



## Early birds are sexy: male age, dawn song and extrapair paternity in blue tits, *Cyanistes* (formerly *Parus*) *caeruleus*

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Sexual selection theory predicts that signals reflecting the relative quality of individuals should be used in mate choice. Females could base their choice of copulation partners on male secondary sexual traits that honestly signal male age, as predicted by the age-based indicator mechanism. Studies have shown that female blue tits prefer older males and that aspects of dawn song reflect male quality, but it remains unknown whether dawn song characteristics correlate with male age. We compared dawn song characteristics of second-year (SY) and older (ASY) male blue tits (cross-sectional analysis), and tested for age-related changes within individuals (longitudinal analysis) and differential overwinter survival of SY males. We further investigated the relation between dawn song and paternity gain and loss. We found that ASY male blue tits began to sing earlier relative to sunrise than did SY males. This difference in the onset of dawn singing was due to age-related changes in individual performance rather than differential survival of individuals with varying expression of the trait. Males that began to sing earlier at dawn had more mating partners, and were more likely to gain extrapair paternity. Our findings suggest that the onset of dawn song can provide a simple mechanism for females to assess the relative quality of their mate and of neighbouring males. We propose that females use the onset of singing as a cue for their choice of extrapair partners.

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The hypothesis that older males should be preferred mating partners of choosy females (Trivers 1972; Manning 1985) has received much theoretical attention (e.g. Brooks & Kemp 2001; Proulx et al. 2002) and is supported by empirical studies across taxa (reviewed in Brooks & Kemp 2001; see also Conner 1989; Poole 1989; Jones & Montgomerie 1991; Enstrom 1993). Older males may demonstrate their superior genetic quality simply by showing that they have survived more episodes of viability selection (Trivers 1972). Females may thus increase their reproductive success by mating with older males, because their

offspring will inherit these 'good genes' for viability (e.g. Wetton et al. 1995).

In the blue tit about 40–65% of broods contain young that are fathered by males other than the social mate (Kempnaers et al. 1992, 1997; Leech et al. 2001; Delhey et al. 2003) and these extrapair matings increase variability in male reproductive success because they are not reciprocal (Kempnaers et al. 1992). Paternity analyses in different populations of blue tits have consistently shown that older males have a much higher success in gaining extrapair paternity than do young males (Kempnaers et al. 1997; Delhey et al. 2003). Behavioural observations suggest that females actively choose these older males, because females leave their territory in search of extrapair copulations, particularly at dawn (Kempnaers et al. 1992).

How do females find extrapair partners and discriminate between older and younger males? Theory predicts that females can use traits dependent on condition or experience, which will be more developed in older males than in younger males, as an honest indicator of male age (Grafen

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1990; Kokko 1997, 1998; Getty 2002). In songbirds, singing behaviour may function as such a viability indicator (e.g. Gil et al. 2001). Birdsong can function both in territorial defence and in female attraction (Catchpole & Slater 1995) and age and experience may influence a male's performance in both contexts. Several song features change with age of the singer (reviewed in White & Mooney 1999). In species with relatively large repertoires where individuals can learn new song types over the years, repertoire size reliably indicates male age (e.g. canary, *Serinus canaria*: Nottebohm & Nottebohm 1978; song sparrow, *Melospiza melodia*: Searcy et al. 1985; yellow warbler, *Dendroica petechia*: Cosens & Sealy 1986; European starling, *Sturnus vulgaris*: Mountjoy & Lemon 1995, 1996). In species with small repertoires and discontinuous singing, song output rather than complexity may reflect aspects of male quality. For example, male black-capped chickadees, *Poecile atricapillus*, with a high dominance status at winter feeders had a higher song rate (Otter et al. 1997), whereas strophe length predicted survival in great tits, *Parus major* (Lambrechts & Dhondt 1987). Females may base their choice of a mate on a combination of these different song characteristics as well as visual traits (e.g. Partan & Marler 1999).

In temperate-zone songbirds singing activity varies throughout the year and is highest during the breeding season, when males establish territories and attract mates (Catchpole & Slater 1995). Besides this seasonal variation, there is also daily variation in singing activity (e.g. Thomas 2002; Amrhein et al. 2004) and, in several species, male song output peaks around dawn, resulting in the so-called dawn chorus (Catchpole & Slater 1995). In some species, dawn song is most pronounced after territory establishment and pairing, that is, during the period of female fertility (e.g. great tit: Mace 1987; European starling: Eens et al. 1994; willow tit, *Poecile montanus*: Welling et al. 1995), suggesting a role in paternity loss or gain. Some features of the dawn song seem to reflect aspects of male quality. For example, in the black-capped chickadee, the start of singing before sunrise correlated with the social rank of a male in the winter flock (Otter et al. 1997), and strophe length in the blue tit was related to success in gaining extrapair paternity (Kempnaers et al. 1997). Furthermore, dawn song features, such as repertoire size, strophe length and percentage performance time (a measure of song output), relate to male performance in singing interactions during territorial intrusions later in the day (Poesel et al. 2004).

Females often foray into neighbouring territories around dawn (Kempnaers et al. 1992; see also Double & Cockburn 2000), when, because of low light levels, signals such as plumage colour may not be assessable. Given the consistent finding of higher extrapair paternity for older male blue tits, we predicted that some features of dawn song reflect male age, and that females use these cues for their extrapair mate choice.

Our aim in this study was to investigate the relation between dawn song characteristics, male age and success in gaining paternity. First, we investigated whether second-year and older males differed in dawn song features (cross-sectional analysis). Second, we tested for age-related

changes in dawn song characteristics at the individual level (longitudinal analysis) and whether age-related differences in those characteristics could be explained by differential overwinter survival. Finally, we investigated how age-related dawn song characteristics related to a male's reproductive success.

## METHODS

### Study Population

During March and April 1998–2002, we studied a population of 52–104 blue tit pairs breeding in nestboxes in a deciduous woodland at Kolbeterberg in Vienna, Austria (48°13'N, 16°20'E). The study area of about 35 ha is dominated by oak, *Quercus robur*, beech, *Fagus sylvatica*, and ash, *Fraxinus excelsior*, and encompasses about 250 nestboxes, each 40 m apart. Most blue tits in this population form pairs in autumn and defend territories from early winter until the end of the breeding season. Males engage in singing interactions with conspecifics over territory borders (see also Poesel et al. 2004). Male blue tits show high singing activity at dawn before and during the egg-laying period. This dawn song is characterized by continuously high song output, which seems to end when the female joins her mate. Males sing bouts of songs of the same song type and cycle through a repertoire of two to five song types (Poesel & Kempnaers 2000), three of which are used by all males in the population (unpublished data).

During the breeding seasons, we checked nestboxes regularly to determine the onset of nest building, egg laying, hatching and fledging as part of a long-term research programme on reproductive biology in this blue tit population. Birds were captured with mist nets (during the day) or in the nestboxes (at night) and transported in bird bags to a nearby field laboratory for banding and measuring. When an individual was caught for the first time, a 20–100- $\mu$ l blood sample was taken from the brachial vein for paternity analysis. Individuals caught during the day were released within 30 min near their territory. Those caught at night were kept in the dark in individual wooden containers until dawn and then released at the forest edge. All birds were observed on their territory afterwards. We recorded dawn song of males between 1 and 112 days after capture. Capturing the birds may have influenced their singing behaviour immediately afterwards, so we excluded the one male that was recorded on the first day after capture from further analysis. All other males had at least one morning between capture and dawn song recording. Nestlings were taken from their nestboxes at 14–16 days old and transported in bird bags to the outskirts of the territory for banding, measurement and blood sampling (10–50  $\mu$ l). They were removed from the nestbox while the parents were away. We handled only half the brood at a time, while sitting at a sufficient distance from the nestbox to allow the parents to continue feeding the other half of the brood. Processing an entire brood took less than 20 min. All blood samples were taken from the brachial vein. Blood sampling had

no obvious adverse effects on adult or nestling condition or survival.

Individuals were uniquely colour-banded, sexed and aged. Based on previous banding records, we could determine the exact age for individuals ringed as nestlings or second-year birds. Unbanded blue tits could be categorized only as second-year (SY) birds and after second-year (ASY) birds following Svensson (1992). Male blue tits in this population are, on average, 1.6 years old (range 1–8 years; unpublished data). In all further analyses, we compared SY males and ASY males where the latter class consists of birds in their third calendar year or older. Individual survival was estimated from local recaptures: individuals that were caught in the study area at the end of February or later were classified as having survived the winter.

Our work was done under licence from the Magistrate of Conservation in Vienna and the Magistrate of Forestry and Agriculture.

### Recording and Analysis of Dawn Song

We recorded the dawn song of 61 territorial male blue tits during the period of presumed fertility of their social mate, that is, from 8 days before the first egg until 1 day before the last egg was laid (Birkhead & Møller 1992). We waited near the nestbox of the pair from 1 h before sunrise, noted at which time the male began to sing and recorded continuously from the first song until the male stopped singing for more than 5 min. Once dawn song had stopped we followed the male until we could see the colour of his bands for identification.

During 1998–2000, recordings were made with a Telinga Stereo-condenser microphone (Stereo-Dat-Mic), mounted in the focus of a Telinga pro 5 parabolic sound reflector (57 cm diameter) and connected to a SONY WM-D6C cassette recorder. In 2001 and 2002, we used a Sennheiser MKH 816 T directional microphone connected to a Sony TCD-D8 DAT recorder. For sonographic analyses we used the software package Avisoft SASLab Pro 3.5 (analysis bandwidth 112 Hz, time resolution 8.9 ms; Specht 1993).

### Dawn Song Characteristics

We focused on the following six characteristics of dawn song: (1) onset of song (start of singing in minutes before sunrise); (2) repertoire size (the number of different song types sung per 100 strophes during a single dawn chorus); (3) song rate (the number of strophes sung/min); (4) mean strophe length (s); (5) mean percentage performance time (PPT; calculated as strophe length divided by the sum of strophe length and subsequent interstrophe pause and multiplied by 100); and (6) proportion of common song types (proportion of strophes that belong to the three most common song types sung in the population).

One recording of a dawn chorus is probably not enough to obtain the entire repertoire size of a male, even though there are good indications that birds cycle through a large part of their repertoire during one morning (e.g. Doutrelant et al. 2000). We used the number of song types per

100 strophes as a proxy of repertoire size to account for differences in the duration of recordings between males.

We calculated the three measures of song output (song rate, strophe length and PPT) using only the three most common song types sung in the population. This was done for two reasons: (1) it makes our measures comparable to those reported in previous studies (Bijnens 1988; Kempnaers et al. 1997; Poesel & Kempnaers 2000); and (2) the three common song types are used by all males in the population and constitute the majority of songs that a male sings. Thus, individuals can potentially use performance of these song types, such as song rate, as a direct comparison between potential opponents or partners. Measures obtained from only the three most common song types were highly correlated with measures obtained from all song types (Pearson correlation: song rate:  $r_{59} = 0.87$ ; song:  $r_{59} = 0.85$ ; PPT:  $r_{59} = 0.88$ ; all  $P < 0.001$ ).

In blue tits, some dawn song variables change over the breeding season, probably in response to changes in female fertility (Poesel et al. 2001). We therefore included day of recording in relation to female egg laying (number of days before or after the female laid the first egg) as a covariate in our analyses.

### Paternity Analysis

Paternity of offspring was determined as part of the long-term research programme on reproductive biology in this blue tit population by using five (1998), six (1999–2001) or eight (2002) polymorphic microsatellite markers: *Pca3*, *Pca4*, *Pca7*, *Pca8*, *Pca9* (Dawson et al. 2000); *Pocc1*, *Pocc6* (Bensch et al. 1997); *Phtr3* (Fridolfsson et al. 1997); *Mcyu4* (Double et al. 1997). The combined probability of exclusion for these marker sets was  $>0.995$  (five markers) and  $>0.999$  (six to eight markers). Paternity was excluded if two or more loci showed mismatches between putative fathers and offspring. Detailed descriptions of the methods are given in Delhey et al. (2003), Foerster et al. (2003) and Johnsen et al. (2003). We determined whether a male lost paternity in his own nest and whether he sired extrapair offspring. We also counted the female partners with which a male sired offspring during one breeding season (number of mating partners).

### Statistical Analysis

We used SPSS 9.0 for Windows (SPSS Inc., Chicago, IL, U.S.A.) for all statistical analyses. PPT and the proportion of common song types were arcsine square-root transformed and repertoire size was log transformed to achieve a normal distribution (Kolmogorov–Smirnov test: NS); the other variables were normally distributed and showed homoscedasticity. Results (untransformed data) are reported as mean  $\pm$  SE. All tests are two tailed.

For the cross-sectional analysis, we used data from 41 SY and 19 ASY males. We constructed general linear models with normal errors (ANCOVAs) with each song variable as the dependent variable, and male age (factor), year (factor) and relative recording day (covariate) as the explanatory variables. Explanatory variables were sequentially deleted

in order of decreasing significance. Only terms with  $P < 0.1$  remained in the final model. Excluded terms were re-entered one by one into the final model to confirm that they did not explain a significant part of the variation. For one male the onset of dawn singing was not noted, so only 59 males were included in analyses of onset of dawn song.

For the longitudinal analysis, we used data from seven males that were recorded as both SY males and ASY males, that is, during their first and second ( $N = 5$ ) or third ( $N = 2$ ) year of breeding. To compare song variables across age, we needed to control for differences in recording day between the years. Thus, we used a repeated measures ANCOVA with the difference in relative recording day as a covariate. We also calculated the between-year repeatability of each song variable (Falconer & Mackay 1996).

To investigate differential survival of SY males with respect to characteristics of dawn song, we compared the characteristics from 16 males that did and 25 males that did not survive their second winter. We used an ANCOVA with the age-related song characteristic as the dependent variable and male survival (factor), year (factor) and relative recording day (covariate) as the explanatory variables.

Data from 53 males were available for analyses concerning paternity gain and loss. We used a logistic regression with paternity gain or loss (yes/no) as the dependent variable, and tarsus length and strophe length (two variables shown to affect paternity loss, Kempnaers et al. 1997) and the onset of dawn song (corrected for relative recording date by forcing this variable in to the model) as the explanatory variables. We sequentially eliminated nonsignificant terms ( $P > 0.10$ ) from the model in order of smallest effect size. The final model contained only terms with  $P < 0.05$ .

## RESULTS

### Male Age and Dawn Song

Male age explained a significant proportion of the variance in the onset of dawn song, but not in any other song parameter (Table 1). The ASY males began to sing on average 5.8 min earlier relative to sunrise than did the SY males (Fig. 1), but they did not sing for longer (Table 1). Overall, the onset of dawn song was not correlated with its duration (Pearson correlation:  $r_{57} = -0.13$ ,  $P = 0.32$ ), probably because the end of dawn song depended strongly on female behaviour, that is, the male stopped singing as soon as his own female approached.

Characteristics of male dawn song were influenced by year and recording day relative to egg laying of the social mate. The duration of dawn song, the proportion of common song types and the repertoire size varied between years (Table 1). Later in the laying period, males began to sing later, that is, closer to sunrise, and sang shorter strophes with a lower PPT (Table 1). The longitudinal analysis showed that only strophe length and PPT were highly repeatable between seasons (repeated measures ANCOVA:

**Table 1.** Effects of male age on characteristics of dawn song of 60 blue tits recorded from 1998 to 2002

Dependent variable	Explanatory variable*	df	F	P	Effect size $\eta^2$
Onset of dawn song†	Age	1,56	14.6	<0.001‡	0.21
	Recording day	1,56	4.45	0.04	0.07
Duration	Age	1,54	0.27	0.60	0.01
	Year	4,54	7.48	<0.001‡	0.36
Proportion of common song types	Age	1,54	1.54	0.22	0.03
	Year	4,54	5.41	0.001‡	0.29
Repertoire size	Age	1,54	0.01	0.93	0.00
	Year	4,54	4.01	0.006‡	0.23
Song rate	Age	1,58	0.01	0.94	0.00
Strophe length	Age	1,57	0.09	0.76	0.002
	Recording day	1,57	4.91	0.03	0.08
Percentage performance time	Age	1,57	0.12	0.73	0.002
	Recording day	1,57	9.55	0.003‡	0.14

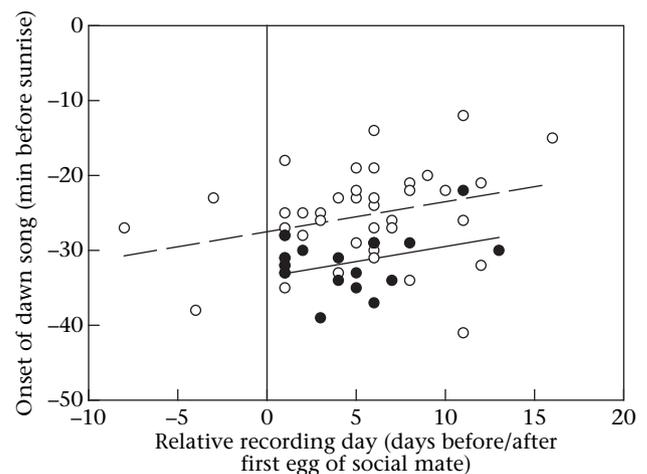
\*Year and recording day (relative to the start of laying of the female partner) were included in the full model. Only the results from the final models are shown here.

†We failed to note the onset of dawn song for one male.

‡Significant after Bonferroni correction for multiple testing (seven tests,  $\alpha' = 0.007$ ).

strophe length:  $R = 0.66$ ,  $F_{6,7} = 4.91$ ,  $P = 0.028$ ; PPT:  $R = 0.88$ ,  $F_{6,7} = 16.34$ ,  $P = 0.001$ ; all other  $P > 0.08$ ).

The effect of age on the onset of dawn song could not be explained by differential survival of SY males. Males that survived did not differ in the onset of dawn song from those that did not survive (ANCOVA: survival:  $F_{1,37} = 0.09$ ,  $P = 0.77$ ; relative recording day:  $F_{1,37} = 3.48$ ,  $P = 0.07$ ). However, individual males started dawn song earlier as they became older, although not significantly so (adjusted mean  $\pm$  SE: SY males:  $28.7 \pm 1.0$  min before



**Figure 1.** The onset of dawn song of male blue tits in relation to recording day.  $\circ$ , — — —: Second-year males ( $N = 41$ );  $\bullet$ , —: after second-year males ( $N = 18$ ). Regression lines are based on predicted values from the general linear model (see Methods).

sunrise; ASY males:  $31.7 \pm 1.8$  min before sunrise; repeated measures ANCOVA: age:  $F_{1,5} = 4.16$ ,  $P = 0.097$ ; effect size: 0.45; difference in recording day:  $F_{1,5} = 1.71$ ,  $P = 0.25$ ; effect size: 0.26).

### Extrapair and Within-pair Success

Males that sired extrapair young (EPY) started singing earlier at dawn than did those that did not sire EPY (logistic regression:  $\chi^2_1 = 4.91$ ,  $P = 0.027$ ; Fig. 2a) and early singing males sired offspring with more females (Spearman correlation:  $r_s = -0.37$ ,  $N = 53$ ,  $P = 0.006$ ). Males that sired EPY did not differ in tarsus length ( $\chi^2_1 = 0.11$ ,  $P = 0.74$ ) or in mean strophe length ( $\chi^2_1 = 0.001$ ,  $P = 0.97$ ) from males that did not sire EPY. Males that were cuckolded did not differ in onset of dawn song from males that achieved full paternity in their own nest (logistic regression:  $\chi^2_1 = 0.36$ ,  $P = 0.55$ ; Fig. 2b), nor did they differ in tarsus length ( $\chi^2_1 = 0.19$ ,  $P = 0.66$ ) or in mean strophe length ( $\chi^2_1 = 0.04$ ,  $P = 0.85$ ).

## DISCUSSION

ASY male blue tits began to sing earlier, and early singers gained extrapair paternity and had more mating partners. The difference in the onset of dawn singing tended to be caused by age-related changes in individual performance rather than by differential survival of individuals with varying expression of the trait.

Early onset of dawn song and high song output (PPT) were observed just before and during the early egg-laying stage, that is, during the peak of female fertility. This result confirms those from earlier studies and further suggests that dawn song has an intersexual function in the Paridae (see also Mace 1987; Welling et al. 1995; Poesel et al. 2001). Individual males might time their peak singing activity to when most paternity can be gained or lost. Our results indicate that dawn song in the blue tit may function to attract extrapair females, especially given the

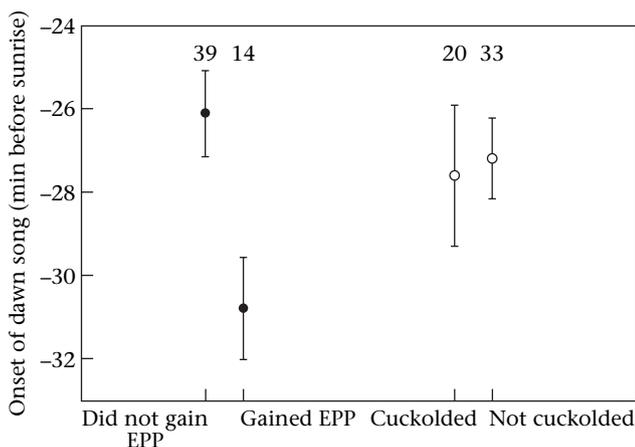
highly synchronized breeding activity (Kempnaers 1997). Between-year differences in several dawn song characteristics may reflect environmental conditions. Different weather conditions may have influenced, for example, the duration of the dawn chorus, because song activity may be related to temperature (e.g. Slagsvold 1977). Social factors such as availability of fertile females in the neighbourhood may have differed between years and affected dawn song characteristics (e.g. Galeotti et al. 1997).

If females are the intended receivers at dawn and are attentive to dawn song (Mace 1986; Gorissen & Eens 2004), it will pay a male to sing as early as possible. By singing early, a male may signal his presence to his social mate who is still sitting on the nest, which may make it more difficult for her to fly off into neighbouring territories to pursue extrapair copulations (early dawn song as a form of mate guarding). Our results do not support this hypothesis, however, because males paired to faithful females did not start singing earlier than males that were cuckolded.

Alternatively, females may use song as a trigger to leave the nest and as a cue to locate a potential extrapair partner. A male already singing while all his neighbours are still quiet may increase his success at attracting females (Mace 1986). Supporting this prediction, males in our study starting to sing earlier at dawn had more mating partners and were more likely to gain extrapair paternity. The correlation between onset of dawn song and male age can thus explain why older male blue tits are more successful at gaining extrapair paternity (Kempnaers et al. 1997; Delhey et al. 2003). The average difference in the onset of singing between juvenile and adult males (6 min) seems sufficient for females to leave the territory and attempt to copulate with an early singing male. The age effect on gaining extrapair paternity is found only when extrapair males are close neighbours (Foerster et al. 2003), and thus probably within hearing distance of the focal female (Blumenrath et al. 2004). The signal-to-noise ratio is only slightly reduced inside the nestbox (Blumenrath et al. 2004), which suggests that females can hear and get reliable information on at least neighbouring males.

In the black-capped chickadee, high-ranking males began to sing earlier and sang longer at dawn (Otter et al. 1997), and high-ranking males obtained higher extrapair success (Mennill et al. 2004). We cannot exclude the possibility that the higher success of early singing males in gaining extrapair paternity was due to female choice for another correlated trait, instead of choice for early singing per se. Female blue tits may have information on potential partners from previous encounters and may combine multiple characteristics to choose an extrapair mate. In any case, the start of singing was the only dawn song feature that differed significantly between second-year and older males in our population (Table 1). Unlike Kempnaers et al. (1997), we did not find that older males sang longer strophes than did second-year males.

To obtain matings with older or higher-quality males, female blue tits could also base their choice on plumage characteristics, such as the male's highly UV-chromatic crown (Sheldon et al. 1999; Delhey et al. 2003). However,



**Figure 2.** Mean  $\pm$  SE onset of dawn song in blue tits for (a) males that did or did not gain extrapair paternity (EPP) and (b) males that lost paternity (cuckolded) or did not lose paternity in their own nest. Sample sizes are shown above data points.

this sensory channel requires visual contact between individuals. Thus, whereas plumage coloration can be assessed only at shorter distances and under adequate light conditions, song can be assessed without close approach, even in total darkness. It is still unknown whether and how song characteristics relate to plumage colour in blue tits.

If males gain more extrapair paternity by starting to sing earlier at dawn than do their neighbours, why do not all males start earlier? Put differently, what is the cost of singing early? We suggest two potential costs. (1) It may be energetically costly to wake up early and consequently be active before there is sufficient light to allow successful foraging. Males singing earlier have to spend more time without food while having a higher metabolic rate than during sleep. Thus, only males with sufficient or surplus energy reserves would be able to afford to sing early (see also McNamara et al. 1987; Hutchinson et al. 1993). (2) The honesty of the signal may be imposed by competition with other males. If neighbouring males were also attentive to dawn song, they may engage territory owners in a singing interaction. This may inflict costs on the territory owner if such interactions escalate into a physical fight (A. Poesel, personal observation), or if performing poorly in such a singing contest leads to loss of reproductive success (e.g. Mennill et al. 2002). The cost of cheating has also been shown in studies of birds in which badges of status (e.g. bib size, forehead patch size) were manipulated; individuals with experimentally enlarged signals were harassed and persecuted by naturally large-badged individuals (Møller 1987; Qvarnström 1997).

The fact that older males started singing earlier could also be explained by variation in light conditions within the study area. It is well known that light pollution (e.g. from street lamps) causes birds to start to sing earlier (e.g. Bergen & Abs 1997). Thus, if older males are more likely to occupy areas with lighter conditions, then this would explain our results. However, there is no evidence that this is the case in our study area. Nevertheless, the hypothesis that singing early at dawn influences the chance of a male obtaining extrapair young could be tested experimentally by providing artificial light in some territories. Female blue tits may benefit from basing their choice of extrapair partners on the onset of dawn song for several reasons. First, by assessing the onset of singing, females can monitor all males in their neighbourhood simultaneously without leaving their territory, and they can evaluate differences between many males in a population to determine the highest-quality male available. Forays into neighbouring territories are potentially costly for females because intruding females are often aggressively chased by the resident female (Kempnaers et al. 1992). Second, the onset of dawn singing allows females to decide swiftly which neighbouring male to visit. By leaving their own territory for a short period before dawn, females may avoid being detected by their own mate, and therefore avoid costs of extrapair copulations such as aggression or reduced paternal effort from their social partner (e.g. Birkhead & Møller 1995). Third, by choosing early singers, and thus older males, as extrapair partners, females may obtain 'viability genes' for their offspring (Brooks & Kemp 2001).

Our results provide support for an age-based indicator mechanism for female choice (Brooks & Kemp 2001). In the blue tit, older males are more successful in obtaining extrapair paternity (Kempnaers et al. 1997; Delhey et al. 2003), and this is probably a result of active female choice for genetic benefits (Kempnaers et al. 1992; Foerster et al. 2003). Our study shows that older males start to sing earlier during the fertile period, suggesting a mechanism by which females could select these older males. Accordingly, males singing earlier sired young with more females. Researchers have proposed that characteristics of dawn song are honest signals, reflecting aspects of male quality or resource-holding potential (Lambrechts & Dhondt 1987; Otter et al. 1997; Welling et al. 1997). The underlying assumption of the age-based indicator mechanism, that age indicates genetic quality, has been questioned by Hansen & Price (1995). Their model indicated that the oldest individuals are not necessarily genetically superior, and that individuals of young or intermediate age are often the most fertile ones. We compared young (SY) and intermediate-aged (ASY) male blue tits, and it remains to be shown whether the oldest individuals in the population advertise at the highest levels and are preferred by females.

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