



SEXUALLY SELECTED SIGNALING IN BIRDS: A CASE FOR BAYESIAN CHANGE-POINT ANALYSIS OF BEHAVIORAL ROUTINES

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ABSTRACT.—Responses of organisms to environments or to conspecifics may abruptly change once the organism has changed its state. For example, the expression of sexually selected signals often depends on the pairing status of the sender. A likely change in signaling routines at the point of pair formation should thus be taken into account when investigating a sexually selected trait like birdsong. However, female breeding behavior is elusive in many species, and the date of pair formation may be unknown. We developed a change-point model in a Bayesian context to analyze the seasonally changing singing activity in male Nightingales (*Luscinia megarhynchos*) for which the pairing status was assumed to be unknown. We used our change-point singing activity model to estimate the pairing status of the males as well as the dates of pair formation (i.e., the unobserved switches of states). We obtained results on pairing success and date of pair formation that were consistent with our data from mist netting and with the results of earlier studies. We also found that the peak in nocturnal and dawn singing activity was after the period of female arrival and was later in the season in unpaired males than in paired males. On the basis of our analyses, we argue that change-point models are powerful analytical tools for many fields of research and can be used whenever animals abruptly switch behavioral routines. Received 12 March 2012, accepted 24 July 2012.

Key words: female arrival, *Luscinia megarhynchos*, model-based approach, Nightingale, piecewise regression, state-space models, switch-point analyses.

La signalisation sélectionnée sexuellement chez les oiseaux : un cas pour l'analyse bayésienne du point de rupture des routines comportementales

RÉSUMÉ.—Les réponses des organismes aux environnements ou aux congénères peuvent brusquement changer une fois que l'organisme a changé d'état. Par exemple, l'expression des signaux sélectionnés sexuellement dépend souvent du statut d'appariement de l'individu qui émet. Un changement apparent dans les routines de signalisation au moment de la formation des couples devraient donc être pris en considération lors de l'étude d'un trait sélectionné sexuellement comme le chant des oiseaux. Cependant, le comportement reproducteur des femelles est difficile à définir chez plusieurs espèces et la date de formation des couples peut être inconnue. Nous avons développé un modèle de point de rupture dans un contexte bayésien afin d'analyser l'activité de chant changeant selon les saisons chez les mâles de *Luscinia megarhynchos* pour lesquels le statut d'appariement était supposé être inconnu. Nous avons utilisé notre modèle de point de rupture pour l'activité de chant afin d'estimer le statut d'appariement des mâles ainsi que les dates de formation des couples (c'est-à-dire le changement non observé des statuts). Nous avons obtenu des résultats sur le succès d'appariement et la date de formation des couples qui étaient compatibles avec nos données de capture au filet japonais et avec les résultats d'études antérieures. Nous avons aussi trouvé que le pic dans l'activité de chants nocturnes et crépusculaires avait lieu après la période d'arrivée des femelles et se produisait plus tard dans la saison chez les mâles non appariés que chez ceux appariés. Sur la base de nos analyses, nous pensons que les modèles de point de rupture sont des outils analytiques puissants pour plusieurs champs de recherche et peuvent être utilisés à chaque fois que les animaux changent brusquement de routines comportementales.

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RESPONSES OF ORGANISMS to environments or to conspecifics may abruptly change once a threshold has been crossed or once the organism has changed its state. Abruptly changing responses may occur in space; for instance, along an environmental gradient, the population size of a species may abruptly decrease when a threshold of available habitat is reached (Swift and Hannon 2010). Likewise, abrupt responses may occur in time; for instance, an individual advertising to attract a mate may instantly change its behavior after pair formation (Krebs et al. 1981, Nemeth 1996, Staicer 1996, Amrhein et al. 2002). The exact time or threshold when such abrupt changes in responses take place are usually called “change-points” (Thomson et al. 2010). Accurate estimation of the change-points is important because subsequent estimation of ecological quantities depends on the position of the change-points, and not accounting for the change-points may lead to misleading results (Beckage et al. 2007).

Birdsong has evolved under both inter- and intrasexual selection, and male song mostly serves to attract females and to repel rival males (Catchpole and Slater 2008). Singing activity has often been shown to change depending on the stages of the female’s breeding cycle; such stages include the fertile period of the female before the first egg is laid, the egg-laying period, and the incubation period. Singing activity in birds is a case where not accounting for change-points has possibly led to contradictory results in the published literature. Møller (1991) reviewed studies on male singing activity that mostly did not account for change-points between the individual stages of the breeding cycle, and he concluded that >70% of the studied bird species showed a peak of singing activity during the time of the year when females are fertile. Gil et al. (1999), however, reviewed studies on singing activity that were mostly based on analyses that accounted for the change-points between the individual stages of the breeding cycle; the authors concluded that in most species, the males did not show a peak of singing activity during the fertile period of their mates. The contradictory conclusions in the reviews by Møller (1991) and Gil et al. (1999) may be due, in part, to the different treatments of the change-points in the studies they reviewed.

In songbirds, the singing activity of males often decreases immediately after pair formation. Thus, the switch in pairing status leads to a change-point in singing activity (Krebs et al. 1981, Hayes et al. 1986, Gibbs and Wenny 1993, Otter and Ratcliffe 1993, Amrhein et al. 2002, Hennin et al. 2009). However, investigating temporal patterns of singing with sudden changes of singing activity upon pair formation is challenging because female breeding behavior is elusive, and the exact dates of pair formation and of the stages of the breeding cycle may be unknown for many or most of the males.

Here, we suggest the use of change-point models in a Bayesian framework to overcome such difficulties. Change-point models were recently proposed for addressing ecological estimation problems when abrupt changes in states occur, even if these switches of states are not observed (Beckage et al. 2007). Change-point estimation problems are addressed via regression methods, wavelet-based methods and others, and are not restricted to Bayesian approaches (Lund and Reeves 2002, Wilson et al. 2010, Chen et al. 2011, Schütz and Holschneider 2011). However, a major advantage of Bayesian change-point techniques is that the models are very flexible and can easily be adapted to the specific situation in the studied organism (Chen et al. 2011, Schütz and Holschneider

2011). Thus, Bayesian change-point techniques seem perfectly suited to analyzing ecological time series and to adapting the statistical model to the specific situation in the studied species (Thomson et al. 2010).

Here, we provide a change-point model to analyze the nocturnal singing routines from dusk to dawn in individual male Nightingales (*Luscinia megarhynchos*) for which the exact dates of female arrival were unknown. The nocturnal singing of Nightingales conforms to one of two distinct types of singing routines (Amrhein et al. 2002, Thomas 2002), and the switches between the singing routines are related to switches in pairing status (Amrhein et al. 2002, 2004; Roth et al. 2009). The “bachelor singing routine” is characterized by high singing activity during most of the night; it is sung by males that remain unpaired throughout the breeding season (bachelors) and by paired males before arrival of the mate (Amrhein et al. 2002, Roth et al. 2009). Following pair formation, the males typically stop singing at night, which we call the “paired-male singing routine.”

We developed a change-point singing activity model that accounts for unknown male pairing success and unknown date of female arrival. By including male pairing success and female arrival as unknown parameters in the model, we formalized the assignment of male pairing success and the estimation of female arrival. Such formalizations make the assignment of male pairing success and female arrival more consistent and also allow estimating the precision of the assignments. This is in contrast to earlier studies, in which we usually assessed male pairing success from nocturnal singing activity of subjects by manually defining subjects as paired if they ceased regular nocturnal song after the beginning of the breeding season (e.g., Kunc et al. 2006, Schmidt et al. 2008, Sprau et al. 2012). We show that purely observational data on male nocturnal singing activity are sufficient to estimate accurate dates of female arrival and of male pairing success, without the necessity to empirically collect data on females. Given that similar switches in behavioral routines are likely to occur in many different fields of research, we argue that change-point models also open up new opportunities for studies on other topics in ecology and evolution.

METHODS

Study site and field protocol.—Data collection took place from 10 April to 20 May 2008 at the Petite Camargue Alsacienne in the Upper Rhine Valley in France. The study site (~1 km²) comprises a mosaic of forest patches, pastures, fields, reeds, ditches, and artificial ponds. To survey the singing activity of male Nightingales, we made standardized rounds of inspection throughout our study site and recorded for each territory whether or not a bird was singing (Amrhein et al. 2004, 2007). Singing activity of a male was defined as the probability that the male was heard singing during a round of inspection. The nocturnal rounds lasted 50–65 min and followed a fixed route 8.5 km in length; the direction of the rounds was fixed for a particular night, but the direction was changed from one night to the next. We made nine rounds of inspection per night (Roth et al. 2009). The first round started at sunset (dusk round), and the last round started 75 min before sunrise (dawn round). The seven remaining rounds (N1 to N7) were spaced out regularly between the dusk and the dawn round. Thus, the exact starting time of the rounds slightly changed from day to day

because of the seasonal changes of sunset and sunrise. The mean starting times (\pm SD in minutes) were 20:44 \pm 20 (dusk round), 21:47 \pm 14 (N1), 22:50 \pm 9 (N2), 23:54 \pm 4 (N3), 0:57 \pm 2 (N4), 2:00 \pm 6 (N5), 3:03 \pm 12 (N6), 4:06 \pm 17 (N7), and 5:09 \pm 22 (dawn round). Territories with singing males were excluded from the analyses if males deserted their territories during the study period or if all the song posts of a male were >100 m away from our route of inspection (perpendicular distance). We obtained suitable data on singing activity of 31 males. In our observations of ringed individuals in previous studies, we have never recorded a replacement of a territory owner by another male, except in the first few days of the breeding season, when territories are established (V. Amrhein et al. unpubl. data). Thus, we are confident that an individual singing in a territory was the same individual throughout the study period. At the study site, the first male started to sing in its territory during the night of 11–12 April. Thus, the data cover 39 nights, 9 rounds per night, and 31 occupied territories, yielding 10,881 observations of male singing activity, defined as whether or not a male was singing on a particular round of inspection.

To test the plausibility of the results obtained from the change-point singing activity model, the identity and pairing status of the studied males were ascertained by capturing and ringing the male and, if present, its mate (Amrhein et al. 2002, 2004, 2007). Pairing status of males was further confirmed by monitoring the territories of males for female alarm calls. Mist nets were usually opened before sunrise and stayed open for ~5 h. Mist nets were checked every 30 min; birds were ringed in their territory and were released within 30 min of capture. Because mist-netting sessions were distributed throughout the field season and often did not take place exactly at the time of female arrival, the exact time of female arrival and pair formation was unknown in most cases. Furthermore, we never attempted to capture birds on more than three mornings in a row in a particular territory. Thus, in some territories the male or the female could not be captured.

Change-point singing activity model.—Suppose that a population of $i = 1, \dots, N$ occupied territories are sampled during $t = 1, \dots, T$ days over the course of the breeding season. During each day t , the territories are surveyed at $r = 1, \dots, R$ rounds of inspection performed at different times of the day, yielding the observed singing state variable $X_{i,r,t}$. If a male in territory i was heard singing at day t during round of inspection r , then $X_{i,r,t} = 1$; otherwise, $X_{i,r,t} = 0$. Let the parameter $M_{i,r,t}$ be the probability that a male is singing at day t during round of inspection r in territory i . From the day after a male was heard in territory i for the first time ($a_i + 1$), we assumed that the singing state variable $X_{i,r,t}$ is Bernoulli distributed with the singing probability $M_{i,r,t}$ as its parameter. Thus, the singing state variable $X_{i,r,t}$ is given by the model

$$X_{i,r,t} \sim \text{Bernoulli}(M_{i,r,t}) \quad (1)$$

$$\text{for } i = 1, \dots, N, r = 1, \dots, R, \text{ and } t = (a_i + 1), \dots, T$$

A consistent pattern of the dusk-to-dawn singing of Nightingales is that individual males sing according to one of two distinct types of singing routines (Amrhein et al. 2002, Thomas 2002). We define singing routine $k = 1$ for the “bachelor singing routine” and $k = 2$ for the “paired-male singing routine.” We modeled the singing activity $M_{i,r,t}$ on the logit scale and assumed a random male effect α_i , and for each round r and each singing routine k a different intercept $\mu_{r,k}$ as well as different linear $\beta 1_{r,k}$ and quadratic $\beta 2_{r,k}$

temporal trends of the singing activity in the course of the season. We used a quadratic trend because there is often a peak in singing activity within a breeding season. The singing activity $M_{i,r,t}$ was thus formulated as follows:

$$\log\left(\frac{M_{i,r,t}}{1 - M_{i,r,t}}\right) = \alpha_i + \mu_{r,k} + \beta 1_{r,k} t + \beta 2_{r,k} t^2 \quad (2)$$

with $\alpha_i \sim N_i(0, \sigma_\alpha)$

Equations 1 and 2 constitute a formal description of the dusk-to-dawn singing in Nightingales over the breeding season that allows for $k = 1, \dots, K$ distinct singing routines (in the case of Nightingales, we assume $K = 2$). However, so far the singing routine k (or the individual stages of the breeding cycle that predict the singing routines) needs to be known for each of the males in their territories i and for all days t . Because this is not the case in our data and will often not be the case in similar studies on song of territorial male birds, we assumed random processes for the latent (i.e., not directly observable) pairing status and the latent day of female arrival. We assumed that the singing routine k is a deterministic function of the realizations of these two random processes. Denote the singing routine state variable $y_{i,t}$; if a male in territory i at day t sings the “bachelor singing routine” ($k = 1$), then $y_{i,t} = 1$; otherwise, if the male in territory i at day t sings the “paired-male singing routine” ($k = 2$), then $y_{i,t} = 2$. Denote the latent pairing state variable ps_i ; if a male in territory i remains unpaired throughout the breeding season (bachelor), then $ps_i = 0$. Otherwise, if a female pairs to a male and settles in its territory i at some time during the season, then $ps_i = 1$. We assumed the pairing state variable ps_i to be the outcome of a Bernoulli trial with the average pairing probability π as its parameter:

$$ps_i \sim \text{Bernoulli}(\pi) \quad (3)$$

In Nightingales, bachelors conform to the “bachelor singing routine” ($k = 1$) throughout the season (Amrhein et al. 2002). Thus, we assumed $y_{i,t} = 1$ for all males with $ps_i = 0$ and for all days t . The dusk-to-dawn singing routine of paired Nightingales, however, depends on the latent female arrival (i.e., the date when a female settles in a territory to pair with the male of that particular territory). Upon female arrival, the male immediately switches from the bachelor to the paired-male singing routine (Amrhein et al. 2002, 2004). Denote the latent female arrival time fa_i as the day t a female settles in territory i . We assumed the day of female arrival fa_i (i.e., the change-point) to be normally distributed with average female arrival ϕ and standard deviation σ_ϕ , but the arrival of a female fa_i in territory i was restricted to the date the male arrived in that territory (a_i) and a latest possible date e of female arrival (see below):

$$fa_i \sim \text{Norm}(\phi, \sigma_\phi) \quad (4)$$

with $a_i \leq fa_i \leq e$

A formal description of the singing routine state $y_{i,t}$ is then given as

$$y_{i,t} = \begin{cases} 1 & \text{for } ps_i = 0 \\ 1 & \text{for } ps_i = 1 \text{ and } t < fa_i \\ 2 & \text{for } ps_i = 1 \text{ and } t \geq fa_i \end{cases} \quad (5)$$

Thus, only paired males (i.e., $ps_i = 1$) from day t , when the female arrived in their territory, sing the “paired-male singing routine” (i.e.,

$y_{i,t} = 2$). The entire change-point singing activity model (Equations 1–5) is thus specified with 58 parameters: the pairing probability π , the mean female arrival ϕ , the standard deviation of female arrival σ_ϕ , an intercept $\mu_{r,k}$, linear slopes $\beta_{1,r,k}$ and quadratic slopes $\beta_{2,r,k}$ for each of the nine rounds of inspection and the two singing routines, and the standard deviation σ_α of the random male effect.

Bayesian analyses and test of the model.—We used a Bayesian analysis based on Markov-chain Monte Carlo methods (MCMC; Link et al. 2002). The MCMC simulations were conducted using WinBUGS, version 1.4 (Gilks et al. 1994), executed in R using the R add-on library R2WinBUGS (Sturtz et al. 2005). We ran three parallel chains to assess convergence using the Gelman-Rubin diagnostic (Brooks and Gelman 1998). Posteriors were based on the three parallel chains with 15,000 iterations each, discarding the first 10,000 values and thinning the remainder by using only every fifth value. For all estimates of the parameters, we give the mean and the 95% credible interval (CI; i.e., the Bayesian analogue to the 95% confidence interval). The specification of the model was as follows: the study duration was from the day when the first male was heard singing in its territory ($t = 1$: night from 11 to 12 April) to the night from 19 to 20 May ($t = 39$). During these $T = 39$ days, each of the $N = 31$ occupied territories were visited daily during $R = 9$ rounds of inspection ($r = 1$: dusk round; $r = 2..8$: nocturnal rounds N1 to N7; $r = 9$: dawn round). We restricted the latest possible day of female arrival to 10 May ($e = 30$) because we have never observed a female arriving after 10 May in earlier studies (V. Amrhein et al. pers. obs.; Amrhein et al. 2007). We assumed diffuse prior distributions for the parameters, which were uniform $U(0,1)$ for the pairing probability π , $U(0,25)$ for the mean female arrival ϕ , $U(0,10)$ for the standard deviation of female arrival σ_ϕ , $U(0,1)$ for all of the intercepts on the probit scale $e^{\mu_{r,k}} / (1 + e^{\mu_{r,k}})$, normal $N(0,2)$ for linear slopes $\beta_{1,r,k}$ and for quadratic slopes $\beta_{2,r,k}$ and uniform $U(0,2)$ for the standard deviation of the random male effect σ_α . In the Appendix, we provide the model description in the BUGS language.

Unfortunately, we do not have complete empirical data on the dates of arrival and pairing for many of our subjects. To validate our model, we therefore compared the results of the change-point singing activity model with the results from our earlier studies on the same Nightingale population (Amrhein et al. 2002, 2004, 2007; Roth et al. 2009; Naguib et al. 2011). Furthermore, we compared the results obtained from the change-point singing activity model with the results from a traditional generalized linear mixed model (GLMM) on singing activity that accounts for neither the stages of the breeding cycle nor the different pairing status of the males. For the GLMM, we used the lme4 package (Pinheiro et al. 2011) in R, version 2.12.1 (R Development Core Team 2011). For each of the rounds, we fitted a separate GLMM with a logistic link function. We regressed a linear and quadratic temporal term on the binary singing activity (singing or not singing); to account for the repeated measures, we also included individual male as a random factor. For the GLMMs, as for the change-point singing activity model, we used only data starting from the day after the male was heard singing for the first time.

RESULTS

We described a change-point model for singing activity in Nightingales that does not incorporate prior information on pairing status and date of pair formation of the males but allows for two distinct types of dusk-to-dawn singing routines. Using this model, we estimated the percentage of paired males in our population to be 76% (95% CI: 60–89%; Fig. 1, left). This estimate corresponded well to our mist-netting data on the same subjects collected during the same year, from which we concluded that 25 of the 31 studied males (81%) were paired (Roth et al. 2009). Note that the mist-netting data were not used in the current change-point singing activity model and that in the present study, the pairing status was estimated using only the observational data on

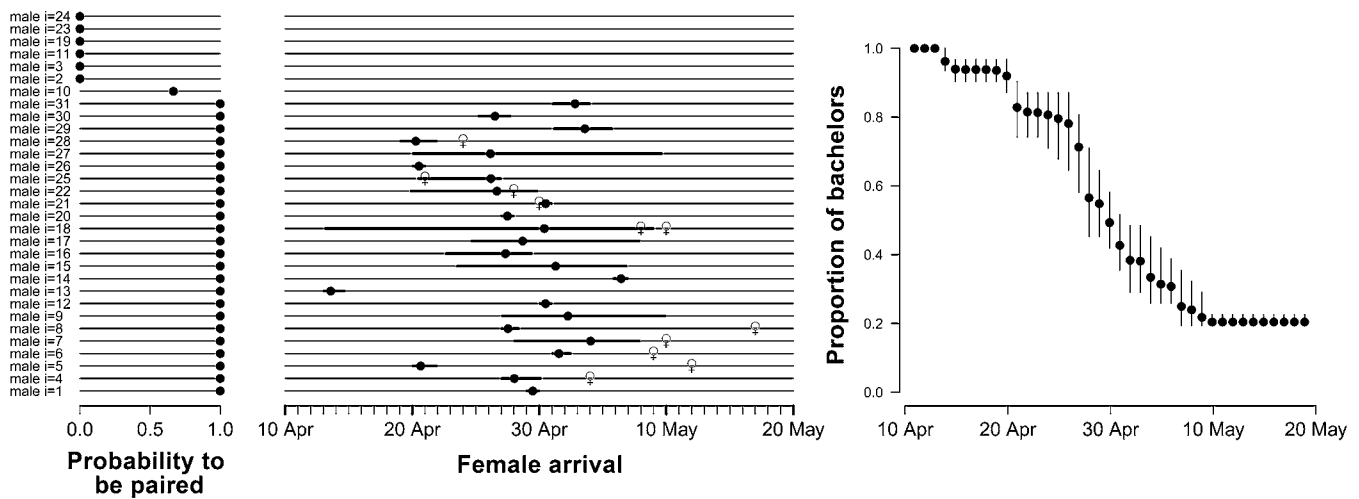


FIG. 1. Estimates of pairing success and female arrival in Nightingales obtained from the change-point singing activity model. (Left) The probability of being paired is given for each of the 31 males. (Middle) For each male that is estimated to be paired, the estimates of the dates of female arrival (averages and 95% credible intervals [CIs] of the posterior distributions) are given. Also given are the dates when the females were captured (♀). (Right) Proportion of males singing the bachelor singing routine, as estimated for each day over the course of the season. Given are averages and 95% CIs of the posterior distributions.

male singing activity. The estimated average female arrival was in the night from 27 to 28 April (95% CI: 25–26 April to 30 April–1 May), which corresponds to an earlier study at the same study site, in which the mean female arrival date was 26 April (Amrhein et al. 2007). Furthermore, all capture dates of females were consistent with the model predictions for female arrival dates: the capture date of a female was always within or later than the 95% CI of the arrival date of the female in a given territory (i.e., no female was captured before its arrival date as predicted by the model; Fig. 1, middle). As a result of the different dates of female arrival, the proportion of males singing the bachelor singing routine decreased from 100% at the start of the breeding season to ~20% at the end of the study period (Fig. 1, right), which corresponded to the 6 (of 31) males that remained unpaired throughout the breeding season (Roth et al. 2009).

Overall, nocturnal and dawn singing activity was higher in bachelors than in paired males (Fig. 2). The largest differences in nocturnal and dawn singing activity were found at the end of the season, which was due to the distinct seasonal increase in nocturnal singing activity of bachelors (Table 1). For both bachelors and paired males, the peak in singing activity was after the period when most females arrived at the study site, which in our study was between 20 April and 4 May (Fig. 1, middle; cf. Amrhein et al. 2007, in which females settled between 21 April and 3 May). Irrespective of the time of day, singing activity of paired males was highest in the first week of May, when females are usually laying eggs and starting incubation (Amrhein et al. 2004), whereas the peak in singing activity of bachelors was in the second or third week of May. This corresponds to our earlier studies that reported highest diurnal singing activity of paired males during the laying period, whereas the diurnal singing activity of bachelors continuously increased until the end of the incubation period (Amrhein et al. 2002, 2004, 2007).

The traditional GLMMs accounted for neither the pairing success of the males nor the change-points of female arrival and suggested different patterns of seasonal singing activity: the singing activity of the third nocturnal round (N3) linearly decreased over the season (quadratic term: $z = 1.6$, $P = 0.12$; linear term: $z = 3.5$, $P < 0.001$), whereas no temporal trend was detected for the first two nocturnal rounds (quadratic term: both $z < 1.0$, both $P > 0.30$; linear term: both $z < 0.6$, both $P > 0.52$). The seasonal singing activity at all other rounds peaked in the middle of the study period (quadratic term: all $z > 3.3$, all $P < 0.001$). This peak in singing activity was estimated to be around the period of female arrival at the end of April (see Fig. 3 for dusk round, N4, and dawn round). Therefore, the results of the GLMMs suggested an earlier peak in singing activity, whereas the change-point singing activity model revealed a peak in singing activity of bachelors and paired males after most females have arrived at the study site, which is consistent with our earlier empirical data on dawn and daytime singing (Amrhein et al. 2002, 2004, 2007).

DISCUSSION

We described a change-point model of Nightingale signaling routines that was based on observations of nocturnally singing males. The model did not use empirical data on the presence and behavior of females, but incorporated general knowledge about

nocturnal singing routines from previous studies (Amrhein et al. 2002, 2004, 2007; Roth et al. 2009). Compared with our earlier studies on Nightingales from the same study population, our model provided realistic estimates of the pairing success of males and of the date when one of the most important change-points in the singing activity occurred, which is the event of female arrival (i.e., female settlement in the territory of a male). Using the change-point model, we were also able to detect patterns of seasonal trends in singing activity that were obscured when using a traditional GLMM that accounted for neither the two different singing routines nor the change-points.

In a bird population, individual pairs usually do not breed in perfect synchrony (Gil et al. 1999), and the dates of the stages of the breeding cycle may vary from male to male. Because the daily signaling routines of birds usually depend on the stages of the breeding cycle (Nemeth 1996; Staicer 1996; Amrhein et al. 2002, 2004), it is likely that different males follow different daily signaling routines at a given time. However, if different males follow different daily signaling routines, the proportion of singing individuals (i.e., the population-wide singing activity) is influenced by the proportion of individuals using the particular signaling routines. Therefore, the population-wide signaling activity does not necessarily reflect patterns of individual signaling behavior. Accordingly, studies that investigate seasonal singing activity at the population level without accounting for individual stages of the breeding cycle may come to different conclusions than studies that consider singing activity at an individual level, including individual stages of the breeding cycle. This is exemplified by the contradicting conclusions by Møller (1991), who reviewed studies on singing activity that mostly did not account for change-points between the individual stages of the breeding cycle, and by Gil et al. (1999), who reviewed studies that did account for such change-points.

In the case of Nightingales, at the beginning of the season the males sang according to the “bachelor singing routine.” Because the individual singing activity of bachelors increased in the course of the season, the population-wide singing activity in our study population increased at the beginning of the breeding season before the females arrived. Thus, as estimated from the traditional GLMM, the highest population-wide singing activity was at the period of female arrival, and from then the population-wide singing activity decreased. This decrease in population-wide singing activity after female arrival is mostly due to the decreasing number of males singing the bachelor singing routine and is in contrast to the increasing singing activity of bachelors revealed from the change-point singing activity model. Therefore, when analyzing temporal patterns of singing activity, it is important to take male pairing status and different singing routines of paired and unpaired males into account.

After female arrival, paired males often resume nocturnal singing during a short period mainly during the first week of May, which is linked to the female’s egg-laying period (Amrhein et al. 2002, Kunc et al. 2007). In an earlier study, 13 of 15 paired males resumed nocturnal singing for ~3 nights once the females started egg laying (Amrhein et al. 2002). The functions of this second period of nocturnal song in paired Nightingales are unclear but are likely related to both intrasexual and intersexual behavior (Amrhein et al. 2002, Naguib et al. 2011). A potential intersexual function could be to encourage the mate to increase investment in the brood (Amrhein et al. 2002),

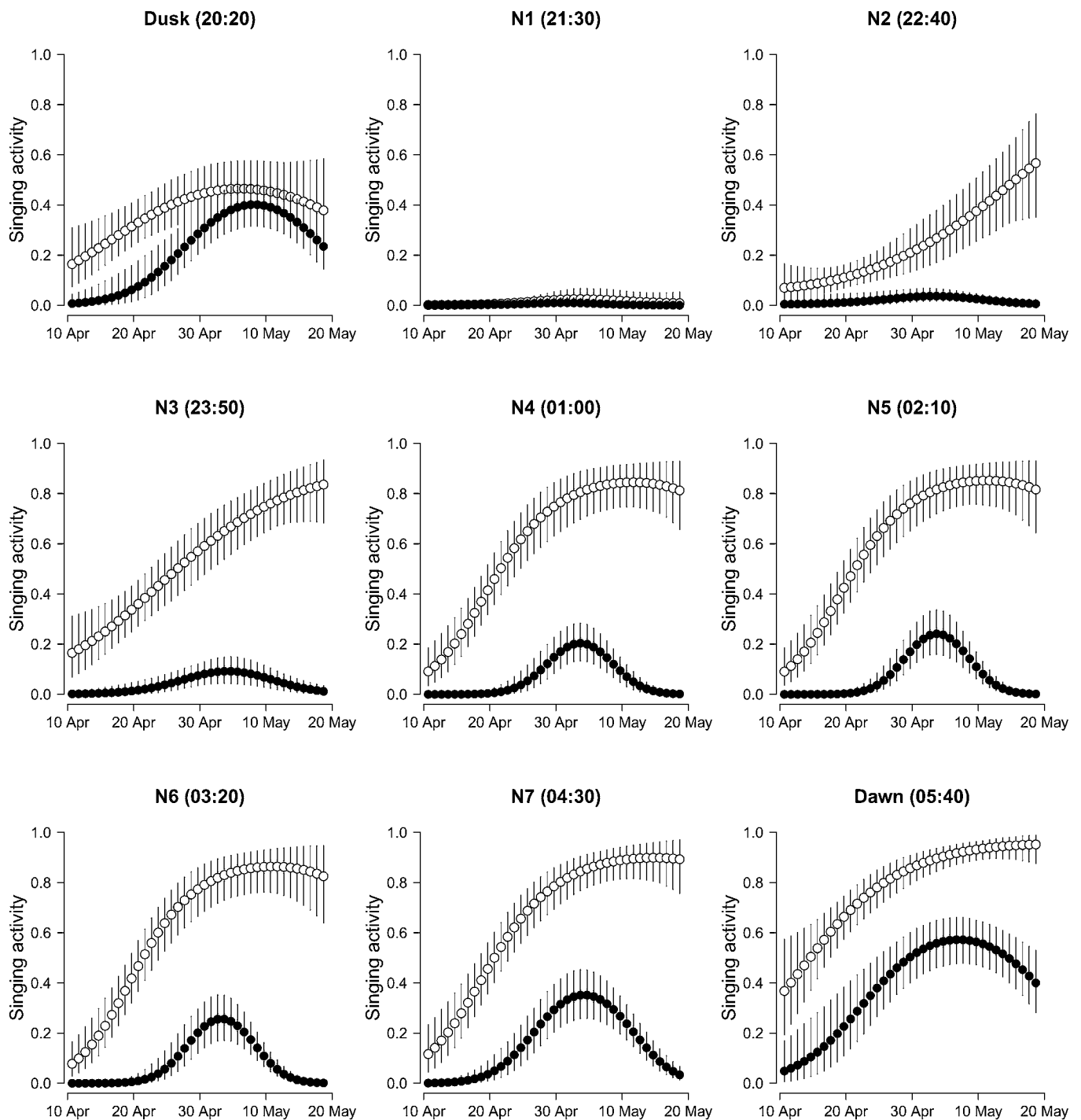


FIG. 2. Seasonal development of nocturnal singing activity (i.e., probability that a male was encountered singing) in Nightingales, for 9 daily rounds of inspection (dusk round, nocturnal rounds N1–N7, and dawn round; see text). Given are averages and 95% credible intervals of the posterior distributions of the singing activities for bachelors (○) and paired males (●); singing activity and pairing status of males were estimated from our change-point model. The average starting times of the rounds are given in the headers of the respective panels.

TABLE 1. Credible intervals (CIs) of the linear (L) and quadratic (Q) temporal trends of nocturnal singing activity of male Nightingales in the course of the season, for the “bachelor singing routine” and the “paired-male singing routine.” A significant linear (+) or curvilinear (∩) trend of singing activity is indicated by CIs that do not include zero.

Round	Bachelors				Paired males			
	L-effect	L-trend	Q-effect	Q-trend	L-effect	L-trend	Q-effect	Q-trend
Dusk	0.13 to 0.61	+	-0.47 to 0.01		0.59 to 1.85	+	-0.11 to -0.03	∩
N1	-0.39 to 2.17		-2.50 to 0.10		-1.46 to 3.12		-4.13 to 0.09	
N2	0.54 to 1.13	+	-0.27 to 0.29		-0.22 to 3.23		-2.92 to -0.38	
N3	0.73 to 1.23	+	-0.34 to 0.15		0.03 to 2.34	+	-2.47 to -0.65	∩
N4	0.80 to 1.31	+	-0.70 to -0.21	∩	0.86 to 3.35	+	-4.05 to -1.82	∩
N5	0.80 to 1.30	+	-0.72 to -0.23	∩	0.69 to 3.12	+	-3.67 to -1.69	∩
N6	0.83 to 1.34	+	-0.77 to -0.28	∩	0.24 to 2.69	+	-3.33 to -1.41	∩
N7	0.94 to 1.46	+	-0.69 to -0.18	∩	0.32 to 1.63	+	-1.68 to -0.77	∩
Dawn	0.79 to 1.40	+	-0.38 to 0.18		0.28 to 1.18	+	-0.83 to -0.23	∩

whereas a potential intrasexual function is that increased singing during egg laying serves to repel neighboring males, to minimize the risk of cuckoldry (Møller 1991). The estimates provided by the change-point singing activity model indicate that the nocturnal singing activity of paired males during the approximate time of egg laying was much lower than that of bachelors during the same period. Although the main function of nocturnal song in bachelors is most likely to attract females (Amrhein et al. 2002, Roth et al. 2009), the lower nocturnal singing activity of paired males compared with bachelors suggests that the nocturnal singing of paired males during egg laying is probably unlikely to serve in attracting females for extra-pair copulation (Amrhein et al. 2002).

We analyzed our data in a Bayesian framework, which is very flexible and can easily be adapted to the specific situation of the studied organism (Chen et al. 2011, Schütz and Holschneider 2011). In the case of Nightingales, we were thus able to include knowledge from previous studies in the model. For example, in our change-point singing activity model, we accounted for the fact that bachelors and paired males have distinct daily singing routines and switch between these routines at the event of female

arrival (Amrhein et al. 2002, 2004). Thus, Bayesian change-point techniques provide a formal way to account for previous knowledge of a study system when analyzing new data from the same study system. In its current form, our change-point singing activity model on Nightingales estimates a single change-point in singing activity, which is the date of female arrival. However, it would be straightforward to increase the complexity of that model. For example, the beginning and end of nocturnal song in paired males during egg laying are additional change-points that could be included in the singing activity model. It might even be possible to include an unknown number of change-points in the model and let the model estimate how many change-points would best fit the data (Thomson et al. 2010). Further, one could also include covariates of the change-points in the model or adapt the model to different sampling situations. For example, if data on territory quality are available, our model could be used to investigate whether the date of female settlement is correlated with characteristics of a male’s territory such as food availability or scrub structure (Wilson et al. 2005). In the present study, we showed that even a very simple change-point model can

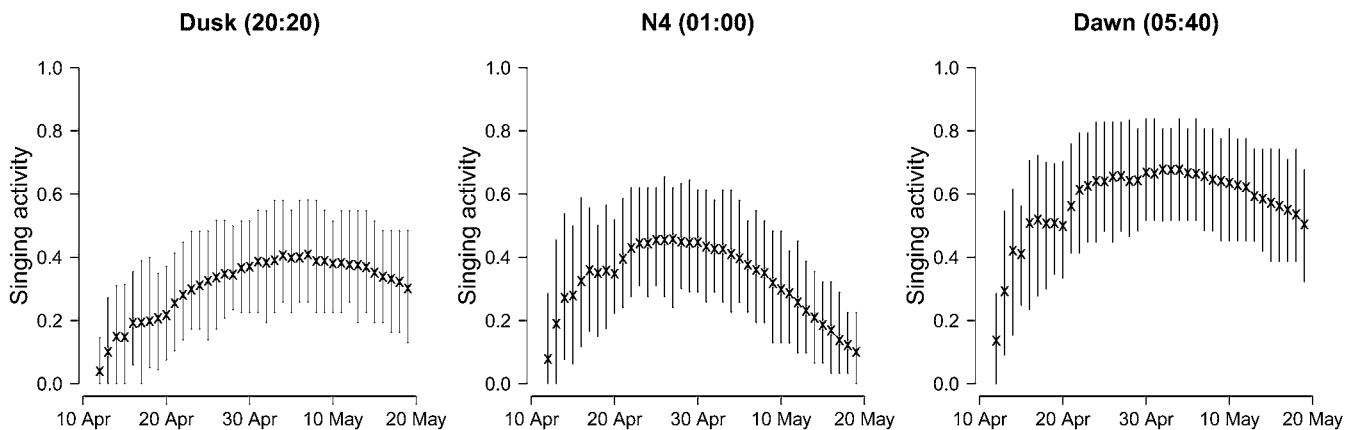


FIG. 3. Seasonal development of nocturnal singing activity in Nightingales, during the dusk round of inspection, during the round in the middle of the night (N4), and during the dawn round. Given are averages and 95% credible intervals of the posterior distributions of traditional generalized linear mixed models, which used the same data as in Figure 2 but could not account for different singing routines in bachelors and paired males, nor for change-points at the dates of female arrival. The average starting times of the rounds are given in the headers of the respective panels.

considerably improve inferences on signaling activity compared with the results from a traditionally used GLMM, and additionally can estimate important change-points such as the date of female arrival.

In many fields of research, data do not have a linear functional relationship with time or space but show abrupt changes in this relationship. Such is the case with the nocturnal singing activity of Nightingales, which abruptly decreases once a male pairs with a female. In such cases, change-point models reliably identify the events of changes in the temporal dynamic of populations (Thomson et al. 2010). Abrupt changes are expected to occur in most behavioral contexts, and examples are likely to include predator-prey interactions in which a predator may switch between different prey species depending on the abundance of the prey (Garrott et al. 2007), perhaps leading to changes in the vigilance of preferred and nonpreferred prey; contest behavior in which rivals switch between strategies to assess the fighting ability of the opponent (Hsu et al. 2008), which may lead to sudden changes in the intensity of a contest; or territory defense behavior in which an activation of the immune system following infection with a pathogen affects song production of the territorial male (Munoz et al. 2010). We argue that change-point models provide a flexible and reliable tool for analyzing data with abrupt changes in functional relationships that are caused by often unobserved switches of state in the studied subjects.

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APPENDIX. The change-point singing activity model in the BUGS language.

```

model {

### Define Priors
### *****
pi ~ dunif(0,1)          ### Pairing success
phi ~ dunif(1,25)       ### Average female arrival
sigma.phi ~ dunif(0,10) ### SD of female arrival
tau.phi <- pow(sigma.phi, -2)
for(r in 1:R) {
  for(k in 1:K) {
    mu[r,k] ~ dunif(0,1)  ### Intercept of singing probability of round
                        ### r and singing routine k
    lmu[r,k] <- log(mu[r,k]/(1-mu[r,k]))
    beta1[r,k] ~ dnorm(0,0.25)I(-5,5)  ### Linear effect of time and
                                        ### singing routine k
    beta2[r,k] ~ dnorm(0,0.25)I(-5,5)  ### Quadratic effect of time and
                                        ### singing routine k
  }
}
sigma.alpha ~ dunif(0,2)  ### SD of random male effect
tau.alpha <- pow(sigma.alpha, -2)
for(i in 1:N) {
  alpha[i] ~ dnorm(0,tau.alpha)  ### Random male effect
}

### Model for singing activity MU[i,t,r]
### *****
for(i in 1:N) {
  for(t in (a[i]+1):T) {
    for(r in 1:R) {
      logit(MU[i,t,r]) <- alpha[i] + lmu[r,y[i,t]] + beta1[r,y[i,t]]*((t-
20)/10) + beta2[r,y[i,t]]*((t-20)/10)*((t-20)/10)
      X[i,t,r] ~ dbern(MU[i,t,r])
    }
  }
}

### Model for the singing routine state (y[i,t])
### *****
for(i in 1:N) {
  ps[i] ~ dbern(pi)
  fa[i] ~ dnorm(phi, tau.phi)I(a[i],30)
  for(t in 1:T) {
    ty[i,t] <- ps[i] * step(t-fa[i])
    y[i,t] <- ty[i,t] + 1
  }
}
}

```