

Male and female Penduline Tit *Remiz pendulinus* can reverse their desertion decisions

Hane och hona av pungmes Remiz pendulinus kan ändra sina beslut om att överge äggkullen

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Abstract

The Penduline Tit *Remiz pendulinus* is a species that displays uniparental care. Either the female or the male parent abandons the clutch before incubation commences, and both parents desert about 30% of clutches. Deserting individuals may nest again and have up to six partners over a breeding season. We describe five cases of an apparent reversal of the decision to desert by four male and one female Penduline Tit in Sweden and Poland. Several days after abandoning a clutch, the individuals returned

to their nests and began incubation. All clutches were successful.

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Parental care is costly, and there is a conflict between parents over the amount of care invested in their offspring (Trivers 1972, Parker et al. 2002). For an individual male or female the best option is to pass their parental care duties onto someone else, usually their partner (Arnquist & Rowe 2005). Although the female provides care alone in many avian species, regular clutch desertion is relatively rare in birds, and if it occurs, it is usually the male who deserts (Lack 1968, Davies 1991). Sexual conflict over care is well displayed in the breeding system of the Penduline Tit *Remiz pendulinus*. The main features were described by Persson & Öhrström (1989) and can be as follows: The male usually initiates nest building but a female may join him at any stage. Only one parent, male or female, provides parental care. Clutches are deserted before incubation commences, and both parents abandon about 30% of the clutches. Deserting males and females may nest again and have up to six partners in sequence over the breeding season.

Szentirmai et al. (2007) showed that both male and female Penduline Tits might benefit from desertion by remating with a new partner. However, in some situations such as low remating opportunities, desertion by the other parent or mating to a partner of high quality, it may be better to invest in the present brood (Székely et al. 2000). To inves-

tigate the factors underlying individual Penduline Tits' decision whether to provide parental care, we have studied populations in Sweden and Poland since 1980 and 2002 respectively. In this report we describe five cases of an apparent reversal of desertion decision: A few days after abandoning a clutch, the individuals returned to their nests and started incubation.

Study area and methods

The observations were made at several different sites in SW Sweden and at the Milicz fishponds in SW Poland. The habitats in which Penduline Tits built their nests were similar at the Swedish and Polish sites, consisting mainly of ponds and marshes bordered by reeds *Phragmites australis*, willows *Salix spp.* and birches *Betula spp.* For a description and maps of the Swedish sites, see Persson & Öhrström (1989, 1994).

Our core areas were monitored at least twice a week starting when the first Penduline Tits arrived to the breeding sites. In South Sweden the first birds arrived in April, occasionally earlier. Egg laying usually occurred from early May through June. At the Milicz fishponds the first Penduline Tits arrived in the end of March and the egg laying period began in the second half of April and ended in mid July. We

considered a pair to be formed if the mates were observed copulating near the nest or if they were found building the nest together. The birds were caught and individually colour-ringed using a mist net and song playback. We usually refrained from nest inspections during the egg laying period to minimise the risk of disturbing the birds while still mated. Furthermore, eggs may be buried in the nest. Should an egg become visible, this may influence a decision of whether to stay or desert (Valera et al. 1997). Nests where one or both parents seem to have deserted were watched for at least 15 minutes, which normally is sufficient to record the presence of the mates (Van Dijk et al. 2007). If one or both mates were not observed, observation time was extended unless they were found elsewhere in the study area. In problematic cases, we often visited the nest a second time on the same day. The different nest building stages were categorised from A (earliest stage) to F (finished) according to Figure 1. Since these stages can convey information about the state of the breeding attempt, we present a short account of the nest building process. For more details, see Schönfeld (1994). Plant fibres are attached to the selected twig and stage A can be reached within a day. At stage B the forks are connected and a ring is formed. The ring is expanded and widened to a hammock, C. This stage could be reached after three days of work. The nest is gradually expanded to a basket, D. Nest built by an unmated male may remain at this stage for weeks. If a female is present, the nest is further enlarged, mainly from the inside. One side is selected as the entrance while the other side becomes closed, resembling a bag, E. Egg laying, one per day, usually occurs at this stage, but sometimes at the previous stage (Schönfeld 1994). Finally the spout is constructed, but it is initially short and appears first only as a roof over the entrance of the near finished nest, F-. We have never found a nest at this stage without an egg clutch. Deserted nests are usually found at this stage or at stage E. The long spout of the finished nest F is completed by the incubating bird. The total building time varies considerably, depending on time of year, weather conditions and if a female is present. Under ideal conditions stage F- could be reached within a week, but 10 to 14 days is more common.

Results

We observed four males and one female who reversed their previous decision to desert a nest, having then returned and begun to incubate after apparently abandoning the clutch. In all described

cases we have observed a pair in joint nest building up to a stage E (without spout) or where the entrance spout was initiated (stage F-). All males were found to construct a new nest after their desertion but no eggs were laid in these. The observations are outlined in Figure 2.

Male 1, 1984, Lomma, Sweden (55°41'28'' N, 13°03'26'' E)

Male 1 was first observed on 23 April, when he was building a ring-nest (B). He remained nest building at this site but a female was not observed until 20 May, by when the nest was complete with a short spout (F-). On 24 May Male 1 was found building on a small basket (D) 350 m south of the first nest. There was no indication of any females in the area. On 27 May the male was found incubating in the first nest and four young fledged in late June. With an estimated incubation period of 14 days and a nestling period of 20–22 days (Schönfeld 1994) incubation should have commenced on May 25. This infers that eggs were present in the first nest while the male was constructing the new one. The latter was abandoned, containing no eggs. The nearest observed nest-building males were 13 km SE and 16 km NW, but no females were observed at these sites.

Male 2, 1985, Lake Börringe, Sweden (55°30'05'' N, 13°18'52'' E)

Male 2 was first observed on 26 May when he was found nest building (C). On 29 May he was still single but on 1 and 2 June a ringed female was present building at the bag-nest (E). By 4 June the nest had been completed (F-), although Male 2 was observed building a new nest (C) 350 m to the south of the original nest. The female was not observed at either nest at this time. On 8 June Male 2 was incubating in his original nest, while the female was found nest building with a new male 4.3 km to the northwest. The second nest was deserted with no eggs. Nestlings were being fed on 20 June; hence incubation would have started no later than 7 June. The female was the only known in this study area. Previously in this season she deserted three clutches with other males, her next clutch was also deserted while she finally assumed care at the last one.

Male 3, 1997, Lake Kranke, Sweden (55°42'04'' N, 13°26'25'' E)

On 26 May the male was constructing his third nest (C), aided by an unringed female, while on 30 May

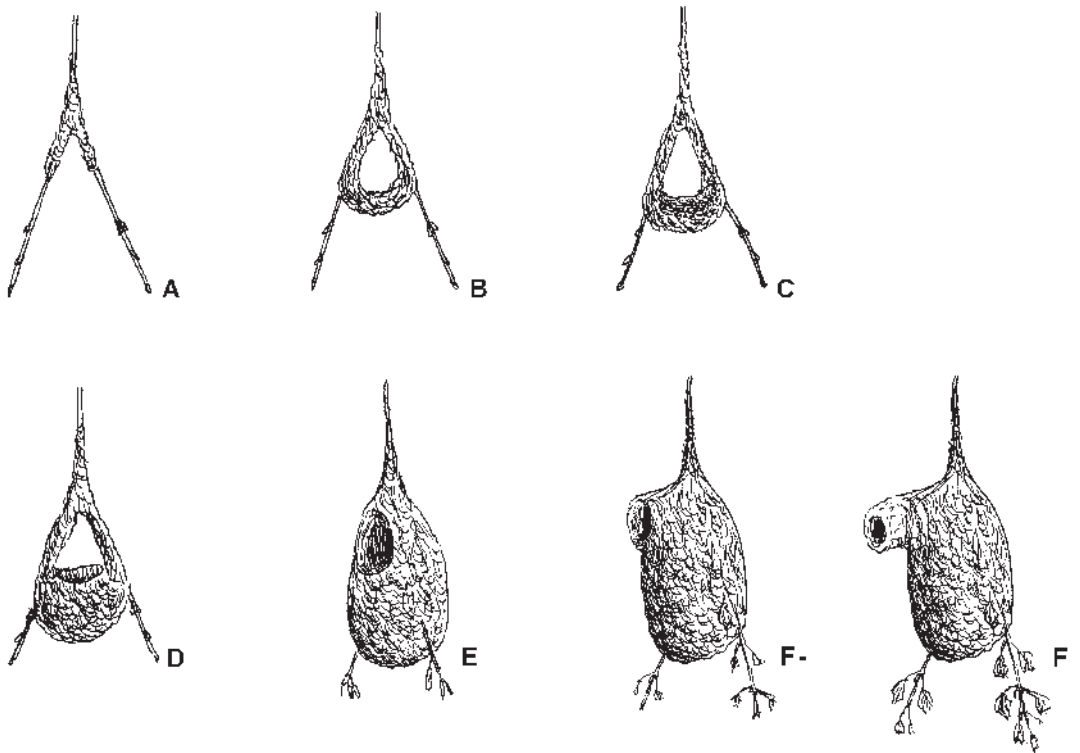


Figure 1. Nest building stages in the Penduline Tit. (Drawing by O. Persson, modified from Persson & Öhrström 1980). *Bobygnadsstadiet hos pungmes. (Teckning O. Persson, modifierad från Persson & Öhrström 1980).*

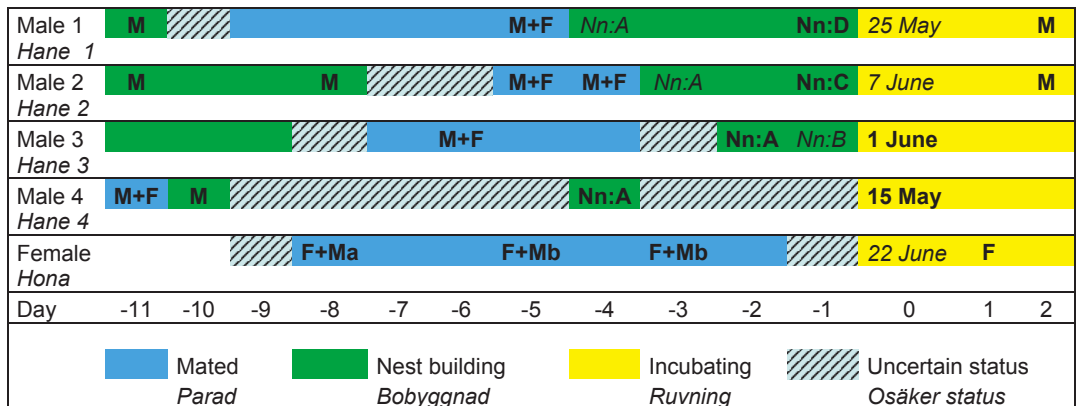


Figure 2. Observations of each individual displayed on timelines. Direct observations are shown in bold letters, estimates in italics. M = male, F = female, Nn: X = new nest: stage. Day 0 represents the day incubation commenced. The mating period of males 1, 2 and 3 was estimated as clutch size + 1 day. Note that male 4 was mated from day -20 which is not shown in this figure.

Observationer av varje individ visad utmed en tidslinje. Direkta observationer anges i fet stil, beräknade värden anges kursivt. M = hane, F =hona, Nn:X = nytt bo: stadium. Dag 0 är dagen då ruvning inleddes. Parningsperioden för hane 1, 2 och 3 beräknades som kullstorlek +1 dag. Observera att hane 4 var parad sedan dag -20 vilket inte visas i denna figur.

he had commenced building a fourth nest at an early stage (A) 500 m away and was accompanied by a different (ringed) female. The third nest, now near-finished (F-), was inspected, containing three partly buried eggs. Male 3 had returned to the third nest by 1 June, assumed care, and the young were fledged by 10 July. The fourth nest was deserted at stage B. The two females mentioned were the only ones (out of 9) not involved in providing care at the end of May, having previously deserted one clutch each. Both females remated and were found incubating on 10 June.

Male 4, 2006, Milicz Fish ponds, Poland
(51°32'55'' N, 17°22'33'' E)

Male 4 was first observed as part of a pair that was building a nest at the ring-stage (B) on 25 April. Both Male 4 and the female were still present on 27 April, although the female was not observed on 1 May. On 4 May both birds were again engaged in building the nest, which lacked only the entrance spout (E). Male 4 was observed at the nest on 5 May, while the female had deserted. Male 4 was not observed until 11 May, when he was working on a new nest 250 m SE of the original nest. Meanwhile, on 8 May, the female had appeared at the nest of another male 250 m SW. Male 4 was again observed at his first nest on 15 May while he was completing the entrance spout. Incubation should also have started on that date since the nestlings hatched on 29 May. After two young had fledged from this nest in June, Male 4 began building a new nest, although no further breeding was observed. During the described period (from Male 4's desertion to his return) the proportion of unmated males to unmated females in the studied population was 7:2.

Female, 1983, Lake Kranke, Sweden
(55°42'04'' N, 13°26'25'' E)

This female's first breeding attempt failed due to nest predation on 10 or 11 June, but on 14 June she was observed nestbuilding with her partner at a large nest that lacked only the spout (E). On 17 June she was seen actively building with another male at a new nest (D) situated 1.0 km to the northeast, while her first partner continued building the original nest alone (F-). Two days later, this original male began building another nest while the female remained with the second male at their near-finished nest (E). On 22 June the female had returned to the first nest, commenced incubation,

and four young fledged in July. The nest of the second male contained no eggs. This female was the only one (out of 8) not engaged in parental duties in mid June. There was only one other nestbuilding male remaining in the area, aside from the two males mentioned above.

Discussion

To our knowledge, these are the first records of Penduline Tits reversing their desertion decisions. A potential problem is that the presence of a clutch at the time of the desertion was only confirmed at one nest, and inferred at a second one. It might be argued that other females could have laid eggs while the male was constructing his new nest. This is however unlikely under the circumstances we describe and would require unknown females in the areas of which there were no indications. Other alternative interpretations would be that a male could build two nests at the same time either to attract another female simultaneously or to prepare for desertion. We do not regard these explanations as likely, since we have never observed a male being mated to two females simultaneously, nor is it described in the literature. In addition, we only have one observation of a male initiating a new nest while still being mated, and in this case the female assumed care at the first nest (B. Czyż pers. obs). The conflict over care between a male and female Penduline Tit can be described as an arms race. It has been suggested that each mate should disguise any intention to desert, and detailed observations seem to support this (van Dijk et al. 2007). By building a new nest a male clearly shows his intention to remate, so this should be done after the female has deserted or assumed care. Since we observed pairs jointly building on advanced breeding nests, we can be confident that clutches also were present when the nests were first deserted.

The interpretation of the behaviour of the female reversing her decision also touches another issue. It seems possible, or even likely, that both males contributed to her clutch. Extra pair paternity, albeit on a low level of 7%, was reported in this species (Schleicher et al. 1997). Provisional results indicate a similar frequency in Sweden (O. Persson unpubl) but much higher (40% of nests) in Poland (B. Czyż unpubl.). Multiple mates may yield several benefits to a female (Fossøy et al. 2007). Our observation suggests a possible way for a female to increase the genetic diversity of her offspring without the risk of clutches being deserted.

Each of the observations appeared as typical in-

stances of desertions by both mates, until one of them returned. Desertion is a common strategy by males and females of this species; previous studies show that between 82–92 % of nests are abandoned by males and 35–53 % by females (Franz 1988, Franz 1991, Persson & Öhrström 1989, Czyż 2008). Desertion decision may depend on many factors e.g. remating opportunities, body reserves, attractiveness etc. (Szekely et al. 2000). Our observations seem to have one thing in common, namely that there were few opportunities for birds to mate with new partners at the time of reversing the decision to desert. Although recent studies suggest that remating opportunities seem to play a little role in determining which parent should desert (Szentirmai 2005, Czyż 2008), it seems possible that reversing decision was influenced by lack of potential mates. Our observations also indicate that this strategy is more frequent among males, and occurring in 4 out of 123 records of male care.

These observations may have some interesting implications for understanding the process of clutch desertion. Data from a study in Hungary (van Dijk et al. 2007) suggest that female and male make the decision simultaneously, while observations from Sweden and Poland show that females frequently desert earlier than males (Persson & Öhrström 1989, Czyż unpubl.). The female mentioned in this report did actually leave a male and desert first, but for the other Swedish individuals the order of desertion was unclear. At the described nest from Poland the female deserted before the male.

An observation of reversing desertion decision was also made in Little Egrets *Egretta garzetta* (Fujioka 1989), in which either the male or female may abandon the nest approximately three weeks after hatching. One female that had deserted her 17-day-old chicks returned after 20 days and resumed feeding. During her absence the male took all parental duties.

The observations we present here suggest that desertion may be a complex process, and that individual birds may actually reverse their previous decision. Although this strategy is rare, it shows that Penduline Tits can change their behaviour, which might increase their chances to rear offspring.

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Sammanfattning

Att vårda sina ungar är kostsamt och för en förälder kan det vara att låta någon annan, vanligtvis sin partner, att ta hand om uppfödandet. Därmed uppstår en konflikt mellan könen vilken är speciellt tydlig hos pungmesen där bara en av föräldrarna tar hand om ungarna. Kullen lämnas innan ruvningen inletts, och cirka 30 % av alla kullar överges av båda föräldrarna. Både hanen och honan kan inleda nya parförhållanden och den enskilde individen kan därmed få fördel av att lämna en kull (Szentirmai et al. 2007). Det skulle emellertid ibland kunna vara bättre att stanna kvar, till exempel om det finns få nya parningsmöjligheter, man har blivit övergiven eller partnern har uppvisat goda kvaliteter. Vi har studerat pungmespopulationer i Sverige och Polen sedan 1980 respektive 2002 för att undersöka vad som påverkar en pungmesindivids beslut om att ta hand om en kull. I denna rapport beskriver vi fem fall där pungmesar uppenbarligen har ändrat ett beslut. Några dagar efter att ha övergett en kull återvände de till sina bon och inledde ruvning.

Studieområde och metod

Observationerna gjordes på flera lokaler i Skåne samt vid fiskdammarna nära Milicz i sydvästra Polen. Våra kärnområden inventerades minst två gånger i veckan under häckningssäsongen. Vi bedömde att ett parband upprättats när ett par såg kopulera nära ett bo eller de sågs gemensamt bygga på ett bo. Fåglarna fångades med hjälp av nät och en bandspelare och blev individuellt färgmärkta. Vi avstod från boinspektioner under äggläggningsperioden för att undvika störningar. Bon där en eller båda föräldrarna verkade ha övergivit bevakades i minst 15 minuter vilket normalt är tillräckligt (van Dijk et al. 2007). Tiden kunde utökas om fåglarna inte observerades någon annanstans i studieområdena och i problematiska fall gjorde vi oftast ytterligare besök samma dag. Bobyggnadsstadierna beskrevs från A till F enligt figur 1. Eftersom de olika stadierna kan visa i vilket skede häckningsförsöket befinner sig presenterar vi en sammanfatt-

ning av byggnadsförloppet. Växtfibrer fästs i den utvalda klykan och A-stadiet kan nås inom en dag. Därefter binds klykan samman och en ring bildas (B). Ringen vidgas och breddas till en hängmatta (C) vilken kan vara klar inom tre dagar. Boet förstoras successivt till en korg (D) och bo byggda av ensamma hanar kan kvarstå i detta skede i flera veckor. Om en hona är närvarande kommer boet ytterligare att förstoras, huvudsakligen från insidan. Ena sidan blir ingång, medan baksidan försluts och boet blir en säck (E). Äggläggningen sker vanligtvis i detta skede men kan påbörjas redan i korgbon (D). Slutligen byggs ingångsröret, men i början är detta kort och bildar först ett litet tak över ingången till det nästan fullständiga boet (F-). Vi har aldrig funnit ett bo i detta skede utan att det har innehållit ägg. Bon med övergivna kullar är också i detta stadium eller i E-stadiet. Det långa ingångsröret på det fullständiga boet (F) färdigställs av den ruvande fågeln. Den totala bobyggnadsstadiet varierar, men under ideala förhållanden kan stadiet F- uppnås efter en vecka, men oftare efter 10–14 dagar.

Resultat

Vi observerade fyra hanar och en hona som ändrade sina beslut genom att återvända till sina övergivna bon och inleda ruvning. I samtliga fall observerade vi par som byggde bon fram till stadierna E eller F-. Alla hanar observerades bygga nya bon men några ägg lades inte i dessa. Observationerna redovisas också i tidslinjerna i figur 2.

Hane 1, 1984, Lomma, Sverige. Hane 1 sågs bobygga den 23 april men ingen hona observerades förrän den 20 maj då boet var nästan färdigt med ett kort rör (F-). Den 24 maj sågs hanen vid ett nytt bo (D) 350 m söder om det första medan honan verkade ha lämnat området. Den 27 maj ruvade hanen i det första boet och 4 ungar blev flygga de sista dagarna i juni. Med en ruvningstid på 14 dagar och botid på 20–22 dagar (Schönfeld 1994) bör ruvningen ha inletts den 25 maj. Det betyder att ägg fanns i boet medan hanen påbörjade det nya boet. De närmaste kända pungmesarna, två ensamma hanar, fanns 12 km respektive 16 km bort.

Hane 2, 1985, Börringesjön, Sverige. Hane 2 sågs först vid ett C-bo den 26 maj. Den 29 maj var han fortfarande ensam men den 1 och 2 juni byggde en ringmärkt hona på boet som nu var i D-stadiet. Den 4 juni var det färdigt (F-) men hanen byggde nu på ett nytt bo 350 m söderut medan honan inte sågs någonstans i området. Den 8 juni ruvade hanen i det första boet medan honan återfanns hon en annan hane 4,3 km bort. Ungar matades den 20 juni

vilket betyder att ruvningen inleddes senast den 7 juni. Honan var den enda kända i detta studieområde. Tidigare hade hon lämnat tre kullar med andra hanar, en femte kull övergavs också medan hon slutligen tog hand om den sista kullen

Hane 3, 1997 Krankesjön, Sverige. Den 26 maj byggde denna hane på sitt tredje bo (C) med hjälp av en omärkt hona. Den 30 maj hade påbörjat ett nytt bo (A) 500 m bort och en ringmärkt hona fanns också närvarande. Det tidigare boet kunde inspekteras och innehöll tre ägg. Hane 3 hade återvänt till detta bo den 1 juni och inlett ruvning medan det nya boet var övergivet i skede B. De två nämnda honorna var de enda av 9 honor som inte hade tagit hand om några kullar i slutet av maj. Båda honorna parade sig på nytt och ruvade den 10 juni.

Hane 4, 2006, Milicz, Polen. Hane 4 sågs först bobyggande (B) med en hona den 25 april. Den 4 maj var de fortsatt tillsammans och boet var nästan klart (E). Den 5 maj var hanen ensam. Därefter sågs han inte förrän den 11 maj då han hade ett nytt bo 250 m sydöst om det förra. Honan observerades den 8 maj vid ett nytt bo 250 m sydväst tillsammans med en annan hane. Hane 4 sågs åter den 15 maj vid sitt första bo då han inledde ruvningen. Förhållandet mellan hanar och honor vid denna tidpunkt var 7 till 2.

Hona 1, 1983, Krankesjön, Sverige. Honans första häckningsförsök misslyckades då boet rövades den 10 eller 11 juni. Den 14 juni observerades hon bygga tillsammans med en hane på ett stort bo (E). Den 17 juni sågs hon bygga med en ny hane på ett nytt bo (D) 1,0 km bort, medan den förste hanen var kvar och byggde vidare på det nästa fullständiga boet (F-). Honan var kvar hos den nya hanen den 19 juni medan den första hanen såg bygga ett nytt bo. Den 22 juni hade honan återvänt till det första boet och ruvade. Honan var vid mitten av juni den enda av 8 som inte tagit hand ägg och ungar, och det fanns bara 3 oparade hanar kvar i området.

Diskussion

Såvitt vi vet är detta de första observationerna av pungmesar som ändrat sina beslut. Ett potentiellt problem är att vi bara i ett fall kunde bekräfta att det fanns ägg i boet när det först övergavs medan det kunde beräknas i ytterligare ett fall. Det skulle kunna hävdas att andra honor lagt ägg i bona medan hanen byggde på ett nytt. Det är knappast troligt

under de omständigheter vi beskrivit och förutsätter okända honor i områdena vilket vi inte har någon antydning om. Andra alternativa förklaringar är att hanarna byggt på två bon samtidigt för att ha samtidig polygyni eller för att förbereda ett snabbt övergivande. Vi anser inte heller att dessa är troliga. Samtidig polygyni är aldrig beskrivet hos pungmesen och vi har bara en observation av en hane som inledde ett bobygge samtidigt som han fortfarande var parad med en hona. I detta fall tog honan hand om kullen. Konflikten mellan könen kan beskrivas som en kapprustning och i denna situation bör det vara bästa vara att inte uppvisa några tecken till att överge kullen vilket också stöds av detaljerade observationer (van Dijk et al 2007). Genom att inleda ett nytt bobygge visar hanen tydligt att vill para sig på nytt men det bör inte göras förrän honan tagit hand om kullen eller lämnat den.

Tolkningen av beteendet hos honan som ändrade sitt beslut berör också en annan fråga. Det är möjligt att båda hanarna bidrog till hennes kull. Utomsparringar förekommer hos pungmesen med en varierande frekvens. Att ha flera fäder till en kull kan ge flera fördelar (Fossøy et al. 2008). Våra observationer visar på en möjlighet för en hona att få en större genetisk diversitet bland sina ungar utan att riskera att få någon kull övergiven.

De händelseförlopp vi beskrivit är typiska för när kullar överges av båda föräldrarna ända till den tidpunkt då en av dem återvände. En gemensam faktor tycks ha varit att det fanns få möjligheter för föräldrarna till att para sig på nytt när de ändrade sina beslut. Denna strategi verkar vara vanligare hos hanar än honor och har observerats i 4 av 123 fall där hanen tagit hand om en kull. Observationerna kan ha betydelse för förståelsen av processen när en kull skall överges. En studie i Ungern tyder på att hanen och honan fattar sina beslut samtidigt (van Dijk et al. 2007) medan observationer från Sverige och Polen tyder på att honan oftast lämnar först (Persson & Öhrström 1989, Czyz opubl). Honan som beskrivs i denna rapport och honan vid häckningen i Polen lämnade också boet först, medan turordningen i de andra fallen är okänd. Våra observationer antyder att övergivandet är en komplex process, och att enskilda individer faktiskt kan ändra ett tidigare beslut. Beteendet är ovanligt, men visar att pungmesar kan ändra sig vilket kan öka deras möjligheter till att få avkommor.