preferring certain males over the others. Interestingly, females seemed clearly to prefer bold males over males that behaved cautiously in personality test. We did not find any evidence for the assortative mating with respect to the BT. Finally, we did not find support that cricket BT would predict its survival under opportunist bacterial infection. To better understand the associations between personality, mate choice, and parasite resistance, we encourage further studies on this topic. The further studies would reveal whether females show assortative mating preferences with respect to the BTs in other populations, and whether BTs would predict resistance against other pathogens and parasites.

Acknowledgments This research has been supported by the Academy of Finland; projects 127398 (RK, AV) and 1130724 (JL). We would like to thank anonymous referees for the valuable comments on the earlier version of the manuscript. We would like to thank the University of Oulu Zoo and its staff for the help with experiments and maintenance of our cricket population. We thank also Annie Leonard, Ann Hedrick and Markus Rantala, who helped us to establish the laboratory population used in this study. The authors declare that they have no conflict of interest. All the experiments were conducted according to the Finnish legislation of animal care.

References

- [1] R. D. Alexander, *Aggressiveness, territoriality and sexual behavior in field crickets (Orthoptera: Gryllidae)*, *Behaviour*, 17 (1961), 130–223.
- [2] I. Barber and N. J. Dingemans, *Parasitism and the evolutionary ecology of animal personality*, *Philos Trans R Soc Lond B Biol Sci*, 365 (2010), 4077–4088.
- [3] A. M. Bell, *Future directions in behavioural syndromes research*, *Proc Biol Sci*, 274 (2007), 755–761.
- [4] P. A. Biro and J. A. Stamps, *Are animal personality traits linked to life-history productivity?*, *Trends Ecol Evol*, 23 (2008), 361–368.
- [5] N. Boyer, D. Réale, J. Marmet, B. Pisanu, and J. L. Chapuis, *Personality, space use and tick load in an introduced population of Siberian chipmunks *Tamias sibiricus**, *J Anim Ecol*, 79 (2010), 538–547.
- [6] A. D. Briscoe and L. Chittka, *The evolution of color vision in insects*, *Annu Rev Entomol*, 46 (2001), 471–510.

- [7] S. R. X. Dall, A. I. Houston, and J. M. McNamara, *The behavioural ecology of personality: consistent individual differences from an adaptive perspective*, *Ecol Lett*, 7 (2004), 734–739.
- [8] N. J. Dingemanse and D. Réale, *Natural selection and animal personality*, *Behaviour*, 142 (2005), 1159–1184.
- [9] V. P. Friman, T. Hiltunen, M. Jalasvuori, C. Lindstedt, E. Laanto, A. M. Örmälä, et al., *High temperature and bacteriophages can indirectly select for bacterial pathogenicity in environmental reservoirs*, *PLoS One*, 6 (2011), e17651.
- [10] D. A. Gray and W. H. Cade, *Quantitative genetics of sexual selection in the field cricket, *Gryllus integer**, *Evolution*, 53 (1999), 848–854.
- [11] P. A. Grimont and F. Grimont, *The genus *Serratia**, *Annu Rev Microbiol*, 32 (1978), 221–248.
- [12] M. Halpern, D. Raats, and S. Lev-Yadun, *Plant biological warfare: thorns inject pathogenic bacteria into herbivores*, *Environ Microbiol*, 9 (2007), 584–592.
- [13] B. Hart, *Behavioral defence*, in *Host-Parasite Evolution: General Principles and Avian Models*, D. Clayton and J. Moore, eds., Oxford University Press, Oxford, UK, 1997, 57–77.
- [14] A. V. Hedrick, *Female preferences for male calling bout duration in a field cricket*, *Behav Ecol Sociobiol*, 19 (1986), 73–77.
- [15] A. V. Hedrick, *Crickets with extravagant mating songs compensate for predation risk with extra caution*, *Proc Biol Sci*, 267 (2000), 671–675.
- [16] A. V. Hedrick and R. Kortet, *Hiding behaviour in two cricket populations that differ in predation pressure*, *Anim Behav*, 72 (2006), 1111–1118.
- [17] A. V. Hedrick and R. Kortet, *Effects of body size on selectivity for mating cues in different sensory modalities*, *Biol J Linn Soc Lond*, 105 (2012), 160–168.
- [18] A. V. Hedrick and T. Weber, *Variance in female responses to the fine structure of male song in the field cricket, *Gryllus integer**, *Behav Ecol*, 9 (1998), 582–591.
- [19] H. A. Hofmann and K. Schildberger, *Assessment of strength and willingness to fight during aggressive encounters in crickets*, *Anim Behav*, 62 (2001), 337–348.
- [20] R. Kortet and A. V. Hedrick, *Detection of the spider predator, *hololena nedra* by naïve juvenile field crickets (*Gryllus integer*) using indirect cues*, *Behaviour*, 141 (2004), 1189–1196.
- [21] R. Kortet and A. V. Hedrick, *The scent of dominance: female field crickets use odour to predict the outcome of male competition*, *Behav Ecol Sociobiol*, 59 (2005), 77–83.
- [22] R. Kortet and A. V. Hedrick, *A behavioural syndrome in the field cricket *Gryllus integer*: intrasexual aggression is correlated with activity in a novel environment*, *Biol J Linn Soc Lond*, 91 (2007), 475–482.
- [23] R. Kortet, A. V. Hedrick, and A. Vainikka, *Parasitism, predation and the evolution of animal personalities*, *Ecol Lett*, 13 (2010), 1449–1458.
- [24] R. Kortet, M. J. Rantala, and A. V. Hedrick, *Boldness in anti-predator behaviour and immune defence in field crickets*, *Evol Ecol Res*, 9 (2007), 185–197.
- [25] G. A. Lozano, *Optimal foraging theory: a possible role for parasites*, *Oikos*, 60 (1991), 391–395.
- [26] Y. Moret and M. T. Siva-Jothy, *Adaptive innate immunity? Responsive-mode prophylaxis in the mealworm beetle, *Tenebrio molitor**, *Proc Biol Sci*, 270 (2003), 2475–2480.
- [27] N. T. Nehme, S. Liégeois, B. Kele, P. Giammarinaro, E. Pradel, J. A. Hoffmann, et al., *A model of bacterial intestinal infections in *Drosophila melanogaster**, *PLoS Pathog*, 3 (2007), e173.
- [28] P. Niemelä, A. Vainikka, A. V. Hedrick, and R. Kortet, *Integrating behavior with life history: boldness of the field cricket, *Gryllus integer*, during ontogeny*, *Funct Ecol*, 26 (2012), 450–456.
- [29] P. T. Niemelä, A. Vainikka, S. Lahdenperä, and R. Kortet, *Nymphal density, behavioral development, and life history in a field cricket*, *Behav Ecol Sociobiol*, 66 (2012), 645–652.
- [30] T. R. Raffel, L. B. Martin, and J. R. Rohr, *Parasites as predators: unifying natural enemy ecology*, *Trends Ecol Evol*, 23 (2008), 610–618.
- [31] M. J. Rantala, I. Jokinen, R. Kortet, A. Vainikka, and J. Suhonen, *Do pheromones reveal male immunocompetence?*, *Proc Biol Sci*, 269 (2002), 1681–1685.
- [32] M. J. Rantala and R. Kortet, *Courtship song and immune function in the field cricket *Gryllus bimaculatus**, *Biol J Linn Soc Lond*, 79 (2003), 503–510.
- [33] M. J. Rantala and R. Kortet, *Male dominance and immunocompetence in a field cricket*, *Behav Ecol*, 15 (2004), 187–191.
- [34] M. J. Rantala, R. Kortet, J. S. Kotiaho, A. Vainikka, and J. Suhonen, *Condition dependence of pheromones and immune function in the grain beetle *Tenebrio molitor**, *Funct Ecol*, 17 (2003), 534–540.
- [35] D. Réale, S. M. Reader, D. Sol, P. T. McDougall, and N. J. Dingemanse, *Integrating animal temperament within ecology and evolution*, *Biol Rev Camb Philos Soc*, 82 (2007), 291–318.
- [36] J. R. Rohr, A. Swan, T. R. Raffel, and P. J. Hudson, *Parasites, info-disruption, and the ecology of fear*, *Oecologia*, 159 (2009), 447–454.
- [37] P. Schmid-Hempel, *Immune defence, parasite evasion strategies and their relevance for ‘macroscopic phenomena’ such as virulence*, *Philos Trans R Soc Lond B Biol Sci*, 364 (2009), 85–98.
- [38] A. Sih, A. Bell, and J. C. Johnson, *Behavioral syndromes: an ecological and evolutionary overview*, *Trends Ecol Evol*, 19 (2004), 372–378.
- [39] L. W. Simmons, *Inter-male competition and mating success in the field cricket, *Gryllus bimaculatus* (de Geer)*, *Anim Behav*, 34 (1986), 567–579.
- [40] J. Stamps and T. G. Groothuis, *The development of animal personality: relevance, concepts and perspectives*, *Biol Rev Camb Philos Soc*, 85 (2010), 301–325.
- [41] M. L. Thomas and L. W. Simmons, *Short-term phenotypic plasticity in long-chain cuticular hydrocarbons*, *Proc Biol Sci*, 278 (2011), 3123–3128.
- [42] S. Väänänen, R. Kortet, and M. J. Rantala, *Dominance and immune function in the F1 generation of wild caught field crickets*, *Behaviour*, 143 (2006), 701–712.
- [43] I. Vallet-Gely, B. Lemaitre, and F. Boccard, *Bacterial strategies to overcome insect defences*, *Nat Rev Microbiol*, 6 (2008), 302–313.
- [44] N. Wedell and T. Tregenza, *Successful fathers sire successful sons*, *Evolution*, 53 (1999), 620–625.
- [45] D. S. Wilson, K. Coleman, A. B. Clark, and L. Biederman, *Shy-bold continuum in pumpkinseed sunfish (*Lepomis gibbosus*): an ecological study of a psychological trait*, *J Comp Psychol*, 107 (1993), 250–260.