

# Diel variation in a dynamic sexual display and its association with female mate-searching behaviour

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Dynamic sexual signals often show a diel rhythm and may vary substantially with time of day. Diel and short-term fluctuations in such sexual signals pose a puzzle for condition capture models of mate choice, which assume a female preference for male traits that reliably reflect a male's quality. Here we experimentally manipulated the food supply of individual male field crickets *Gryllus campestris* in their natural habitat in two consecutive seasons to determine (i) the effect of male nutritional condition on the fine-scaled variation of diel investment in acoustic signalling and (ii) the temporal association between the diel variation in male signalling and female mate-searching behaviour. Overall food-supplemented males signalled more often, but the effect was only visible during the daytime. In the evening and the night, signal output was still high but the time spent signalling was unrelated to a male's nutritional condition. Females' mate-searching behaviour also showed a diel rhythm with peak activity during the afternoon, when differences among calling males were highest, and where signal output reliably reflects male quality. These findings suggest that males differing in nutritional condition may optimize their investment in signalling in relation to time of day as to maximize mating success.

**Keywords:** circadian rhythm; honest signalling; female mate choice; condition dependence; ambient temperature

## 1. INTRODUCTION

Diel rhythms in behavioural traits are common in most animal species. The migratory restlessness of passerines (Berthold *et al.* 2003), the dawn chorus of birds (Catchpole & Slater 1995) and the acoustic displays of insects and anurans (Gerhardt & Huber 2002) are among the most striking examples for diel rhythms in animal behaviours. The best explanation for the gross activity patterns lies in the distinct 24-hour period of the solar radiation which generates diel environmental cycles. This variation in environmental conditions is an important force shaping an individual's life history and its temporal investment in fitness-related traits (Dunlap *et al.* 2004). Life-history theory predicts that any deviation from the mean activity pattern most likely reflects an optimized, adaptive strategy of an individual that depends on its genetic background, condition and additionally on environmental factors that interact with its current state (Stearns 1992). Despite extensive research on diel and

circadian rhythms in behavioural sciences (e.g. Takahashi *et al.* 2001; Dunlap *et al.* 2004), the causes of the fine-scaled variation in activity patterns are poorly studied and its adaptive function is largely unexplored.

Sexual signals offer a unique possibility to investigate the proximate and ultimate causes for variation in diel investment in traits, which are related to fitness. The time spent signalling, that is, the signalling effort of a displaying male is a sexually dynamic trait where the signal output can be modulated within a short time period and often follows a diel rhythm. While the mechanism of sexual selection is not necessarily female choice or male-male competition (Murphy 1998), the signalling effort of a male into mate attraction is expected to be a main trait under sexual selection owing to its direct effect on mating success. Theoretically, the optimal investment in current signalling depends on the fitness returns per unit of extra-investment in current reproduction at the cost of future reproduction (Stearns 1992). The resulting trade-off and thereby a male's optimal investment in current signalling will depend on factors affecting a male's state and additionally on its local environment.

Variation in calling effort may be explained by internal factors like male nutritional condition (Holzer *et al.* 2003;

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Jacot *et al.* 2004), immune status (Jacot *et al.* 2004) and also on its age (Bertram 2000; Hunt *et al.* 2006) and mating status (Amrhein *et al.* 2004). In nightingales (*Luscinia megarhynchos*), bachelor males invested more in singing activity but only during the early morning (Amrhein *et al.* 2004). In addition, external factors such as the availability of receptive females within the day may affect the strength of sexual selection and thereby also the willingness of a male to invest in costly signalling. As soon as females invest differentially in mate search activity in relation to daytime or environmental factors (e.g. predation pressure), males are expected to use this information about female activity in their decisions to invest in sexual display. These examples indicate that variation in dynamic male sexual displays is not only reflecting a male's condition or state but also additionally interacts with a strategic investment of a male into signalling.

In this field study with the field cricket *Gryllus campestris*, we experimentally investigate the effects of male nutritional condition on variation in signalling effort, diel signalling pattern and its consequences on temporal mate choice patterns of females. Male field crickets use their modified forewings to emit the long-range calling song. Field crickets kept under superior nutritional condition called more often and produced a more attractive calling song compared with controls (Wagner & Hoback 1999; Holzer *et al.* 2003; Scheuber *et al.* 2003a,b). Furthermore, recent experimental and correlational studies have demonstrated that the acoustic display of orthopterans confers reliable information about the availability of specific macronutrients (Bertram *et al.* 2006), current immune status (Ryder & Siva-Jothy 2000, 2001; Jacot *et al.* 2004; Simmons *et al.* 2005), age (Bertram 2000) and heritable longevity (Hunt *et al.* 2006). However, probably the most important calling song characteristic determining female attraction is the proportion of time spent calling (Holzer *et al.* 2003). In short, this study investigates a proximate cause (i.e. nutritional condition) for diel variation in a dynamic sexual display and its association with female mate-searching behaviour.

## 2. MATERIAL AND METHODS

The studies took place in 2 years (2000 and 2002) on an uncut meadow located near Hinterkappelen, Bern, Switzerland (46°58'10" N, 7°23'35" E). Further specifications about the study site are described in detail in Holzer *et al.* (2003), and the life cycle of *G. campestris* is well documented in Rost & Honegger (1987).

### (a) Male temporal signalling patterns

The effect of food availability on male diel signalling patterns was recorded between April and July 2002. We used a randomized block experimental design to balance out the potential influence of between-day variation in environmental conditions (e.g. ambient temperature, wind, and humidity) across the control and food-supplemented treatment groups. In this design, groups of up to 10 males entered the experiment on the same day, and within blocks, males were randomized over the control and food supplementation group. Experimental males were randomly selected among the calling males, weighed with an electronic balance (PT150, Sartorius, Göttingen, Germany) to the nearest 0.01 g and assigned to one of two food treatments. Each male

was transferred to a tent-like enclosure of 1 m<sup>2</sup> covered by a mosquito net of 50 cm in height, containing an artificial burrow and a sheltered feeding dish. Cages were randomly distributed over the meadow with minimum distances of 1.5 m to each other. To manipulate nutritional condition of males, we supplemented extra food over a period of 3 days. Food-supplemented males were fed ad libitum with fish food (NovoBel Aquarium fish food, JBL GmbH, Neuhofen, Germany) whereas control individuals received an empty feeding dish. All feeding dishes were exchanged daily with new ones. The use of enclosures allowed us to regularly monitor male body mass and survival. The netting also ensured that the male had exclusive access to the food supplement and that his calling behaviour was not affected by direct physical contact with females or other males.

Four males from the control treatment and three males from the food-supplemented treatment escaped and all were excluded from future analyses. The remaining control ( $N=44$ ) and food-supplemented ( $N=47$ ) males did neither differ in body mass at the beginning of the experiment ( $F_{1,79}=0.94$ ,  $p=0.34$ ) nor in the structural size (pronotum, tibia and harp size; all  $p>0.3$ ). We used the change in body mass from the start of the experimental period until the recording of the calling song (day 3) as a measure of body condition in individual males (cf. Scheuber *et al.* 2003a; Jacot *et al.* 2004). This measure is a reliable indicator of change in body condition following food supplementation (Scheuber *et al.* 2003a).

From day 2 to 3, we recorded daily calling rate for a period of 23–24 hours using a data logger (Mindstorms RCX 1.0 programmable brick, LEGO, Baar, Switzerland) with a microphone (DCP Microsense, DCP Microdevelopments Ltd, Norfolk, UK). The logger was programmed to measure loudness (dB) every 3 min resulting in 480 data points in 24 hours. Data points, which were 25 dB above background noise, were scored as 'singing' or 1, while data points less than 25 dB above background noise were scored as 'not singing' or 0. Males sing on average  $49 \pm 3.28$  dB above background noise, and our threshold value has proven to reliably discriminate singing males from background noise (Jacot *et al.* 2004).

On day 3, we recorded calling song quality, using a digital audio tape recorder (TCD-D100, Sony, Tokyo, Japan) and a stereo microphone (ECM-MS957, Sony, Tokyo, Japan). To reduce temperature-induced variation in calling song characteristics, we recorded all males in the evening when the whole meadow was in the shade. The analysis of calling song characters was performed using Canary software (Charif *et al.* 1995). We measured chirp rate (no. of chirps s<sup>-1</sup>), chirp duration (ms), interchirp duration (ms), syllable number (no. of syllables/chirp), chirp intensity (fW m<sup>-2</sup>) and carrier frequency (kHz) using standard criteria (e.g. Scheuber *et al.* 2003b).

### (b) Temporal mate choice patterns

Data on acoustic signalling by males and attractiveness of males to females (i.e. number of females trapped at male burrows) were obtained in two separate years, spring 2002 (Jacot *et al.* 2004) and spring 2000 (Holzer *et al.* 2003), respectively. During a field experiment in the year 2000, we measured female attraction in a similar experimental set-up (see Holzer *et al.* 2003). Females were caught in four pitfall traps (7 cm in diameter and 9 cm in depth) that were placed around the cages that contained an experimental male differing in nutritional condition. Pitfall traps were checked every hour between 12.00 and 21.00 and the number of

females caught was noted for each experimental male. The trapped females were individually marked with a numbered opalith plate glued onto the pronotum (Bienen-Meier, Switzerland), and finally released 1 m above the site of capture. Food-supplemented males attracted overall more females than control males (see Holzer *et al.* 2003). Here we present the reanalysis of these data investigating temporal variation in attractiveness of males to females and to associate this variation to variation in male calling song.

### (c) Statistical analyses

All statistical analyses were performed with the freeware R v. 2.4.0 (R Development Core Team 2006). A seasonal decline in body mass ( $N=91$ ,  $r=-0.29$ ,  $p<0.01$ ) indicates the importance of including seasonal effects in our analyses. All statistics were therefore controlled for group effects. For the analyses of daily calling activity, we divided the 24-hour period into six blocks of 4 hours starting at 13 hours. For each time block, we calculated mean  $\pm$  s.e. per cent time spent calling. To investigate treatment effects on daily calling patterns, we added the six time blocks as repeats in a repeated measure ANOVA. This analysis allows determining an overall treatment effect on calling rate and additionally treatment effects on daily calling patterns. In a further step, we analysed each time block separately using mixed effect models (NLME package: Pinheiro *et al.* 2006) with individual nested within the group as random effect and food treatment as fixed effect.

In a next step, we analysed whether treatment-specific differences on diel calling rate patterns can be explained through variation in ambient temperature. Owing to diel fluctuations in solar radiation, ambient temperature shows a consistent diel pattern with lowest temperatures around sunrise and highest temperatures at approximately 14 hours (data not shown). The effect of environmental temperature on calling rate was analysed using generalized linear mixed models with a Poisson distribution (LME4 package; Bates & Sarkar 2006). For each hour, we used the counts in which a male was calling (max. 20 counts per hour) as dependent variable, food treatment and group as fixed factors, individual as random factor and temperature as covariate. Temperature entered the model as the residuals from a daytime to temperature regression, accounting for the circularity of this variable (i.e. we used the sine and cosine of daytime; Jammalamadaka & Sengupta 2001). We used the best-fitting model, comparing linear as well as quadratic relationships between temperature and singing activity. Temperature data were obtained from the Swiss Meteorological Institute in Liebefeld (46°55'43" N, 7°25'15" E), approximately 5 km from the field site.

The sum of attracted females over a 6-day period was used as a measure of male sexual attractiveness. For statistical analysis, we pooled capture data creating three blocks of 3 hours (block 1: 12–15 hours; block 2: 15–18 hours; and block 3: 18–21 hours) and one block of 15 hours (block 4: 21–12 hours). Note that block 4 accumulates capture data over a 15-hour period, since pitfall traps were not checked between 21.00 and 12.00 the following day. Each block was analysed separately using general linear models with a Poisson error distribution with food treatment as fixed effect, and date of the year and the number of days a male was in the experiment as covariates. To account for underdispersion of the data, we used Pearson's  $\chi^2$  to adjust the scale parameter (i.e. using quasi-Poisson family), and the significance of predictor variables was tested by an  $F$ -test instead of the  $\chi^2$  test (Crawley 2002, pp. 518–519).

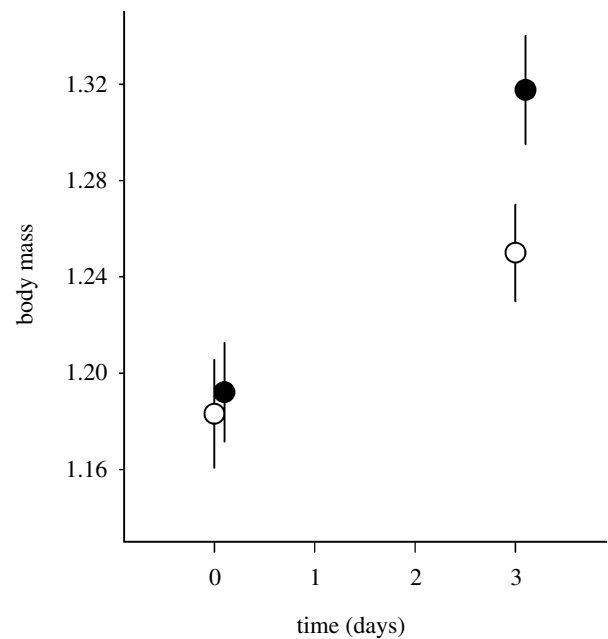


Figure 1. Change in the mean body mass ( $\pm$  s.e.) for control males (open circles) and food-supplemented males (closed circles) over the experimental period.

## 3. RESULTS

### (a) Effects on body mass

The change in body mass over the experimental period was significantly different between the two food treatments (REML mixed model, food treatment  $\times$  time:  $F_{1,85}=11.01$ ,  $p=0.001$ ). Males in both treatments increased in body mass but the increase among food-supplemented males was greater than in control males (figure 1).

### (b) Effects on daily calling rate and temporal signalling patterns

From day 2 to day 3, we measured the effects of the food treatment on daily calling song activity. Over a 24-hour period, calling rate was  $35 \pm 2.4\%$  for food-supplemented males whereas control males called  $26 \pm 2.5\%$  of the time period. Controlling for group effects ( $F_{10,79}=5.10$ ,  $p<0.001$ ), the food treatment had a significant effect on overall daily calling rate (repeated measures ANOVA, food treatment:  $F_{1,79}=11.83$ ,  $p=0.001$ ) and on variation of calling rate within the day (repeated measurement ANOVA, food treatment  $\times$  time:  $F_{5,75}=2.67$ ,  $p=0.022$ ). The variance in signalling within the day is explained by significant treatment effects in calling activity between 09.00 until 21.00 while calling rates were similar for the rest of the day (table 1; figure 2a).

When incorporating temperature as a covariate into the model, we found a significant interaction between environmental temperature and food treatment on calling activity (table 2). This analysis was performed on the total 24-hour period as well as on daytime (12–21 hours) only, and the results are consistent (table 2). The best fit for both treatments is a quadratic relationship where individuals show highest calling rate at intermediate temperatures (approx. 23°C). Individuals that received supplementary food, showed a steeper relationship between environmental temperature and calling rate under low

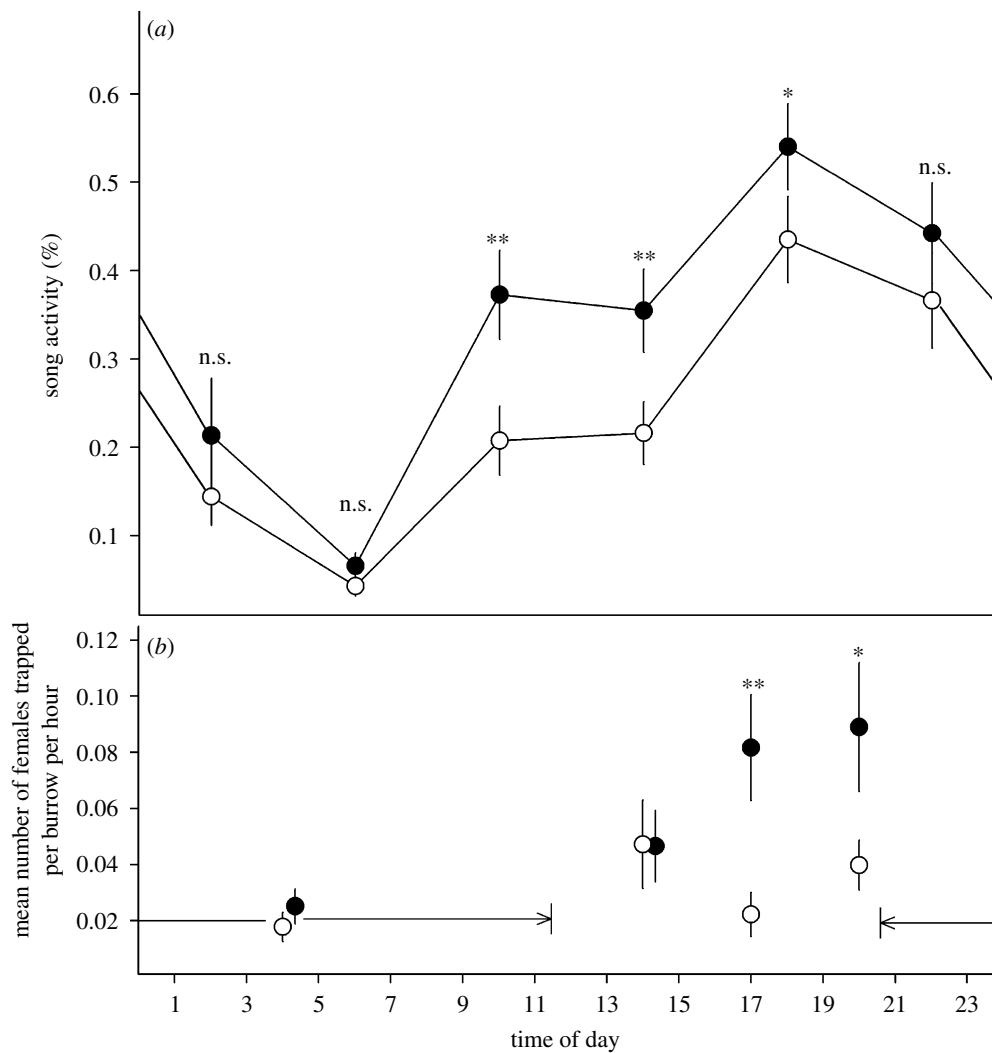


Figure 2. The effect of the food treatment on (a) male temporal signalling pattern and (b) female mate-searching behaviour. The arrow in (b) indicates the 15-hour block during the night and morning over which the number of females trapped was not determined hourly. Open circles indicate control males while closed circles indicate food-supplemented males. The significance is indicated by asterisks, where \* $p < 0.05$ , \*\* $p < 0.01$ .

Table 1. The effect of the food treatment on daily calling activity. (Indicated are means ( $\pm$ s.e.) and test statistics for the six blocks of 4 hours starting at 13 hours.)

time blocks	food treatments		d.f.	<i>F</i> -value	<i>p</i> -value
	control	food supplemented			
1–4	0.14 $\pm$ 0.03	0.21 $\pm$ 0.04	1,79	2.46	0.121
5–8	0.04 $\pm$ 0.01	0.07 $\pm$ 0.01	1,79	1.82	0.181
9–12	0.19 $\pm$ 0.04	0.37 $\pm$ 0.05	1,79	13.54	<0.001
13–16	0.21 $\pm$ 0.04	0.35 $\pm$ 0.05	1,79	13.24	<0.001
17–20	0.42 $\pm$ 0.05	0.54 $\pm$ 0.05	1,79	6.28	0.014
21–0	0.34 $\pm$ 0.05	0.44 $\pm$ 0.06	1,79	1.38	0.244

temperatures and song activity remained on a higher level under high environmental temperatures (figure 3).

#### (c) Effects on calling song characteristics

Food treatment affected chirp rate (REML mixed model, food treatment:  $F_{1,44} = 6.84$ ,  $p = 0.012$ ). This increase in chirp rate is mainly explained through a decreased interchirp duration (REML mixed model, food treatment:  $F_{1,44} = 8.26$ ,  $p = 0.006$ ). Syllable number, chirp duration, chirp intensity and carrier frequency were not affected by the food treatment (all  $p > 0.2$ ).

#### (d) Effects on female mate choice

The effect of food supplementation on the number of females trapped varied with daytime (repeated measures ANOVA, time  $\times$  food treatment:  $F_{3,59} = 3.35$ ,  $p = 0.025$ ). Food-supplemented males attracted more females than control males in the late afternoon and early evening (i.e. time periods 15–18 and 18–21 hours), but not during other time periods (figure 2b). Males of both nutritional conditions attracted a similar number of females during the night-time and morning hours (21–12 hours: treatment:  $F_{1,62} = 1.30$ ,  $p = 0.260$ , covariates day and day of the

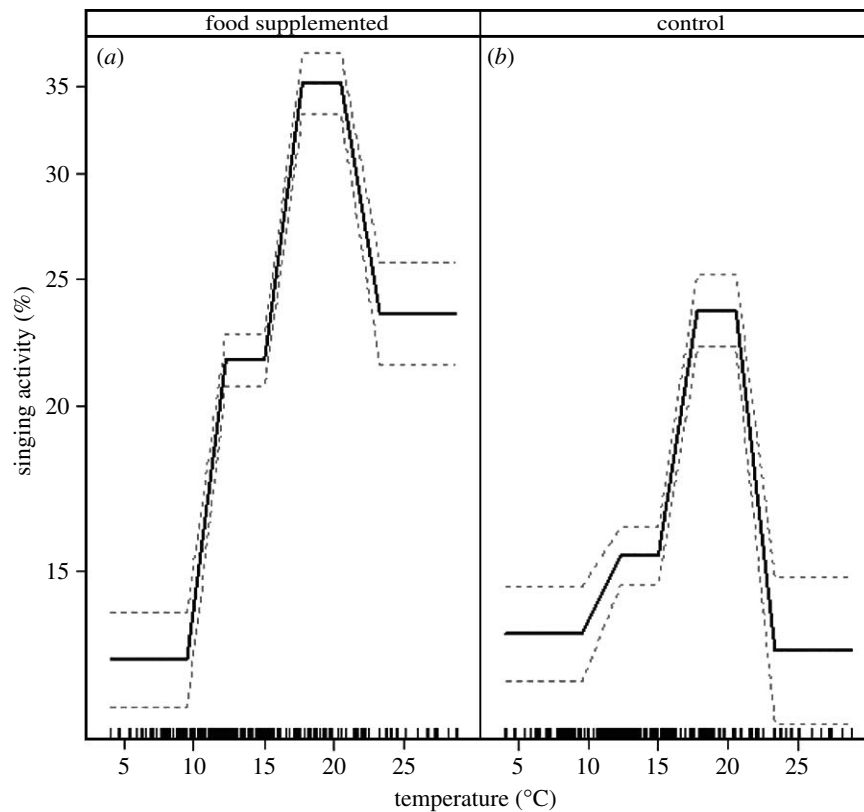


Figure 3. Effect display for the interaction of food treatment on song rate in relation to environmental temperature: (a) food supplemented and (b) control. A 95% pointwise confidence interval is drawn around the estimated effect. For statistical details, see §2.

year  $p < 0.01$ ) and early afternoon (12–15 hours: treatment:  $F_{1,62} = 0.002$ ,  $p = 0.969$ , covariate day of the year  $F_{1,61} = 9.244$ ,  $p < 0.01$ ). In contrast, in the time between 15 and 18 hours (treatment:  $F_{1,62} = 10.439$ ,  $p = 0.002$ , covariate day of the year  $F_{1,61} = 4.54$ ,  $p = 0.037$ ) and between 18 and 21 hours (treatment:  $F_{1,62} = 5.584$ ,  $p = 0.021$ , covariate day of the year  $F_{1,61} = 5.290$ ,  $p = 0.025$ ), food-supplemented males attracted more females than control males.

#### 4. DISCUSSION

Most if not all sexual displays have dynamic components (Gerhardt 1991), for example, the time an individual displays its intense coloration or delivers its complex song to a potential mate. Unfortunately, most studies to date have focused on static sexual traits (reviewed in Cotton *et al.* 2004), largely neglecting temporal aspects of sexual signals. The findings of this study highlight the importance of quantifying diel variation in signalling effort when investigating the condition dependence of dynamic sexual traits. Male calling effort followed a distinct temporal pattern within a 24-hour period that differed between males in good and poor nutritional conditions. The effect of the food treatment on song output was detectable during the morning and afternoon while there was no treatment effect in the evening and the night. Female mate-searching behaviour also followed a diel rhythm that resembled the males' calling pattern. Most males were chosen when treatment-induced differences in calling activity were high and where signal output reflected male nutritional condition. By choosing mates with a high signalling rate, females may obtain both indirect genetic

Table 2. Test statistics for the effect of environmental temperature on daily calling rate in the two food treatments. (Included are only individuals which sang at least once during the 24-hour recording period. For statistical details, see §2.)

coefficient	estimates	s.e.	$z$ -value	$p$ -value
intercept	1.089	0.254	4.28	<0.001
treatment	-0.478	0.207	-2.315	0.021
residual	0.084	0.005	15.79	<0.001
temperature				
residual	-0.005	<0.001	-7.34	<0.001
temperature <sup>2</sup>				
group	0.093	0.033	2.80	0.005
treatment ×	< -0.001	0.008	-0.10	0.919
temperature				
treatment ×	0.006	0.001	4.71	<0.001
temperature <sup>2</sup>				

benefits and eventually also safe and superior feeding grounds.

Male signalling effort was honest on average as predicted by a model of dynamic sexual signalling (Johnstone & Grafen 1993). However and more interestingly, there were certain times within the day when the signal became a heightened indicator of condition. These results indicate that diel allocation patterns in signalling reflect optimized strategies in relation to a male's state. Males in poor condition may adopt a best of a poor situation strategy, investing in signalling when the net benefits are highest. The quantification of factors affecting the decision to invest in signalling is challenging and at the moment we can only speculate which selective forces play

the major role in shaping a male's optimal signal display in relation to daytime.

Low nutritional condition is known to have a detrimental impact on song activity and male longevity (Jacot *et al.* 2004), two life-history traits that are expected to be strongly related to lifetime reproductive success (Stearns 1992). To compensate for the negative effects of low food availability, males in poor condition are expected to invest extra time in foraging in order to increase their energy reserves before the time peak of female mate search activity. In our study, males in poor condition primarily invested in sexual signalling during the late afternoon, which coincides with female peak activity. Variation in a male's daily time budget would herewith mirror a male's state and may reflect an optimal allocation of time in maintenance and mate attraction. Alternatively, predators that eavesdrop on acoustic advertisement calls can have a strong impact on a male's decision to signal (Zuk & Kolluru 1998). Diurnal signalling often requires special protection from predators (Belwood 1990), as seen in the burrows of territorial male field crickets. The physical ability to perceive and escape a predator is probably related to physiological or nutritional condition (Lindström *et al.* 2006). Thus, variation in predation pressure might exert a stronger selective force on low-quality compared with good-quality males, which could partly explain treatment-related differences in diel signalling effort.

A male's strategy to signal can additionally be influenced by abiotic factors affecting basal metabolic rate and the activity of a calling male. Similar to the observed patterns in calling rate, most abiotic factors, like temperature, oscillate over the daily cycle. It is well established that optimal muscle performance in ectotherms is temperature dependent (Machin *et al.* 1962; Verdu *et al.* 2006) and will thereby affect qualitative as well as quantitative aspects of acoustic signals (Pires & Hoy 1992; Martin *et al.* 2000; Walker & Cade 2003). Owing to the high energetic costs of the acoustic display (Hoback & Wagner 1997) and its resulting energetic constraints, individuals will refrain from investing in costly signalling under suboptimal environmental conditions (e.g. maximum or minimum solar radiation; Huey & Stevenson 1979). These constraints are expected to be especially pronounced in individuals of poor body condition and may explain why males in superior physiological condition invested relatively more in signalling at low and very high temperatures.

To conclude, the results of this study are of general interest to sexual selection theory since they demonstrate that variation in dynamic sexual traits incorporate condition-related as well as strategic information about a signaller. This suggests that females may assess male quality less reliably on the basis of separate dynamic traits as compared with multiple traits (Candolin 2003). The multitude of intrinsic and environmental factors affecting a male's decision to signal might deliver an explanation why females of most species use multiple traits in mate choice decisions and why sexual selection has driven female mate preferences for static male traits that incorporate a male's condition or quality over a longer time period.

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## REFERENCES

- Amrhein, V., Kunc, H. P. & Naguib, M. 2004 Seasonal patterns of singing activity vary with time of day in the nightingale (*Luscinia megarhynchos*). *Auk* **121**, 110–117. (doi:10.1642/0004-8038(2004)121[0110:SPOSAV]2.0.CO;2)
- Bates, D. & Sarkar, D. 2006 LME4: linear mixed-effects models using S4 classes. R package, version 0.9975-10. See <http://cran.r-project.org>.
- Belwood, J. J. 1990 Anti-predator defences and ecology of Neotropical forest katydids, especially the Pseudophyllinae. In *The Tettigoniidae: behaviour, systematics, evolution* (eds W. J. Bailey & D. C. F. Rentz), Bathurst, Australia: Crawford House Press.
- Berthold, P., Gwinner, E. & Sonnenschein, E. 2003 *Avian migration*. Berlin, Germany: Springer.
- Bertram, S. M. 2000 The influence of age and size on temporal mate signalling behaviour. *Anim. Behav.* **60**, 333–339. (doi:10.1006/anbe.2000.1473)
- Bertram, S. M., Schade, J. D. & Elser, J. J. 2006 Signalling and phosphorus: correlations between mate signalling effort and body elemental composition in crickets. *Anim. Behav.* **72**, 899–907. (doi:10.1016/j.anbehav.2006.02.012)
- Candolin, U. 2003 The use of multiple cues in mate choice. *Biol. Rev.* **78**, 575–595. (doi:10.1017/S1464793103006158)
- Catchpole, C. K. & Slater, P. J. B. 1995 *Bird song: biological themes and variations*. Cambridge, UK: Cambridge University Press.
- Charif, R. A., Mitchel, S. & Clark, C. W. 1995 *Canary 1.2 user's manual*. Ithaca, NY: Cornell Laboratory of Ornithology.
- Cotton, S., Fowler, K. & Pomiankowski, A. 2004 Do sexual ornaments demonstrate heightened condition-dependent expression as predicted by the handicap hypothesis? *Proc. R. Soc. B* **271**, 771–783. (doi:10.1098/rspb.2004.2688)
- Crawley, M. J. 2002 *Statistical computing: an introduction to data analysis using S-plus*. Chichester, UK: Wiley.
- Dunlap, J. C., Loros, J. L. & DeCoursey, P. J. 2004 *Chronobiology: biological timekeeping*. Sunderland, MA: Sinauer Associates, Inc., Publishers.
- Gerhardt, H. C. 1991 Female mate choice in treefrogs: static and dynamic acoustic criteria. *Anim. Behav.* **42**, 615–635. (doi:10.1016/S0003-3472(05)80245-3)
- Gerhardt, H. C. & Huber, F. 2002 *Acoustic communication in insects and anurans: common problems and diverse solutions*. London, UK: The University of Chicago Press.
- Hoback, W. W. & Wagner, W. E. 1997 The energetic cost of calling in the variable field cricket, *Gryllus lineaticeps*. *Physiol. Entomol.* **22**, 286–290.
- Holzer, B., Jacot, A. & Brinkhof, M. W. G. 2003 Condition-dependent signaling affects male sexual attractiveness in field crickets, *Gryllus campestris*. *Behav. Ecol.* **14**, 353–359. (doi:10.1093/beheco/14.3.353)
- Huey, R. B. & Stevenson, R. D. 1979 Integrating thermal physiology and ecology of ectotherms—discussion of approaches. *Am. Zool.* **19**, 357–366.
- Hunt, J., Jennions, M. D., Spyrou, N. & Brooks, R. 2006 Artificial selection on male longevity influences age-dependent reproductive effort in the black field cricket *Teleogryllus commodus*. *Am. Nat.* **168**, E72–E86. (doi:10.1086/506918)

- Jacot, A., Scheuber, H. & Brinkhof, M. W. G. 2004 Costs of an induced immune response on sexual display and longevity in field crickets. *Evolution* **58**, 2280–2286.
- Jammalamadaka, S. R. & Sengupta, A. 2001 *Topics in circular statistics*. Singapore: World Scientific Publishing Company.
- Johnstone, R. A. & Grafen, A. 1993 Dishonesty and the handicap principle. *Anim. Behav.* **46**, 759–764. (doi:10.1006/anbe.1993.1253)
- Lindström, L., Ahtiainen, J. J., Mappes, J., Kotiaho, J. S., Lyytinen, A. & Alatalo, R. V. 2006 Negatively condition dependent predation cost of a positively condition dependent sexual signaling. *J. Evol. Biol.* **19**, 649–656. (doi:10.1111/j.1420-9101.2005.01043.x)
- Machin, K. E., Pringle, J. W. S. & Tamasige, M. 1962 The physiology of insect fibrillar muscle. IV. The effect of temperature on a beetle flight muscle. *Proc. R. Soc. B* **155**, 493–499. (doi:10.1098/rspb.1962.0014)
- Martin, S. D., Gray, D. A. & Cade, W. H. 2000 Fine-scale temperature effects on cricket calling song. *Can. J. Zool.* **78**, 706–712. (doi:10.1139/cjz-78-5-706)
- Murphy, C. G. 1998 Interaction-independent sexual selection and the mechanisms of sexual selection. *Evolution* **52**, 8–18. (doi:10.2307/2410915)
- Pinheiro, J., Bates, D., DebRoy, S. & Sarkar, D. 2006 NLME: linear and nonlinear mixed effects models. R package, version 3.1-77. See <http://cran.r-project.org>.
- Pires, A. & Hoy, R. R. 1992 Temperature coupling in cricket acoustic communication. 1. Field and laboratory studies of temperature effects on calling song production and recognition in *Gryllus firmus*. *J. Comp. Physiol. A* **171**, 69–78.
- R Development Core Team 2006 *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. ISBN 3-900051-07-0. See <http://www.r-project.org>.
- Rost, R. & Honegger, H. W. 1987 The timing of pre mating and mating behavior in a field population of the cricket *Gryllus campestris* L. *Behav. Ecol. Sociobiol.* **21**, 279–289. (doi:10.1007/BF00299965)
- Ryder, J. J. & Siva-Jothy, M. T. 2000 Male calling song provides a reliable signal of immune function in a cricket. *Proc. R. Soc. B* **267**, 1171–1175. (doi:10.1098/rspb.2000.1125)
- Ryder, J. J. & Siva-Jothy, M. T. 2001 Quantitative genetics of immune function and body size in the house cricket, *Acheta domesticus*. *J. Evol. Biol.* **14**, 646–653. (doi:10.1046/j.1420-9101.2001.00302.x)
- Scheuber, H., Jacot, A. & Brinkhof, M. W. G. 2003a Condition dependence of a multicomponent sexual signal in the field cricket *Gryllus campestris*. *Anim. Behav.* **65**, 721–727. (doi:10.1006/anbe.2003.2083)
- Scheuber, H., Jacot, A. & Brinkhof, M. W. G. 2003b The effect of past condition on a multicomponent sexual signal. *Proc. R. Soc. B* **270**, 1779–1784. (doi:10.1098/rspb.2003.2449)
- Simmons, L. W., Zuk, M. & Rotenberry, J. T. 2005 Immune function reflected in calling song characteristics in a natural population of the cricket *Teleogryllus commodus*. *Anim. Behav.* **69**, 1235–1241. (doi:10.1016/j.anbehav.2004.09.011)
- Stearns, S. C. 1992 *The evolution of life histories*. New York, NY: Oxford University Press.
- Takahashi, J. S., Turek, F. W. & Moore, R. Y. 2001 *Handbook of behavioral neurobiology. Circadian clocks*, vol. 12. New York, NY: Springer.
- Verdu, J. R., Arellano, L. & Numa, C. 2006 Thermoregulation in endothermic dung beetles (Coleoptera: Scarabaeidae): effect of body size and ecophysiological constraints in flight. *J. Insect Physiol.* **52**, 854–860. (doi:10.1016/j.jinsphys.2006.05.005)
- Wagner, W. E. & Hoback, W. W. 1999 Nutritional effects on male calling behaviour in the variable field cricket. *Anim. Behav.* **57**, 89–95. (doi:10.1006/anbe.1998.0964)
- Walker, S. E. & Cade, W. H. 2003 The effects of temperature and age on calling song in a field cricket with a complex calling song, *Teleogryllus oceanicus* (Orthoptera: Gryllidae). *Can. J. Zool.* **81**, 1414–1420. (doi:10.1139/z03-106)
- Zuk, M. & Kolluru, G. R. 1998 Exploitation of sexual signals by predators and parasitoids. *Q. Rev. Biol.* **73**, 415–438. (doi:10.1086/420412)