

## **UC Davis**

### **UC Davis Previously Published Works**

**Title**

Environmental condition-dependent effects on a heritable, preferred male trait

**Permalink**

<https://escholarship.org/uc/item/5955k76z>

**Journal**

Animal Behaviour, 70

**ISSN**

0003-3472

**Author**

Hedrick, A

**Publication Date**

2005-11-01

Peer reviewed



## Environmental condition-dependent effects on a heritable, preferred male trait

ANN HEDRICK

Neurobiology, Physiology & Behavior, University of California, Davis

(Received 5 August 2004; initial acceptance 7 October 2004;  
final acceptance 14 February 2005; published online 3 October 2005; MS. number: A9958)

Models for the evolution of female mating preferences suggest that preferred male traits may be condition dependent. In the field cricket, *Gryllus integer*, a preferred male trait (calling-bout duration) shows high additive genetic variance. I found that this preferred trait is also condition dependent. Under food deprivation, males lose body mass and correspondingly shorten the durations of their calling bouts. This result implies that females might be able to gain cues from calling-bout durations about a male's body condition.

© 2005 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

Female mating preferences are important in evolutionary biology because of their potential to shape the evolution of male traits and female sensory systems. As a consequence, many biologists have proposed models to account for the evolution of female mating preferences (Andersson 1994). Generally, these models require that male traits preferred by females have high additive genetic variance. The models show that for female mating preferences to evolve for particular male traits, these traits must confer either direct or indirect (genetic) benefits on females. A variety of both 'indirect' and 'direct' benefits models have suggested that preferred male traits are dependent on the male's body condition (i.e. his health and nutritional status). For example, some indirect-benefit ('good genes') models (Andersson 1986, 1994) propose that females use the male traits they prefer as indicators of male body condition. Presumably, these indicator traits inform females about not only male genotypes, but also how well those genotypes are faring in the current environment. By mating with a male in good body condition, a female might ensure that her offspring have genotypes that will allow them to achieve high fitness in a similar environment. Other models suggest that condition-dependent male traits may allow females to choose males in good body condition, because these males provide the best direct (nongenetic) benefits to females and/or their offspring (e.g. Price et al. 1993).

Although many studies have shown that preferred male traits are affected by body condition (e.g. Zuk et al. 1990;

Jennions & Backwell 1998; McGraw et al. 2002; Rantala et al. 2003), only a fraction have shown that these traits are also high in additive genetic variance (but see e.g. Wilkinson & Taper 1999; David et al. 2000; Jia et al. 2000; Kotiaho et al. 2001). Thus, in many cases, females may not be able to gain any cues from condition-dependent male traits about male genotypes. Rather, differences among males may reflect environmental variation, for example in the food that they obtain during development. Nevertheless, these differences may be important in female choice of mates.

Here, I demonstrate that a male trait that is preferred by females is both heritable (requiring it to have high additive genetic variance) and condition dependent. To investigate condition dependence in a preferred male trait, I used the field cricket, *Gryllus integer*. In this cricket, males call to attract sexually receptive females, and males differ in their durations of uninterrupted calling (Hedrick 1986). The song of this cricket is made up of chirps, each chirp consisting of two to three short sound pulses (10 ms long at 25°C). These chirps are organized into trains of chirps (hereafter, calling bouts, defined as a period of calling containing no pause greater than 0.1 s), which sound to the human ear like a trill. Some males trill for a long time without stopping (up to 5–6 h), whereas others break up their trills at regular intervals, and many males have intermediate sorts of calls (Hedrick 1986, 1988). Calling-bout length is not correlated with body size in this species (A. Hedrick, unpublished data).

In an earlier work on the population of *G. integer* in Davis, California, U.S.A., I showed conclusively that females prefer calls with longer calling bouts, even when all variables in the call other than bout length are controlled (Hedrick 1986), and that bout length is heritable,

Correspondence: A. Hedrick, Neurobiology, Physiology & Behavior, University of California, One Shields Avenue, Davis, CA 95616, U.S.A. (email: [avhedrick@ucdavis.edu](mailto:avhedrick@ucdavis.edu)).

with a high heritability of 0.75 (Hedrick 1988). Therefore, calling-bout length is a preferred male trait with high additive genetic variance in *G. integer* from this population.

Several lines of evidence suggested that calling might be a condition-dependent trait in this population of crickets. First, calling in crickets is energetically costly, requiring up to 16 times basal metabolic rates for some trilling species (Prestwich & Walker 1981; Hoback & Wagner 1997). Second, some components of cricket song are condition dependent in other species of crickets (Wagner & Hoback 1999; Scheuber et al. 2003). Third, food limitation and condition dependence of song elements occur in some cricket populations under natural conditions (Holzer et al. 2003).

Thus, I tested whether calling-bout duration, a preferred, heritable trait, is condition dependent in this population of crickets. To address this question, I hypothesized that food deprivation would detract from male body condition (males would lose mass), and in response to this deprivation, males would decrease calling-bout duration. I also hypothesized that decreases in mass would be positively correlated with decreases in calling-bout duration.

## MATERIALS AND METHODS

Forty virgin laboratory-reared males (unrelated first-generation offspring of 40 females caught in the field) were randomly assigned to one of two groups, either 'fed' ( $N = 20$ ) or 'fasted' ( $N = 20$ ). All males were weighed ( $\pm 0.001$  g) and placed into individual cages (waxed paper ice-cream cups), from which their calling activity could be monitored continuously. To obtain a record of each male's calling activity and bout lengths over a 4-day period, I used an audio monitor (Hedrick & Mulloney 2004) connected to a computer. Males were kept at 25°C and on a 12:12 h light:dark cycle. They were spatially and acoustically isolated, each in his own cage, surrounded by acoustic foam, which blocked sounds from outside the cage. A small microphone was inserted into the lid of each male's cage. Acoustic output from the microphones was converted by the audio monitor into a digital signal that was sent to a computer. I then used software developed in my laboratory (Hedrick & Mulloney 2004) to analyse the calling records of individual males. Following Hedrick (2000), I used the mean duration of all bouts longer than 10 min to characterize a male's calling behaviour.

For the first 2 days of the experiment, all males received ad libitum food (Purina chick starter) and water supplied in a vial stuffed with cotton. After 2 days, I opened each cage, removing the food cup from the fasted males while picking it up and replacing it for the fed males. Water was left unchanged. I continued monitoring all calling activity for an additional 2 days, then removed all males from the experimental set-up and weighed them again.

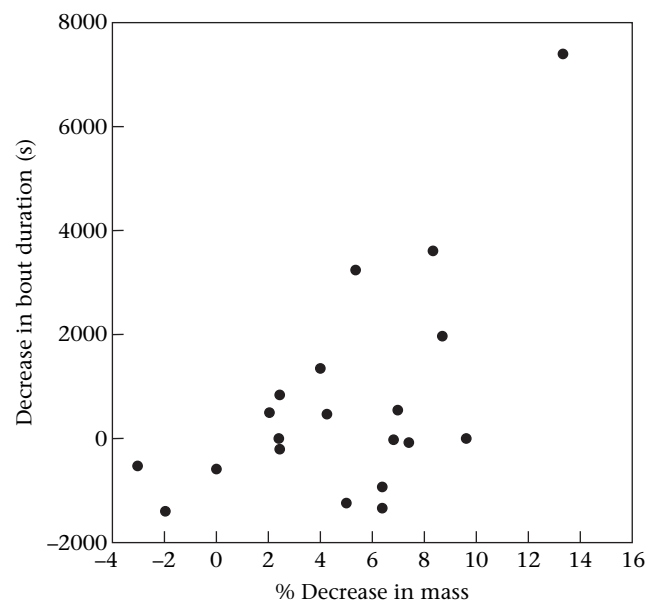
I then evaluated whether fasted males had lost more mass than fed males, and whether fasted males decreased their calling-bout lengths relative to fed males. I used loss in mass as a measure of decline in condition (Blanckenhorn & Hosken 2003). Data were analysed with parametric tests when data fit a normal distribution, and with

nonparametric tests when data did not. I used one-tailed tests for directional hypotheses (e.g. the hypothesis that fasted males would lose more mass than fed males). Neither the masses nor the bout lengths of males in the fed and fasted groups differed from one another at the beginning of the experiment (masses: two-tailed  $t$  test:  $t_{38} = 1.37$ ,  $N = 20$  males/group,  $P = 0.18$ ; bout lengths: Mann-Whitney  $U$  test:  $U = 465$ ,  $N_1 = N_2 = 20$  males/group,  $P = 0.14$ ). Also, there was no significant correlation between mass and bout length at the start of the experiment (Spearman rank correlation:  $r_s = -0.114$ ,  $N = 40$ ,  $P = 0.48$ ), nor at the end of the experiment ( $r_s = -0.05$ ,  $N = 40$ ,  $P = 0.75$ ).

## RESULTS

Fasted males lost more mass than did fed males (one-tailed  $t$  test:  $t_{38} = -3.00$ ,  $N = 20$  males/group,  $P = 0.0025$ ), losing, on average, around 6% of their body weight ( $\bar{X} \pm \text{SE} = -0.029 \pm 0.006$  g from a mean  $\pm \text{SE}$  mass of  $0.477 \pm 0.01$  g); fed males gained, on average, a slight amount of weight ( $0.0025 \pm 0.006$  g). Moreover, fasted males decreased their bout lengths significantly compared to fed males ( $\bar{X} \pm \text{SE}$  bout length for all males =  $4209.84 \pm 535.39$  s, median bout length = 2898.958 s, median change for fasted males =  $-731.77$  s, median change for fed males = 233.45 s; one-tailed Mann-Whitney  $U$  test:  $U = 325$ ,  $N_1 = N_2 = 20$  males/group,  $P = 0.01$ ).

Decreases in mass were positively correlated with decreases in bout length (Kendall's tau = 0.33,  $N = 20$  males, one-tailed  $P = 0.02$ ; Fig. 1). As the fasted males lost a higher percentage of their mass, they correspondingly dropped the mean durations of their calling bouts (Kendall's tau = 0.33,  $N = 20$  males, one-tailed  $P = 0.02$ ; Fig. 1).



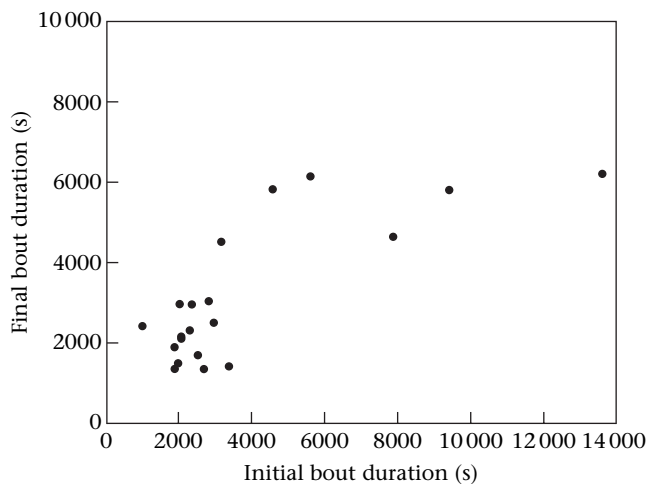
**Figure 1.** Decrease in bout duration (s) versus percentage of decrease in mass for fasted males. Each point represents an individual male ( $N = 20$ ).

The same significant relationship was found for the percentage decrease in bout duration versus the percentage decrease in mass (Kendall's tau = 0.33,  $N = 20$  males, one-tailed  $P = 0.02$ ). There was a trend for fasted males with longer initial bouts to lose proportionally more of their bout duration as a result of fasting than did males with shorter initial bouts (percentage drop in bout length versus initial bout length, Spearman rank correlation:  $r_s = 0.44$ ,  $N = 20$ , two-tailed  $P = 0.055$ ). However, the five males (25%) that had the longest bout lengths at the beginning of the experiment ( $> 4000$  s) still had relatively long bout lengths after fasting ( $> 4000$  s versus  $< 4000$  s for 14 of the 15 other males; Fig. 2). Furthermore, males with longer initial bout lengths did not lose proportionately more of their initial body mass, relative to other males (initial bouts versus percentage of mass lost, Spearman rank correlation:  $r_s = 0.166$ ,  $N = 20$ , one-tailed  $P = 0.48$ ).

## DISCUSSION

In this study, fasting decreased both body mass and calling-bout durations of male crickets. Moreover, there was a significant relationship between percentage of mass lost and the amount, as well as the percentage, by which male bout durations decreased. Males that lost more mass decreased their bout lengths more than did other males. This result suggests that calling is energetically costly, and hence that females might use calling-bout length as a reliable indicator of male condition.

Given that calling-bout duration is a preferred, heritable trait in this population of crickets (Hedrick 1986, 1988), bout duration could simultaneously provide females with cues about a male's body condition and his genotype. Under at least some conditions, such as those in this experiment, males with longer bouts are both in good nutritional condition and have the long-calling genotype. In the absence of significant genotype-environment interactions, information on bout duration might allow females to choose mates whose genotypes are



**Figure 2.** Final calling-bout durations (s) versus initial calling-bout durations for fasted males. Each point represents a single male ( $N = 20$ ).

favourable under current environmental conditions. An alternative, but not mutually exclusive, possibility is that females could use this indicator of male condition to find specific locations where environmental conditions are particularly favourable, for the benefit of either the females or their offspring. In this population, males call for females from cracks in the ground, which are sometimes but not always surrounded by protective cover and adequate food, and which differ in temperature (Hedrick et al. 2002). It is not known whether females usually oviposit in a male's crack after mating with him. Females often leave cracks soon after mating, and in the laboratory, do not start laying eggs until 1–2 weeks after insemination. Finally, it is possible that female preferences for longer calling-bout durations are nonadaptive.

Despite the strong association across males between decrease in mass and decrease in bout length, males with longer bouts at the beginning of the experiment did not lose a greater percentage of their mass than did other males. Thus, these males were apparently more able to maintain long bouts in the face of a food shortage than were other males, again suggesting that calling-bout length is reliably correlated with male condition. The hypothesis that bout length may reflect additive genetic variance in condition, as well as environmental variation in condition, awaits further study (Rowe & Houle 1996; Blanckenhorn & Hosken 2003). For example, some genotypes might be better at acquiring or conserving nutritional reserves than others.

Although males were not observed visually during this experiment, one proximate explanation for the shorter calling bouts in the fasted males might be that these males shortened their calling bouts to forage for food. Calling and feeding are mutually exclusive activities in these crickets, so hungry males might spend more time searching for food and therefore less time calling.

Studies in other species of crickets have shown that body condition affects calling song (Wagner & Hoback 1999; Holzer et al. 2003; Scheuber et al. 2003), and in some cases, affects female choice (Wagner & Hoback 1999; Holzer et al. 2003). In contrast, body condition in *G. texensis* does not affect courtship song, which is quieter than calling song and directly precedes mating (Gray & Eckhardt 2001).

Anecdotal evidence from *G. integer* suggests that food deprivation does not affect song carrier frequency, a male trait that is not subject to sexual selection (A. Hedrick, unpublished data). Thus, the change in calling-bout length with food deprivation may fit a prediction from the handicap model of sexual selection (Zahavi 1975), that sexual ornaments will show greater condition dependence than will other traits (Cotton et al. 2004). Unfortunately, my monitoring system did not allow me to track changes in additional variables within male song, such as syllable and chirp duration. These variables might yield more information than carrier frequency, because song carrier frequency largely depends on adult morphology, which is stable after maturation. Body size and calling-bout duration are not correlated in this species, eliminating the need for body size scaling of the present results (Cotton et al. 2004).

Finally, the removal of food for 2 days from males in the fasted group was unlikely to have exceeded the range of environmental conditions in nature, because the weight lost by these males (approximately 6% of body mass) compares directly with the weight gain of males from the field when they are brought into the laboratory and given ad libitum food (A. Hedrick, unpublished data). The effects of food deprivation when administered for a shorter period (e.g. 1 day) or with a less nutritious diet (e.g. with lower protein) are unknown.

In summary, condition-dependent signals have been identified in a variety of animals, but the degree of genetic variance (heritability) in these signals has been measured less frequently (but see e.g. Wilkinson & Taper 1999; David et al. 2000; Kotiaho et al. 2001). This study provides direct evidence that a heritable condition-dependent signal preferred by females is reliably correlated with male body condition.

### Acknowledgments

I thank Raine Kortet, Brian Mulloney, William Wagner, Anne Leonard, Laura Berger and two anonymous referees for helpful comments. This work was supported by National Science Foundation grant IBN 007-6484.

### References

- Andersson, M. 1986. Evolution of condition-dependent sex ornaments and mating preferences: sexual selection based on viability differences. *Evolution*, **40**, 804–816.
- Andersson, M. 1994. *Sexual Selection*. Princeton, New Jersey: Princeton University Press.
- Blanckenhorn, W. U. & Hosken, D. J. 2003. Heritability of three condition surrogates in the yellow dung fly. *Behavioral Ecology*, **14**, 612–618.
- Cotton, S., Fowler, K. & Pomiankowski, A. 2004. Do sexual ornaments demonstrate heightened condition-dependent expression as predicted by the handicap hypothesis? *Proceedings of the Royal Society of London, Series B*, **271**, 771–783.
- David, P., Bjorksten, T., Fowler, K. & Pomiankowski, A. 2000. Condition-dependent signaling of genetic variation in stalk-eyed flies. *Nature*, **406**, 186–188.
- Gray, D. A. & Eckhardt, G. 2001. Is cricket courtship song condition dependent? *Animal Behaviour*, **62**, 871–877.
- Hedrick, A. 1986. Female preferences for male calling bout duration in a field cricket. *Behavioral Ecology and Sociobiology*, **19**, 73–77.
- Hedrick, A. 1988. Female choice and the heritability of attractive male traits: an empirical study. *American Naturalist*, **132**, 267–276.
- Hedrick, A. 2000. Crickets with extravagant mating songs compensate for predation risk with extra caution. *Proceedings of the Royal Society of London, Series B*, **267**, 671–675.
- Hedrick, A. & Mulloney, B. 2004. A multichannel electronic monitor of acoustic behaviors, and software to parse individual channels. *Journal of Neuroscience Methods*, **133**, 201–210.
- Hedrick, A., Perez, D., Lichti, N. & Yew, J. 2002. Temperature preferences of male field crickets (*Gryllus integer*) alter their mating calls. *Journal of Comparative Physiology A*, **188**, 799–805.
- Hoback, W. W. & Wagner, W. E. 1997. The energetic cost of calling in the variable field cricket, *Gryllus lineaticeps*. *Physiological Entomology*, **22**, 286–290.
- Holzer, B., Jacot, A. & Brinkhof, M. W. G. 2003. Condition-dependent signaling affects male sexual attractiveness in field crickets, *Gryllus campestris*. *Behavioral Ecology*, **14**, 353–359.
- Jennions, M. & Backwell, P. 1998. Variation in courtship rate in the fiddler crab *Uca annulipes*: is it related to male attractiveness? *Behavioral Ecology*, **9**, 605–611.
- Jia, F., Greenfield, M. D. & Collins, R. D. 2000. Genetic variance of sexually selected traits in waxmoths: maintenance by genotype  $\times$  environment interaction. *Evolution*, **54**, 953–967.
- Kotiaho, J. S., Simmons, L. W. & Tomkins, J. L. 2001. Towards a resolution of the lek paradox. *Nature*, **410**, 684–686.
- McGraw, K. J., McKillop, E. A., Dale, J. & Hauber, M. E. 2002. Different colors reveal different information: how nutritional stress affects the expression of melanin- and structurally based ornamental plumage. *Journal of Experimental Biology*, **205**, 3747–3755.
- Prestwich, K. N. & Walker, T. J. 1981. Energetics of singing in crickets: effect of temperature in three trilling species (Orthoptera: Gryllidae). *Journal of Comparative Physiology*, **143**, 199–212.
- Price, T., Schluter, D. & Heckman, N. 1993. Sexual selection when the female directly benefits. *Biological Journal of the Linnean Society*, **48**, 187–211.
- Rantala, M., Kortet, R., Kotiaho, J., Vainikka, A. & Suhonen, J. 2003. Condition dependence of pheromones and immune function in the grain beetle *Tenebrio molitor*. *Functional Ecology*, **17**, 534–540.
- Rowe, L. & Houle, D. 1996. The lek paradox and the capture of genetic variance by condition dependent traits. *Proceedings of the Royal Society of London, Series B*, **263**, 1415–1421.
- Scheuber, H., Jacot, A. & Brinkhof, M. W. G. 2003. Condition dependence of a multi-component sexual signal in the field cricket *Gryllus campestris*. *Animal Behaviour*, **65**, 721–727.
- Wagner, W. E. & Hoback, W. W. 1999. Nutritional effects on male calling behaviour in the variable field cricket. *Animal Behaviour*, **57**, 89–95.
- Wilkinson, G. & Taper, M. 1999. Evolution of genetic variation for condition-dependent traits in stalk-eyed flies. *Proceedings of the Royal Society of London, Series B*, **266**, 1685–1690.
- Zahavi, A. 1975. Mate selection: a selection for a handicap. *Journal of Theoretical Biology*, **53**, 205–214.
- Zuk, M., Thornhill, R., Ligon, J. & Johnson, K. 1990. Parasites and mate choice in red jungle fowl. *American Zoologist*, **30**, 235–244.