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The frequency and timing of copulations in the Willow Tit *Parus montanus*

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The frequency and timing (in relation to season and time of day) of copulations were studied in the Willow Tit *Parus montanus*. We monitored 124 pairs in four years. Copulations were solicited by both sexes and they occurred both in the suspected fertile and non-fertile periods of the females. Similarly, there was no significant decline in the copulation frequency after the laying period started. The frequencies of copulations and copulation attempts were estimated as 0.37–0.52/h/pair and 0.21–0.43/h/pair, respectively. Copulations occurred from 03:42–11:00 hours, but they peaked early in the morning. No copulations were seen in the afternoon. The results imply that, like in many other territorial species, the copulation frequency of the Willow Tit is relatively low and thus, probably not influenced by sperm competition. Other functions of copulations (in addition to fertilization) and the reasons for early morning copulation peak are discussed.

1. Introduction

The frequency and timing of copulations in birds vary in relation to taxa and life history (Birkhead et al. 1987, Birkhead & Møller 1992). High copulation rates are often associated with intense sperm competition and male inability to guard his mate (for instance in raptors and colonial species). Frequent copulations are considered to work as a paternity guard by two mechanisms: (1) a proportional increase in the number of sperm from the male partner enhances the probability of fertilizing an egg and (2) the last male usually has the best chances to sire the offspring (Møller & Birkhead 1991, Birkhead & Møller 1992). In territorial species with low population densities, and thus possibly smaller cuckoldry risks, copulation rates may be relatively low.

Most monogamous species have the highest copulation rates a few days before egg-laying starts (Birkhead et al. 1987, Birkhead & Møller 1993a). This is probably mainly due to the fact that copulations become more inefficient when the egg-laying starts: the developing egg may prevent new sperm from entering the infundibulum, where fertilization takes place (Birkhead & Møller 1992). Since stored sperm from earlier copulations are usually sufficient to fertilize an entire clutch, no further copulations are necessary.

Also diurnal variation in copulations has been frequently found (Birkhead et al. 1987). Usually a peak in copulations occurs early in the morning (Birkhead et al. 1987), but as mentioned before, copulations often become rarer after the first egg is laid. In most species, females lay their eggs early in the morning and ovulation of the following egg probably happens within 30 min (Birkhead & Møller 1992). This short period between laying and ovulation, the insemination window (Cheng et al. 1983), is the last chance to fertilize the next egg to be laid. However, many studies of passerine birds have found no clear evidence for an increased copulation frequency at this time (e.g. Birkhead et al. 1989, Sheldon & Burke 1994, see also Birkhead et al. 1996).

The Willow Tit *Parus montanus* is a socially monogamous and territorial species in which copulations are very difficult to observe because of the suddenness of their initiation, their brief duration and the dense forest habitat in which they occur. If the within-pair copulations are rarely seen, then extra-pair events are even rarer: only once has a successful extra-pair copulation been reported (Haftorn 1995), and even that happened after clutch completion. Young Willow Tits establish their pair bonds in the winter flocks during their first autumn (Ekman 1979, Haftorn 1990). The majority of pair bonds are maintained through the lifetime of individuals, but divorces occur now and then (Orell et al. 1994). Females tend to prefer old (non-yearling) males as new mates. In the study area, egg laying begins on average on 17 May and females lay 7.6 ± 1.1 (mean ± SD) eggs per clutch (Orell & Ojanen 1983a, b). One egg is laid per morning (own observations). We have found some evidence for a mixed reproductive strategy (sensu Trivers 1972) and sperm competition: a low frequency of extra-pair paternity (4.2% of nests and 0.89% of nestlings) was revealed by DNA-fingerprinting (Orell et al. 1997) and males seem to guard their fertile mates (Koivula et al. 1991, Welling et al. 1995b).

The aims of this study are: (1) to describe the copulation frequency of the Willow Tit and (2) to examine how the copulations occur in relation to female fertility, egg laying, and time of day. Our objective was to determine whether sperm competition affects the Willow Tit's copulation behaviour.

2. Methods

2.1 Study area

The study area (ca. 22 km^2) lies near Oulu, northern Finland (65°N, 25°30´E), and contains mostly coniferous and mixed forests of different ages. A detailed description can be found in Orell and Ojanen (1983a). All birds were individually colour-banded and the size of the breeding population varied between 70 and 120 pairs over the past decade.

2.2 Data collection

We monitored a total of 124 Willow Tit pairs over the four-year period from 1991–92 and 1994–95. To ensure statistical independence, each pair was included in this study only once. The focal pair was monitored as long as possible. Whenever copulations occurred, the time and any associated behaviour were recorded. Birds were observed for a total of 1 830 min, ranging from 1 to 80 min and averaging 14.8 min (± 12.8 SD, Md = 10) per observation bout. Observations were made from dawn — females emerge on average 35 min after sunrise (Welling et al. 1995a) — to late afternoon. We made only a few observations after 17:00 hours, but females in our study area roost soon after this time (own observations). All age groups are present in the data.

There is no information concerning the duration of the fertile period and the sperm-storing ability of Willow Tit females (although there is every reason to believe that they do store sperm, just like their relatives; see Kempenaers et al. 1993). Therefore, female fertility was defined with the information originally derived from the Zebra Finch *Taeniopygia guttata* (Birkhead et al. 1989). The fertile period in our study begins on day – 11 (where 0 = the day the first egg is laid) and ends on the day when the penultimate egg is laid. Birkhead et al. (1989) define the end of the fertile period as a day before the penultimate egg is laid, since in practice there is only a short insemination window available for fertilization during the penultimate day. (In other words, both fertile and nonfertile periods are present in the penultimate day and it is impossible to define the exact limits.) However, since one of the goals of this study was to find out whether copulations occur outside the fertile period, it would have been more erroneous to score copulations that take place in the fertile period as non-fertile than vice versa. Thus, our choice of the fertility limits is conservative. Females of eleven non-breeding pairs and pairs whose nest was destroyed at an early stage (and not rebuilt) were scored as non-fertiles (ca. 21% of all non-fertiles). One copulation and one copulation attempt from these pairs was included in the observations. The proportions of observation time were 60% for the fertile and 40% for the non-fertile period. The determination of female breeding status (prelaying/laying/incubation; the corresponding proportions of observation time were 60%, 26%, 14%) was confirmed by routine visits to nests.

In the analyses, time of day was divided into three categories. The first is defined as lasting from female emergence at dawn to 06:00 hours, the second as from 06:01–12:00 hours, and the third from 12:01 hours onwards. The proportions of total observation time were 38%, 42% and 20%, respectively.

2.3. Statistics

To analyse copulation behaviour (copulation vs. no copulation), we used GLIM4 for the PC (Crawley 1993) to test log-linear models with a binomial error distribution and logit link function. The link function links the expected values with the explanatory values as implemented in the program. The modelling allows the stepwise addition of factors in the analysis of variance sense. Model fitting produces parameter estimates, which in the case of a factor, denote the position of the slope of the i:th factor level in relation to the first factor level. We then can apply t-tests to see whether the parameter estimate deviates from zero by dividing it with the standard error. Thus, we can compare the differences between the first and the higher factor levels. Since the duration that each pair was monitored varied considerably (see Section 2.2.), we considered this effect by including the observation time as a continuous variable into the model. The other independent factors were female fertility (fertile/non-fertile), breeding stage (prelaying, laying, incubation) and time of day (before 06:01, 06:01–12:00, after 12:00).

3. Results

3.1. Copulation behaviour in general

Only one copulation or copulation attempt per pair was seen, but we know from previous observations (unpublished) that Willow Tits copulate more than once per clutch. Copulations included typical "si-si-si" vocalizations, wing fluttering and a pair briefly chasing each other (cf. Cramp & Perrins 1993). The duration of a copulation sequence was usually 5–20 (but sometimes even 60) seconds, but the mounting itself lasted approximately only a second. Sixteen copulations were observed; the earliest on day – 17 (where 0 = the day the first egg is laid) and the last on day + 12, i.e. three days after the last egg. Additionally, we observed six copulation attempts (where we could confirm that mounting did not occur in spite of the typical display) and seven cases where we observed a copulation display (sounds, wing fluttering, etc.), but could not be sure whether the copulation was successful. We scored these 6 + 7 cases as copulation attempts.

Both sexes solicited copulations. Because solicitation is hard to observe (and interpret), we have no quantitative data. In those six attempts where we were sure that mounting did not happen, it was usually the female who did not respond to the display or prevented the male from mounting. Only once was a female seen trying to copulate but failing due to the lack of response by the male. During this study we observed one extra-pair copulation attempt (but in the analyses we used only within-pair copulations). The female involved refused to copulate.

3.2. Temporal pattern of copulations

Copulations occurred both in the fertile and the non-fertile periods. The frequency of copulations was 0.52/h/pair and the frequency of copulation attempts 0.43/h/pair (the data were pooled over all observation bouts) (Table 1). The logit model revealed that the duration of an observation bout affected the probability of witnessing copulations, but there was no indication that birds copulated more often when females were fertile, nor was there any interaction between the length of observation time and fertility (Table 2). The frequency of copulations did not differ significantly between prelaying, laying and incubation periods. Again, the time spent monitoring was a significant variable, but there was no interaction between it and the periods (Table 3).

3.3. Diurnal pattern of copulations

The diurnal pattern of copulations is presented in Table 4. The logit model showed that time of day had a significant effect on copulation frequency (Table 5). The values of the parameter estimates show that the birds had less copulation behaviour between 06:01–12:00 hours than before 06:01 (estimate = – 0.3146, SE = 1.015), and less in the afternoon than before 06:01 (estimate = – 8.574, SE = 22.37). When a pair copulated at dawn, it usually happened within a few minutes after the female had emerged from her roost, although the available data are limited (N = 6, mean ± SD = 6.5 ± 7.4 min). The same was true for the copulation attempts (N = 7, mean ± SD = 3.9 ± 5.5 min). The time spent monitoring proved again to be a significant factor with no interaction between it and time of day (Table 5), indicating that the length of observation time was similar on different times of day.

After the egg-laying has started, the last chance to fertilize the egg to be laid next morning, is during the so-called insemination window (Cheng et al. 1983, Birkhead et al. 1996). We included the days when females ovulate (i.e. from day – 1 to the penultimate egg) to the logit model and compared the hours before 06:01 with the rest of the day. The early hours should approximately coincide with the supposed insemination window.

Table 1. The temporal pattern in copulations and copulation attempts in regard to (a) the fertility status of the females and to (b) the prelaying, laying and incubation periods. The rates are counted as N/observed hours/pair from pooled observation bouts. Note that the non-fertile period includes both pre- and postfertile phases. See Section 4.1. for further comments.

Period	Copulation		Attempt		Copulation + Attempt		No copulation
	N	Rate	N	Rate	N	Rate	N
(a) Fertile	9	0.49	10	0.55	19	1.04	53
Non-fertile	7	0.57	3	0.24	10	0.81	42
(b) Prelaying	11	0.60	8	0.43	19	1.03	51
Laying	3	0.38	5	0.62	8	1.01	30
Incubation	2	0.49	0	0.00	2	0.49	14
Σ	16	0.52	13	0.43	29	0.95	95

Table 2. Logit model of factors affecting copulation behaviour in the Willow Tit (copulations and copulation attempts combined). Factors included in the null model are observation time and female fertility (fertile/non-fertile).

Variable	Deviance	df	Change in Deviance	Change in df	P
Null model	134.89	123			
+ Observation time	129.69	122	– 5.202	– 1	< 0.05
+ Fertility	128.91	121	– 0.779	– 1	> 0.1
+ Observation time × Fertility	127.67	120	– 1.235	– 1	> 0.1

Table 3. Logit model of factors affecting copulation behaviour in the Willow Tit (copulations and copulation attempts combined). Factors included in the null model are observation time and seasonal period (prelaying/laying/incubation).

Variable	Deviance	df	Change in Deviance	Change in df	P
Null model	134.89	123			
+ Observation time	129.69	122	– 5.202	– 1	< 0.05
+ Period	127.97	120	– 1.714	– 2	> 0.1
+ Observation time × Period	125.38	118	– 2.591	– 2	> 0.1

According to the model, none of the factors affected copulation behaviour — not even observation time, which shows the insufficiency of the data (N = 42 pairs, 3 copulations and 11 no-copulations before 06:01 hours, 5 copulations and 31 no-copulations from 06:01 hours onwards). When the same analysis was applied to the preovulation (before day – 1) pairs (N = 66), the logit model revealed the same kind of pattern as in the pooled data: both the observation time and the time of day affected copulation behaviour.

4. Discussion

4.1 Copulation solicitation and frequency

During recent years, there has been a change of emphasis in the study of sexual behaviour in respect to the relative importances of male and female behaviour (Birkhead & Møller 1993b). For example, the initiation of copulations is now considered to be controlled by females (cf. Smith 1988 and Otter et al. 1994 for results in a closely related species). Our observations are consistent with this view: if a copulation did not succeed, the refusing partner was — with one exception — the female.

High copulation rates are used as a paternity guard in species in which males cannot be sure of their mate's fidelity (Birkhead et al. 1987, Birkhead & Møller 1992). These include colonial species (where population densities are high) and birds of prey (where males have to leave females while hunting). Instead, species with low population densities and/or mate guarding have usually low copulation rates. The Willow Tit seems to belong to the latter group. There is a relatively low population density in our study area (3–7 pairs/km^2) and the forests are quite dense, allowing no visual contact between neighbours. Moreover, the males seem to guard their mate, even though this is not very intense (Koivula et al. 1991).

Extrapolating from our results gives a theoretical maximum of ca. 8 copulations/female/day (if the active time for copulations lasts 8 hours per day and the frequency of copulation behaviour is about 1/female/h, see Table 4). This is certainly an overestimation, because all observed copulation attempts were not successful and copulations occurred more often early in the morning. A more realistic estimate is achieved if we weight the frequencies in Table 4 by the proportional observation time in a corresponding time of day. If we assume that a typical day of a female contains 13 hours (05:00–18:00), then the early morning

Table 4. The diurnal pattern of copulations and copulation attempts in the Willow Tit. The rates are counted as N/observed hours/pair from pooled observation bouts. See Section 4.1. for further comments.

Time of day	Copulation		Attempt		Copulation + Attempt		No copulation
	N	Rate	N	Rate	N	Rate	N
Before 06:01	7	0.59	9	0.76	16	1.36	13
06:01–12:00	9	0.71	4	0.32	13	1.03	54
After 12:00	0	0.00	0	0.00	0	0.00	28
Σ	16	0.52	13	0.43	29	0.95	95

Table 5. Logit model of factors related to copulation behaviour in the Willow Tit (copulations and copulation attempts combined). Factors included in the null model are observation time and time of day (before 06:01/06:01–12:00/after 12:00).

Variable	Deviance	df	Change in Deviance	Change in df	P
Null model	134.89	123			
+ Observation time	129.69	122	– 5.202	– 1	< 0.05
+ Time of day	105.42	120	– 24.27	– 2	< 0.001
+ Observation time × Time of day	103.41	118	– 2.013	– 2	> 0.1

period (before 06:01) represents ca. 8%, the morning period (06:01–12:00) ca. 46% and the afternoon period (after 12:00) ca. 46% of the day. Thus, the weighted copulation frequency (see Table 4) becomes $0.08 \times 0.59 + 0.46 \times 0.71 + 0.46 \times 0.00 = 0.37$ (copulations/h/day). Similarly calculated frequency of copulation attempts is 0.21 copulations/h/day and frequency of copulations and attempts (combined) 0.58 copulations/h/day.

The low copulation frequency implies that sperm competition has not been a major factor in the evolution of Willow Tit copulation behaviour. Other tit species with similarly low copulation rates as the Willow Tit include the Great Tit *Parus major* (Björklund & Westman 1986, Kempenaers et al. 1993) and the Black-capped Chickadee *P. atricapillus* (Briskie in Birkhead et al. 1993a). The Blue Tit *P. caeruleus* is a contrary example with a copulation rate up to 7–28 per day (Kempenaers et al. 1992, 1993). It would be interesting to know to what extent these differences are caused by different habitats (e.g. park-like vs. dense forest) and population densities.

4.2. Temporal pattern of copulations

Willow Tits begin to copulate at least a week before the putative fertile period (even though the fertile period was defined to begin rather early) and continue well past the postfertile period, even during incubation. The following hypotheses may account for copulations in the non-fertile stage. (1) The social bond hypothesis (see Birkhead et al. 1987) states that pairs copulate frequently to strengthen their pair bonds. This may be especially important with migratory birds as pair formation occurs over a very short time frame. For instance, in the Willow Warbler *Phylloscopus trochilus*, the copulation rate is highest soon after a female has arrived on a male territory; thereafter the frequency decreases, and then rises again when the date of the first egg approaches (Arvidsson 1992). In the Willow Tit, pair bonds are usually established in autumn (Ekman 1979, Haftorn 1990), so the birds are certainly not strangers to each other. However, strengthening of the pair bond might still play a part in copulations outside the fertile period. If there is a risk of divorce (Orell et al. 1994), it might be advantageous for the "threatened" partner to maintain its mate's interests to retain the pairbond. The observed copulation behaviour by some non-breeding pairs also supports this hypothesis. Moreover, this could explain why females (with their probable control over copulations) want to copulate during incubation. Copulation solicitations may be a way to persuade males to invest in parental care (cf. Venier & Robertson 1991, Birkhead & Møller 1993a). (2) The stimulation of follicle growth (e.g. Erickson & Zenone 1976, but see also Birkhead et al. 1987) is a possible explanation for the prefertile copulations. This hypothesis is not necessarily incombatible with others, but (3) the observed prefertile copulations occurred so close to fertility that they could also be caused by males unaware of female status. (4) Birkhead (1979) states that in order to make extra-pair copulations harder to achieve, males disguise the exact time of female fertility with copulations during the non-fertile stage. For the Willow Tit, this is unnecessary, since neighbours are usually quite far away. The quietness of the copulation display also suggests that the pairs do not advertise their behaviour.

We found no differences in copulation frequency between prelaying, laying and incubation periods. In addition, we have witnessed spontaneously (i.e. with no simultaneous time measurements and thus not included in these data) three copulations (ranging from Day 0–3) and three attempts (Days 2–3) in the laying period, and one copulation in the incubation period (Day 6). So, it seems that copulations are not at all rare after the first egg. Most species cease to copulate when laying starts, although this is not abrupt (Birkhead et al. 1987). In their interspecific comparisons, Birkhead and Møller (1993a) concluded that the most likely explanation for this cessation is a decrease in copulation efficiency, mostly due to the difficulty of sperm passing a developing egg. They also found that when sperm competition is very intense, as in polyandrous species, there is a tendency to continue copulations for as long as females are fertile. It is unlikely that Willow Tits continue copulations because of a cuckoldry risk, since the proportion of extra-pair fertilizations does not indicate intense sperm competition (Orell et al. 1997). In some species, post-fertile copulations are attributed to possible renesting attempts in case the nesting fails (e.g. Møller 1987). In the

Willow Tit, this too is unlikely, since renesting attempts are very rare (Orell & Ojanen 1983a). Thus, the most reasonable explanation for the observed non-fertile copulations seems to be the maintenance of the pair bond.

4.3. Diurnal pattern of copulations

In contrast to our earlier interpretation (Welling et al. 1995a), we found that copulation activity peaked early in the morning, which is typical of the majority of bird species (Birkhead et al. 1987), and ceased completely in the afternoon (but we know from unpublished observations that sometimes Willow Tits do copulate in the afternoon). The reason for this pattern has usually been accounted for by the insemination window (Cheng et al. 1983) which is the short period following egg-laying (which in turn usually happens at dawn). In fact, alternative hypotheses have rarely been presented, not to mention tested (cf. Birkhead & Møller 1992). Just recently, Birkhead et al. (1996) showed how the concept of the insemination window has largely been misunderstood in the literature. Unlike often assumed, it is not the best time for fertilization in general, but merely the last chance to fertilize the following egg. Moreover, the morning peak in copulations occurs in many species before the first ovulation (Birkhead et al. 1996), i.e. before the putative insemination window, and this is only what should be expected, since copulations in most cases cease after egg-laying has started. Because the Willow Tit seems to be somewhat of an exception among monogamous birds, in that copulations continue after the first egg, we divided the pooled data into preovulation and ovulation periods. The early morning copulation peak was indeed present in the former, but unfortunately we did not have enough data for testing the ovulation period separately. We nevertheless conclude that the insemination window is unlikely to occur in the Willow Tit, because a pronounced use of it should be evident even in a small data set. Our results are an addition to a list of recent studies where no unambiguous evidence for the insemination window has been found (Birkhead et al. 1989, Venier & Robertson 1991, Arvidsson 1992, Briskie 1992, Sheldon & Burke 1994).

The question remains, why did the birds prefer to copulate in early mornings. Sheldon and Burke (1994) proposed that the reduction of copulations in the Chaffinch *Fringilla coelebs* could be due to the depletion of sperm reserves. This is possible but unlikely in the Willow Tit since the copulation frequency is low (unlike in Chaffinches). A more plausible possibility could simply be female availability (cf. Venier & Robertson 1991) after their emergence from overnight roosts. However, we have no data to test this, and the reason for the morning peak in copulations stays at a speculative level.

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Selostus: **Hömötiaisen parittelufrekvenssi ja -ajoitus.**

Tutkimme hömötiaisen parittelufrekvenssiä ja parittelujen ajoittumista suhteessa naaraan fertiilisyyteen, pesintäkauden etenemiseen ja vuorokaudenaikaan. Kohteena oli 124 oululaisen hömötiaisparin populaatio vuosina 1991–1992 ja 1994–1995. Parittelujen kesto oli hyvin lyhyt — varsinainen kloaakiyhteys kesti tuskin sekuntiakaan, koko tapahtuma ääntelyineen ja kisailuineen usein vain parikymmentä sekuntia. Molemmat sukupuolet tekivät aloitteita. Hömötiaiset parittelivat sekä naaraiden fertiilissä että ei-fertiilissä vaiheessa, jopa haudonnan alettua. Arvio paritteluiden frekvenssistä oli 0.37–0.52/h/pari ja vastaavasti paritteluyrityksistä 0.21–0.43/h/pari. Vuorokaudenajan suhteen parittelut keskittyivät aikaiseen aamuun (auringonnousun ja noin klo 06:00 väliin), kun taas iltapäivällä niitä ei havaittu lainkaan. (Tosin tiedämme tämän aineiston ulkopuolelta, että iltapäivisinkin hömötiaiset parittelevat.)

Hömötiaisella on useiden muiden reviirilintujen tavoin verrattain alhainen parittelufrekvenssi. Tämä viittaa siihen, että ns. spermakilpailu ei ole vaikuttanut lajin parittelukäyttäytymisen evoluutioon. Ei-fertiilissä vaiheessa tapahtuvat parittelut selittynevät parhaiten hypoteesilla, jonka mukaan linnut näin vahvistavat parisuhdettaan. Se, ettei parittelufrekvenssi näytä laskevan muninnan aloittamisen jälkeen, on muihin lajeihin verrattuna harvinaista. Sen sijaan parittelujen ajoittuminen juuri varhaisaamuun on linnuilla hyvin yleistä.

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