

A case of polyterritorial polygyny in European Nightjar *Caprimulgus europaeus*

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(Med et dansk resumé: Et tilfælde af polyterritorial polygyni hos Natravn)

Abstract A case of polyterritorial polygyny among European Nightjars was observed in the summer of 2011 in a breeding population in Thy National Park in NW Jutland, Denmark. A male was found to have two territories with a female in each, and with a distance of c. 5 km between them. Polyterritorial polygyny is not previously reported from European Nightjars. Polygyny is known in particular from a number of passerines, raptors, waders and from three other nightjar species. The reason for this behavior is considered to be a combination of several factors, with the main objective of maximizing the production of chicks within the short breeding period available.

Introduction and methods

During a study of behavior and habitat use in a European Nightjar breeding population, we discovered a case of polyterritorial polygyny, a behavior not previously described among European Nightjars. Earlier observations indicate rare cases of monoteritorial polygyny, and double-brooding and female mate-switching between broods are known as well (Cramp 1985, Cleere & Nurney 1998).

We here define polyterritoriality as cases where a male defends two clearly separated territories, i.e.

with an area between the two territories which the male does not defend. This area may contain territories of other males, or it may be clearly unsuitable as breeding habitat. Polyterritoriality is seen only in a minor part of polygynous species (Møller 1986).

The study was carried out during the summers of 2011 and 2012 in a Nightjar population in Thy National Park in NW Jutland. The breeding population in Thy holds around 120 pairs and has been stable over the past 20 years (Jensen 2010).

The main purpose of the study was to investigate habitat use of the Nightjars around their breeding sites. For this purpose birds were tagged with VHF radio transmitters and monitored using

† Niels Odder Jensen perished in an accident on 4 August 2013

radio receivers throughout the breeding season. The transmitters were tail mounted and weighed about 1 g. They could be tracked at distances of up to a few hundred meters when the birds sat on the ground, and up to 3 km in open landscapes, when the birds were in the air. A total of 16 males were tagged, eight in 2011 and eight in 2012. The study took place in two breeding areas. In June and the first half of July tracking generally took place every other night in the two areas. We used 1-5 hours in the field each time. In the rest of July and in August tracking was generally more sporadic with searches about 2-3 times a week.

A surprising result of the monitoring was the discovery of a case of double territories in 2011. After the male performing polyterritorial behavior was discovered, we attempted to track it at least once per day. Although our focus on this particular behavior was intensified, it was not possible to allocate sufficient resources to identify other possible cases of polyterritoriality 2011. In 2012 we made an additional effort but without further observations of polyterritoriality.

Results

Seven of the eight males in 2011 kept fairly well-defined territories, while one male clearly alternated between two territories c. 5 km apart (Fig. 1). The male moved between the two places to defend territories, usually every other day, but with slightly varying frequency (Fig. 2).

Behavior at territory A: In five instances, the male was observed flying with a female during June and July. In July, the male stayed for a period of three weeks in the territory (Fig. 2), and on 20 July, the male, female and 1-2 young were seen flying together, indicating that the male was on territory A in the period after the chicks had hatched; possible in late June. After helping to raise chicks it moved again partly to territory B.

Behavior at territory B: The female on territory B was only seen twice; once flying with the focal male. When the male stayed here, it was relatively active, singing and flying around. We often heard the male and female calling to each other, indicating pair-bond, but we did not find any proof of breeding success in this territory.

The male was tracked over six full nights, and the results showed that it stayed in the same territory all night, interrupted only by short trips into neighboring male's territories. Other registrations were limited to single observations of a few minutes

duration. Activity patterns were the same each time the male moved between territories. After sunset he sang for a few minutes then flew to the other territory. Here he claimed territory the rest of the night and was resting there the next day, only to return to the first territory and repeating the pattern. The nights where the male was not present on territory A and B, respectively, neighboring males were calling and claiming territories much closer to the non-guarded territories. None of the surrounding males seemed to be able to enter territory A or B, however, even though the two territories were defended only every second night or less.

Discussion

It is now common knowledge that some European Nightjars have two clutches, the second usually initiated c. 2 weeks after the first brood has hatched, whereupon the male takes care of the young from the first brood (Lack 1930, 1932, Cramp 1985). In couples with two broods, an 'extra' male helping the female to raise her second brood has been observed in some cases (Schlegel 1969, Cresswell & Alexander 1990).

Cleere & Nurney (1998) mention that in rare cases dominant males can court two females. Nest sites can be up to 40 m apart, and the timing of the two broods spaced with 14 day intervals. The male may mate again later with one of the females and get a third brood. In our case, however, the incident involved polyterritorial polygyny, where the male's two territories were clearly separated from each other.

Several studies indicate that in polygynous relations there is usually a primary and a secondary female. Young of secondary mates in a variety of species received less parental care than those of primary mates, and less parental care often leads to lower reproductive success among the secondary females (e.g. Korpimäki 1988, Temrin & Arak 1989, Alatalo *et al.* 1990, Searcy & Yasukawa 1996, Qvarnström *et al.* 2003, Huk & Winkel 2006).

In this study, the female in territory A may be described as the primary female and the female in territory B the secondary female. The primary female in territory A was found with fledglings in July, while the breeding success of the secondary female in territory B remained unknown. Due to the male's long presence in territory A in July, any chicks in territory B must have been left with the female to care for.

The biological purpose of polyterritorial polygyny is still uncertain despite the presence among several bird species. In a review of mating systems



Fig. 1. The location of the two territories (A and B), held by one male, together with neighboring territories in 2011. The area is situated in NW Jutland inside Thy National Park. *Placeringen af de to territorier (A og B), der blev holdt af den samme han i sommeren 2011, samt naboterritorier. Området er beliggende i Nordvestjylland i en del af Nationalpark Thy.*

of European passerines, Møller (1986) reported that most of the species that practice polyterritorial polygyny are long-distance migrants. Most long-distance migrants have relatively short reproductive 'windows' and hence particularly strong pressure to optimize the breeding period. It is possible that simultaneous breeding by both females in the optimal breeding period with a dominant male can explain polyterritorial polygyny, as opposed to a normal monoterritorial reproductive cycle with two broods in a sequence, thus spread over a longer time period.

Another possible explanation could be that paired males can establish extra territories when there are plenty of good breeding areas, simply because advertising from multiple locations increases their chances of being discovered by unpaired females (Ford 1996).

The choice of two separate territories can also lead to other advantages. By defending two territories separated by a long distance, males can effectively prevent or reduce contact between their two mates (Temrin & Arak 1989), and it can furthermore prevent females from discriminating between the mating statuses of males (Alatalo *et al.* 1990).

The polygyny-threshold model (Verner & Willson 1966, Orians 1969) has been discussed as a possible explanation for polygyny. The model is based on the assumption that a female can obtain a higher reproductive quality by choosing a strong male that is already mated, and that this can compensate for the lack of a permanent male. The model has been the subject of numerous discussions since it was first published, but the basic hypothesis of a long-term genetic advantage when choosing the best adapted individuals as partners seems justified.

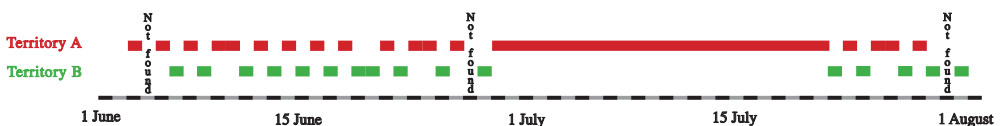


Fig. 2. Time allocation of the male Nightjar between two territories, A and B, during the season 2011. *Fordelingen af Natravnehannens ophold i de to territorier A og B gennem sæsonen 2011.*



Nightjar at a typical day roost on a branch in a pile of old pine branches. Photo: Niels Odder Jensen.
Natravn der 'overnatter' på typisk dagrastesteds på en gren i en bunke gamle fyrregrene.

However, the model was developed for monoterritorial situations and assumes that the female knows the male's mating status which is not given in polyterritorial males. It is therefore possible that the model is not sufficient to explain polygyny when polyterritorial (Korpimäki 1988, Searcy & Yasukawa 1989, Alatalo & Rätti 1995).

Polygyny is known only from a few nightjar species, White-winged Nightjar *Caprimulgus candicans* (Pople 2003), Standard-winged Nightjar *Macrodipteryx longipennis* and Pennant-winged Nightjar *M. vexillarius* (Holyoak 2001), whereas polyterritorial behavior so far is unknown in the nightjar family Caprimulgidae.

As discussed above, it is not possible to provide a complete answer to why some nightjars choose polyterritorial polygyny, but it may be speculated that it is caused by a combination of optimal feeding conditions in a particular period of the breeding season, vacant territory opportunities, strong dominant males and breeding females available.

Although the case described here represents the only observed occurrence of polyterritorial behavior there may have been more polyterritorial males

in the studied breeding population. It requires intensive monitoring to identify incidences of polyterritorial behavior. In the light of the present discovery a few older observations of ringed males from the local area in Thy, which were recaptured during the breeding season far from their original breeding site, could possibly be related to poly-territoriality. It must be assumed that this type of behavior is only practiced by a small proportion of the Nightjar population in the area, yet it may give cause for reflection, when population censuses are carried out.

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A male European Nightjar was found to have two territories with a female in each in Thy National Park, Denmark, in 2011. Photo: Claus Halkjær Nielsen.

I 2011 fandtes en Natravnehane i Thy Nationalpark, der havde to hunner i hvert sit territorium.

Resumé

I forbindelse med habitat- og adfærdsstudier af Natravne på deres ynglelokaliteter i Thy i Nordvestjylland blev der fundet et tilfælde af polygyni og polyterritorial adfærd. Observationen blev gjort hos en han, der var forsynet med en radiosender og derfor kunne spores over et større geografisk område.

Hannen holdt to territorier med to forskellige hunner og med en afstand på ca. 5 km mellem territorierne (Fig. 1). Hannen befandt sig skiftevis på de to territorier; i reglen hver anden nat på hvert af dem, men med en vis uregelmæssighed (Fig. 2). I en periode i juli opholdt den sig udelukkende på territorium A. Her sås den flyve med hun og unger, hvilket tages som udtryk for, at den valgte at være med til opfostringen af ungerne her. I slutningen af juli vendte den tilbage til at veksle mellem de to territorier. Ynglesuccesen hos hunnen på territorium B kendes ikke.

Selv om hannerne fra de omkringværende territorier jævnligt forsøgte at trænge ind på både territorium A og B, når hannen her ikke var til stede, lykkedes det aldrig andre hanner at overtage nogen af de to territorier.

Det er efterhånden almindelig kendt, at en del Natravne får to kuld unger. Det sker som regel ved, at hunnen lægger et nyt kuld æg ca. 2 uger efter at første kuld er klækket, hvorefter hannen overtager pasningen af ungerne fra første kuld. Hos par, der lægger to kuld, er det iagttaget, at en ekstra han i visse tilfælde kan være med til at opfostre andet kuld, således at hannen på den måde har hjælp fra to hanner til yngleplejen. I sjældne tilfælde

kan det forekomme, at dominante hanner kan spille for to hunner. Redestederne kan være op til 40 m fra hinanden, og de to kuld kan være lagt med op til 14 dages mellemrum, altså polygyni inden for det samme territorium. I det undersøgte tilfælde er der imidlertid tale om polyterritorial polygyni, hvor hannens to territorier ligger klart adskilt fra hinanden.

Polyterritorial polygyni er et velkendt fænomen fx blandt visse spurvefugle, rovfugle og vadefugle. Den evolutionære baggrund for polyterritorial polygyni er trods forekomsten hos adskillige fuglearter stadig usikker. Flere undersøgelser peger på, at den sekundære hun ofte har ringere ynglesucces end den primære.

Polygyni kendes kun fra andre natravnearter, nemlig Hvidvinget Natravn *Caprimulgus candicans*, Standartvinge *Macrodipteryx longipennis* og Vimpelvinge *Macrodipteryx vexillarius*, alle i en monoterritorial form, hvorimod polyterritorial adfærd hidtil har været ukendt hos natravnefamilien Caprimulgidae.

Det er ikke muligt at give et fyldestgørende svar på, hvorfor nogle individer vælger polyterritorial polygyni. Det kan skyldes en kombination af optimale fødemuligheder i en bestemt periode af ynglesæsonen, ledige territorier, stærkt dominerende hanner samt yngleledige hunner. En større tæthed af observationer i nærværende undersøgelse kunne måske have afsløret flere fund af polyterritorial adfærd. Det må dog antages, at denne adfærdsform kun praktiseres af en mindre andel af Natravnebestanden i området.

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