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Competitor phenology as a social cue in breeding site selection

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Summary

1. Predicting habitat quality is a major challenge for animals selecting a breeding patch, because it affects reproductive success. Breeding site selection may be based on previous experience, or on social information from the density and success of competitors with an earlier phenology.
2. Variation in animal breeding phenology is often correlated with variation in habitat quality. Generally, animals breed earlier in high-quality habitats that allow them to reach a nutritional threshold required for breeding earlier or avoid nest predation. In addition, habitat quality may affect phenological overlap between species and thereby interspecific competition. Therefore, we hypothesized that competitor breeding phenology can be used as social cue by settling migrants to locate high-quality breeding sites.
3. To test this hypothesis, we experimentally advanced and delayed hatching phenology of two resident tit species on the level of study plots and studied male and female settlement patterns of migratory pied flycatchers *Ficedula hypoleuca*. The manipulations were assigned at random in two consecutive years, and treatments were swapped between years in sites that were used in both years.
4. In both years, males settled in equal numbers across treatments, but later arriving females avoided pairing with males in delayed phenology plots. Moreover, male pairing probability declined strongly with arrival date on the breeding grounds.
5. Our results demonstrate that competitor phenology may be used to assess habitat quality by settling migrants, but we cannot pinpoint the exact mechanism (e.g. resource quality, predation pressure or competition) that has given rise to this pattern.
6. In addition, we show that opposing selection pressures for arrival timing may give rise to different social information availabilities between sexes. We discuss our findings in the context of climate warming, social information use and the evolution of protandry in migratory animals.

Key-words: climate, competition, habitat selection, heterospecific attraction, mate choice, protandry, public information, social learning, species interactions, timing

Introduction

Habitat selection is an integral part of successful reproduction in animals, yet predicting habitat quality is difficult, as components affecting it may fluctuate over both spatial and temporal scales (Orians & Wittenberger 1991). By default, animals have to base their settlement decisions on incomplete information, because sampling the environment is time-consuming or because food required for successful breeding will only become available later in the

season. Individuals may achieve this by using habitat information from previous breeding attempts or alternatively they may use integrative cues by eavesdropping on social information provided by other individuals with a similar niche and copying their choice (Parejo, Danchin & Avilés 2005). Such inadvertent social information (Danchin *et al.* 2004) may create a shortcut towards novel resources (Cortés-Avizanda *et al.* 2014; Teague O'Mara, Dechmann & Page 2014) or towards high-quality patches required for reproduction.

Social information use in breeding site selection has been confirmed in a wide variety of taxa. Passerine birds

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adjusted their choice of breeding patch the next year based on presence (Doligez, Pärt & Danchin 2004; Kivelä *et al.* 2014) and reproductive success (Doligez, Danchin & Clobert 2002; Citta & Lindberg 2007; Parejo *et al.* 2007) of conspecifics, naive female fruit flies *Drosophila melanogaster* copied oviposition sites of demonstrator flies regardless of site quality (Battesti *et al.* 2012), juvenile *Anolis aeneus* lizards preferentially settled near territorial residents independent of habitat quality (Stamps 1988), and females of the lek-breeding antelopes *Kobus leche* and *Kobus kob* preferred territories with olfactory cues from successfully mated females (Deutsch & Nefdt 1992). Interestingly, social cues use may apparently override a theoretically expected ideal free distribution based purely on resource presence in the breeding habitat, but this is only expected if animals lack personal information about these resources (Coolen *et al.* 2005). In short, animals prospect among a range of environmental and social components to optimize breeding site selection, because patch quality limits current and possibly future reproductive opportunities.

Social information use is not limited to conspecifics, as heterospecifics with similar niches are potentially a more reliable information source (Seppänen *et al.* 2007). For migratory animals with limited time to sample the environment themselves (Mönkkönen *et al.* 1999), resident heterospecifics provide information that is otherwise costly to obtain. For example, due to their earlier phenology, heterospecific residents might have completed broods, the size of which is used as an information source for settlement decisions by migrants (Forsman & Seppänen 2011; Loukola *et al.* 2013). However, within habitats there is also variation in breeding phenology, which is partly driven by the quality of the breeding patch. Selection pressures that may advance or delay reproductive phenology include food abundance and predation pressure. Food abundance affects reproductive timing by allowing animals to reach a nutritional threshold faster (Drent & Daan 1980). For example, resident blue tits *Cyanistes caeruleus* bred earlier in food-rich

habitat (Svensson & Nilsson 1995; Lambrechts *et al.* 2004), and similar patterns were found in great tits *Parus major* (Riddington & Gosler 1995; but see Van Balen 1973). Furthermore, nest predation might delay reproduction by inducing replacement clutches. For example, researchers were able to delay reproductive phenology of a great tit population by more than 2 weeks by inducing replacement clutches after clutch completion in great tits (Verhulst & Tinbergen 1991). Consequently, later reproducing great tits may signal heightened competition, as flycatcher mortality in tit nest boxes was higher in years with more phenological overlap between tits and flycatchers (Ahola *et al.* 2007), and most flycatcher mortality occurred during the egg-laying phase of tits (Merilä & Wiggins 1995), demonstrating that competitor phenology may play a role in shaping competitive interactions. In summary, habitat quality may express itself as a higher amount of resources required for breeding or safety from predation, all of which may impact upon reproductive phenology and as a consequence may affect interspecific competition. Therefore, early breeding phenology of competitors might be a potentially useful information source for arriving migratory birds cueing in on high-quality nesting sites (Fig. 1). Interestingly, competitor timing has so far not been studied as a social cue in breeding site selection.

Social cues may change over time, and their accessibility may also be time bound. Later, arriving individuals are more likely to use social information in selecting a breeding site (Seppänen & Forsman 2007; Jaakkonen *et al.* 2015), because they may have more social information available or because they have less local experience. Experienced individuals often arrive earlier at the breeding grounds, but in many species, males also arrive earlier than females. Two commonly contrasted hypotheses for the evolution of such protandrous arrival timing include the Rank Advantage Hypothesis and the Mate Opportunity Hypothesis (Morbey & Ydenberg 2001). The Rank Advantage Hypothesis postulates that competition for high-quality territories selects for early male arrival in

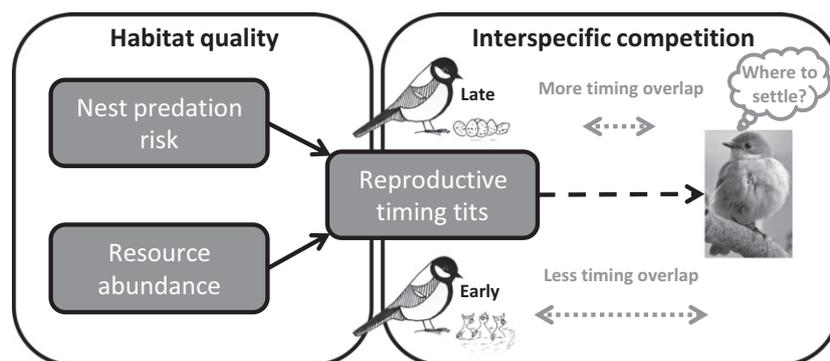


Fig. 1. Do flycatchers (right) use heterospecific (tit) timing cues in selecting a breeding site? Processes that affect reproductive timing in tits (middle drawings) include nest predation (inducing replacement clutches), and resource abundance (advancing female nutritional thresholds). Flycatchers may perceive late great tits as indicators of poor habitat quality, and may be faced with more interspecific competition due to phenological overlap as a consequence. Flycatchers were expected to prefer settling near early breeding tits.

species where males defend territories (Kokko 1999). The Mate Opportunity Hypothesis is not mutually exclusive, and postulates that males arrive earlier to have higher mating opportunities (Morbey & Ydenberg 2001). Theoretical work suggests that the Rank Advantage Hypothesis alone cannot explain the evolution of protandry, and that an integration with the Mate Opportunity Hypothesis, for example in the form of male-biased operational sex ratios (OSR), provides a stronger framework (Kokko *et al.* 2006). However, empirical research to test this framework is limited. One study found no evidence that the degree of protandry was higher when OSR was more male biased, but this study used a comparative approach at a migration capture site (Saino *et al.* 2010). It is unclear whether the sex ratio at a migration capture site is translatable to the OSR at the breeding grounds, so more studies from within breeding populations are needed to test whether later arriving males have lower mating opportunities in systems with male-biased adult sex ratios (Morbey, Coppack & Pulido 2012). Moreover, protandry may have differential effects between the sexes on the potential to incorporate social information in settlement decisions. However, these differences have so far not been considered in an intersexual context. In species with protandrous arrival timing, we therefore hypothesize that females are more able to incorporate social information in breeding site selection than males.

In this study, we aimed to answer three questions. First, does the breeding phenology of resident competitors affect settlement decisions of a migratory bird? Earlier phenology of residents may signal resource-rich areas, safety and lower competition, and were therefore expected to be preferred. Second, does mating probability of males decline with arrival date in a population with a male-biased sex ratio? Females were in principle expected to prefer earlier males, as these may occupy the higher quality breeding sites. Last, do intersexual differences in arrival date limit the potential to incorporate social information in breeding site selection? It was expected that the later arriving sex had more opportunity to incorporate social information in selecting a breeding site.

Materials and methods

STUDY SPECIES

Great tits and blue tits are resident insectivorous passerines widely occurring in Europe, and pied flycatchers migrate each year from West Africa to European temperate forests (Ouwehand *et al.* 2016), crossing the Sahara desert in one non-stop flight (Ouwehand & Both 2016). Female pied flycatchers arrive on the breeding grounds 1 week after males (Both, Bijlsma & Ouwehand 2016). All species are secondary cavity nesters that readily breed in nest boxes. On flycatcher arrival, there may be intense competition for nest boxes with resident tits, which regularly leads to fatalities among flycatchers (Slagsvold 1975; Merilä & Wiggins 1995; Ahola *et al.* 2007; J.M. Samplonius, pers. obs.). Moreover, experimental removal of tits demonstrated that flycatcher

reproductive success is subject to interspecific density dependence (Gustafsson 1987). In contrast to these negative effects, flycatchers have been shown to prefer settling near tits (Forsman, Seppänen & Mönkkönen 2002) and copied their perceived choice of nest box type (Seppänen & Forsman 2007). Interestingly, this copying behaviour by flycatchers switched to rejection when tits had low perceived brood sizes (Forsman & Seppänen 2011; Seppänen *et al.* 2011). Flycatchers appear to balance the costs of interspecific competition with the benefits of receiving social information from tits.

STUDY POPULATIONS

This study was performed in four nest box plots in National Park Dwingelderveld (52° 49' 05" N, 6° 25' 41" E) in 2014 and 2015 and in Boswachterij Ruinen (52° 43' 37" N, 6° 24' 00" E) in 2015. The forest composition is moderately heterogeneous, and is mostly dominated by pedunculate oak *Quercus robur*, scots pine *Pinus sylvestris* and silver birch *Betula pendula*. In our larger metapopulation of 1050 nest boxes, the number of breeding pairs average 269 pied flycatchers, 197 great tits, 55 blue tits, and 12 nuthatches *Sitta europaea* between 2007 and 2015 (Table S1, Supporting Information). Blue and great tits did not differ in their breeding phenology, but their hatch dates preceded flycatcher breeding phenology by c. 15 days on average in our population (Table S1).

HETEROSPECIFIC HATCH DATE MANIPULATIONS

Sixteen subplots of between 1.2 and 4.5 ha were selected in our nest box population (nest box size W × D × H: 9 × 12 × 23 cm), containing 0.9 to 5.9 tits ha⁻¹ (median 2.0 tits ha⁻¹). Nest box availability varied from 2.2 to 8.1 boxes ha⁻¹ (median 4.7 boxes ha⁻¹). In 2014, 12 subplots were assigned, but in 2015, six of these were dropped due to low tit densities, and four were added. All nest boxes were checked at least twice weekly in the earlier stages of the breeding season, and blue and great tit first egg dates were established. To examine whether pied flycatchers use heterospecific breeding phenology as a social cue for habitat quality, we experimentally established a gradient of hatching phenologies in resident blue and great tits from early (-5.7 days) to late (+8.1 days) at the subplot level. Treatments were randomly assigned, and in subplots that were used in both years, treatments were switched between years. Subplot level phenological manipulations of tit hatch dates were achieved by swapping early and late clutches from all over the metapopulation between tit nests during the incubation phase (2014: 76 great tits and 21 blue tits, 2015: 72 great tits and 22 blue tits). Subplots were situated within larger study plots of 100 nest boxes, so that flycatchers could choose between subplots without having to move far. On the early end of the spectrum, the earliest clutches were moved to forest patches assigned as early during the incubation phase, so that incubation time was shortened for these tits. On the late end of the spectrum, late clutches were moved to tit nests in forest patches assigned as late. A further hatch date delay was achieved by storing clutches in the ground for a maximum of 1 week (2014: *n* = 14 clutches, 2015: *n* = 27 clutches), providing dummy eggs to the female until we gave her the experimental clutch, prolonging her incubation time by a maximum of 1 week (for details on this method, see Samplonius *et al.* 2016). Incubated clutches were transported to their foster mother as quickly

as possible in small containers with cotton and heat pads. As the swapping operations were always done in sequence and never at the same time, incubated clutches were outside of the nest for only about 5 minutes before being placed in the new nest. All clutches were cross-fostered, and we monitored hatching date of the experimental tit broods by daily nest box visits around the expected hatch date.

By swapping early and late broods to the appropriate locations, a gradient of tit hatch dates was created among subplots (see results and Fig. 2 for effect sizes). For the analyses on flycatcher arrival patterns, we used the mean hatch date per experimental subplot rather than two discrete experimental treatments as an explanatory variable, to include also the variation in degree of change. We will refer to this as 'tit timing treatment'. As there was some heterogeneity (see results) among plots in the planned hatch date by the tits, we also use this as a covariate in our models to control for natural timing variation among subplots, which will be referred to as 'planned tit timing'. 'Planned tit timing' was calculated for each tit nest by adding 13 incubation days to the first day of tit incubation, which is the average incubation time for tits in our population before hatching.

We are aware that our experimental manipulations of tit phenology increased and decreased incubation times for the females, and that this may have caused changes in their behaviour. However, we found no differences in egg hatching success between treatments, so we assume that the results reported in this study are caused by differences in tit phenology. Moreover, variation in hatch dates within subplots was reduced, as we moved the earliest clutches from the whole laying date distribution to the advanced plots, and nests from the late tail of the distribution to the delayed plots. As the reduction in this variation is equal among treatments, we assume this has no effect on flycatcher settlement patterns.

PIED FLYCATCHER ARRIVAL PATTERNS

Male and female presence was scored at least every other day to establish settlement patterns along the gradient of tit hatch dates. On arrival, males usually monopolize one or two empty nest boxes and sing vigorously, making them relatively easy to spot during checks. For each individual male that was spotted, its characteristics were scored including blackness with the seven-point Drost score (Drost 1936), amount of white on the tertial feathers, the size and shape of a forehead patch, the amount of side patch and throat patch, and the presence and location of aluminium and colour rings (for details on the scoring method, see Both, Bijlsma & Ouweland 2016). Combined with the observation that males are highly box faithful, we were able to distinguish individuals and assign individual arrival dates. Female arrival date was determined when she was spotted near a male and nest building activity was taking place inside the nest box. These arrival dates were accurate compared to arrival of the same individuals with geolocator loggers (± 1.5 days), and repeatable among years in both males and females (Both, Bijlsma & Ouweland 2016). Pied flycatchers have protandrous arrival timing: males in our population arrive on average 1 week earlier than females (Both, Bijlsma & Ouweland 2016). About 12% of males remain unpaired (mean for 2007–2015), and keep displaying and singing near their nest box throughout the breeding season without attracting a mate, but in the experimental years, this number was higher (2014: 21%, 2015: 16%; Both *et al.* in press).

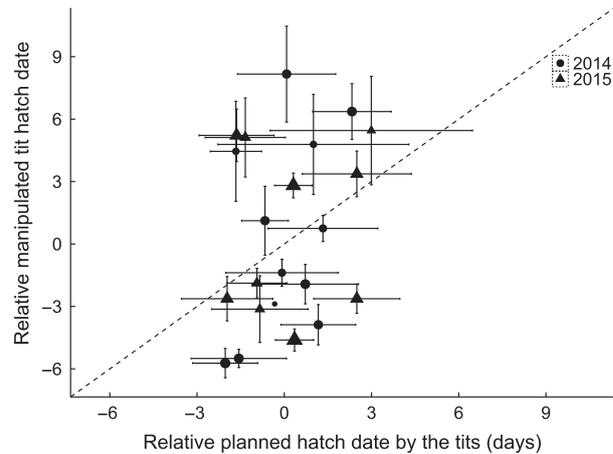


Fig. 2. Hatch date of resident tits was experimentally manipulated in forest patches (*y*-axis). Each data point represents a forest patch. The *x*-axis depicts the planned hatch date by the tits if we had not performed manipulations, which was approximated by adding 13 days to the start of incubation. Error bars are standard errors of the mean. Hatch dates below the $x = y$ line were advanced relative to the planned hatch date, whereas the points above that line were delayed.

STATISTICAL ANALYSIS

In order to elucidate whether tit timing treatment affected flycatcher male and female arrival patterns, statistical analyses were performed in R 3.3.1 (R Development Core Team 2016) with the lme4 package (Bates *et al.* 2015) using binomial Generalized Linear Mixed effect Models (GLMM). Male pied flycatcher arrival was modelled as the probability of an available nest box being chosen by a male (hereafter 'settlement probability') with 'tit timing treatment', 'planned tit timing' and 'year' as fixed effects and 'subplot' as a block random effect. Be aware that 'male arrival date' or 'male identity' could not be used in this model, as nest boxes without flycatchers could not be assigned male parameters. Furthermore, in order to test whether mean male arrival dates differed between tit treatments, we modelled relative male arrival date as a function of 'tit timing treatment', 'planned tit timing' and 'year' with 'subplot' and 'male identity' as block random effects using Linear Mixed Effect models (LME).

Male pairing probability was modelled as the probability of a male being chosen by a female using a binomial GLMM with 'relative male arrival date' (days relative to annual mean), 'tit timing treatment', 'planned tit timing', 'year', the interaction between 'treatment' and 'male arrival date' as fixed effects and 'male identity' and 'subplot' as block random effects. Backward elimination of non-significant terms was used until only (marginally) significant variables remained. Be aware that 'female identity' could not be used in this model, as only paired males received a female, rendering it a meaningless predictor for male pairing probability. Moreover, to test whether mean female arrival dates differed between tit timing treatments, we modelled relative female arrival date with 'tit timing treatment', 'planned tit timing' and 'year' as fixed effects and 'female identity' as block random effect using LME. We used relative female arrival here, subtracting the mean arrival date for each year, in order to eliminate year effects in the arrival date estimate, as we were interested in whether females might arrive relatively early or later depending on tit treatment.

To assess female arrival patterns across treatments in detail, we used a Cox proportional hazards model provided by the survival package in R (Therneau 2015) to evaluate the fraction of unpaired males over time in relation to 'year', 'tit timing treatment' and 'planned tit timing'. Cox proportional hazard models are semiparametric, as a baseline hazard is assumed that does not depend on the covariates. A common implementation is in survival analysis. It is modelled as the time until a certain event (e.g. death) occurs at certain points in time. Stated otherwise, it is the probability of an event occurring at a certain time, under the condition that the subject has survived until that time given a certain baseline hazard. Cox models assume that for all groups, there is a baseline hazard, with certain factors increasing or decreasing this baseline hazard. For example, smoking may increase the baseline hazard of death in humans, whereas a healthy diet may increase this baseline hazard. In our models of male and female settlement over time, the baseline hazard is best described as the diminishing number of unpaired males over time. This baseline hazard is however expected to differ between relatively 'early' and 'late' tit timing treatments, because the later arriving females are hypothesized to be more able to use the tit timing information, which affects the proportionality assumption of these Cox models. Therefore, a so called time dependence is introduced using a response variable that depended both on the start and end times of pairing events ('male arrival, female arrival, pairing event'). This is a commonly used approach in Cox proportional hazards models to deal with time interactive covariates (Therneau, Crowson & Atkinson 2016). For males that did not receive a female (zeros), the end of the evaluation period was assigned the latest date a male got paired in our study, 4 June.

All graphs in this paper were produced with ggplot2 package in R (Wickham 2009).

Results

HETEROSPECIFIC HATCH DATE MANIPULATIONS

The hatch dates of tits were about 10 days earlier in the warm spring of 2014 than the cold spring of 2015, and differed across treatments. Mean absolute tit hatch dates in 2014 were 1.7 ($n = 38$) and 10.0 ($n = 25$) May in advanced and delayed subplots respectively, and 12.6 ($n = 40$) and 19.9 ($n = 39$) May in 2015. The mean relative hatch date (calculated as the deviation of the manipulated hatch date within subplots from the mean population hatch date) of tits across advanced subplots in both years was -3.0 days, and $+4.7$ days in delayed plots, ranging from -5.7 to $+8.1$ days (Fig. 2). Between subplots, there was no correlation between 'tit timing treatment' and 'planned tit timing' (Spearman's rank correlation $r = 0.28$, $P = 0.22$). The difference in tit phenologies between years coincided with differences in April temperatures (2014 April temperature, 11.4 °C; 2015 April temperature, 7.9 °C; data retrieved from the Royal Dutch Meteorological Institute KNMI).

FLYCATCHER ARRIVAL PATTERNS

In the two study years, a total of 159 flycatcher males arrived and 114 females, leading to an estimated

male-biased OSR of 0.58. Flycatcher male arrival averaged 19.1 ($n = 72$) and 22.2 ($n = 87$) April, and female arrival averaged 30.2 ($n = 48$) and 29.0 April ($n = 66$) in 2014 and 2015 respectively. Both male and female relative arrival dates were unrelated to the experimentally manipulated tit hatch dates (LME arrival date ~ 'tit timing treatment': $P > 0.74$ for males, $P > 0.73$ for females). Moreover, males did not appear to use tit timing information in their breeding site selection, as their settlement probability per available nest box was unrelated to the experimental manipulation (GLMM nest box occupancy probability ~ 'tit timing treatment': $Z_{4,269} = 0.85$, $P > 0.39$; Table 1). This lack of experimental effect is not surprising, as almost all males settled before the experimental treatment became apparent (i.e. hatching of great tits).

In contrast to males, we found an experimental effect of tit timing on female settlement in both years, with females preferring males located in areas with early tits (GLMM male pairing probability ~ 'tit timing treatment': $Z_{6,152} = -2.03$, $P = 0.042$; Fig. 3, Table 2). Moreover, male pairing success declined strongly with arrival date ($Z_{6,152} = -3.91$, $P < 0.0001$; Fig. 3, Table 2). Average male pairing probability in tit advanced and delayed plots was 0.75 ($n = 40$) and 0.56 ($n = 32$) in 2014, and 0.81 ($n = 36$) and 0.73 ($n = 51$) in 2015 respectively. The difference in female settlement patterns between early and late tit timing treatments became more pronounced in the second half of the female arrival period, when tits in the early treatments had started hatching (Fig. 4), suggesting a disproportionate hazard for males that did not receive a female before this time.

A Cox proportional hazards model on male and female arrival patterns over time demonstrates that the hazard function declined more steeply for males in relatively 'early' tit timing areas compared to relatively 'late' ones (Cox model effect of 'tit timing treatment' $P < 0.009$, Table 3). In other words, the state of being unpaired disappeared more rapidly and steeply for males in areas with relatively early tits (Fig. 4). Biologically, this meant that females apparently preferentially settled in areas with relatively early breeding resident tits.

Table 1. Male flycatcher arrival patterns across tit hatch date treatments and year (corrected for planned tit timing), modelled as the probability that an available box was chosen by a male (binomial Generalized Linear Mixed effect Models). Male settlement patterns only varied between years, but not among tit timing treatments

Male box choice*	Estimate	SE	<i>z</i> value	Pr(> <i>z</i>)
(Intercept)	-0.093	0.195	-0.477	0.633
Tit timing treatment	0.031	0.036	0.854	0.393
Planned tit timing	-0.004	0.102	-0.042	0.966
Year 2015	0.946	0.284	3.336	<0.001

*Random effect variance \pm SD 'subplot' = 0.092 ± 0.304 .

Discussion

Here, we showed that the breeding phenology of a heterospecific competitor is used as a social cue in the breeding site selection of a migratory bird, but this effect differed between sexes. We replicated the experiment and found that the pattern was similar in two consecutive breeding seasons. Early arriving flycatcher males settled randomly in our experimental plots, but their probability of attracting a female was lower in forest patches where tit phenology was experimentally delayed and also declined strongly with male arrival date. Moreover, the effect of the heterospecific timing manipulation on female preference for early subplots increased over the course of the season. Selection on protandry may therefore constrain the potential to incorporate interspecifically derived social information in settlement decisions for the early arriving sex.

Phenological components of social information use have, to our knowledge, not received any experimental attention. We showed that female flycatchers preferred settling in plots with early breeding resident tits, and that this effect increased later in the season. We asked which heterospecific timing cues flycatchers could use. Intuitively, we argue post-hatching cues are more readily eavesdropped upon than pre-hatching cues, because tit provisioning behaviour can be observed from a distance, whereas pre-hatching behaviour cannot. However, our data show that in both years female settlement patterns already started to diverge before the onset of tit hatching in our treatments (Fig. 4), suggesting pre-hatching cues also contributed to differential flycatcher settlement. Such pre-hatching cues could include prenatal parent-offspring communication as reported in fairy wrens (Colombelli-Négrel *et al.* 2012, 2016), which may signal to flycatchers that tit eggs are close to hatching. This would require prospecting flycatchers to be near tit nests, a behaviour that is indeed found to occur (Forsman & Thomson 2008). Future research into phenological cues could focus on separating pre- and post-hatching information use.

Phenologies across trophic levels have been extensively studied in relation to climate change, where in general lower trophic levels are more responsive to climatic changes than higher levels, potentially leading to mismatches in species depending on peaked resources (Visser *et al.* 1998; Both *et al.* 2009; Thackeray *et al.* 2010). If the phenology of resident species is indeed used as a habitat quality cue, then the faster advancement of food peaks compared to consumer phenology (Visser & Both 2005; Thackeray *et al.* 2010, 2016) may have repercussion for the predictability of heterospecific phenological cues and lead to an ecological trap (Robertson & Hutto 2006). For example, high-quality habitats may have more food resources and earlier breeding competitors, but are also more seasonal in food abundance (Burger *et al.* 2012), so these areas might become increasingly unsuitable for later breeding migrants. However, if habitat unsuitability is not evident from the phenological cues provided by competitors, these cues may become unreliable in selecting a habitat. A climate warming induced mismatch between for example tit and caterpillar timing (Visser *et al.* 1998) may therefore erode heterospecific information value for arriving flycatchers.

Phenological adjustments of animals are not just found between years, but also within years. Recent research

Table 2. Male flycatcher pairing probability in relation to tit timing treatment and male arrival date, corrected for original tit timing. Female flycatchers settled more in areas with relatively early heterospecific competitors (tits)

Male pairing*	Estimate	SE	z value	Pr(> z)
(Intercept)	1.141	0.211	5.397	<0.001
Tit timing treatment	-0.101	0.050	-2.030	0.042
Planned tit timing	-0.074	0.125	-0.591	0.554
Male arrival date	-0.111	0.028	-3.908	<0.001
Year 2015	0.526	0.386	1.363	0.173

*Random effect variance \pm SD 'subplot' = 0 ± 0 , 'male identity' = $4e-14 \pm 2e-07$.

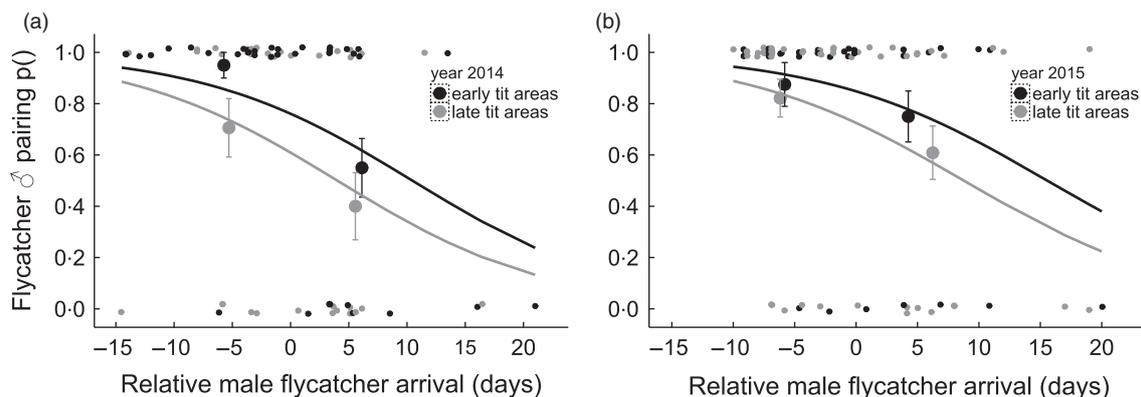


Fig. 3. Male pied flycatchers in areas with late tit timing had a lower pairing probability compared to males in areas with early tit phenology ($Z_{6,152} = -2.03$, $P = 0.042$). Later arriving males also had lower pairing probability ($Z_{6,152} = -3.91$, $P < 0.0001$). Small jittered data points are paired and unpaired males, the larger data points are four arrival date groups (2014 from left to right: $n = 19, 16, 15, 20$; 2015: $n = 28, 16, 20, 23$). Lines are model fits corrected for year and male identity.

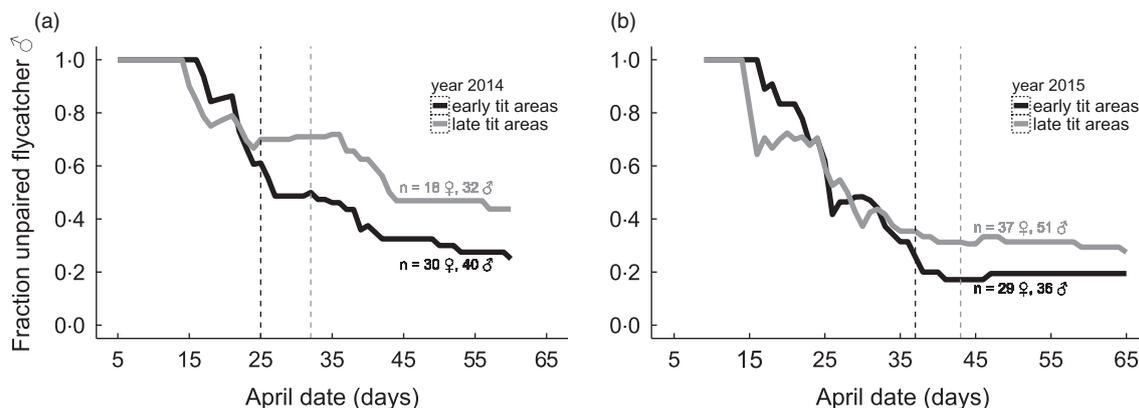


Fig. 4. Raw data plot of female flycatcher settlement patterns in relation to seasonal timing, expressed in two discrete groups of tit phenology. The dashed vertical lines indicate the start of tit hatching in early vs. late plots, and divergent patterns of female settlement appear to coincide with this moment in both years. Further evidence that treatment had a stronger effect later in the season is presented in Table 2 using a Cox proportional hazards model.

Table 3. Results of a Cox proportional hazards model testing female arrival order (proportion of unpaired males over time) in relation to tit timing treatment and year, corrected for 'planned tit timing'. Females were over time increasingly unlikely to settle in plots with later hatching tits (see Fig. 4)

Male pairing over time	Estimate	Exp (coef)	SE (coef)	z value	P value
Tit timing treatment	-0.065	0.936	0.025	-2.61	<0.009
Planned tit timing	0.053	1.055	0.064	0.833	0.405
Year 2015	0.622	1.86	0.195	3.18	<0.002

suggests that birds adjust their breeding phenology across spatial scales with one study showing that great tits bred earlier in forest patches with a relatively earlier food and oak bud-burst phenology (Hinks *et al.* 2015). Interestingly, this finding leads to opposite predictions from what we found: if heterospecific timing is used as a food phenology cue, then the later breeding flycatchers should select forest patches with late breeding great tits, because they should be able to match their phenology better with the local food peak and consequently raise their offspring more successfully (Samplonius *et al.* 2016). So why did flycatchers act in the opposite manner? The answer may be twofold. First, food abundance rather than food phenology may be a better predictor of habitat quality. For example, the contrast in tit timing between high- and low-quality habitat was 8.4 days in Corsican blue tits breeding in oak vs. evergreen forests (Lambrechts *et al.* 2004), 9.5 days in food supplemented blue tits breeding in rich vs. poor deciduous forest (Svensson & Nilsson 1995), 6.2 days in great tits breeding in deciduous woodland vs. gardens (Riddington & Gosler 1995) and 0 days in great tits breeding in deciduous vs. coniferous woods (Van Balen 1973). On the other hand, the contrast between great tits breeding in an oak forest with early and late

bud-burst was the same order of magnitude with 1.5 days per standard deviation of oak bud-burst timing (Hinks *et al.* 2015). Clearly, both variation in habitat quality and variation in tree phenology affect tit timing, but whether one effect is larger than the other may be context dependent. Moreover, if we only consider studies with similar forest types to ours without food supplementation experiments (e.g. Van Balen 1973; Hinks *et al.* 2015), then we may tentatively conclude that early tit phenology to some extent signals early tree phenology, but not higher habitat quality. The question remains why flycatchers in our study chose habitats in which the residents might signal an earlier caterpillar peak. Perhaps, the fitness costs of competition with resident species is higher for migrants than the benefits gained from local phenological matching with the habitat, but the evidence for fitness costs of phenological overlap between species is limited (Ahola *et al.* 2007). Alternatively, the later phenology of tits could have been perceived as a local nest predation cue resulting from reneating after predation. Research into the fitness consequences of phenological overlap between species is required to draw conclusions about the underlying mechanisms that gave rise to the patterns reported in this study.

Male pairing probability declined steeply when arriving later, demonstrating that early males have an advantage when it comes to finding a mate (Fig. 3). These results are consistent with the Rank Advantage Hypothesis and the Mating Opportunity Hypothesis to explain the evolution of protandry. This is in line with theoretical predictions by Kokko *et al.* (2006), and provides an empirical demonstration that the combined framework of rank advantage and mating opportunity may explain the evolution of protandry in a population with a male-biased OSR. Moreover, with opposing selection pressures acting on male and female arrival timing, protandry causes intersexual differences in the potential to use social cues. Our results clearly demonstrate that males pay a high fitness cost of

arriving late, which potentially overrides benefits they might get from arriving late in the form of a higher availability of social information. Although previous research found increased propensity of later arriving flycatchers to use social information (Seppänen & Forsman 2007; Jaakkonen *et al.* 2015), this has so far been interpreted as an effect of local breeding experience: later arrivers are inexperienced breeders and therefore have a higher need for social cues. However, we show that the potential to use social information may also differ between sexes in a protandrous species. Such differences may be of crucial importance when considering the effect of timing on assessing habitat suitability. We speculate that in the absence of personal information, females of relatively short-lived species may profit from arriving later than males in order to assess habitat suitability using social information. Although males may also need to assess habitat suitability, mating opportunity and male–male competition drive them to arrive earlier than females, potentially decreasing their potential to assess social information in selecting a breeding habitat.

Conclusion

Timing is of crucial importance in breeding site selection, both within individuals to maximize fitness, and between individuals as a social cue for resource quality, competition or predation. Moreover, optimal arrival timing may differ between sexes, acting as a filter that alters the potential to use social information. Such temporal aspects of social information use have so far received little attention, but may be crucial in understanding trade-offs between information density and competition intensity. These results call for careful consideration of differential effects of climate change on the phenologies of resident and migratory species.

Authors' contributions

J.M.S. and C.B. designed the study, and performed the field work. J.M.S. performed statistical analyses, and wrote most of the manuscript with critical input from C.B. All authors approved the content at all stages of the manuscript.

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Data accessibility

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.bs427> (Samplonius & Both 2017).

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Supporting Information

Details of electronic Supporting Information are provided below.

Table S1. Population metrics of the four most common nest box breeders in our metapopulation of 1050 nest boxes based on 4794 first nests between 2007 and 2015. “Pop. Size” is the average population size per year, “First egg” and “Hatch date” are in mean April date (1 May = 31 April), “Clutch size” is the mean clutch size across years.