



Original Article

Playback of predator calls inhibits and delays dawn singing in a songbird community

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Recent studies have demonstrated that experimental increases in perceived predation risk can substantially impair breeding behavior and reduce reproductive success. Perceived predation risk may also occur in the context of sexual signaling, with potential consequences for sexual selection. In songbirds, singing at dawn is an important sexual signal but may also attract predators. Here, we report on 2 experiments designed to test whether perceived predation risk affects the occurrence and timing of dawn singing in a songbird community. In a pilot experiment, we broadcast predator playbacks intermittently across half a forest plot and nonpredator playbacks across the other half throughout early spring. In the second experiment, we repeated the treatments in 16 independent but smaller plots (8 with predator calls and 8 with nonpredator calls). In the predator treatment, most species were less likely to sing at dawn (small, nonsignificant effects) and started later if they did sing (significant for 2 species). Meta-analyses combining the data from both experiments showed an overall significant effect of the treatment on both the likelihood and timing of singing. Species that were less likely to sing also sang later if they did sing, corroborating that an increase in perceived predation risk was the common cause of the effects on both measures.

Key words: dawn chorus, extrapair paternity, fear, perceived predation risk, sexual signaling, songbird.

INTRODUCTION

Predation is a major selective force. Traditionally, studies emphasized the direct effects related to the predator killing the prey. However, there is growing evidence that predators can additionally have nonconsumptive effects on prey species. Several studies have now demonstrated that an increase in the perceived risk of predation is sufficient to cause substantial negative effects on breeding behavior and reproductive success (often referred to as “fear effects”; Cresswell 2008; Creel and Christianson 2008; Lima 2009; Zanette et al. 2011; Hua et al. 2014; LaManna and Martin 2016). In species where males use elaborate displays to attract (extrapair) females or deter competitors, the perceived risk of predation may also affect sexual signaling. If this is the case, perceived predation risk may not only lower mean reproductive success of a population but also have consequences for how reproductive success is distributed among males, with potential implications for the process of sexual selection (Andersson 1994; Jennions and Petrie 1997). Indeed, several studies have shown that perceived predation risk may affect visual and acoustic sexual displays in birds (Fontaine and Martin 2006; Schmidt and Belinski 2013; Akcay et al. 2016;

Abbey-Lee et al. 2016) and other animals (Ryan 1985; Cordes et al. 2014; Michelangeli and Wong 2014; Rypstra et al. 2016).

One of the most ubiquitous and conspicuous sexual signals is the dawn chorus of male songbirds (Staicer et al. 1996; Catchpole and Slater 2008). Indeed, this is so ubiquitous and conspicuous that the fact it could be silenced was evocatively used to highlight dangers to the environment by Rachel Carson (1962) in *Silent Spring*. Dawn singing can effectively keep other males out of the territory, but it can also attract (extrapair) females, and thus has an important function as an intrasexual as well as an intersexual signal (Krebs 1977; Mace 1986; Cuthill and Macdonald 1990; Staicer et al. 1996; Kunc et al. 2005; Catchpole and Slater 2008). Recent work showed that the timing of dawn singing may be especially important because in several species, it reflects male quality and the earliest-singing males were the most successful in attracting females and siring extrapair offspring (Poesel et al. 2006; Dolan et al. 2007; Murphy et al. 2008; Kempenaers et al. 2010).

Dawn singing attracts the attention of not only potential mates and competitors but potentially also that of predators, and singing might thus increase the probability of being preyed on (Zuk and Kolluru 1998; Mougeot and Bretagnolle 2000; Krams 2001). Male songbirds therefore may face a trade-off between the benefits they gain from singing early (e.g., in terms of

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paternity) and potential survival costs, which will depend on the risk of predation (Zuk and Kolluru 1998; Hughes et al. 2012). Additionally, perceived predation risk may indirectly affect dawn singing, for instance through its effects on foraging efficiency or sleep quality (Lima and Dill 1990; Stuber et al. 2014). Energy reserves are a key determinant for how individuals optimize their daily routines (Houston and McNamara 1987; McNamara et al. 1987; Hutchinson et al. 1993), and several empirical studies have highlighted its importance for dawn singing (Cuthill and Macdonald 1990; Otter et al. 1997; Thomas 1999; Murphy et al. 2008). Surprisingly, however, whether and how perceived predation risk affects dawn singing remains untested, despite a highly cited review having identified that perceived predation risk seems particularly likely to silence the dawn chorus (Lima 2009).

Here, we investigate whether perceived predation risk inhibits (silences) dawn singing by songbirds or delays the onset of singing if they do sing. To test this, we manipulated perceived predation risk by intermittently broadcasting predator calls throughout early spring. In a pilot experiment, we intermittently broadcast predator calls over half a forest plot and nonpredator calls over the other half. Analyses of this experiment revealed substantial effects on the occurrence and timing of dawn singing. We then performed a second experiment in which we repeated the treatments in 16 independent but smaller plots (8 with predator and 8 with nonpredator playbacks).

METHODS

Experimental procedures

First, we conducted a pilot experiment (see details below) in a 40-ha unmanaged part of the Westerholz forest in Southern Germany (48°08'26"N, 10°53'29"E; see Supplementary Figure S1a). We aimed to increase perceived predation risk in half of the study area by placing 25 speakers (Foxpro Shockwave, Foxpro Inc., Lewistown, PA) that intermittently broadcast calls of avian predators from 30 March to 2 May 2016. The other half of the study area served as a control and contained 25 speakers that intermittently broadcast nonpredator calls during the same period. Speakers were placed near active blue tit (*Cyanistes caeruleus*) nests as part of a larger study examining the effects of perceived predation risk on blue tit breeding behavior (Santema et al. in preparation). The playbacks were audible throughout the experimental and control plots but not across plots because plots were separated by a buffer area with no treatment. This allowed us to investigate the effects on the dawn singing behavior of the entire local songbird community. To avoid treatment effects on settlement patterns and spatial distribution of birds, we started the experiment relatively late in the season, after territory settlement. Indeed, detailed monitoring of the blue tit population (Santema et al. in preparation) revealed no effects of the treatment on the spatial distribution of individuals. To avoid habituation, we changed the location of the speakers within each plot every second day. We installed 85 weatherproof sound recorders (Song Meter SM2, Wildlife Acoustics, Concord, MA; <http://www.wildlifeacoustics.com>) throughout the study area and programmed them to record sounds daily between 2 h before and 1 h after sunrise.

Although the pilot experiment included a large number of individuals from different species, we only used one (large) plot for each treatment and the sample size can therefore be considered as $N = 1$ per treatment. Because this does not allow robust conclusions,

we performed a follow-up experiment in 2017, in which we selected 16 independent but smaller plots in a 300-ha forest surrounding the study area used in experiment 1 (and excluding this area; see Supplementary Figure S1b). Between 27 March and 26 April, half of these plots received the predator playback treatment, whereas the other half received the nonpredator control treatment. Each plot contained 3 speakers, placed 140 m apart (in a triangular shape), that broadcast calls in the same manner as in experiment 1. To avoid habituation, we programmed the speakers to play on a 2-day-on/2-day-off schedule. We placed a sound recorder in the center of each plot and recorded dawn song in the same manner as in experiment 1 (see below).

Calls were played following a protocol demonstrated to have substantial effects on breeding behavior and reproductive success in other songbirds (Zanette et al. 2011; Hua et al. 2014; LaManna and Martin 2016). For the predator treatment, we used 6 nocturnal and 12 diurnal predator species that occur in Southern Germany and that include small birds in their diet (Supplementary Table S1). For the nonpredator control treatment, we used 4 nocturnal and 14 diurnal bird species that occur in Southern Germany but that neither prey on nor compete with forest-living songbirds (Supplementary Table S1). We used a total of 281 recordings of predators and 253 recordings of nonpredators that were obtained from the online repository Xeno Canto (www.xeno-canto.org). We normalized the peak amplitude of each exemplar using the software Audacity (www.audacityteam.org). At the start of the experiment, we played back a recording consisting of constant white noise (set to the same peak amplitude as the exemplars) and we set the volume such that we measured 85 dB at 1 m distance (using a Voltcraft SL-100 sound pressure meter). Recordings were intermittently broadcast throughout the day from 2 h before sunrise to 1 h after sunset at a 1:1.5 sound-to-silence ratio (e.g., a 60-s recording was followed by 90-s silence; see Zanette et al. 2011). Calls of nocturnal species were played before sunrise and after sunset, calls of both nocturnal and diurnal species were played in the first hour after sunrise, and calls of diurnal species were played the rest of the day. Calls had no apparent effect on the occurrence of real predators, as the number of predator sightings was comparable between the plots (Supplementary Table S2). The experiments were approved by the Bavarian government and the Bavarian regional office for forestry (LWF).

We manually extracted data from the sound recordings using Song Scope 4.1.3 (Wildlife Acoustics, Concord, MA; <http://www.wildlifeacoustics.com>). For each recorder on each day, we noted whether or not a species was singing and, if so, the time (to the nearest second) of its first song. We extracted data for the 10 most common songbird species at our study site: European robin (*Erithacus rubecula*), common blackbird (*Turdus merula*), song thrush (*Turdus philomelos*), great tit, blue tit, common chaffinch (*Fringilla coelebs*), marsh tit (*Poecile palustris*), coal tit (*Periparus ater*), Eurasian nuthatch (*Sitta europaea*), and European wren (*Troglodytes troglodytes*). In experiment 2, we additionally included Eurasian treecreeper (*Certhia familiaris*) and short-toed treecreeper (*Certhia brachydactyla*). All of these species were recorded on the majority of plots and most species were recorded on every plot (see Supplementary Figure S2 for the relative abundance of each species). We noted the presence of rain, which was easily recognizable on the sonogram as broad-frequency, low-amplitude, continuous noise. We excluded recordings on days where heavy rainfall made song detection unreliable (2 days in experiment 1 and none in experiment 2). We analyzed a total of 1269 and 559 recorder days in experiments 1

and 2, respectively (see [Supplementary Figures S2 and S3](#) for a graphical summary of the data). Two out of 3 data extractors were blind to the aims and hypotheses of the study, and restricting the data set to recordings extracted by these 2 people (>70% of the data) did not change the conclusions of the study.

Statistical analyses

All statistical analyses were performed with R (versions 3.1.2 and later; [R Development Core Team 2014](#)). First, we tested for an overall, across-species effect of the treatment on the occurrence of dawn singing using a generalized linear mixed-effect model with a binomial error structure (lme4 package; [Bates et al. 2015](#)). The response variable was whether a species sang on a particular morning (yes/no). We tested the effect of the treatment on the timing of dawn singing using a linear mixed-effect model (nlme package; [Pinheiro et al. 2013](#)) with onset of singing (in minutes relative to sunrise) as the response variable. In all models, we included the explanatory variables “treatment” (predator/control), “rainfall” (yes/no), and recording “date” (mean-centered); the latter 2 factors were included because they strongly influence dawn singing ([Da Silva et al. 2014, 2015](#)). For the data from experiment 1, we included a correlation structure with the coordinates of the location of the sound recorders in the models examining the onset of singing to account for potential spatial autocorrelation. In the models examining whether or not a species was singing, we included recorder identity as a random intercept. For the data from experiment 2, we included plot identity as a random intercept. In all models, we also included “species” as a random intercept and “date” as a random slope for both “plot” and “species.” We then tested for an overall, across-experiment effect by performing meta-analyses with the estimated effect sizes and standard errors (SE) obtained from the across-species models for each experiment using the “rma” function from the R package “metaphor” ([Viechtbauer 2010](#)).

Second, we ran models for each species separately to test for species-specific treatment effects on the occurrence and timing of dawn singing using the same models as described above but without “species” as a random intercept. For robins, the effect of the treatment on the occurrence of dawn singing could not be estimated in experiment 2 because this species was singing in almost all recordings (>98%). We used the R package “multcomp” ([Hothorn et al. 2008](#)) to correct the *P*-values for multiple testing.

RESULTS

Playbacks of predator calls reduced the likelihood of singing at dawn on any given day in the majority of species (>70% of species; [Figure 1a](#)) in both experiments (8 out of 10 in experiment 1, 8 out of 11 in experiment 2). However, after correcting for multiple comparisons, this effect was significant for only one species (coal tit) in experiment 1 ([Supplementary Table S3](#)) and for none of the species in experiment 2 ([Supplementary Table S4](#)). Across-species analyses revealed that there was a significant treatment effect on the likelihood of singing in experiment 1 but not in experiment 2, although the effect was in the same direction ([Figure 1b](#); [Supplementary Table S5](#)). Combining the across-species estimates from both experiments in a meta-analysis revealed a significant overall effect of the predator treatment, with birds being less likely to sing at dawn in areas where predator calls were broadcast ([Figure 1b](#); estimate compared with control = -0.44 , $z = -2.06$, $P = 0.038$).

When species did sing, playbacks of predator calls on average delayed the start of singing in the majority of species ([Figure 2a](#); 7 out of 10 in experiment 1, 8 out of 12 in experiment 2), with birds exposed to predator calls singing up to 16 and 11 min later in experiments 1 and 2, respectively ([Figure 2a](#)). After correcting for multiple comparisons, this was significant for 5 species in experiment 1 ([Supplementary Table S6](#)) and for 2 species in

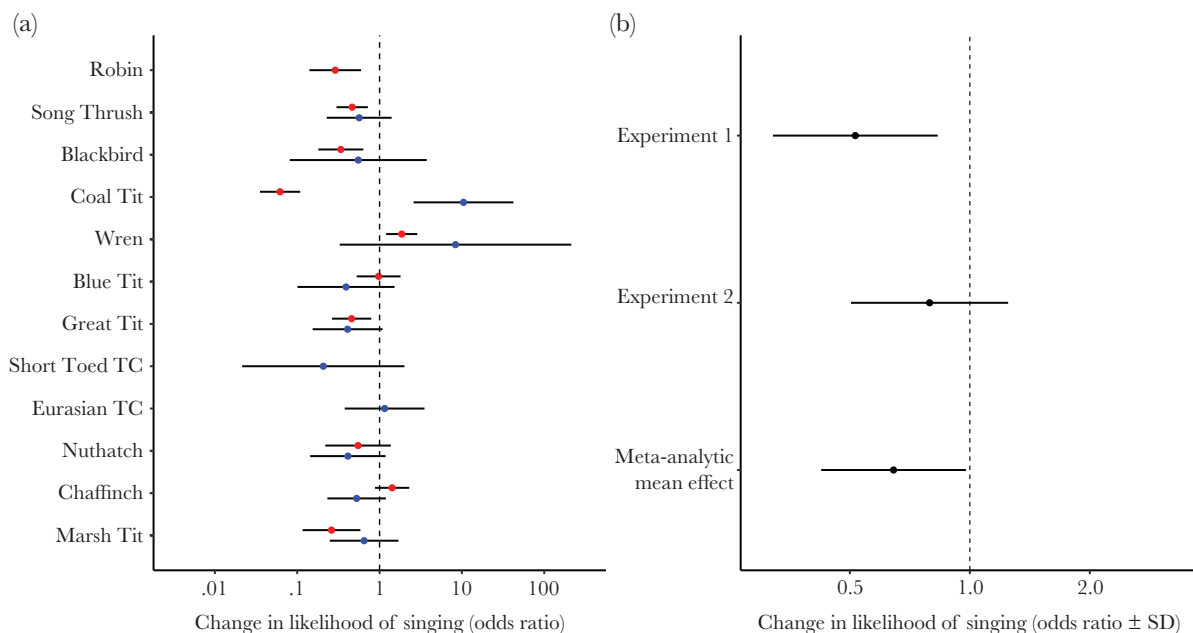


Figure 1

Effects of exposure to predator playback calls (relative to a control treatment with nonpredator calls) on the occurrence of dawn singing in 12 songbird species. (a) Estimates (mean \pm SE) for each species separately. Red and blue dots indicate results from experiment 1 and 2, respectively. Species are ordered by their natural onset of dawn singing relative to sunrise, with the earliest-singing species at the top. TC, treecreeper. (b) Estimates (mean \pm SE) from the across-species meta-analysis combining both experimental estimates and those for experiments 1 and 2 separately.

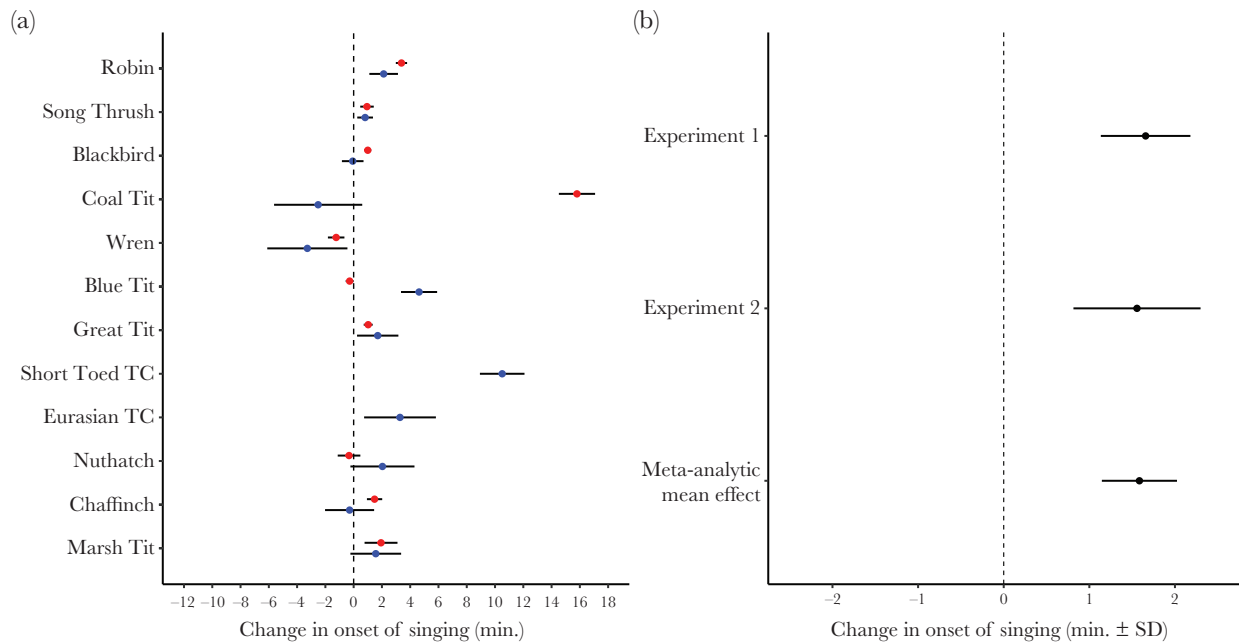


Figure 2

Effects of exposure to predator playback calls (relative to a control treatment with nonpredator calls) on the timing of dawn singing in 12 songbird species. (a) Estimates (mean \pm SE) for each species separately. Red and blue dots indicate results from experiment 1 and 2, respectively. Species are ordered by their natural onset of dawn singing relative to sunrise, with the earliest-singing species at the top. TC, treecreeper. (b) Estimates (mean \pm SE) from the across-species meta-analysis combining both experimental estimates and those for experiments 1 and 2 separately.

experiment 2 (Supplementary Table S7). Across-species analyses revealed a highly significant treatment effect on the timing of singing in both experiment 1 and experiment 2 (Figure 2b; Supplementary Table S8). Combining the across-species estimates from both experiments in a meta-analysis revealed a highly significant overall treatment effect on the onset of dawn singing ($z = 7.41$, $P < 0.001$), with birds exposed to predator calls singing 1.6 min later on average (Figure 2b).

Species that were less likely to sing on any given day also sang later if they did sing (Figure 3), indicating that both measures, inhibition and delay, reflected an impairment of sexual signaling induced by the increase in perceived predation risk. The correlation between the 2 measures was significant in both experiments (Spearman rank correlations; experiment 1: $\rho = -0.78$, $N = 10$, $P = 0.012$; experiment 2: $\rho = -0.71$, $N = 11$, $P = 0.015$).

DISCUSSION

In response to exposure to predator playback calls during the early breeding season, songbirds were overall less likely to sing at dawn, and when they did sing, they started later in the morning. Not singing and delaying singing were associated (Figure 3), indicating that they reflected the same underlying process: an impairment of singing induced by an increase in perceived predation risk.

Not singing at dawn can obviously be costly because mates are not attracted and competitors not deterred. Delaying singing still allows attracting mates or deterring competitors but can also come at a cost. For instance, a delay in singing of 2.7 min by blue tit males in nonilluminated compared with illuminated territories was associated with a 2-fold reduction in the likelihood of siring extrapair offspring (Kempnaers et al. 2010) and a delay in the start of dawn singing of 5 min marked the difference between males that did not

sire extrapair offspring and those that did (Figure 2 in Poesel et al. 2006). The delays in our study were relatively small (1.6 min on average and up to 16 min) but of the same magnitude and may thus have substantial biological consequences. On the other hand, not singing at all obviously has the benefit of reducing the risk of attracting a predator's attention and delaying singing even by a few minutes may have substantial benefits in this respect as well. During the period of dawn singing (typically between astronomical twilight and sunrise; Da Silva et al. 2014), the illumination of the environment changes fast in both intensity and spectral quality (Kishida 1989; Spitschan et al. 2016) such that the observed delays are probably sufficient to improve predator detection abilities (Lima 2009).

The dawn chorus has been described as an "interactive communication network" (Burt and Vehrencamp 2005), suggesting that male singing is influenced not only by receivers in the surrounding social network (e.g., potential mates) but by other signalers as well (Peake 2005; Snijders and Naguib 2017). Our results demonstrate that those other signalers can include vocalizing predators (see also Zuk and Kolluru 1998; Abbey-Lee et al. 2016). However, the timing of dawn singing is affected not only by predator vocalizations but potentially also by the singing of other conspecific males in the local environment (Hodgson et al. 2018, but see Kempnaers et al. 2010). The local social network of male signalers may thus affect both the occurrence and timing of dawn singing (Burt and Vehrencamp 2005; Snijders and Naguib 2017), as well as the response to predator calls (Cordes et al. 2014; Abbey-Lee et al. 2016, 2018). Correspondingly, differences in the composition of the local communication network can help explain why the effect of the treatment on the likelihood of singing was absent in the second experiment. In experiment 2, playbacks were broadcast over a smaller area in each plot, such that the "treated" birds were surrounded by nonexposed signalers, which may have influenced their behavior.

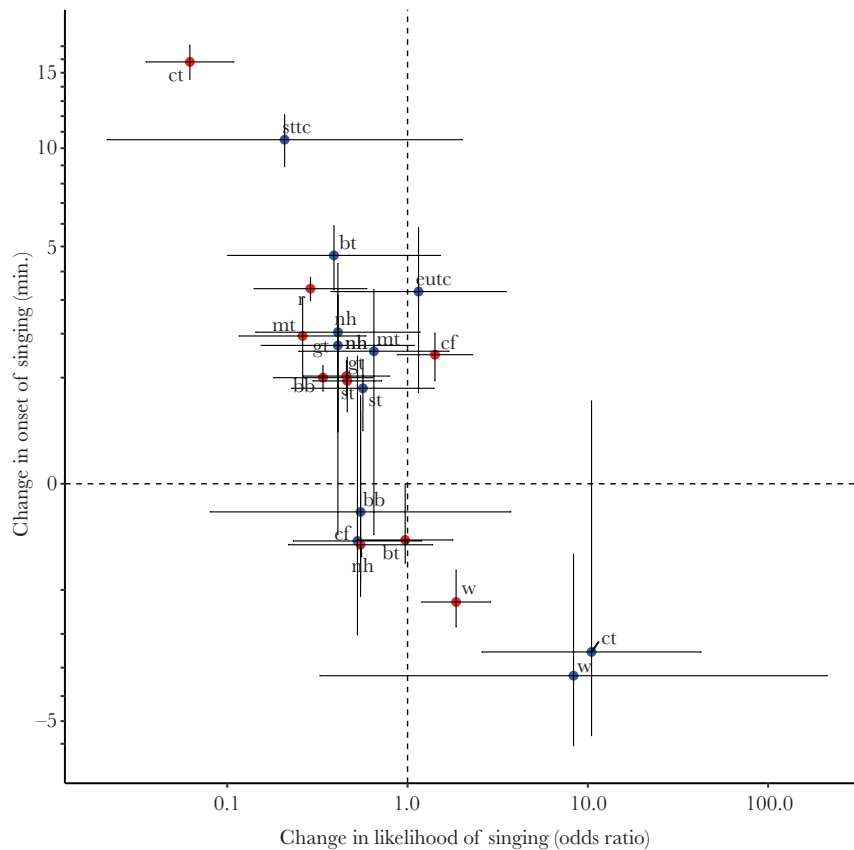


Figure 3

Relationship between the estimated effect of the predator playback treatment on the likelihood of singing for each species and the estimated effect on the onset of singing for each species in experiment 1 (red dots) and experiment 2 (blue dots). Shown are means \pm SE. Species abbreviations: bb, blackbird; bt, blue tit; cf, common chaffinch; ct, coal tit; eutc, Eurasian treecreeper; gt, great tit; mt, marsh tit; nh, Eurasian nuthatch; r, European robin; st, song thrush; sttc, short-toed treecreeper; w, European wren.

In contrast, birds in experiment 1 were surrounded by a community of birds all exposed to predator (or control) playbacks. This suggests that the effect of the local communication network may have had a stronger effect on the timing and occurrence of dawn singing than the effect of perceived predation risk.

The experiments caused a general delay in the onset of singing and reduced the likelihood of singing, but some species showed different responses in the 2 experiments. Most notably, coal tits showed a strong and highly significant reduction in the likelihood and a delay in the timing of singing in experiment 1 but no significant response in experiment 2. One potential explanation for this is that individuals of the same species differ in their responsiveness to changes in predation risk (Abbey-Lee et al. 2016, 2018), and that the number of responsive individuals that was present at the sampling sites differed between the experiments. For instance, individuals with prior experience with predators (e.g., having directly observed one or having been attacked by one) may be more responsive to predator calls than individuals without such experience. Alternatively, some males may have more to gain from dawn singing than others (e.g., older or more attractive males that have greater chances to obtain extrapair copulations) such that they trade-off dawn singing and predation risk differently (Cordes et al. 2014).

Recent work has highlighted that perceived predation risk can impair breeding behavior and reduce reproductive success (Cresswell 2008; Creel and Christianson 2008; Lima 2009; Zanette et al. 2011; Hua et al. 2014; LaManna and Martin 2016). Our results demonstrate that perceived predation risk additionally impacts the occurrence and timing of dawn singing, a sexual signal that plays a key role in attracting (extrapair) mates and deterring competitors (Staicer et al. 1996; Catchpole and Slater 2008). An increase in perceived predation risk may thus also affect sexual selection. Exploring how the effects of perceived predation risk on sexual signaling and communication networks in turn affect variation in male and female mating and reproductive success should prove productive.

SUPPLEMENTARY MATERIAL

Supplementary data are available at *Behavioral Ecology* online.

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Data accessibility: Analyses reported in this article can be reproduced using the data provided by Santema et al. (2019).

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