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Fluctuations in neighbourhood fertility generate variable signalling effort

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Studies of sexual signalling generally focus on interactions between dyadic pairs, yet communication in natural populations often occurs in the context of complex social networks. The ability to survey social environments and adjust signal production appropriately should be a critical component of success in these systems, but has rarely been documented empirically. Here, we used autonomous recording devices to identify 118 472 songs produced by 26 male common yellowthroats (*Geothlypis trichas*) over two breeding seasons, coupled with detailed surveys of social conditions on each territory. We found strong evidence that common yellowthroat males adjusted their total song production in response to both changes in within-pair social context and changes in the fertility of neighbouring females up to 400 m away. Within the social pair, males drastically reduced their song production when mated, but the magnitude of this reduction depended on both the time of day and on the fertility status of the social mate. By contrast, when fertile females were present on nearby territories, males increased their song output, especially during daytime singing. At this time, it is unclear whether males actively gathered information on neighbouring female fertility or whether the patterns that we observed were driven by changes in social interactions that varied with neighbourhood fertility. Regardless of the mechanism employed, however, subtle changes in the social environment generated substantial variation in signalling effort.

1. Introduction

Decades of studies on sexual signalling have explored the way that signals evolve in the context of dyadic interactions between signallers and receivers (reviewed in [1,2]). More recently, it has become clear that the ability to flexibly adjust signals also plays a role in shaping the outcomes of these dyadic interactions [3–6]. Fewer studies, however, address the larger communication network of signalling and receiving conspecifics in which dyadic interactions occur [7]. Yet, a growing body of literature demonstrates that communication beyond dyadic pairs can structure signalling systems through—for example—eavesdropping on signalling contests [8,9], heterogeneity in response to social situations [10] and social niche construction [11]. When fitness depends on interactions between both social partners and nearby conspecifics, surveillance of, and response to, complicated social environments may play a crucial role in shaping signalling systems [12,13].

Despite recognition of the importance of networks in understanding communication [7,14], there are still relatively few empirical examples of social information outside of dyadic pairs influencing sexual signal production (but see [8,9]). Ideally, a study of flexible signalling in response to extra-dyadic social environment should include: (i) a species with a highly variable social environment with social changes clearly linked to fitness pay-offs, (ii) continuous, complete and fine scale monitoring of changes in the social environment for both focal individuals and all relevant neighbours and (iii) detailed information on signal production for each focal individual across changing social conditions (i.e. *many* days of observation for *many* individual signallers). Although the first condition may be met in many natural populations, there are considerable logistical difficulties in meeting the second and third conditions, as most studies of

bird song evaluate aspects of signalling on only one or a few days for each focal individual in a population.

Further, even in situations where relevant social information is available, it is unclear how often and under what conditions we should expect signallers to adjust signalling effort to match changing social environments. There is now strong evidence that both male and female songbirds glean information by observing the social interactions of conspecifics [8,9,15–19]. In these studies, a focal individual is generally allowed to observe a simulated or natural social interaction and then subsequent behaviour is assayed. Often, subsequent behaviour is adjusted to match the information gained by eavesdropping [17,19]. For example, males may modulate aggressiveness in response to the perceived reputation of an intruder [17], while females may alter paternity allocation in response to the perceived reputation of their mate [19]. Clearly, then, eavesdropping on extra-dyadic communication is an important component of sexual signalling in both mate choice and aggressive contexts. It is still unclear, however, how often signallers monitor and respond to more subtle changes in the social environment, such as fluctuations in neighbour fertility. This type of information may be more difficult to obtain by eavesdropping alone and adjusting signalling effort appropriately requires balancing the costs and benefits of signalling to multiple receivers that may make different demands (i.e. within- versus extrapair mates). Thus, gathering, evaluating and responding to complex social information may be time-consuming and cognitively demanding.

Here, we used autonomous recording devices to study the influence of both within-pair social context and neighbourhood social context (i.e. the fertility of females on nearby territories) in relation to total song production during the dawn chorus and daytime in common yellowthroat warblers (*Geothlypis trichas*). Common yellowthroats are socially monogamous wood-warblers; males possess a carotenoid-based yellow bib, a melanin-based facial mask and a single perch song that is repeated throughout the season. Females arrive on breeding grounds asynchronously and experience high nest predation followed by re-nesting throughout the breeding season. Thus, social context in focal territories and the number of fertile females in any neighbourhood of the study site vary stochastically.

Both within-pair and extrapair mating success contribute substantially to seasonal fitness in our population [20,21]. Additionally, male song performance is related to social pairing status and extrapair reproductive success [22]. Given the variable social environment and apparent need to signal to both within- and extrapair mates, yellowthroats represent an ideal study system in which to examine flexibility in signal production with respect to changing social conditions in the focal and neighbouring territories. We predicted that (i) males would reduce their song production when mated, especially when the social mate was fertile and males shift their effort towards mate guarding and (ii) after controlling for within-pair social context, males would increase song production in proportion to the current number of potential extrapair mates (i.e. fertile females) on nearby territories.

2. Material and methods

(a) Study population and general methodology

We studied 26 male common yellowthroat warblers breeding in Saratoga Springs, NY (43°10'24.6" N, 73°53'19.7" W) over two

breeding seasons (2010–2011). Of these 26 males, 11 were present in both years, resulting in a total of 37 observed male breeding attempts. Our field site consisted of a linear power line cut, which created a series of suitable yellowthroat territories surrounded on all sides by dry woodland habitat unsuitable for yellowthroats (described in detail in [20,21]). Thus, social interactions with birds beyond our observation area were negligible, allowing us to describe the complete social environment experienced by each male that we observed.

Early in each breeding season, males and females were captured in mist nets to collect a small blood sample (less than 50 μ l) for microsatellite-based paternity analysis and to measure body size, plumage ornamentation size and plumage coloration as part of a related, ongoing study [20–24]. At this time, we marked birds with an aluminium USGS band and a unique combination of coloured plastic leg bands, to allow for later visual identification.

We conducted a detailed census of each territory in the field site on every day of the breeding season (approx. 5 May to 20 July). During census visits, we noted pairing status and, after females arrived, watched for nest construction. We found nests by following females during construction and subsequently visited nests every 1–2 days to record the number of eggs, initiation of incubation and predation or fledging events. Nestlings were visited on day 5 after hatching to collect a small blood sample, take morphological measurements, and affix an aluminium USGS band. In 2011, some males also received a sub-dermal testosterone ($n = 8$) or control implant ($n = 8$) as part of a separate experiment [25]. We included control implanted birds in our analyses, but excluded recordings from testosterone-implanted birds made after the implant was given. We also re-analysed our data including recordings from testosterone-implanted birds and adding a fixed effect for implant status to each of our models; results from this analysis were qualitatively unchanged and we report only the results from our reduced dataset excluding recordings from testosterone-implanted males. This intense observation allowed us to record all changes in social status (e.g. female arrival, nest initiation and nest predation) to within 1 day of occurrence throughout each breeding season.

For each male, we demarcated the outer territorial boundaries using a combination of behavioural observations, aerial photos and GPS readings (detailed methodology in [20]). Using ARCVIEW v. 9.3 (ESRI), we defined the centroid of each male's territory. This central location was used to determine which nearby territories fell within a signalling neighbourhood for each male. Neighbouring males with a centroid less than 400 m from a focal male's territory were defined as sharing a neighbourhood. We chose a 400 m limit because 97% of extrapair young in this population are sired by males with a home territory less than 400 m away from the nest [20]. Because the density of territories varied across our site (see extensive description of territory density and distribution at our field site in [20]), the numbers of territories included in a neighbourhood varied (range 1–9, mean 5.6 ± 1.8). Territory size is highly variable and dependent on habitat characteristics throughout the site, but even the largest territories were much smaller than the 400 m neighbourhood that we defined around each centroid.

We also collected focal song recordings from each male in the study site. These recordings consisted of at least one bout of 20 songs recorded after positive visual identification. Songs from these recordings were used as known ID references when processing our longer recordings (see below). For these recordings, we approached to within 10–20 m of a singing male and recorded with a Sony MZ-M200 Hi-MD mini-disc recorder equipped with a Sennheiser ME 66 handheld shotgun microphone (as in [22]).

(b) Definition of fertility windows and social context

In most birds, fertility windows include the period of egg laying and additional days prior to egg laying during which sperm may

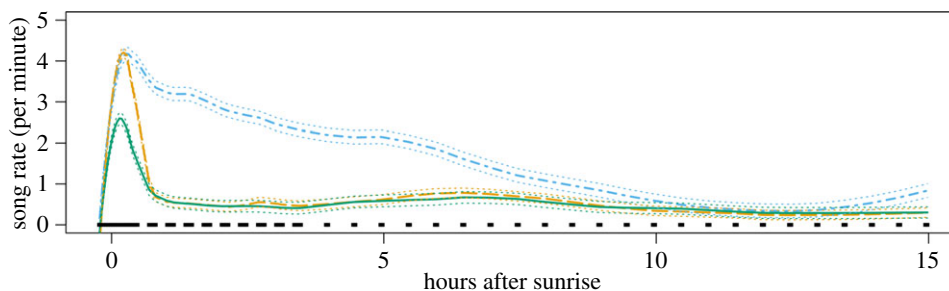


Figure 1. Average singing rate with respect to within-pair social context pooling across all males. Thick, coloured lines are loess smoothed estimates of songs produced per minute based on 250 min of recording across each day for males that were unmated (blue, dot-dash), had a fertile mate (green, solid), or a post-fertile mate (orange, long-dash). Thin dashed lines show smoothed estimates for the mean \pm s.e. for each social condition. The bold black lines along the x-axis show the sampling schedule during which recordings were taken. Sample size ranged from 106 to 185 days for each recording period depending on time of day and social context. (Online version in colour.)

be stored for later fertilization. The exact period of fertility for common yellowthroat females has not been studied and it is thus unclear how many days prior to laying a female should be considered fertile. We followed typical practices from other songbird studies [26] in defining female fertility windows as beginning 5 days before laying the first egg and lasting until the day that the penultimate egg was laid.

Females arrived at our field site asynchronously (7 May to 8 June; mean 20 May \pm 8 days) and experienced high nest predation rates. During the 2 years of study described here, only 28% of 125 observed nests produced fledglings (72% failed from predation or, less commonly, abandonment). After predations, females typically re-nested; most females built several nests in each season, with some building up to five nests. Given the differences in arrival dates and the stochastic nature of predation and re-nesting, the number of fertile females in any area of the field site varied unpredictably throughout the breeding season. This variability in neighbourhood fertility created an opportunity to observe male responses to changes in neighbourhood social context decoupled from seasonal date and within-pair breeding stage.

For each male, we defined two social context parameters for every day on which autonomous recordings were made. First, we defined a categorical variable for within-pair social context with three possible values: (i) unmated (before female arrived or, rarely, after a female predation or desertion), (ii) fertile mate (during the social mate's fertility window(s)) or (iii) post-fertile (while the social mate was incubating or caring for nestlings or fledglings). Second, we defined a continuous variable for neighbourhood fertility status by counting the number of currently fertile neighbouring females within 400 m of the focal male's territory (excluding his within-pair mate). The number of fertile females in 400 m on a given day ranged from 0 to 6 (mean 1.6 ± 1.5).

(c) Autonomous song recordings

We used five Song Meter SM2+ recording devices, each equipped with an SMX-II weatherproof microphone, to autonomously record singing behaviour of individual males in our population (Wildlife Acoustics, Inc., Concord, MA). To record target males, we attached the Song Meter to the trunk of a tree at approximately 2 m height. In each male's territory, we chose a central tree and used this same tree for the entire breeding season. We positioned the Song Meter so that the microphone was aimed towards the centre of the territory. Devices were rotated between territories every other day to ensure adequate sampling of each male across different contexts. Each time that a device was deployed in a male's territory, we recorded two consecutive mornings of dawn chorus and one full day of singing activity. In total, we recorded 6.0 ± 2.8 full days, 9.6 ± 2.2 partial days, and 11.0 ± 3.5 dawn choruses for each male in each year of the study. For logistical reasons, we generally

rotated one device around a group of four to five territories; thus, neighbouring males were rarely recorded on the same day and we could not analyse the influence of neighbourhood song output on focal male singing behaviour with our dataset. We replaced and downloaded recordings from SD memory cards every one to two weeks throughout the season.

Yellowthroat territories in our site are small and open, with only low bushes, grass and marsh plants; thus, the active recording area of a unit placed near the centre of a male's territory extended well beyond the territory boundaries. Because males rarely sing beyond the borders of their territories, a single unit was able to capture all songs from a focal individual. Typically, our units also recorded the songs of one to three neighbouring males (depending on neighbour distance), so these songs were separated from those produced by focal males as described below.

To maximize storage capacity, our devices were set to record on Mono with a 32 KHz sampling rate. Rather than recording continuously, we programmed the units to record on a sampling schedule each day (illustrated in figure 1). The units turned on 15 min before civil sunrise and recorded one 45 min bout (dawn chorus). After this initial recording, the unit alternated between 10 min off and 10 min recording for 3 h (covering the morning period when singing rate is still relatively high), followed by a programme of 25 min off and 5 min recording for 11.5 h (when singing rate is relatively low). Because the time of sunrise changed throughout the season, all recording windows are presented relative to the time of sunrise, rather than time of day. Although the start time of recordings varied with sunrise, our schedule ensured that the same total number of minutes were recorded on each full day of recording.

To facilitate day-to-day comparisons, we restricted our analyses of daytime singing behaviour to days on which the Song Meter was in a territory for the entire recording schedule. For dawn chorus analyses, we included every day in which the full 45 min dawn chorus was recorded. For both daytime and dawn chorus recordings, we excluded days with no identified focal songs from our analyses. Males occasionally leave their territory for extended periods during the breeding season—possibly to follow potential mates off territory (C.C.T. 2014, personal observation); thus, on days with no identified songs, it was unclear whether males were not present or were present but did not sing. We also reanalysed our data including days with no focal songs and our results were qualitatively similar, except that the uncertainty among our candidate models was increased.

Our Song Meter units were programmed to measure temperature with a built-in thermal sensor every 5–25 min (depending on time of day). To account for variation related to conditions at the deployment location (e.g. direct sun), we combined and averaged the temperature readings from all five Song Meters to generate a single temperature profile for the field site on each day of the breeding season; in general, temperatures from all five units

Table 1. Model sets and AIC weights for candidate models to explain song output during the dawn chorus ($n = 301$ days) or daytime ($n = 173$ days). Variable codes are: #fertile (number of fertile females within 400 m excluding social mate); social (social context: unmated, fertile or post-fertile); low (night-time low temperature for previous night), high (daytime or dawn chorus high temperature on day of recording); date (days from 1 May). All models included a random effect for male ID.

	ΔAIC	k	w_i
dawn chorus models			
~ #fertile + social	0.0	6	0.92
~ social	5.3	5	0.06
~ #fertile + social + low + dawnhigh + date	7.8	9	0.02
~ 1 (null model)	15.5	3	<0.01
~ low + dawnhigh + date	17.1	6	<0.01
daytime song models			
~ #fertile + social	0.0	6	0.90
~ #fertile + social + low + dayhigh + date	4.8	9	0.08
~ social	8.0	5	0.02
~ low + dayhigh + date	60.2	6	<0.01
~ 1 (null model)	74.1	3	<0.01

were very similar. For each day of recording, we included the previous night low temperature and daytime high or dawn chorus high temperature as predictors of song production.

(d) Song analysis

Our autonomous recording units produced a total of 334 h of dawn chorus recording and 1455 h of daytime recording over the 2 years of study. To facilitate the extraction of useable data from these recordings, we developed a semi-automated workflow as follows. First, we built a detection algorithm using SONG SCOPE software (Wildlife Acoustics, Inc.). To build this algorithm, we used a set of training data taken from randomly selected Song Meter recordings. Our training set included 324 songs from 22 individual males and our detection algorithm was built in SONG SCOPE using the default settings, except that maximum syllable length was adjusted to 25 ms.

The detection algorithm worked by matching recording segments to the template derived from the training data and registering a hit any time that a similarity threshold was met. Because we were interested in identifying every song produced by our focal individuals, we intentionally set our threshold very low (SONG SCOPE settings: quality = 5, score = 55). Using a low threshold resulted a high incidence of false positives (83% of hits), but ensured that very few focal songs were missed. We verified that our detection algorithm was picking up most yellowthroat songs by manually identifying songs in 43 randomly chosen recording files from 2010 that totalled 5 h of recording time; in this subset of recordings, 90.3% (353 out of 391) of visually detected songs were also detected by our algorithm. Among the 43 testing files, song counts obtained by visual inspection or our detection algorithm were remarkably consistent (Pearson's correlation = 0.987; repeatability = 0.985). Additionally, most undetected songs were recorded at low amplitude because they were produced by neighbouring males relatively far from the recording unit; thus, more than 95% of songs by focal males were detected. After running batches of raw field recordings through our detection algorithm, we proceeded to manually reject false positives. The annotated spectrogram associated with each detection was visually inspected by CCT and all non-yellowthroat songs were deleted from the detection output. While filtering out false positives, we also identified each song as belonging to the focal male or to a neighbouring male.

Several pieces of information allowed us to determine the identity of each singing male. First, yellowthroat males rarely sing beyond the borders of their territory. Thus, the location of a recording unit limited the number of possible singing males to one to four individuals (depending on neighbourhood density). Second, yellowthroats have a single song type rather than a repertoire and individual males repeat a single song with the same structure throughout their life [27]. In contrast to this within-individual similarity, there is considerable variation in fine scale song structure between males. Using the known ID reference samples from focal recordings described above, we were able to unambiguously assign each song in a recording to the focal male or to one of his close neighbours; our full dataset included a total of 118 472 songs produced by focal males from 1789 total hours of recording. We could not ensure that all songs from neighbouring males were recorded (because of greater distance to the recording unit); thus, we restricted all of our analyses to songs produced by the focal males.

(e) Statistical analysis

We analysed total singing output using a model selection approach with alternative models compared by Akaike information criterion (AIC) values. Dawn chorus and daytime singing were analysed separately, but with identical candidate model sets, except that dawn chorus models included high temperature during the dawn recording as a predictor, rather than daytime high temperature. In each case, the response variable was the total number of songs produced during the recording period (45 continuous minutes for dawn chorus; 205 min spaced throughout the day for daytime singing, as described above). Potential predictors of song production included abiotic factors (date, night low temperature, day or dawn high temperature), social pairing status (mated, fertile mate or post-fertile mate) and neighbourhood fertility context (number of fertile females within 400 m).

From these predictors, we generated a candidate set of five models (table 1). First, we fit a null, intercept-only model. Second, we fit a model that included only abiotic factors with no social information. Third, we fit a model that included only social pairing information. Fourth, we fit a model that included both social pairing information and neighbourhood fertility. Finally, we fit a full model that included social pairing, neighbourhood fertility and abiotic factors. Each model also included a

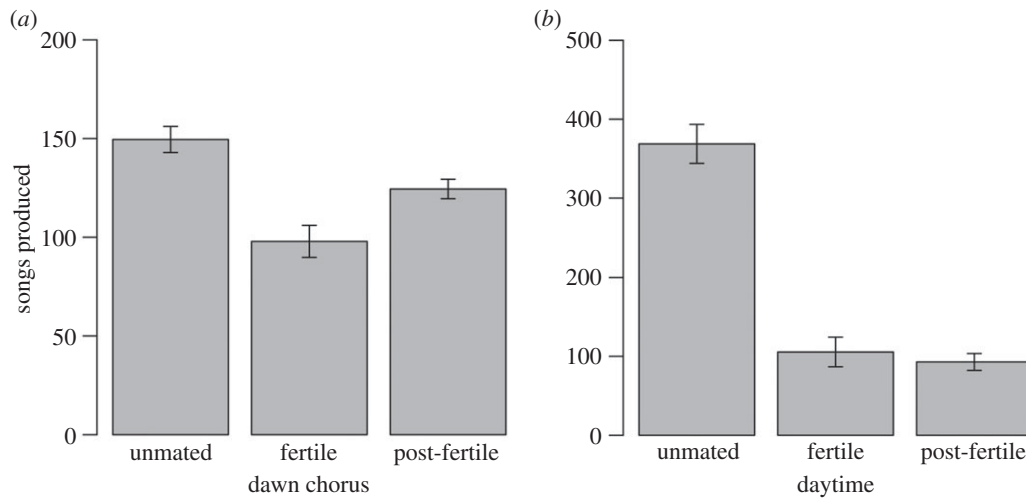


Figure 2. Empirical mean numbers of songs produced \pm s.e. for each of three social mating contexts during (a) dawn chorus or (b) daytime singing. Sample sizes range from 43 to 138 observations depending on context and recording period.

random effect for male ID (to account for the many observations made on each individual).

We fit our count data with the R package *glmmADMB* v. 0.8.0 using a negative binomial distribution to allow for overdispersion. We evaluated the support for each model based on differences in AIC values between fit models. AIC values in the *glmmADMB* package are calculated without conditioning for random effects as $-2 \times \log(L) + 2k$. Each model that we fit varied in fixed effects, but included the same random effect structure; thus, this formulation of AIC allowed for valid comparisons between our candidate models. For both dawn chorus and daytime song, we present the fit parameter estimates from the best-supported model; in both cases, all other models had Δ AIC values greater than or equal to 4. We illustrate the effects of within-pair status on song production by plotting raw data for singing profiles (figure 1) and total number of songs (figure 2*a,b*). The magnitude of the effect of within-pair social status on song output was considerably larger than the effect of neighbourhood fertility; thus, the relationship between neighbourhood fertility and song production only emerged after controlling for within-pair context. To illustrate this relationship, we plotted the predictions from the best-supported dawn chorus and daytime singing models ($w_i > 90\%$, tables 1 and 2) along with a subset of empirical data taken from the unmated social stage (figure 3*a,b*). All analyses were performed in R v. 3.0.2 (R Core Development team).

3. Results

The final dataset used to fit our models consisted of 817 h of recording from 301 dawn chorus recordings and 173 full-day recordings from 26 males. These recording days yielded a total of 37 622 identified dawn chorus songs and 31 782 identified daytime songs produced by focal males. This dataset represents 21.5 ± 13.5 h of recording from each focal male in each year, from which we identified 1827 ± 1052 songs per male. We paired these data with complete information on pairing status and neighbourhood female fertility. To our knowledge, the comprehensive characterization of changing social environment coupled with repeated assessment of signal production for a large number of individuals make this dataset unique.

(a) Response to social mate

Males drastically adjusted their song output in response to changes in social mating status (figures 1 and 2). For both

Table 2. Parameter estimates from best-supported negative binomial GLMMs for dawn and daytime models. The default social status is unmated.

parameter	estimate	s.e.
dawn chorus \sim #fertile + social $w_i = 0.92$		
intercept	4.88	0.09
#fertile neighbours	0.08	0.03
fertile social mate (yes = 1)	-0.50	0.11
non-fertile social mate (yes = 1)	-0.20	0.10
daytime song \sim #fertile + social $w_i = 0.90$		
intercept	5.64	0.14
#fertile neighbours	0.16	0.05
fertile social mate (yes = 1)	-1.33	0.18
non-fertile social mate (yes = 1)	-1.32	0.16

dawn and daytime singing, AIC values strongly supported models that included an effect of social pairing (cumulative w_i for models including social pairing: dawn: more than 99%; daytime: more than 99%, table 1). The magnitude of these effects was large (table 2), with males reducing their daytime song output by 74% immediately after attracting a social mate.

During the dawn chorus, the magnitude of this reduction depended on the social mate's fertility status, with the biggest reduction (39%) corresponding to a fertile mate and an intermediate reduction (18%) for a post-fertile mate (figure 2). Inspection of the average singing profiles (figure 1) indicates that these differences were driven by variation in both the maximum rate and the length of the dawn chorus. At all stages, males rapidly increased their song rate just after dawn, but males with fertile mates peaked at an average song rate just over 50% of that observed in males that were unmated or mated to post-fertile females (figure 1). By contrast, males with mates that were post-fertile sang at rates similar to

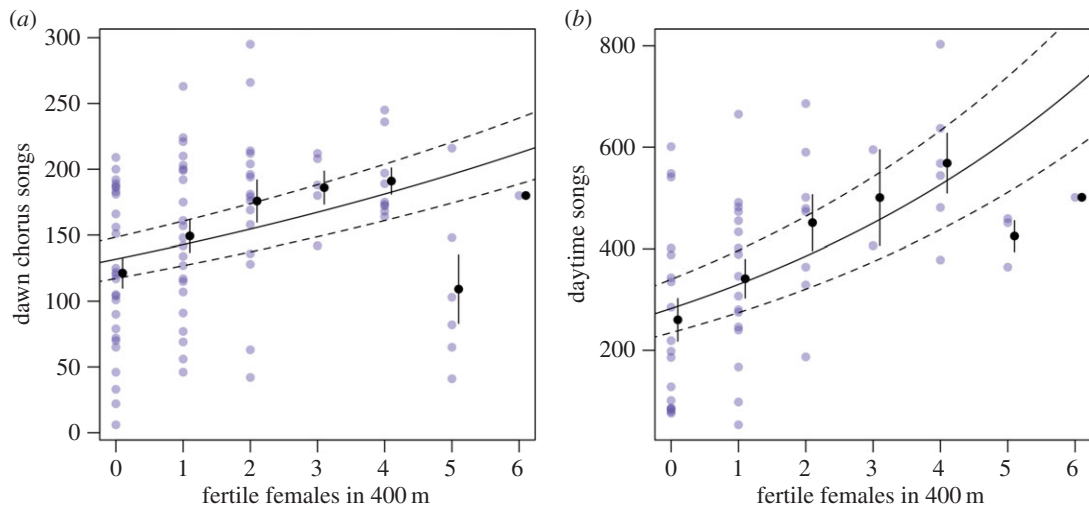


Figure 3. Model predicted relationship between the number of fertile females within 400 m of a focal male's territory, not including his own mate and (a) dawn chorus and (b) daytime song production. For simplicity, we show the expected relationship when males are unmated. Blue dots represent empirical observations of 87 dawn chorus and 55 daytime recordings made while males were unmated. Black dots and vertical lines are the empirical mean \pm s.e. for each number of fertile neighbours. Solid black line is the maximum-likelihood estimate and dashed black lines are maximum likelihood estimates (MLE) \pm s.e.; both are derived from the fit model that received the most support ($\text{Song} \sim \# \text{Fertile} + \text{Social}$, tables 1 and 2). (Online version in colour.)

those observed in unmated males; these high rates, however, were sustained for longer in unmated males, leading to the intermediate song production of males with post-fertile mates (figure 1).

During the daytime, song production was very low for mated males regardless of the fertility status of their social mate (figure 2). By contrast, unmated males maintained relatively high singing rates throughout much of the day, only dropping to levels observed in mated males about 10 h after sunrise (figure 1).

(b) Response to neighbourhood fertility

Models that included the number of fertile females in the neighbourhood received strong support (cumulative w_i for models including neighbourhood fertility: dawn: 94%; daytime: 98%, table 1). For both dawn and daytime recordings, the presence of fertile females increased the expected song production after accounting for changes attributable to pairing status (table 2). However, the magnitude of these effects differed. During dawn chorus, there was only a moderate effect of neighbourhood fertility, with each additional fertile female increasing song production by an estimated 5–10%. For daytime singing, the effect was more pronounced, with each additional fertile female predicted to result in a 15–20% increase in song production (table 2). Because some males experienced neighbourhoods with up to six fertile females at a time, the maximum predicted increase in song production in response to neighbourhood fertility was substantial (figure 3).

(c) Response to abiotic factors

In contrast to social information, there was little evidence that abiotic factors contributed substantially to variation in song production. For both dawn and daytime singing, the full model that included temperature and date received little support (dawn $w_i = 2\%$, day $w_i = 8\%$, table 1). At both dawn and daytime, the model that only included abiotic factors received essentially no support (w_i dawn $< 1\%$, w_i daytime $< 1\%$, table 1). It is important to note that, for daytime singing,

models with only abiotic factors still received substantially more support than the null model (ΔAIC of abiotic only to null model for daytime = 13.9). Thus, an analysis including only abiotic factors without social information might have concluded that song variation was driven by temperature and date. Our results suggest that the effects of social conditions are so large that any contribution of abiotic factors is rendered insignificant.

4. Discussion

By focusing on the dyadic signalling interactions that occur between mates, researchers often implicitly ignore the fact that signalling in natural populations generally occurs in a complex social environment with many signallers and many receivers. When signaller fitness is influenced by the responses of receivers both within and outside of the dyadic pair, the structure of signalling systems can only be understood by incorporating information beyond the dyadic pair [8,9,15–19]. In common yellowthroats, we found that males *decrease* their song production when paired with a fertile social mate, but *increase* their song production when neighbouring females are fertile. Because these events often occur simultaneously, males are forced to compromise their signalling behaviour to balance the demands of signalling to within-pair and potential extrapair mates. Thus, daily and seasonal patterns of singing are shaped by subtle changes in the social environment and males must gather, process and respond to complex social information.

Currently, it is unclear how males accomplish the task of neighbourhood surveillance. One possibility is that males eavesdrop on the changes in song production of rivals on nearby territories. This scenario is likely, because attending to the songs of neighbours is a relatively low cost way to acquire social information, and eavesdropping on aggressive song interactions of neighbours is well documented in a variety of species [15–18]. In this case, males may inadvertently advertise the fertility of their own mate to their rivals by the act of *not* singing. If eavesdropping is common, males may be selected

to balance the benefits of attending to a fertile social mate with the costs of advertising fertility to the entire neighbourhood. Thus, it is possible that the patterns that we observed were driven largely by intra-sexual signalling networks. Unfortunately, we could not test this possibility directly in our study, as we did not record full neighbourhoods of males singing on the same day.

Alternatively, males might assess neighbouring female fertility through direct social interactions. For example, males may foray off-territory to visit neighbouring females or neighbouring females may foray off-territory while fertile to visit potential extrapair mates [28]. In either case, increased male song production might result from an increase in encounters with fertile females. Both male and female off-territory forays are common in songbirds, though male forays have been studied more extensively [28]. One study of common yellowthroats in Wisconsin found that males that forayed off territory were more likely to sire extrapair young and that females were more likely to foray off-territory during their fertile period, but male song output was not measured in that study [29]. Gathering information from social interactions and from neighbouring male songs are not mutually exclusive hypotheses, and we suspect that males combine social information gleaned in multiple ways when assessing neighbourhood fertility and allocating signalling effort. Studies that experimentally manipulate each information source independently—as has been done, to some extent, in studies of eavesdropping on aggressive interactions [15–18]—will be helpful in understanding the relative importance of each source of information.

Given the complexity of accurate surveillance and the competing signalling demands that we observed, individual signallers are likely to differ in their ability to respond appropriately to changes in social context. Appropriate behavioural responses to social information in dyadic courtship encounters can have major fitness consequences [5]; we suspect that similar consequences will pertain to behavioural adjustment in the context of signalling networks. In this study, we were constrained in looking for relationships between signal adjustment and extrapair fitness by a relatively small sample size of individual males; only eight males successfully sired extrapair young in our sample and not all males were recorded under all social conditions, making it difficult to assess inter-individual variation in responsiveness. Additionally, within-pair and extrapair fitness are influenced by many other factors in this population that we could not control for (e.g. song consistency, breeding density, predation events, plumage characteristics, male breeding experience and oxidative stress: [20–23,25,30]). We suggest that studies combining autonomous recording of song behaviour with experimental manipulations of social environment (e.g. presentations of fertile females or playbacks of neighbouring male song) will be the most powerful way to test the hypothesis that variation in song adjustment is related to reproductive success.

Even if subsequent work shows that inter-individual variation in signal adjustment is not related to fitness, there are reasons that males—at the population level—might continue to respond to changes in neighbourhood fertility. One possibility is that total song output serves mainly as a form of tonic communication that indicates continued presence and availability as an extrapair mating option. In this scenario, increasing song rate when neighbouring females are fertile may be necessary, but not sufficient, for extrapair mating success. Increased song

may signal availability, with subsequent female choice depending on other factors (e.g. fine-scale song performance or ornamentation). Indeed, previous work in this population has shown that song consistency over short time-scales (within a singing bout) is related to both extrapair mating success and within-pair social context. More consistent singers are more likely to sire extrapair young, but consistency within individual males declines after mating [22]. We did not measure song consistency in this study, so it is unclear how consistency is related to total song production across varying social contexts. It seems likely, however, that trade-offs between total song output and song consistency may limit a male's ability to respond optimally to changing social environments.

Regardless of the fitness outcomes and information acquisition processes employed, males apparently respond to subtle changes in the social environment of neighbouring territories up to 400 m away. Even if males are using neighbour singing behaviour as an indication of female fertility, a simple rule of thumb in which a male bases his own singing on the total number of songs heard would be insufficient to explain the patterns that we observed. Males often had one or two close neighbours who were unmated and singing at high rates, yet this high song output did not prevent males from responding to the subtle changes in fertility on territories up to 400 m away. Thus, it appears that male signal adjustment is calibrated to account for each neighbouring territory on which extrapair young could be sired.

We do not suggest that yellowthroats are uncommon in their attentiveness to changing social contexts. Rather, we suspect that nuanced adjustment of signals in response to subtle changes in social environments is common, but often overlooked because the relevant data are not collected. Indeed, studies of sexual selection often characterize signallers based on a small number of brief observations of signal production (often only a single observation) and rarely include complete information on social context, especially outside of a dyadic pair. Incorporating more observations of individuals coupled with information on social context should lead to a greater understanding of variation in signal production. For example, a recent meta-analysis found that the repeatability of mating behaviours in studies that quantified behaviour multiple times for the same individuals was surprisingly low [31]. However, if social context changed across observations, low repeatability may become the predicted outcome, rather than a surprising result. Autonomous observations like those employed in our study offer a powerful approach to understanding the repeatability of signalling behaviour, because they make it possible to quantify signals many times per individual across changing social conditions [32].

Ethics statement. This research was conducted in accordance with ABS/ASAB guidelines and all procedures were approved by UC Davis IACUC protocol nos. 13329 or 16362 and by Skidmore College IACUC protocol no. 69.

Data accessibility. Data were deposited in the dryad repository (www.datadryad.org): doi:10.5061/dryad.0039d.

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