Does mate-guarding give non-territorial birds the chance to settle?

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SAMENVATTING

Hoewel monogamie bij veel vogelsoorten de norm is, bestaat er binnen soorten vaak enige variatie in het paarsysteem. Merels Turdus merula zijn zeer goed bestudeerd in Engeland. Daar waren alle paren monogaam. De onderhavige studie is het resultaat van zeven jaar onderzoek in twee stadsparken in Szczecin, Polen, waar het paarsysteem van Merels is onderzocht aan de hand van individueel gemerkte vogels. De meeste vogels bleken monogaam te zijn, maar bij 1231 broedpogingen van 437 paar werden negen gevallen opgespoord waarbij één man twee vrouwen had in hetzelfde territorium (polygynie). Verder werd één geval vastgesteld waarbij een man twee gescheiden territoria had met in beide een vrouw en twee gevallen geconstateerd van een vrouw die twee mannen had. Daarnaast werd viermaal waargenomen dat een vrouw haar man verliet kort nadat de jongen waren uitgevlogen. Daarbij nam de man de zorg voor de jongen op zich, terwijl de vrouw met een andere man aan een nieuw nest begon. Eenmaal verliet een man de vrouw direct na het uitvliegen van de jongen, waarna hij een nieuw nest met een andere vrouw begon. Merels blijken dus een ruime schakering in paarsystemen te hebben, maar in dit opzicht blijkt er dus wel variatie tussen regio's te zijn. (CB)

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DOES MATE-GUARDING GIVE NON-TERRITORIAL BIRDS THE CHANCE TO SETTLE?

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Territory defence has been suggested to serve as a means of preventing extra-pair copulations. This hypothesis predicts that territory size is largest during the fertile period, and hence at this time few new territory settlements are expected. I show that Great Tits Parus major show a peak in new territory settlements in between adjacent territories precisely at the time other pairs start egg-laying. These newly settled individuals were mostly known as floaters in the area, and did not seem to be paired before they settled. This observation is in contrast with the territory defence to prevent EPC's hypothesis. I hypothesise that males have to trade-off territory defence and mate-guarding, enabling new birds to settle at the time males mate guard.

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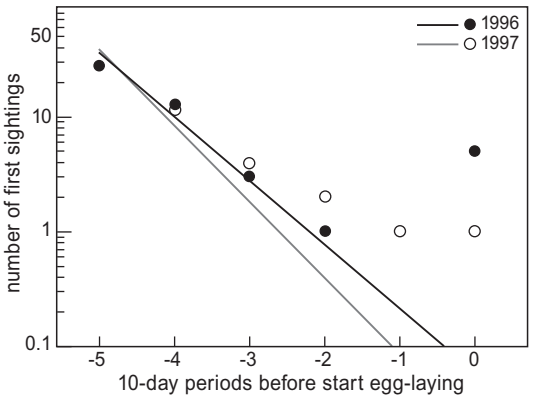
Many bird species defend breeding territories, which probably incur very diverse functions (see Hinde 1956; Stamps 1994). Recently Møller (1990) suggested that an important function of territoriality is to minimise the risk of losing paternity to neighbouring males is. He showed that in several bird species the breeding territory size peaked during the fertile period of females, suggesting that males expand their territory size at this time as a means of mate-guarding. However, several detailed studies have now shown that territory size in some bird species does not increase during the fertile period or is even smallest at this time (Rodrigues 1998). Furthermore, studies show that most extra-pair copulations are initiated by females outside their male's territory (Westneat 1992; Kempenaers *et al.* 1992; Hanski & Laurila 1993; Sheldon 1994), which contradicts the hypothesis that territory size is mainly a means of mate-guarding (Dunn 1992). Thus so far the evidence for mate-guarding as function of territoriality is contradictory. Contrary to the suggestion of Møller (1990) males might have difficulty to combine mate-guarding and territory defence, and hence they compromise one at the expense of the other. If such a trade-off between mate-guarding and territory defence exists, we expect that new territory settlements take place during the fertile period of females. At this time there are still non-territorial birds around, as shown by most removal experiments of territorial pairs (Newton 1992; Sternberg *et al.* 2002). Møller's hypothesis on the contrary would suggest that least new settlements would take place in the period when most females are fertile, since at that time males expand their territory sizes. So far, no data have been presented showing that the pattern in new territory settlements differs between fertile and non-fertile periods of females. Here I report that a new peak of territory settlement occurs in Great Tits *Parus major* around the time other individuals start egg-laying. In Great Tits mate-guarding has been shown to be common (Björklund & Westman 1986). This strongly supports the idea that a trade-off exists between territory defence and mate-guarding, rather than territory defence being a means of mate-guarding.

The study was carried out on the Buunderkamp, central Netherlands, from 1996 to 1997. This area is a mixed forest of 70 ha, dominated by *Pinus sylvestris* and *Quercus rubra*. About 350 nestboxes were provided in a regular grid throughout the area. See Drent (1987) for a more detailed description of the study area. Adults were caught during winter and early spring and provided with unique combinations of colour rings, enabling identification in the field. From mid February the area was visited almost daily to map territories. Observations of movements of individual birds and pairs were mapped as accurately on a map (1:2700), distinguishing behaviour such as foraging with and without scolding, singing, and territorial conflicts. On the basis of these spatial observations, territory boundaries were drawn and the surface of the territory areas was determined. The boundaries of the territories were defined by drawing straight lines between the locations of territorial disputes, outer song posts, and outer foraging places where scolding was heard. Sometimes territories partly overlapped, and not always 100 percent of the study area was observed to be occupied with territories. During both study years about one third of the territorial pairs in half of the study area was removed (and released >25 km away) at the start of April (Both & Visser 2000). The area where the pairs were removed was rapidly taken over by neighbouring pairs. Just a few pairs attempted to settle on the open territories just after removal, and they were were removed as well. The newly settled pairs reported here did not settle just after the removal of other pairs, and the late settlements were observed in three out of six cases in the control area and are thus not the mere consequence of the removal. In 1996 the egg laying period was from 22 April to 6 May (SD = 2.9 days), and in 1997 from 12 April to 13 May (SD = 5.4 days). Population densities were similar in 1996 and 1997 with the average territory sizes before experimental removal being about 1 ha, but 1995 had about 50% lower densities and the recruitment rate from 1995 to 1996 was about 4 times higher than in the next year (Both & Visser 2000). The aim is to show that at the time other birds

started egg-laying more new territories were established than in earlier periods during the spring. A potential problem is that the time a new territorial pair is first observed, is sometimes later than the time they settled, because not all individuals were observed every day. This sighting probability of less then unity can result in new settlements being observed at the time other individuals start egg-laying, while they occurred earlier. I test whether more new pairs were observed during the start of the laying period than expected from mere observation probability only. This is done by dividing the whole observation period into 10-day periods (periods –5 to 0, where the first day in period 0 is the day of the first egg), and calculating the observation probability for each breeding pair, assuming that they were all present at the start of period –5. The average of these observation probabilities per year was used to simulate how many newly observed individuals are expected in each period. Using a random number generator and the sighting probability the birds were assigned to either seen or not seen in the first period. The birds that were not seen in the first period entered the second period, and so on until all birds had been seen. Thousand runs were done with this procedure to get a distribution of numbers seen at period x for the first time or later. This distribution is used to calculate the p-value for the observed number of new pairs settling. In this way I can show whether the peak in new observations at the start of egg-laying is real or just a result of observation bias.

New sightings of territorial individuals decreased rapidly after the start of fieldwork in both years (Figure 1). In the period that egg-laying commenced, there was a clear peak of new territorial pairs first seen, best seen in 1996 (Figure 1). If both years are combined, the number of new pairs seen in the period of egg-laying was 6, which was significantly greater than expected given the observation probability of 0.74 (probability of ≥6 new sightings at period 0 or later, randomization test: $P = 0.036$). These pairs were all seen to sing in their territory, and had some conflicts with their neighbours. Since settlement happened at the start of the laying period, territory



sizes of the new settlers and the consequences for territory size of the earlier established birds could not be measured due to lack of observations. That the newly sighted individuals were indeed non-territorial before, and not just missed territorial birds earlier in the season, is corroborated by earlier observations of these individuals. One male was known to be expelled from his territory three weeks earlier by two other males, and was not seen until he started defending a new territory at the time other birds started egg-laying (Both 1999). His mate was originally paired, but her male disappeared about three weeks before the start of egg-laying. She was subsequently seen to associate with two pairs in the same neighbourhood, but was chased away by the pair females. Another late-settling male was seen several times in the preceding weeks attempting to defend a territory about 100 meters from his final territory. His final mate was seen once to associate with another pair in the neighbourhood of the final territory. A similar pattern was seen in another female: early in the season she was paired, but her mate got another female. She was frequently seen in the neighbourhood, associating with her former mate, and being chased by his new female. She became finally settled with an unringed male, close to the territory of her former mate. Two males were found sleeping in nestboxes about 6 weeks before the breeding season, one at about 200 meters and the other at 50 meters of their final territories. Their mates were unknown. The last pair was caught seven months earlier as first

year birds in the same mist-net about 500 meters of their final territory, and were not seen until they settled. Thus, three of the six females were seen in the territory of their final mate earlier in the spring, where they attempted to get paired with already paired males. Only one male was found close to the place of his final territory, whereas three males were seen earlier in the season but not in the neighbourhood of their final territory.

Great Tits defend their breeding territories already months before they start egg-laying (Hinde 1952; Drent 1983), but just at the time egg-laying started some new territory settlements were observed. These settlements occurred in half of the times at sites where females were seen frequently, whereas for their males there was no suggestion that they were attached to the site of their final territory. These late settlements coincide with the time that males guard their females to prevent extra-pair copulations (Björklund & Westman 1986). This suggests that there is a trade-off between territory defence and mate-guarding, enabling some non-territorial pairs to establish a territory. If territory defence is a means of mate-guarding (Møller 1990), it is expected that territories are largest at the time of mate-guarding. The results of this study show that during the fertile period floaters are able to settle at existing territories, which is unlikely if the settled pairs also enlarge their territories at the same time. In contrast, the settled individuals lose territorial space to those newly settled individuals, suggesting that males have to compromise between territorial defence and mate-guarding. Similarly, Chaffinches *Frinchilla coelebs* decrease the size of their defended territory during the fertile period of the female (Hanski & Laurila 1993), which may as well be due to a trade-off between both activities. Mate-guarding is the result of a conflict between the sexes, with females apparently benefiting from gaining extra-pair copulations, and males clearly losing fitness as a result of the EPC's of their partners. This study suggests that females also may lose fitness if their males' territory defence is compromised, because fitness is strongly related to territory size in Great Tits as shown by manipulations of territory size (Both & Visser 2000). As both males and females pay a cost of mate-guarding because the price is the loss of part of the territory, the conflict over mate-guarding may be less than expected. The phenomenon of late-settling pairs should be compared with the phenomenon of guest breeders as described in Great Tits (Dhondt & Schillemans 1983; Drent 1987). These guest breeders are territorial, but have their nest in another territory because their own territory lacks a suitable nest site. Guest breeders behave inconspicuously, and do not sing in the territory where they breed in (Dhondt & Schillemans 1983). In my case, all birds were at least seen singing during one day, and most had conflicts with their neighbours. Also the history of known birds shows that they were not having a territory before, or lost it some weeks earlier. The late-settling pairs thus were non-territorial prior to their settlement, and were able to defend a territory at the time other pairs start egg-laying.

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SAMENVATTING

Waarom verdedigen mannen van zo veel vogelsoorten in het voorjaar een territorium? Eén idee is dat ze dit doen om buurmannen ver van hun vrouw vandaan te houden, waarmee ze hun vaderschap proberen te verzekeren. Je verwacht dan dat territoria het grootst zijn in de vruchtbare periode van de vrouw. Een andere manier om het eigen vaderschap te verzekeren, is de vrouw gedurende haar vruchtbare periode steeds zorgvuldig in de gaten te houden en haar zodoende de mogelijkheid te ontnemen om met andere mannen te paren. Je verwacht dan dat gedurende de vruchtbare periode mannen juist minder tijd zullen besteden aan het verdedigen van hun territorium en dat deze verminderde territorialiteit de niet-territoriale paren de mogelijkheid biedt om zich alsnog te vestigen en tot broeden te komen. Dit laatste zagen we bij Koolmezen die we op de Zuid-Veluwe gedurende twee jaar bestudeerden. Op het moment dat de meeste vrouwen begonnen met het leggen van eieren, vestigden zich verschillende nieuwe paren. Dit waren er duidelijk meer dan de maand voorafgaand aan de reproductieve periode. Van een aantal vogels wisten we dat ze al een tijd in het gebied aanwezig waren en eerder hun territorium of hun partner (en daarmee ook hun territorium) hadden verloren. Drie van de zes vrouwen die zich zo vestigden, deden dit op de plaats waar ze al een tijd als niet-territoriale vogel aanwezig waren, terwijl we voor mannen geen aanwijzing vonden dat ze zich vestigden op een plaats waar ze al een tijd aanwezig waren. Deze observaties suggereren dat de verdediging van een territorium en het bewaken van een vrouw niet makkelijk samen gaan, en dat mannen een afweging moeten maken tussen beide activiteiten. Andere vogels zonder territorium kunnen hiervan profiteren.

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