

can involve ontogenetic shifts early in life (or prior to each breeding season for seasonal regenerated traits like antlers or breeding plumage) that affect the expression of morphological traits in adults (e.g., Walling et al. 2007; Bailey et al. 2010; Kasumovic et al. 2011; Kahn et al. 2012). Adaptive plasticity can also occur on much shorter timescales: selection can favor rapid, reversible changes in sexual behavior over an individual's lifetime in response to the prevailing level of mating competition (review: Bretman et al. 2011). In many species, especially those producing acoustic signals, males adjust the rate, intensity, timing, duration or complexity of courtship, or advertisement signals in response to the currently perceived level of male–male competition (e.g., insects: Hill 1998; Jia et al. 2001; newts: Aragón 2009; frogs: Rand and Ryan 1981; Schwartz et al. 2002; Martínez-Rivera and Gerhardt 2008; crabs: Backwell et al. 1998; Milner et al. 2012).

Sexual advertisements impose costs in terms of time, energetic expenditure, and the risk of predation or parasitism (review: Kotiaho 2001). Males, therefore, have to balance the benefits of a higher courtship rate, which elevates their attractiveness and likely mating rate, against these naturally selected costs. When females assess males relative to one another (e.g., when there is mate sampling prior to choosing a mate), the net benefits of a given level of courtship partly depend on a male's attractiveness relative to that of sampled rivals (see Reynolds 1993). A male only needs to be more attractive than his rivals to mate, so any additional investment imposes wasteful costs. The observed investment in courtship by a male is likely to vary depending on: 1) the number of rivals, 2) how intensely rivals court, 3) how attractive these rivals are (i.e., physical attractiveness when courting at the same rate), 4) the marginal costs of courtship, which often vary among individuals (Murai et al. 2009) and 5) the extent of direct male–male competition that affects the ability of males to gain access to females and/or higher quality breeding sites (reviews: theory Reynolds 1993; Kokko and Rankin 2006; Kasumovic and Brooks 2011; Kokko et al. 2012; meta-analysis: Weir et al. 2011; case studies: Gerhardt and Huber 2002; Milner et al. 2012 and references therein).

In many taxa, body size and body condition influence male attractiveness, social dominance, and the marginal costs of sexual signaling (e.g., Judge et al. 2008). The behavioral response of a male to rivals should therefore partly depend on his body size or condition. In extreme cases, less competitive males might facultatively forgo producing a sexual display, and pursue alternative mating tactics (Shuster 2010). For example, in frogs and crickets, small subordinate males will often remain silent (“satellite males”) and intercept females attracted to larger males that continue to call (e.g., Leary et al. 2005). Although rarely examined, plasticity in sexual behavior in response to rivals could have flow-on effects on other key life-history traits. One obvious candidate is life span. Although correlational studies often report a positive correlation between courtship display rate and life span (e.g., genetic correlations: Zajitschek et al. 2007; Archer et al. 2012; phenotypic correlations—meta-analysis: Jennions et al. 2001), this appears to arise due to confounding variables that positively affect both traits (e.g., condition). Elevated rates of courtship in response to experimental manipulations (or environmental factors that elevate courtship and act as a “natural experiment”) tend to be associated with increased mortality rates (e.g., Mappes et al. 1996; Hunt et al. 2004).

In this study, we test whether 1) the social environment, specifically the physical presence or absence of a rival, affects the reproductive effort (measured as advertisement call production) of adult male Australian black field crickets (*Teleogryllus commodus*), 2) male body size

(which is strongly correlated with social dominance) influences the direction/magnitude of any observed changes in calling effort, 3) the social environment, possibly due to plastic changes in calling effort, affects male longevity, and 4) whether plasticity in male sexual behavior differed among 3 study populations (e.g., Carroll and Corneli 1995; review: Bretman et al. 2011). It should be noted that whether one predicts that reproductive effort will increase or decrease with the presence of a rival probably depends on the precise assumptions made (e.g., for a comparable situation, compare the theoretically predicted change in ejaculate size in response to the absence vs. presence of a rival, and the presence of 1 vs. many rivals; meta-analysis Kelly and Jennions 2011; see also Parker et al. 2013). In the absence of formal models based on precise assumptions, we therefore refrain from making explicit directional predictions for 1), 2), or 4) (see Discussion). However, based on empirical results from other species that have acoustic signals, we might expect increased competition to result in greater investment into calling (review: Gerhardt and Huber 2002). For 3), we predict that if calling effort increases due to the social environment this will decrease longevity because of a life-history trade-off between reproduction and survival (Roff 2002).

MATERIALS AND METHODS

The study species, *T. commodus*

Male *T. commodus* stridulate their forewings to produce a long-distance sexual advertisement call (Campbell and Shipp 1979; Evans 1988). If a female approaches a male, he then produces a close-range courtship call to induce mating (Loher and Rence 1978; Drayton et al. 2011). In orthoptera, advertisement displays can use up to 56% of a male's daily respiratory budget (Prestwich and Walker 1981), and a high call rate is metabolically expensive (Kavanagh 1987). Female *T. commodus* prefer males that call at a higher rate, so calling effort is a good predictor of male mating success (Hunt et al. 2005; Bentsen et al. 2006; Drayton et al. 2010). Calling effort tends to increase with age, with an eventual senescent decline (Maklakov et al. 2009; Zajitschek et al. 2009; Kasumovic et al. 2012). Calling effort is also diet dependent: males on a high-protein diet call more heavily earlier in life, which appears to decrease their life span (Hunt et al. 2004). The relationship between lifetime calling effort and male survival can therefore vary depending on local conditions (e.g., food availability), which can fluctuate over the breeding season.

Interactions between male crickets are often highly aggressive and a male's mating success is likely to partly depend on his ability to outcompete rivals (Alexander 1961). In *T. commodus*, larger males are socially dominant (Shackleton et al. 2005). A similar positive effect of body size on fighting success is seen in most animals (Kelly 2008), including many orthoptera (e.g., Simmons 1986a; Savage et al. 2005). In contrast, the effect of body size on male attractiveness in orthopterans is less clear-cut. Females prefer larger males in some species (e.g., Simmons 1986b; Bussière et al. 2005), but not in others (e.g., Zuk 1987). There is no robust evidence that larger male *T. commodus* are more attractive to females. Shackleton et al. (2005) found that females did not prefer larger males when tested at close range (i.e., males producing courtship calls). Call dominant frequency is generally negatively correlated with body size in orthopterans (e.g., Simmons and Ritchie 1996), including *T. commodus* (e.g., Drayton et al. 2011; but see Drayton et al. 2010). However, female *T. commodus* do not preferentially approach advertisement calls with lower dominant frequencies in phonotaxis experiment conducted in the field (Bentsen et al. 2006;

but see Drayton et al. 2010) or the laboratory (Brooks et al. 2005). In general, call rate or “time on air” is the best predictor of male mating success in taxa where males produce sexual advertisement calls (e.g., frogs and many insects; review: Gerhardt and Huber 2002). This also appears to be the case for *T. commodus* as males with a higher call rate attract more females (e.g., Bentsen et al. 2006).

Experimental populations

We used crickets that were the offspring of >200 field-mated females collected from 3 locations within Australia in March 2009: Smith’s Lake (SL: 32°24’S, 152°28’E), Lake George near the Australian Capital Territory (ACT: 35°15’S, 149°8’E) and south-west Western Australia (WA: 34°58’S, 116°44’E). Nymphs were maintained in 20×15×13 cm plastic containers at 28±1 °C on a 12:12 light:dark photoperiod and provided with food (Kit Kat Krunch, Uncle Ben’s, Raglan, Australia) and water ad libitum. At approximately 1 cm in length, nymphs were placed in large (80 l) population boxes and monitored weekly for the appearance of wing buds. At the second-last instar (identified by wing formation over the third abdominal segment), males were placed in individual plastic containers (5×5×5 cm). Each cricket was provided with a cotton wool soaked water tube, 3 food pellets, and a cup of an egg carton for shelter. We then monitored males daily for their final molt (appearance of fully developed wings) and then weighed (milligram) them and measured their pronotum width (millimeter).

Experimental design

When males reached maturity (final instar molt), we randomly assigned males to 2 social treatments: “rival present” (2 males housed together) or “solitary.” Males that were housed together for the rival present treatment had both molted within the previous 48 h and, where possible (only when 4 or more males molted within the same 48-h period), were mismatched for size to increase the likelihood that 1 male was dominant. To aid individual identification, we placed a spot of typist correction fluid (Tippex) on the thorax of 1 male in each “rival present” treatment (“marked male”). “Rival present” males were housed in the same size plastic containers (5×5×5 cm) as solitary males to encourage male–male interactions and intensify the level of direct competition. The housing conditions did not differ between the 2 treatments. It should be noted that males from both treatments were kept in the same constant temperature room at 28±1 °C. All males were, therefore, exposed to the calls of other males (not hearing rivals calling would be extremely rare in the natural setting). The key difference between the 2 social treatments is therefore whether or not males had recently had direct physical interactions with other males prior to being isolated and allowed to call (see Measuring calling behavior).

On first placing the 2 males together, we observed their behavioral interactions and scored their dominant–subordinate relationship. Following Shackleton et al. (2005), we defined the dominant male as the one who made at least 3 isolated attacks, identified by aggressive chirping and chasing, during which the other male retreated. In some pairs, we could not assign dominance status due to a paucity of attacks and/or difficulty in unambiguously identifying the winner of an encounter.

Measuring calling behavior

Earlier studies suggest that male *T. commodus* call relatively little until they are >10 days old (e.g., Figure 2 in Hunt et al. 2004). We therefore started to monitor calling at day 15 of adulthood.

Males from both social treatments were placed individually into separate containers to record their calling effort. Call boxes were housed in a constant temperature room at 28±1 °C with a 12:12 light:dark photoperiod. Care was taken to randomize the shelf position of crickets with respect to treatment and population of origin. Calling was monitored throughout the adult life span in cycles of 3 consecutive nights of call monitoring, followed by 5 nights out of the call box. “Rival present” pairs were reunited whenever they were not in a call box. We checked crickets daily to note when they died. In total, we collected data on 256 males: 127 from Smith’s Lake (49 solitary males and 39 pairs of “rival present” males), 50 from Lake George (16 solitary males and 17 pairs of “rival present” males), and 79 from West Australia (31 solitary males and 24 pairs of “rival present” males).

A customized acoustic recording device was used to measure male calling effort for 12 h per night (18:00–06:00). It consisted of 240 individual condenser microphones attached to the lids of 5×5×5 cm plastic containers. A male was recorded as having called if he produced a sound >10 dB above a threshold level (see detail in Hunt et al. 2004). Each plastic container housing a single male was placed in a 20×15×13 cm call box that was acoustically isolated with foam and cotton wool. For each male, we noted the total number of seconds calling divided by the number of nights sampled (hereafter, mean calling effort).

Statistical analysis

Body size

Male pronotum width is highly correlated with body mass (Pearson’s $r = 0.940$, $t_{248} = 43.51$, $P < 0.0001$), so we only present the results of analysis using pronotum width as a measure of body size. To test for differences in pronotum width among populations and between social treatments, we ran a linear mixed-effects model (LME) with population, social treatment, and their interaction as fixed factors. Pair identity (unique for each “rival present” pair) was treated as a random factor here and throughout (unless otherwise specified).

Dominance behavior

To test if pronotum width predicted dominance in “rival present” pairs we ran a logistic regression model. We tested for an effect of the difference in pronotum width (marked male—rival) on the dominance status of the marked male (0 = subordinate, 1 = dominant), as well as testing for population differences and any interaction between these 2 variables. We only used pairs in which dominance was unambiguously assigned. As noted earlier, in some cases too few social interactions were observed and/or classified to fulfil our criteria for assigning dominance. We therefore also ran a logistic regression to test whether there was an effect of the absolute size difference between males on our ability to assign dominance status (0 = No, 1 = Yes).

Calling effort

In all models mean call effort was $\log(x + 1)$ transformed to normalize residuals and reduce heteroscedacity, while retaining zero values. We initially ran an LME model to test whether social treatment, pronotum width or their interaction, and population affected mean call effort (fixed factors). Pair identity (unique for each “rival present” pair) was treated as a random factor because the calling effort of both males was included in the data set. This analysis used data from all males.

After the rival died, half of the “rival present” males spent at least some time alone before they too died. If there is a shorter term plastic response to no longer being exposed to a rival between bouts of call monitoring, this would effectively make the 2 social treatments equivalent at this point (i.e., males are solitary). This could hinder our ability to test for the intended effect of the social treatment (i.e., a response to recent exposure to a rival). We therefore tested if the mean call effort of the surviving male changed significantly after the death of his rival. Of course, any change in calling after a rival died might also be due to age-dependent changes in calling effort (i.e., males are always older after the death of their rival). We therefore needed to compare the before/after call effort of “rival present” males with that of solitary treatment males. But how do we get this baseline measure? First, because the surviving rival males represent a skewed subset of males (i.e., relatively long lived), we decided to only include solitary treatment males that lived at least as long as the shortest lived surviving rival male (34 days), thereby excluding the shortest lived solitary males. In this way, there was no significant difference between the mean longevity of the 2 groups (surviving rivals: 66.8 ± 17.5 days; subset of solitary males: 67.0 ± 22.7 days; *t*-test of log-transformed longevity: $t_{135} = -0.33$, $P = 0.743$). Thus, any difference in calling between the social treatments (or in their interaction with timing) cannot be attributed to an asymmetry in the selection criteria with respect to their longevity for males that “represent” each treatment in the data set.

Next, we needed to assign a before and after benchmark age for each of the remaining solitary treatment male that was comparable with that at which rivals died in the “rival present” treatment. To do this, we randomly sampled (with replacement) from the observed distribution of rival death ages to generate benchmark ages for control males. Solitary males were, however, only assigned benchmarks earlier than their own death (i.e., with data on calling effort before and after the benchmark). While this meant that benchmark assignment was not entirely random, it was in keeping with the before/after data from the surviving rival males (to be the surviving rival, males had to have lived longer than their rivals). Once each solitary treatment male had been assigned a benchmark, an LME model of mean calling effort was produced. The LME tested if mean call effort was affected by the fixed factors of treatment, timing (before/after rival death or benchmark age), their interaction, pronotum width, and population. Male identity was included as a random factor to control for repeated measures (before/after) from the same male. Pair identity was excluded from these LMEs as we only used 1 male per “rival present” treatment. Benchmarks were then reassigned and a new model was run. This was done 1000 times, and the distribution of statistics was investigated. If there is no true effect of a predictor variable on mean call effort then it should, by chance, only be a significant predictor in 5% of the 1000 runs of the model. For these models, $N = 64$ surviving rival males and $N = 73$ solitary treatment males were included. Very similar results (especially the direction and strength of effects of timing, treatment, and their interaction) were obtained when all solitary treatment males were included, or when a fixed benchmark was used for all solitary males (analyses not presented).

Longevity

We ran an LME model to test whether pronotum width, mean call effort, social treatment, and population of origin predicted log-transformed adult life span. This analysis used the full data set.

All analyses were carried out using R version 2.12.2. We did not pursue a model simplification approach. Instead, we decided

a priori which main effects and interactions we thought were biologically relevant, and interpretable, for the key questions at hand (for an excellent review, see Simmons et al. 2011). We also had to exclude testing for some potentially interesting interactions because of limited sample sizes. Summary statistics are presented as mean \pm SD.

RESULTS

Body size

There was a significant difference in body size across the 3 populations ($F_{2,165} = 38.2$, $P < 0.0001$). Crickets from SL (6.38 ± 0.56 , $n = 127$) and ACT (6.24 ± 0.54 , $n = 50$) had wider pronota than those from WA (5.65 ± 0.66 , $n = 79$). There was no body size difference between males assigned to the “solitary” or “rival present” treatments ($F_{1,165} = 1.88$, $P = 0.172$), nor any treatment by population interaction ($F_{2,165} = 0.35$, $P = 0.708$). Because of the population differences in body size, we centered and scaled (divided by standard deviation [SD]) pronotum width so that the mean for each population was 0 ± 1 SD in all subsequent analyses.

Dominance behavior

Using our assay of social status, we assigned dominance for 58 of 80 test pairs. In these cases, the greater the size difference between the marked and rival male, the more likely it was that the marked male was dominant ($\beta = 1.309$, $\chi^2_{1,56} = 23.63$, $P < 0.0001$). There was no difference in this pattern between populations (population by size difference interaction: $\chi^2_{2,52} = 0.34$, $P = 0.843$), nor was there a main effect of population on dominance ($\chi^2_{2,54} = 0.281$, $P = 0.869$) (all $N = 58$ pairs).

There was no effect of the absolute size difference between rivals on whether we were able to assign dominance to a test pair ($\chi^2_{1,78} = 0.01$, $P = 0.909$, $N = 80$ pairs). However, when social status was assigned, the larger male was dominant in 47 of 58 cases. Male size is, therefore, a strong predictor of fighting success (see also previous studies of *T. commodus* by Shackleton et al. 2005; Reaney et al. 2011). Given strong colinearity between dominance and body size, and that we would lose a significant amount of data by excluding pairs where dominance was not assigned, we only included pronotum width as a predictor in subsequent models.

Lifetime calling effort: full data set

The calling effort of males varied greatly, with an average call effort of 2637 s/night (range: 0–18 720 s/night). There were no population differences in mean call effort ($F_{2,166} = 1.933$, $P = 0.204$). Contrary to our predictions, the social treatment had no detectable effect on mean lifetime calling effort when considering all males in both treatments ($F_{1,166} = 0.010$, $P = 0.920$). Larger males had significantly higher mean calling effort ($\beta = 1.177$, $F_{1,76} = 30.16$, $P < 0.0001$), but this relationship did not differ significantly between males assigned to the “solitary” and “rival present” treatments (pronotum width by treatment interaction: $F_{1,76} = 1.27$, $P = 0.263$).

Calling effort and change in rival presence: subset of males

One explanation for the absence of a social treatment effect based on the full data set is that males regularly update information about the current level of competition. Specifically, half the males in the “rival present” treatment spent time alone (i.e., after their rival died). If there is a short-term response to no longer being

exposed to a rival between bouts of call monitoring, the 2 social treatments become equivalent (i.e., males are solitary in both cases). Consequently, any resultant adjustment in calling effort could reduce the difference between treatments when tallying calls across an entire lifetime and ignoring whether or not a rival was actually present. We therefore compared the mean call rates of “rival present” males before and after their rival died with that of “solitary” treatment males before and after a comparable benchmark age. We ran 1000 models each with a benchmark age drawing randomly from the distribution of rival’s age at death. In every case, the mean call rate increased significantly with age (i.e., was higher after the benchmark age; Table 1, Figure 1). Furthermore, paired males always had a significantly higher mean call rate (Table 1). Most importantly, however, in more than 95% of cases there was a significant interaction between before/after and social treatment (Table 1). Previously paired crickets changed their calling effort before their rival died, in a manner that is not explained purely by an age-dependent increase in calling effort (i.e., as seen for “solitary” treatment males). Paired males tended to call at a higher rate than solitary males earlier in life when they were regularly exposed to a rival. After their rival has died, however, formerly paired males called at the same rate as solitary treatment males (Figure 1).

In the majority of runs of the model there was no significant population differences in mean call rate, as in the analysis of the full data set (Table 1). In contrast, unlike the lifetime call effort model, greater pronotum width was no longer a significant predictor of mean call rate (although the coefficient was almost always positive; Table 1). One potential explanation for this is that call rate tends to increase with age (see Hunt et al. 2004) and early dying rivals and solitary males are excluded from the data set used for the current analysis. This implies that the previously reported positive relationship between pronotum width and mean lifetime calling effort is driven by a positive relationship between body size and longevity. We therefore tested directly for such a relationship (see below).

Longevity

Using the full data, on average, adult males lived for 54.8 ± 23.0 days. Larger crickets lived for significantly longer ($\beta = 0.019$, $F_{1,67} = 19.22$, $P < 0.0001$), as did those with a higher mean call rate ($\beta = 0.090$, $F_{1,67} = 121.50$, $P < 0.0001$; Figure 2). Furthermore, males in the “rival present” treatment had a significantly shorter longevity than solitary males ($\beta = -0.115$, $F_{1,160} = 6.81$, $P = 0.010$; 52.4 ± 20.7 vs. 58.6 ± 25.8 days). Finally, there was significant variation in longevity among the 3 populations ($F_{2,160} = 4.45$, $P = 0.013$; SL: 59.4 ± 26.6 days, WA: 47.9 ± 16.8 days, LG: 54.2 ± 18.7 days).

Table 1

Median (and range) of model coefficients and relevant *F*-tests for an LME model of mean call rate (transformed) using randomly generated benchmark ages for control males (see Methods)

Variable	Coefficient	<i>F</i>	df	<i>P</i>	Percent, <i>P</i> < 0.05
After rival death (A)	1.765 (1.153 to 2.326)	25.70 (11.17 to 43.62)	1, 150	<0.001 (0.001 to <0.001)	100.0
Treatment (T)	1.325 (0.870 to 1.772)	11.07 (6.52 to 18.04)	1, 150	<0.001 (0.011 to <0.001)	100.0
Pronotum width	0.108 (-0.028 to 0.265)	0.65 (0.01 to 2.86)	1, 150	0.423 (0.934 to 0.093)	0.0
Population (SL)	-0.010 (-0.295 to 0.353)	2.27 (0.72 to 4.73)	2, 150	0.107 (0.490 to 0.010)	11.7
Population (WA)	-0.843 (-1.249 to -0.375)				
A × T interaction	-1.293 (-1.854 to -0.681)	7.95 (1.95 to 17.51)	1, 150	0.005 (0.165 to <0.001)	95.1

Output based on 1000 randomizations.

DISCUSSION

Male age, size, and calling effort

In general, male nightly calling effort increased significantly with age (see Figure 1), as has been reported in other studies of *T. commodus* (Maklakov et al. 2009; Zajitschek et al. 2009; Kasumovic et al. 2012), as well as for other cricket species (e.g., Archer et al. 2012). It should be noted, however, that this pattern is sometimes partly driven by a rapid increase in nightly calling effort early in life and thereafter calling effort is fairly steady until late senescence occurs (e.g., Figure 3 in Hunt et al. 2006). In general, life-history theory predicts that male reproductive effort will steadily increase with age although alternative outcomes are possible (review: Roff 2002, p. 230). The extent to which *T. commodus* shows a steady increase in calling effort with age, as opposed to a simple transition from non-calling to calling at sexual maturation (i.e., “true” maturation is about 10 days after the adult molt) remains unclear. In our study, however, male calling was only measured from day 15 onward, so the reported increased calling with age is not due to including pre-maturation males in the sample.

We found that larger male *T. commodus* had higher mean nightly calling effort when we used the full data set of all males that were monitored. The relationship between body size and calling effort appears to vary across species in field crickets, with some species showing a clear increase in calling effort with body size (*Gryllus integer*, Bertram 2000), whereas others do not (*Acheta domesticus*, Wilson et al. 2010; *G. pennsylvanicus*, Zuk 1987, Judge et al. 2008; *G. veletis*, Zuk 1987; *Teleogryllus oceanicus*, Kolluru 1999; *G. campestris*, Rodríguez-Muñoz et al. 2010). In other species, this relationship is known to be complex, varying with the social and nutritional environment. For example, in *G. integer* larger males call more at low but not at high population density (Cade and Cade 1992). In *T. commodus*, males reared on a high quality diet eclose at a larger body size and call more per night (Hunt et al. 2004), but crickets reared in a low competition environment eclose at a smaller body size and call more per night (Kasumovic et al. 2011).

We suggest that the higher mean calling effort we report for larger males is partly driven by variation in male longevity in combination with an age-dependent increase in nightly calling effort. There is, indeed, a positive relationship between male size and longevity. Consequently, when we excluded males that died earlier (to permit the analysis of before/after rival death) from our analysis there was no longer a significant relationship between male size and calling effort.

Social environment and plasticity in calling

Using all available males, there was no significant difference in lifetime calling effort in *T. commodus* between solitary males and

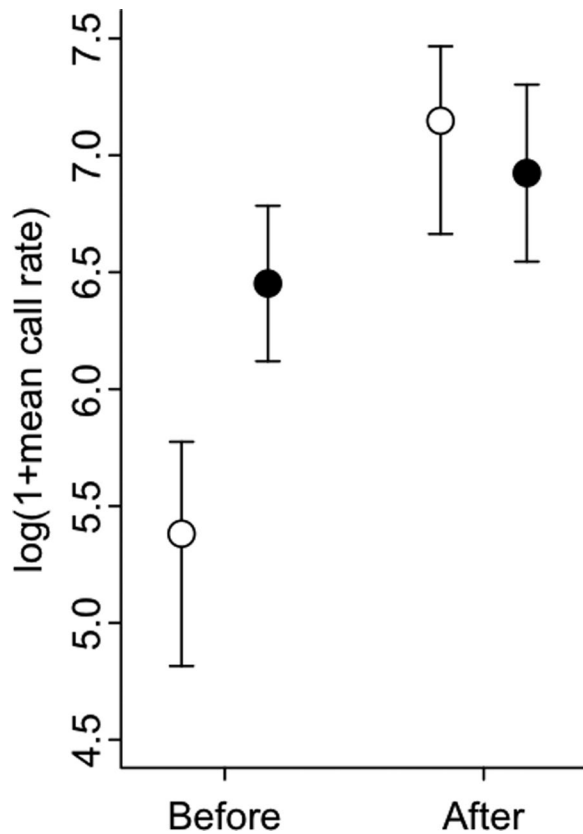


Figure 1

Transformed mean (\pm standard error) calling effort of males assigned to the “rival present” (black) treatment before and after their rival died. For the “solitary” treatment males (white), “before” and “after” are randomly assigned benchmark ages and the median (\pm range) predicted mean calling effort from 1000 runs of an LME model (see Methods for details) are presented.

males that were initially housed with a rival. At face value, this suggests that there is no behavioral plasticity in calling. In general, it is difficult to predict whether plasticity of male sexual advertising/courtship in response to the presence of a rival is favored by selection. Even if it is, it is still unclear in which direction it will shift, and whether the direction will differ depending on male quality. To date, theoretical models of strategic male investment are largely confined to questions about ejaculation (Parker and Pizzari 2010; Bretman et al. 2011). This is different to investment in mating signals because paternity can be shared among a set of males, whereas mating is often confined to a single male in a given set of competitors. Consequently, inferences have to be drawn from models of general shifts in investment with age/time (e.g., Kokko 1997; Lindström et al. 2009). More generally, many authors simply predict that a rival’s presence will increase courtship or advertisement effort based on the results of previous empirical studies, especially those showing that playback of sexual advertisements increases the calling effort or song complexity of the focal male (examples in Gerhardt and Huber 2002).

The allocation pattern for male reproductive effort that maximizes fitness will, as with any life-history trait, partly depend on the trade-off between increasing the likelihood of current reproduction and the costs this imposes on future reproductive success. The cost to males of a higher courtship display rate is often elevated mortality (e.g., because courtship attracts predators,

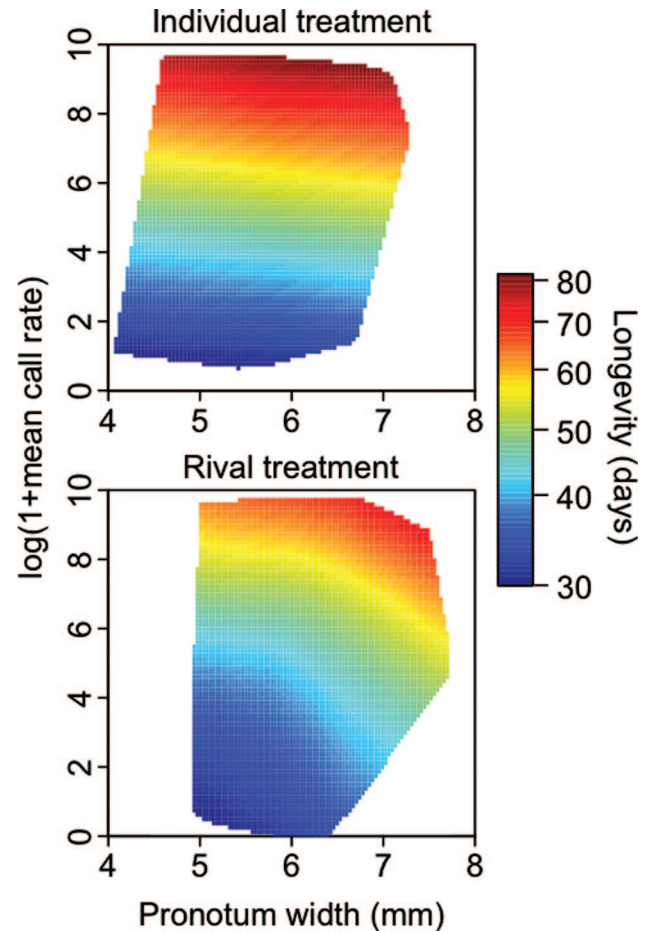


Figure 2

Life span contour map as related to male body size (pronotum width) and calling effort, and separated by treatment. Life span increases as color changes from blue to red (but note that it is on a log-scale to match our analyses). The map was generated using thin-plate splines in the *fields* package of R.

Mappes et al. 1996) and/or a reduced capacity to court at the same level in the future (e.g., because energetic resources are depleted and foraging takes up time). The shape of trade-off functions is rarely known (Roff 2002). Unlike standard life-history traits, however, identifying the optimal response is greatly complicated when considering sexually selected traits because a male’s fitness depends on his rivals’ responses. That is, male mating success depends on the relative investment into attractiveness at the time when females are sampling potential mates (McCauley et al. 2000). Game theoretical rather than static optimality models are required (e.g., Kokko 1997; Lindström et al. 2009). The optimal response depends on future mating opportunities, but these are not simply a function of the ratio of males to females. The future likelihood of mating depends on a male’s mating competitiveness. Competitiveness will partly depend on a male’s intrinsic “quality” relative to that of other males alive at the same time (and the distribution of male quality might change over time if there is differential mortality). In addition, males can elevate their attractiveness by investing more heavily into courtship, even if this increases mortality. Males of differing quality might be under selection to increase their efforts earlier or later in life. It is not even clear whether this will lead to

greater investment into courtship early in life by high or low quality males (e.g., compare Candolin 2000 and Hunt et al. 2004). In sum, we believe there is a need for formal models to predict the optimal level of courtship when the mean and variance in the number of rivals and in male quality vary spatiotemporally.

In the preceding discussion, we assumed that temporal changes in female and male numbers and male competitiveness are predictable. For phenotypic plasticity in courtship to be favored by selection, however, males need reasonable cues to both their current and future likelihood of mating (West-Eberhard 2003). In some cases, unreliable estimates of these parameters might make it more profitable for males to invest in courtship over their life in a manner that is independent of short-term variation in the immediate level of mating competition. It is, therefore, worth considering the extent to which a rival's presence or absence (as in our social treatments or, indeed, many similar experimental designs; e.g., Kasumovic et al. 2011) would actually predict a male's current and future likelihood of mating. A lack of reliable information might account for the apparent absence of an effect of a rival's presence on male *T. commodus* calling effort.

But was there plasticity in calling effort?

Closer inspection of the “rival present” treatment reveals that calling was affected by the presence of a rival, but this insight is confounded by the experimental design. Simply put, once a rival died, the surviving male in the “rival present” treatment was in an identical situation to a solitary treatment male (i.e., no rival was present between call monitoring bouts). We therefore investigated the change in calling effort of the male who outlived his rival before and after his rival's death. To correct for any effect of age on calling (males are always younger before than they are after a rival dies), we had to compare within-male changes in calling once a rival was no longer present with that of a comparable data set from solitary males. We found a smaller increase in calling effort before and after a rival's death than for an equivalent time comparison for solitary treatment males (Figure 1). That is, correcting for age, the longer lived male in the “rival present” treatment tended to have a higher call rate earlier in life when his rival was still present. We interpret this as a phenotypically plastic increase in calling effort in response to a rival's presence. Our analysis relies on a comparison between solitary and paired males. In both cases, there was a systematic bias toward the use of longer lived males. The procedure was, however, not confounded by a difference in the selection criteria between social treatments as the mean longevity of males did not differ between the treatments. The comparison is therefore valid. It is, however, important to acknowledge that the evidence for a phenotypically plastic increase in calling effort in response to a rival's presence was only based on data from longer lived males. Although we think it unlikely that shorter lived males would not express a similar level of phenotypic plasticity in calling this had to be formally tested. At present our results should be viewed with this caveat in mind.

Why did the presence of a rival decrease longevity?

The presence of a rival had a negative effect on male longevity. Males in the “rival present” treatment had a life span that was, on average, 11% shorter than that of males in the “solitary” treatment. This is unlikely to be attributable to greater energetic investment into calling because, over all, there was no difference in call effort

between the 2 treatments. If anything, the longer lived of the 2 males in each “social pairing” tended to call more early in life than an equivalent solitary male, which suggests that the shorter lived male actually called less (otherwise the mean call effort would be greater in the “rival present” than solitary treatment). It, therefore, seems likely that the reduction in life span arose due to direct male–male interactions when males were housed together. Several studies in a range of species show that aggression, direct competition, and stress decrease male life span (e.g., Graves and Mueller 1993, Carey et al. 1995; Gaskin et al. 2002). Consistent with previous findings in this species (Shackleton et al. 2005), larger males were socially dominant. It is, therefore, noteworthy that larger (i.e., socially dominant) males lived significantly longer than smaller males.

In sum, our study reveals the potential importance of plastic behavioral changes in male courtship to life-history strategies because of effects on key life-history traits, such as age dependence of reproductive effort and life span. There are, however, surprisingly few models of the evolution of male investment into sexual traits as they age that explicitly take into account the zero-sum nature of mating competition (e.g., Kokko 1997; Lindström et al. 2009). There are even fewer theoretical studies investigating the conditions under which males should adjust allocation due to shorter term fluctuations in the presence (and possibly competitiveness) of rivals. Given the huge success of models of strategic ejaculation (Parker et al. 2013; review: Parker and Pizzari 2010; meta-analysis: Kelly and Jennions 2011), it is clear that comparable models of strategic courtship are urgently required so that we can actually test predictions rather than simply document patterns.

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