



Signalling males increase or decrease their calling effort according to the proximity of rivals in a wild cricket

Joe A. Wilde^{a,*}, Rolando Rodríguez-Muñoz^b, Safi K. Darden^a, Tom Tregenza^b, Tim W. Fawcett^a

^a Centre for Research in Animal Behaviour, University of Exeter, Streatham Campus, U.K.

^b Centre for Ecology & Conservation, University of Exeter, Penryn Campus, U.K.

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Males that employ dynamic courtship displays to attract females may tactically adjust their courtship in response to their social environment. However, we know little about how sexual signals are adjusted in complex natural settings, where individuals are competing for attention against a backdrop of signals from nearby and distant rivals. We investigated this using data from the WildCrickets project, a wild population of field crickets, *Gryllus campestris*, continuously monitored via CCTV cameras. We used over a million scan samples from 129 males across 51 days to explore how the singing and proximity of other males influenced male singing behaviour. We first quantified the spatial network of the males to understand how the extent of singing overlap is affected by the distance between them, and found a moderate overlap across the whole population, regardless of distance. We then used a finer-grained analysis controlling for the effect of environmental variables. At distances greater than 1 m, we found a stimulatory effect of singing by other males on a focal male's singing behaviour, leading to males singing in the same time intervals. The overlap in singing became weaker as the distance between males increased. Conversely, we found that males were less likely to call when another male was singing very close by (within 1 m), suggesting an inhibitory effect. These findings reveal how, in a dynamic social network in a wild population, males perform fine-scale adjustments to their signalling behaviour in response to signalling by other males both nearby and far away.

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Many animals produce sexual signals to attract potential mates (Andersson, 1994). Some of these signals are thought to be honest indicators of individual quality (Zahavi, 1977; Grafen, 1990). In the last three decades work has uncovered high levels of variation in signalling within individuals, particularly for behavioural displays (Anichini et al., 2018, 2019; Candolin, 1997; Chapman et al., 2009; Gerhardt, 1991; Gerhardt & Huber, 2002; How, Hemmi, et al., 2008; How, Zeil, et al., 2008; Perry et al., 2019; Sullivan-Beckers & Hebets, 2014). Some of this intraindividual variation may be attributed to 'noise' (e.g. variation in signal propagation medium, local disturbances), and some may be due to 'practice effects', whereby certain motor patterns are refined when they are performed repeatedly (Patricelli et al., 2016). However, some of the intraindividual variation may also be due to individuals tactically adjusting their signalling behaviour depending on the context.

Empirical evidence has demonstrated that animals adjust their signalling behaviour in response to environmental factors such as predation risk, light and noise levels (Brumm & Slater, 2006; Chapman et al., 2009; Fuller et al., 2007). For example, when a predator is added to their tank, guppies, *Poecilia reticulata*, reduce the performance of visually conspicuous courtship behaviours (Endler, 1987) and male three-spined sticklebacks, *Gasterosteus aculeatus*, reduce their courtship behaviours closer to their nest, possibly to avoid drawing predators' attention to the nest which is a valuable resource and may contain offspring (Candolin, 1997). By adjusting their signalling behaviour to the perceived predation threat, individuals can therefore reduce their likelihood of being predated.

Social variables, such as the presence and behaviour of potential mates and competing rivals, may also affect the potential fitness payoff of signalling behaviours. For example, if the active space (the distance over which a signal may be effective) of a rival's signal overlaps with that of another individual, potential mates in that area have more signals to evaluate and each

* Corresponding author.

E-mail address: jw777@exeter.ac.uk (J. A. Wilde).

signaller's chances of securing a mate are affected. An individual may then adjust its signalling effort in response to this change in the fitness payoff of a signal. An empirical example is found in male fiddler crabs, *Austruca annulipes*, which increase their waving display rate in response to an increase in the perceived competition from rivals (Milner et al., 2012). Signallers may also adjust their signalling in response to the presence and behaviour of potential mates, as this may also affect fitness payoffs. For example, in greater sage grouse, *Centrocercus urophasianus*, some males increase the rate of their courtship performance in response to the presence and mate-inspecting behaviour of a robotic female (Perry et al., 2019). Males that consistently performed courtship signals at a high level and adjusted signals less in response to the robot female's presence and behaviour secured more matings.

A number of laboratory studies have investigated how signalling behaviour is affected by the behaviour and proximity of rivals. For example, Anichini et al. (2018) found that laboratory-housed male bushcrickets, *Poecilimon ampliatus*, increase their acoustic signal investment as the distance to other males decreases, and that this effect is moderated by focal male body condition. Experimental, laboratory-based studies such as this (see Callander et al., 2013; Dziejewczynski et al., 2009; Kim & Velando, 2014; Milner et al., 2012; Noguera, 2019; Setoguchi et al., 2015 for other examples) are valuable in showing how rival presence and proximity influence signalling behaviour. In the wild, signallers are embedded in a dynamic communication network of rivals at different spatial, and potentially temporal, distances, and potentially influencing one another. It is thus important for us to study signalling and communication within the networks in which they are performed (Greenfield et al., 2021; McGregor & Peake, 2000). Investigating how signallers adjust their behaviour within a complex spatial network of other signallers will give a better understanding of the causes of intraindividual variation in sexual signalling in a biologically realistic setting, as well as an idea of selective pressures that communication networks impose.

This study used a wild population of field crickets, *Gryllus campestris*, to investigate how male calling song is affected by the calling behaviour and proximity of other males. Male *G. campestris* occupy burrows which are used for predator evasion and protection against bad weather. They perform two types of sexual song from the entrance to their burrows: calling songs, which are performed to attract females (Alexander, 1961), and courtship songs, which are performed once a male has come into contact with a female (Tregenza et al., 2006). Here, we quantified how male calling song is affected by the proximity and calling song of other males, as well as the interaction between these two variables, while controlling for nonsocial, environmental factors that may affect all males simultaneously.

We predicted that calling by other males would cause focal males to increase their own calling behaviour as a strategy to outcompete rivals and attract the attention of any females in the vicinity. We also predicted that focal males would increase their own calling to a greater extent when the other males that are calling are close by, as opposed to further away. This second prediction is based on the idea that males may contribute to local calling choruses to attract females to the area more effectively, as observed in Japanese treefrogs, *Buergeria japonica* (Legett et al., 2021) and a species of fiddler crab, *Austruca mjoebergi* (Perez et al., 2019).

METHODS

Study System

We used data encompassing most of the adult life span of 129 male *G. campestris* from the 2019 breeding season, running from 3 May until 20 June when the last adult died. We extracted data from the video library of the WildCrickets project (www.wildcrickets.org), a long-term project monitoring the behaviour of wild *G. campestris* in a meadow in northern Spain. The methods used by the WildCrickets project are described in detail by Rodríguez-Muñoz et al. (2010) and Rodríguez-Muñoz et al. (2019) but are outlined briefly here.

We captured wild crickets as young adults using Flipper Traps (see <https://crickettrapping.wordpress.com/>; Meadows, 2014) from 10 separate populations across northern Spain. We then removed all the nymphs found in the WildCrickets meadow, retaining the females, and collected males from other source populations to be used in an experiment as part of a separate study (see Tregenza et al., 2021). Crickets were weighed (± 0.01 g) and we attached a small waterproof tag to their pronotum using cyanoacrylate glue. Each tag had a unique code to allow for individual recognition. We then made artificial burrows distributed throughout the meadow based on the positions of the natural burrows found in the previous 10 years. We released 132 females from three local source populations and 130 males from 10 source populations into the meadow by placing them at a randomly chosen burrow inside a metal cage to prevent the cricket moving away immediately after release. These cages were removed 2–4 days after release and a high-resolution infrared video camera was placed over each burrow where a male had been released. A mean of 12.9 males (± 0.99 SD) was released from each of the 10 source populations. The cameras ran continuously for 51 days, filming any behaviours the crickets performed in the vicinity of the burrow (which is where most activity occurs in *G. campestris*).

We took account of potential behavioural variation among source populations in our analyses, but such differences are not the focus of our study.

Ethical Note

The study is based on video observations in a natural environment. The only manipulation we did with the wild insects was collecting them from their original location and then releasing them into our study meadow; right before releasing, we took a small haemolymph sample by piercing the membrane behind the hindleg with a very fine (30 gauge needle) which causes the release of a small drop of haemolymph. We removed the last segment of the tarsus of one of the hindlegs and attached a plastic tag by gluing it to the pronotum using cyanoacrylate adhesive. Our tagged crickets live out their natural lives in the meadow and 129 of the 130 males released were observed in the meadow during the breeding season. This study was approved by the University of Exeter's Research Ethics Panel approval number: 513752.

Extracting Behavioural Data from Video

Nine observers who were naïve to the hypothesis and predictions of this study coded the behaviours performed by male *G. campestris* in these videos during periods when males were alone and in the immediate vicinity of their burrow. Videos were

synchronized via time stamps and observers recorded male identity and behaviour by recording behavioural events occurring at each minute. Observers also recorded the position of each male relative to any direct sunlight in the vicinity of the burrow (0: no direct sunlight visible; 1: direct sunlight visible but the male is not in it; 2: the male is in direct sunlight). The ground temperature was recorded every 10 min via a weather station located at the study site.

To exclude any effects of direct physical interactions, we excluded periods when multiple individuals were present in one video. Owing to this, any singing referred to is the calling song and not the courtship song that occurs when a male comes into contact with a female. Any aggressive singing that occurs when males come into contact was also not included in this study.

Data Analysis

We analysed data at two timescales. First, we quantified the overlap in the timing of singing behaviour between males on each day and tested whether this was related to their spatial proximity (Analysis 1). Second, we conducted a finer-grained analysis at the 1 min level, to investigate whether singing behaviour by a focal male was related to the number and proximity of other simultaneously singing males. We used two complementary approaches for this finer-grained analysis. For the first approach, we partitioned the area around the focal male's burrow into discrete distance zones and counted the other males singing in each zone, to see how these counts were related to the focal male's own singing (Analysis 2). For the second approach, we created subsets of the data with the same number of other males singing for all focal males and ran a series of models to investigate how the focal male's singing was related to the mean distance to those other males (Analysis 3).

Because the study meadow is almost flat and relatively homogeneous in plant coverage, we assumed that calling song propagation is homogeneous across the study meadow in all analyses.

Analysis 1: daily song overlap across the meadow

Quantifying spatial positioning relative to conspecific males. Field crickets do not remain at just one burrow throughout the breeding season; in this data set, they sequentially occupied on average 1.16 (± 0.22 SD) burrows per day. To quantify spatial positioning relative to conspecific males, we therefore computed the distance (m) between each pair of males in the meadow, using the spatial positions of the burrows each male occupied at the start of his recorded behaviour for that day.

Quantifying singing overlap. We computed the phi (ϕ) coefficient (Cramér, 2016) as a daily measure of singing overlap between each pair of males across all the time points at which they were both recorded at their burrows (i.e. excluding any time points at which one or both males were not observed). This was calculated each day for males A and B as follows:

$$\phi_{A,B} = \frac{(S_{A,B} \times S_{I_{A,B}}) - (S_{A,!B} \times S_{!A,B})}{\sqrt{S_A \times S_{I_A} \times S_B \times S_{I_B}}} \quad (1)$$

where the S values in the numerator represent the number of occasions (i.e. number of 1-min scan samples) on that day when male A and male B were simultaneously singing ($S_{A,B}$), both male A and male B were performing any nonsinging behaviour ($S_{I_{A,B}}$), male A was singing while male B was performing any nonsinging behaviour ($S_{A,!B}$) or male B was singing while male A was performing any nonsinging behaviour ($S_{!A,B}$). In the denominator, the S values represent the number of occasions when a given male sang (S_A , S_B)

or performed any nonsinging behaviour (S_{I_A} , S_{I_B}), regardless of the other male's behaviour. The phi coefficient yields a standardized measure of association between -1 (perfect avoidance; the males in a pair were never observed singing at the same time) and $+1$ (perfect overlap; the males in a pair were only ever observed singing at the same time); a score of 0 indicates complete independence in singing. We restricted our analysis to phi values where both males were simultaneously observed in more than 50 of the 1 min sampling intervals on that day; any sample smaller than this can lead to less robust estimates of phi (Atilgan, 2013). We therefore had a data set containing a daily phi coefficient for each pair of males that were recorded simultaneously for more than 50 min in 1 day, as well as the distance between the burrows that each male in the pair occupied.

Difference variables. For each pair of males, we also calculated three difference variables: the absolute difference in body mass, the difference in altitude between their source populations ('both high', 'both low' or 'different') and the mean difference in sunlight status across all time points in the day. For the sunlight variable, we labelled each state with a numerical code: 0: no direct sunlight on burrow; 1: direct sunlight on burrow but male not in direct sunlight; 2: both burrow and male in direct sunlight. These codes were assigned for each time point for each male when they were both simultaneously observed. We then took the absolute difference between the two males' numerical codes at each time point and calculated the mean of these absolute differences across a day. Therefore, large values of the sunlight difference variable meant that the males in a pair experienced very different sunlight conditions across the day (e.g. when one male and his burrow were in direct sunlight, the other male's burrow was in shadow, and vice versa).

Statistical analysis. A Bayesian linear mixed model using Markov chain Monte Carlo (MCMC) sampling was used to determine the effect of spatial distance between a pair of males on their phi coefficient. Fixed effects of distance (standardized as a z score and estimated using a spline), the absolute difference in mass, the average absolute difference in sunlight status and the difference in source altitudes were all included in the model. We included random intercepts for date, source population and the identities of both males to account for correlations among nonindependent measurements.

Analysis 2: impact of number of nearby singing males

Sampling design. To investigate the effect of the proximity and number of other singing males on focal male singing, any singing males at each 1 min time point were grouped into metre distance zones (i.e. 0–1 m, 1–2 m, 2–3 m, 3–4 m, 4–5 m) around the focal male's burrow; the number of other males singing within each of these distance zones was counted for each minute, for each focal male. Previous literature suggests that crickets do not respond to auditory cues from conspecifics beyond 5 m away (Hissmann, 1991; Niemelä et al., 2021; Simmons, 1988). Therefore, for each male, we also recorded the number of other males singing beyond 5 m at each 1 min time point, and used this as a means of controlling for unobserved environmental variables that can affect propensity to sing (e.g. wind level, noise from passing trains, temporary human disturbance). This also allowed us to control for any indirect social effects coming from beyond 5 m away (e.g. waves of contagious singing spreading across the entire meadow). The resulting data contained 1026287 scan samples from 129 males across 51 days. Each male was sampled for a mean of 151.81 ± 17.23 SD min each day, averaging across each male's mean number of scan samples across all days.

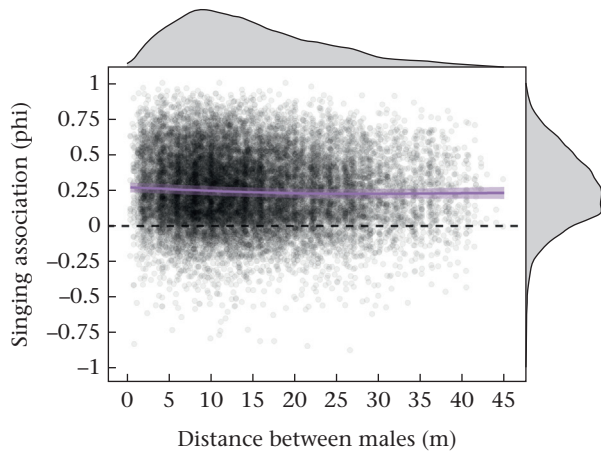


Figure 1. Mean marginal model predictions of the relationship between male pairwise distance and daily singing overlap score (dark purple line) and the 95% credible interval (pale purple ribbon). The dashed line at $\phi = 0$ indicates complete independence in singing, above the dashed line indicates increasing singing overlap and below indicates increasing avoidance. The grey circles show the ϕ coefficients plotted against distance for each pair on each day. The plot above the graph shows the density of pairwise distances; the plot to the right of the graph shows the density of ϕ coefficients. The vertical banding shown by the clusters of grey dots arises due to cricket burrows naturally being spaced 2 m from their nearest neighbour on average.

Statistical analysis. We used MCMC sampling to run Bayesian logistic mixed models to estimate the probability that a male sang in each 1 min interval. The number of other males singing within each distance zone was included, each as a separate fixed effect (number of males within 0–1 m, 1–2 m, 2–3 m, 3–4 m, 4–5 m, 5 m+). Focal male mass, temperature and time of day were converted to z scores and included as fixed effects. Temperature and time of day were included as restricted splines with a maximum of three knots, which allowed us to model nonlinear, quadratic trends for these two variables, as both showed these trends when the raw data were inspected. The male's position relative to any direct sunlight and the altitude (high or low) of his source population were also included as fixed effects. To model variation in the mean odds of singing among dates, burrows, males and source populations (within each altitude level), random intercepts for all these variables were included.

Analysis 3: impact of mean distance to nearby singing males

To investigate the effects of varying mean distance to other singing males on the odds a focal male sang, the data were split into five subsets. The first subset ($c = 1$) contained data from minutes when one other male was singing within 5 m of the focal male (93 252 scan samples from 122 males). The second ($c = 2$) contained data from minutes when two other males were singing within 5 m of the focal male (34 318 scan samples from 111 males),

and so on up to five ($c = 5$) other singing males within 5 m (the sample size became too small to discern any effects above this number of other singing males; $c = 3$: 13 001 scan samples from 93 males; $c = 4$: 4652 scan samples from 73 males; $c = 5$: 1700 scan samples from 46 males). For each of these five subsets of data, we computed the focal male's mean distance to the other singing males at each minute and ran a separate MCMC logistic mixed model to model the odds that the focal male also sang. By subsetting the data in this way, we could control any effects environmental conditions may have had on the males' propensity to sing within each data subset and could investigate the effects of other males singing within 5 m. We included fixed effects of mean distance to the other singing males and z transformed both temperature and time of day, each of which was modelled with restricted splines with a maximum of three knots (allowing nonlinear, quadratic trends). Fixed effects of z-transformed focal male mass, male position relative to any direct sunlight and whether the male had been captured from a high- or low-altitude population were also included. As in the previous analysis, random intercepts for source population, date, burrow and male were included.

Because analyses 2 and 3 use logistic regression analysis, we present the log-odds and odds ratios (ORs) to make interpretation of output easier. Odds ratios indicate how the odds of singing change when the predictor variable increases by 1 unit. An odds ratio of 1 indicates no effect on singing, less than 1 indicates a drop in the odds (i.e. less likely to sing), and greater than 1 indicates an increase in the odds (i.e. more likely to sing). For example, an odds ratio of 1.25 indicates a 25% increase in the odds a male sings. For further details, see Sperandei (2014).

All models were run in R version 4.1.2 (R Core Team, 2022) using the brms package version 2.17.0 (Bürkner, 2017, 2018, 2021).

RESULTS

On each day in the data set, there were an average of 29.71 ± 30.53 SD males recorded (minimum = 1, maximum = 101). Across the entire 51 days, males were recorded singing for 20.6% of the total minute-by-minute scan samples.

Analysis 1: Daily Song Overlap Across the Meadow

The ϕ coefficients calculated ranged from -0.89 to $+1.00$, with a mean of 0.25 ± 0.26 SD. The mean distance between pairs of males in the meadow was 14.44 ± 8.37 m SD, with a minimum distance of 0.53 m and a maximum of 44.72 m.

The MCMC linear mixed model showed that the singing overlap score was unrelated to the distance between the pair of males (see Fig. 1). There was a moderate overlap in the singing of all males across all distances.

The mean difference in sunlight between a pair of males had a negative effect on their song overlap score (β_{sunDiff} 95% highest

Table 1

Summary statistics for the model results from Analysis 1 looking at how singing overlap is associated with distance between males

Term	Posterior mean	Posterior SD	2.5% highest density limit	97.5% highest density limit
Intercept	0.302	0.023	0.258	0.347
Distance spline	0.008	0.002	0.004	0.012
Difference in mass	-0.029	0.016	-0.061	0.002
Altitude: both high → both low	-0.013	0.028	-0.070	0.042
Altitude: both high → different altitudes	-0.015	0.015	-0.045	0.013
Difference in sunlight	-0.194	0.007	-0.208	-0.180

The distributions of marginal effect sizes (β) for each fixed effect included in the model are shown together with the 2.5% and 97.5% highest density interval of the predicted distribution of ϕ values when distance equals the mean distance between pairs, there is no difference in mass, both males are from high-altitude source populations and there is no difference in the mean sunlight (Intercept). Predicted effect sizes of 0 indicate no dependence of the ϕ coefficient on that variable.

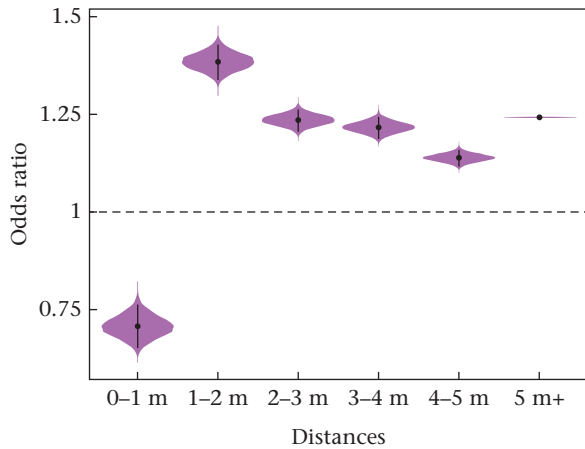


Figure 2. Posterior distributions of marginal odds ratios (ORs) from the model in Analysis 2. Each violin shows the distribution of predicted changes in the odds that a focal male sings when the number of other males singing in the corresponding distance zone increases by one (the effect size of each fixed effect from the model in Analysis 2). The solid lines within the violins span the 95% highest density interval of the posterior distribution and the solid black points show the mean of the posterior distribution. The dashed line at OR = 1 shows where there is no change in the odds of singing.

density interval (HDI) [−0.21, −0.18]), suggesting males that spent more time in similar sunlight conditions (either both in direct sunlight, both near direct sunlight or both not in direct sunlight) had more of an overlap in their singing than those in different sunlight conditions (e.g. one male in direct sunlight, the other not near direct sunlight).

The full model summary for this analysis can be found in Table 1.

Analysis 2: Impact of Number of Nearby Singing Males

The mean number of males recorded singing simultaneously in the whole meadow was 5.97 ± 7.87 SD ($4.6 \pm 6.1\%$ SD of the total study population of males), averaged across all minutes where at least one male was observed. The most males that were recorded in the meadow singing simultaneously in the same minute was 38. The mean number of other males singing within 5 m of a focal male was 0.23 ± 0.65 SD, and the most other males that were singing within 5 m of a focal male in a given minute was 10.

Table 2

Summary statistics for the model results of Analysis 2 looking at the social effects of other males singing within 5 m on a focal male's odds of singing

Term	Posterior mean odds ratio	Posterior SD	2.5% highest density limit	97.5% highest density limit
Intercept	0.022	1.400	0.012	0.044
0–1 m	0.752	1.038	0.700	0.808
1–2 m	1.383	1.016	1.340	1.428
2–3 m	1.233	1.012	1.205	1.262
3–4 m	1.207	1.012	1.179	1.235
4–5 m	1.134	1.009	1.114	1.155
5 m+	1.252	1.001	1.251	1.254
Mass	1.047	1.092	0.882	1.243
Sunlight: no direct sun → sun on burrow	1.189	1.012	1.162	1.216
Sunlight: no direct sun → cricket in sun	1.899	1.012	1.854	1.943
Altitude: high → low	0.972	1.103	0.801	1.174
Temperature spline	1.113	1.008	1.095	1.131
Timestep spline	0.948	1.005	0.939	0.957

The distributions of the marginal change in odds (odds ratio) for each fixed effect included in the model are shown together with the 95% highest density interval of the predicted distribution of odds ratios for each predictor. There is no dependence of focal singing on a given variable if the odds ratio for that variable equals one. The intercept shows the odds a male of mean body mass sings when no males are singing in the rest of the meadow, there is no direct sunlight on him or the burrow, he is from a high-altitude source population, the temperature is equal to the mean temperature and time of day equals the mean of the times at which recordings took place.

The MCMC logistic mixed model showed that a focal male's probability of singing was positively associated with the number of other males singing further than 5 m away (OR_{5m+} 95% HDI [1.25, 1.25]). This corroborates the results from analysis 1, suggesting all males in the meadow had a moderate degree of singing overlap presumably predominantly due to environmental effects (notably the weather) that affected all males at once. This analysis also shows that the probability of singing was positively related to the number of other males singing between 1 and 5 m from the focal male. This positive marginal effect was weakest when other males sang in the 4–5 m distance zone (OR_{4–5 m} 95% HDI [1.11, 1.15]) and increased in strength as those males became closer (OR_{3–4 m} 95% HDI [1.18, 1.24], OR_{2–3 m} 95% HDI [1.21, 1.26], OR_{1–2 m} 95% HDI [1.34, 1.43]; see Fig. 2), consistent with a stimulatory effect of competition. Closer than 1 m, however, the pattern reversed and the model shows a negative marginal effect of other males singing (OR_{0–1 m} 95% HDI [0.70, 0.81]; see Fig. 2), suggesting an inhibitory effect when other males sang nearby.

This model also shows a strong effect of sunlight on focal male singing, with the sun being on the burrow but the male not being in direct sunlight weakly increasing that male's odds of singing (OR_{No direct sun → Sun on burrow} 95% HDI [1.16, 1.22]), and the male being in direct sunlight having a stronger positive influence on the odds he sang (OR_{No direct sun → Cricket in sun} 95% HDI [1.85, 1.94]). The full model summary for this analysis can be found in Table 2.

Analysis 3: Impact of Mean Distance to Nearby Singing Males

The mean distance to other males singing within 5 m of a focal male was 3.32 ± 0.99 m SD, averaged across all minutes with at least one other male singing within 5 m.

The results of the MCMC logistic mixed model show that, with just one other male ($c = 1$) singing within 5 m, the odds that the focal male sang were unrelated to the distance between them (Fig. 3a). This lack of change was also true for two other simultaneously singing males ($c = 2$; Fig. 3b). For three other simultaneously singing males ($c = 3$), however, the probability that a focal male sang was low when those other males were close by, increased as they got further away and reached a peak at a mean distance of 3.5 m (Fig. 3c). As the mean distance to other singing males increased beyond 3.5 m, the predicted probability of the focal male singing began to decrease. A similar pattern was also seen for four ($c = 4$; Fig. 3d) and five ($c = 5$; Fig. 3e) other simultaneously singing males. Taken together, these results suggest that, when one

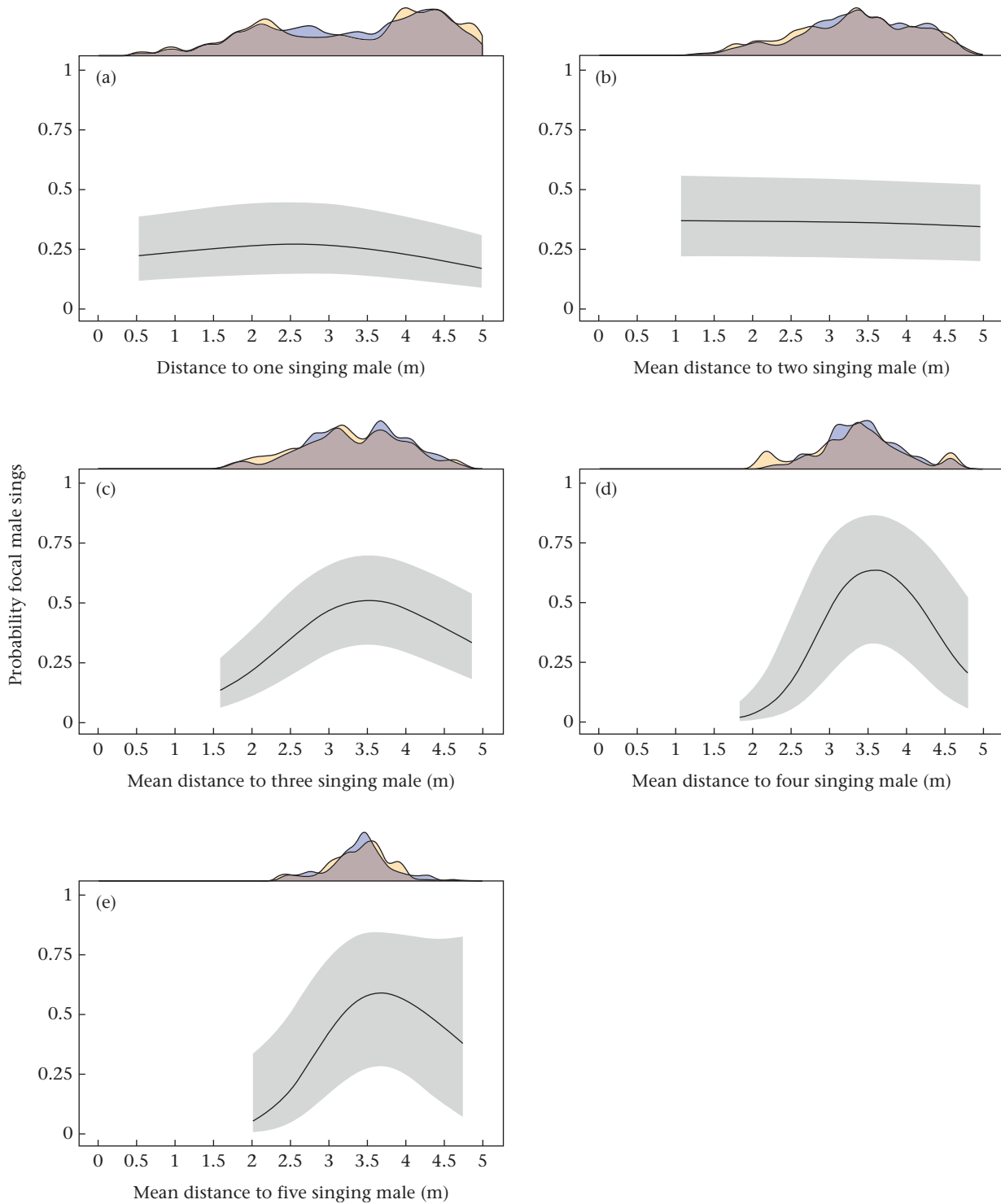


Figure 3. Mean marginal predicted relationship between mean distance to (a) one, (b) two, (c) three, (d) four or (e) five other males singing within 5 m of a focal male and the probability the focal male sings (solid black line), with the 95% credible interval (grey ribbon). The density plots above each graph show the distribution of raw data points for each data subset (yellow = not singing; blue = singing).

or two other males were singing within 5 m of the focal male, their proximity did not have any detectable influence on his singing behaviour. In contrast, when three or more other males were singing within 5 m, there was a nonlinear effect of their proximity

on the predicted probability that the focal male sang, with evidence of an inhibitory effect at shorter distances and a stimulatory effect at intermediate distances (around 3.5 m). The full results for these analyses are available in [Table 3](#).

Table 3

Summary statistics for the five models from Analysis 3 investigating the relationship between the mean distance to other singing males and the odds a focal male sings

Term	Posterior mean odds ratio	Posterior SD	2.5% highest density limit	97.5% highest density limit
c = 1				
Intercept	0.457	1.485	0.214	0.993
Mean distance to singing rivals spline	1.115	1.011	1.092	1.139
Mass	1.010	1.106	0.827	1.232
Sunlight: no direct sun → sun on burrow	1.571	1.025	1.497	1.652
Sunlight: no direct sun → cricket in sun	2.208	1.026	2.102	2.317
Altitude: high → low	0.963	1.101	0.797	1.164
Temperature spline	1.221	1.013	1.190	1.253
Timestep spline	1.768	1.021	1.697	1.842
c = 2				
Intercept	0.735	1.475	0.345	1.551
Mean distance to singing rivals spline	1.025	1.020	0.987	1.065
Mass	1.003	1.105	0.819	1.228
Sunlight: no direct sun → sun on burrow	1.084	1.042	0.998	1.175
Sunlight: no direct sun → cricket in sun	1.551	1.041	1.434	1.677
Altitude: high → low	0.966	1.102	0.799	1.165
Temperature spline	1.278	1.025	1.219	1.341
Timestep spline	1.647	1.039	1.526	1.772
c = 3				
Intercept	1.065	1.508	0.480	2.432
Mean distance to singing rivals spline	0.797	1.038	0.740	0.858
Mass	1.003	1.104	0.828	1.218
Sunlight: no direct sun → sun on burrow	0.888	1.063	0.786	1.000
Sunlight: no direct sun → cricket in sun	1.315	1.061	1.170	1.480
Altitude: high → low	0.979	1.106	0.806	1.192
Temperature spline	1.365	1.071	1.193	1.562
Timestep spline	1.243	1.042	1.146	1.347
c = 4				
Intercept	0.880	1.913	0.245	3.152
Mean distance to singing rivals spline	0.687	1.067	0.605	0.779
Mass	1.002	1.106	0.824	1.222
Sunlight: no direct sun → sun on burrow	0.887	1.078	0.766	1.026
Sunlight: no direct sun → cricket in sun	1.145	1.080	0.985	1.330
Altitude: high → low	0.997	1.104	0.823	1.212
Temperature spline	0.978	1.092	0.821	1.161
Timestep spline	0.951	1.081	0.817	1.106
c = 5				
Intercept	0.938	1.919	0.261	3.390
Mean distance to singing rivals spline	0.722	1.085	0.616	0.848
Mass	1.000	1.106	0.819	1.220
Sunlight: no direct sun → sun on burrow	0.881	1.092	0.741	1.045
Sunlight: no direct sun → cricket in sun	1.048	1.093	0.879	1.248
Altitude: high → low	0.994	1.106	0.816	1.213
Temperature spline	1.056	1.098	0.881	1.266
Timestep spline	0.853	1.083	0.729	0.996

The distributions of the marginal change in odds (odds ratio) for each fixed effect included in the models are shown together with the 95% highest density interval of the predicted distribution of odds ratios for each predictor. There is no dependence of focal singing on a given variable if the odds ratio for that variable equals one. Each model considered a subset of the data where $c = 1, 2, 3, 4$ or 5 indicates the number of other males singing simultaneously within 5 m. The intercept for each model represents the odds a male with mean body mass sings when the other males are singing at the average mean distance away, when there is no direct sunlight on the burrow or male, he is from a high-altitude source population, at mean temperature and time of day equals the mean of the times at which recordings took place.

DISCUSSION

There have been few studies investigating how males adjust their sexual signalling in response to the signalling of conspecific males using wild systems *in vivo*, and fewer still have investigated signalling adjustment within the complex and ever-changing social networks that occur in natural environments. This is important as laboratory studies may not capture the complexity and dynamic nature of a signaller's social environment and may therefore underestimate or overestimate the extent to which sexual signals are adjusted in a natural setting. By monitoring the behaviour of wild male *G. campestris*, we have demonstrated that male crickets overlapped in the timing of their singing across the whole meadow. We also showed that males increased their singing in response to other males singing between 1 and 5 m away, whereas they decreased their singing when other males sang closer than 1 m. This signalling adjustment was dependent on how many other

males were singing within 5 m of a focal male and was most apparent when three or more other males were singing.

We found that males across the whole meadow overlapped in the times at which they sang. This is shown by the positive predicted phi coefficient (a measure of singing overlap) for males across the whole meadow in analysis 1, and by the positive effect of other males singing beyond 5 m away in analysis 2. This overlap is expected since it is well established that environmental variables such as temperature and sunshine have a strong effect on activity in ectotherms including *G. campestris* (Fisher, David, et al., 2015; Fisher, James, et al., 2015). Variation in aspects of the weather and time of day will have similar effects across all males in the meadow which will cause overlapping calling, as will other environmental effects such as human disturbance (Duarte et al., 2019). The meadow-wide overlap is also likely to be strengthened through social transmission. The findings from analyses 2 and 3 show that there was a stimulatory effect of other males singing between 1 and

5 m from a focal male. This stimulatory effect over short distances may be transmitted across the meadow by spreading between males within 5 m of each other, ultimately resulting in further overlap in singing between males at either end of the meadow despite no direct interaction between them (Fitzsimmons et al., 2008). To explicitly investigate sexual signal transmission through networks of interconnected individuals, we would need data at a finer temporal scale than the minute-by-minute intervals used in this study, as the exact timings of singing initiation would be needed to show the temporal sequence of singing across the meadow. This would be an important next step in understanding how individuals tactically adjust their signalling while embedded within complex and dynamic networks of conspecifics.

When meadow-wide environmental effects and indirect (>5 m) social effects were controlled for, we found that singing by other males had a stimulatory social effect on focal male singing (analysis 2). This effect was moderated by how many other males were singing (analysis 3). When just one or two other males were singing, we found no strong evidence that focal males adjusted their singing in response to the distance to those males. However, when three or more other males were singing, focal males adjusted their courtship in response to the distance to those males. This finding may be due to males adjusting their singing in order to sing simultaneously with others, forming local choruses. Anichini et al. (2019) found that features of male song are adjusted in response to differing numbers (and masses) of other males, and it may be that local choruses of three or more males are more effective in attracting females to an area than choruses with fewer males, in which males may not increase investment in auditory signals. Choruses of signallers have been demonstrated in insects, anurans and crustaceans (Gerhardt & Huber, 2002; Larter et al., 2022; Leggett et al., 2021; Perez et al., 2019) and *Plebeiogryllus guttiventris* (another field cricket) has been shown to preferentially position itself so that the active area of its calling songs overlaps with those of other individuals, forming choruses (Mhatre & Balakrishnan, 2006). This may explain why males increase their own calling song when other males sing close by. To investigate this further, research should investigate whether choruses of singing males attract more females than nonchorusing males (as in Leggett et al., 2021), or whether the females that are attracted to choruses are more fecund (as in Lea et al., 2001).

We found a reduction in calling song in response to other males singing less than 1 m away. It has been demonstrated in multiple species that males reduce their signalling effort as the presence of rivals increases (Bretman et al., 2011; Hollon et al., 2023; Weir et al., 2011). Calling song is costly for males to produce (Bailey et al., 1993; Mowles, 2014) and one reason males may inhibit their singing is to reduce costs when there is greater competition from rival males and a lower chance of securing a mate. This may explain the downregulation of calling we saw when other males were calling at close quarters. This explanation, along with the finding of an upregulation of singing in response to males at intermediate distances may suggest that the costs and benefits of singing while other males sing is dependent on the distance to them, and further work should focus on this aspect of dynamic signalling.

When other males are singing nearby, males may also be less likely to invest in calling and more likely to invest in aggressive behaviours to remove intruding males from the vicinity. Burrowing species of field cricket such as *G. campestris* show high levels of aggression and territoriality relative to rarely burrowing species (Alexander, 1961), and these behaviours may be partly responsible for the reduction in singing observed when other males are very close by. Further research should investigate male behavioural changes in response to the calling song of other males at close quarters to confirm the nature of these interactions.

Our study demonstrates that, when observed in a natural setting, males adjust their sexual signalling in response to fine-scale changes in their communication network. Ultimately, this research adds to a body of evidence showing tactical adjustment of sexual signalling, demonstrating that sexual signals are flexible and are deployed as part of a behavioural signalling strategy that may maximize the fitness payoff of the signal depending on the changing context. Further work should seek to address the gap in our theoretical understanding of how these strategies arise and are maintained over evolutionary time, as well as investigating differences in signal adjustment across individuals and the link between this and individual traits such as competitive ability.

Author Contributions

Joe A. Wilde: Conceptualization; Methodology; Software; Validation; Formal Analysis; Investigation; Data Curation; Writing—Original draft; Writing; Review & editing; Visualization. **Rolando Rodríguez-Muñoz:** Data curation; Investigation; Methodology; Writing—Review & editing. **Safi K. Darden:** Conceptualization; Methodology; Formal Analysis; Investigation; Writing—Review & editing; Supervision; Funding Acquisition. **Tom Tregenza:** Conceptualization; Funding acquisition; Investigation; Methodology; Project administration; Writing—Review & editing. **Tim. W. Fawcett:** Conceptualization; Formal analysis; Funding acquisition; Investigation; Methodology; Supervision; Visualization; Writing—Review & editing.

Data Availability

Data are available at <https://figshare.com/s/d2a77aa99f963ff0f997>.

Declaration of Interest

The authors declare no competing interests.

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