

Recruitment of mates and deceptive behavior by male Tengmalm's owls

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Summary. Tengmalm's owl *Aegolius funereus* is a hole-nesting polygynous species in which female nomadism is a reaction to cyclic lows of staple prey. For 2 years during a peak in vole abundance, I examined recruitment of mates and male singing behavior in a local population. Females and about half of the breeding males seemed to arrive successively throughout the breeding period of the first year. In contrast, a majority of the breeding males and likely also females were already on the breeding grounds at the beginning of the breeding season in the second year. Before breeding in the first peak year, males were singing at up to five different nest holes. All early breeding males (67% of total number) continued to sing at secondary nest holes after attracting and installing primary females. Secondary singing locations were never closer than 300 m from primary females' nest holes, although closer locations were used for singing before mating. All bigynous males with nests within the study area were also singing at tertiary nest holes, but none successfully attracted a third female. Polyterritoriality was confirmed by a late male settling between primary and secondary nest holes of a bigynous male. Polyterritorial behavior and reduced breeding success of secondary females are in line with the deception model. Females apparently could not discriminate between paired and unpaired singing males. Females made short visits to different males before mating. During courtship, the number and quality of nest holes defended by males may have been of particular importance to female choice.

Introduction

As early as 1871, Darwin suggested that "mate choice" was made by the female (Darwin 1871). The basis of this choice has been the subject of many studies. Females are often assumed to use assessable features of the territory and/or the male that are correlated to reproductive success. Such features may be abundance of food (Ewald

and Rohwer 1982), nest site quality (Alatalo et al. 1986; Slagsvold 1986), access to shade (Pleszczynska and Hansell 1980), or the male's ability to provide parental care (Searcy 1982), courtship feeding (Simmons 1988a), and courtship display (Simmons 1988b). It is often difficult to separate the effects of territory quality from those of mate quality on female choice because the best males are expected to control the best territories (Searcy 1982; Alatalo et al. 1986; Slagsvold 1986).

In altricial species, one feature of the male that affects female fitness is his pairing status. Females mating with an already-mated male often experience reduced assistance during breeding and therefore reduced breeding success (e.g. Alatalo et al. 1981; Altenburg et al. 1982; Simmons et al. 1986; Carlsson et al. 1987). Females' active choice of already-mated males is not explained by the original "polygamy threshold" model (Verner 1964; Verner and Willson 1966; Orians 1969) and, therefore, this model has been extended by proposing benefits that compensate secondary females (e.g., Weatherhead and Robertson 1979; Heisler 1981; Wittenberger 1981; Searcy 1982; Kodric-Brown and Brown 1984; Davies 1985; Andersson 1986; Armitage 1986; but see Davies 1989 for an alternative view).

In polyterritorial species, mate choice based on pairing status may not be possible (von Haartman 1969; Wittenberger 1976). Therefore, Searcy and Yasukawa (1989) proposed that polygyny in the polyterritorial pied flycatcher (*Ficedula hypoleuca*) is best explained by non-compensation models. Such a model (the deception model) was developed by Alatalo et al. (1981), who suggested that already-paired males deceive secondary females by acting as unmated males in new territories. Alternative hypotheses propose benefits to the male by increased mate retention if the first nesting attempt fails (Slagsvold and Liffjeld 1986) or by reduced aggression between his females (Breiehagen and Slagsvold 1988). Stenmark et al. (1988) noticed that mated males of pied flycatchers singing at secondary nests behaved differently than unmated males. Stenmark et al. (1988) concluded that deception is not an evolutionary stable strategy be-

cause an observant secondary female may discover the male's status. The mate choice and thus the reduced breeding success of these secondary females can be explained by the higher costs of searching for a new mate (Stenmark et al. 1988).

In Tengmalm's owl *Aegolius funereus*, polygynous breeding has recently been shown to be an important reproductive strategy (Solheim 1983; Carlsson et al. 1987; Korpimäki 1988, 1989; Carlsson and Hörnfeldt 1989). Secondary females have a reduced breeding success compared to primary and contemporary monogamous females (Carlsson et al. 1987; Korpimäki 1988). Males seem to defend nest holes only, and not hunting areas (König 1969), and they provide food to the females during laying and incubation (Korpimäki 1981; Carlsson, unpublished work). The contribution of prey delivered by the male to the young is substantial (Korpimäki 1981). Small rodents make up the staple prey, and owl breeding density (per cent boxes with ≥ 1 egg) is correlated with vole abundance (e.g., Linkola and Myllymäki 1969; Korpimäki 1981, 1985; Hörnfeldt et al. 1990). Males are site tenacious, but females and juveniles are nomadic between vole peaks (Löfgren et al. 1986; Korpimäki et al. 1987; Sonerud et al. 1988).

This paper describes (1) consequences of male residency and female nomadism on male mating success, (2) male singing activity associated with a polyterritorial behavior, and (3) different mating options available to settling females.

Methods

Study area and nest box arrangement. The study was carried out in 1984–1985 (with some additional ringing and recovery data from 1986 to 1988) in mixed coniferous woodland north of Umeå in northern Sweden (64°05'N; 20°10'E). The study area covered 100 km² and belongs to the middle boreal zone (Ahti et al. 1968). Wooden nest boxes were mounted from 1981 to 1983 at 80 sites along roads. The distance between these sites varied from 200 m to 500 m. At 40 sites, boxes were mounted in pairs with an intrapair distance of 20–50 m. In all years studied, boxes were in great surplus.

Breeding data. During the breeding season, the boxes and alternative natural nest holes were visited at least every second week to count the number of eggs and nestlings and to ring adults and nestlings. Owls were aged (by primary moult patterns) and classified as 1-year-old or ≥ 2 -year-old (Hörnfeldt et al. 1988). Egg laying (≥ 1 egg) was defined as a breeding event. Laying date was calculated by assuming that eggs were laid at 2-day intervals, that incubation lasted for 29 days (Korpimäki 1981), and by aging the oldest chick according to its wing length (Carlsson and Hörnfeldt, unpublished work). In 1984, 20 females (representing 100% of the number of nestlings recorded) and 14 males (95%), and in 1985, 33 females (97%) and 12 males (35%), were trapped. Males were mostly trapped during the nestling period, and females were trapped during egg laying. The small number of males trapped in 1985 was due to the fact that 62% of the nests were abandoned before the nestling period. This high rate of abandonment occurred when vole abundance declined dramatically over the winter (see also Hörnfeldt et al. 1990).

Identification of singing males. Singing males were located and identified in 1984 (25 February–8 May) and 1985 (25 February–22 March). The area was visited at least once a week and displaying

males were, if possible, tape recorded. Playback was not used. Identification of males was made by comparing sonagrams from separate recordings at different nest holes. Individuals differed in length of the song phrase, number of notes, average length of notes, and average internote length (cf. König 1968). Some birds also had highly characteristic peculiarities in their song. In 1984, all identifications of males from tape recordings (17 singing males out of a total of 18 males) were found to be correct by subsequent trapping males at their nests. Moreover, all bigynous males were trapped at both the primary and secondary nest boxes in 1984. Three breeding males (two bigynous and one monogamous) were also equipped with radio transmitters during the nestling period in order that their home ranges could be mapped. In 1985, it was not possible to check the identifications since the nests were abandoned before the trapping of males took place.

Trapping of owls in autumn. Indices of sex ratio in the autumn were obtained during 5 consecutive years (1984–1988). Owls were caught with two mist nets arranged in a T formation. The owls were attracted to the nets by a tape recorder playing the courtship song of the owl. Both males and females were attracted, and I have no reason to believe that relative netting efficiency of sexes differed among years. Relative sex ratio should thus be comparable. The trappings were performed in the same sites in the different years (except for two trapping sites in 1984 that were later excluded owing to a low number of trapped owls). I do not know any reliable method to sex owls in the autumn. Therefore, sex was determined only in those birds that were both trapped in the autumn and controlled during breeding, at which time they were sexed by weight (Korpimäki 1981; Hörnfeldt et al. 1988).

Food supply. To obtain information about vole abundance, small mammals were snap-trapped each spring (end of May) and autumn (end of September; data from B. Hörnfeldt, personal communication; see Hörnfeldt 1978 and Hörnfeldt et al. 1986 for details on methods). Sampling was conducted in 58 1-ha plots regularly distributed over a 10000 km² area. My Tengmalm's owl study area was situated within this area. The number of voles per 100 trap-nights was used as an index of food supply. Vole abundance was high in the spring of 1984, 1985 (but declined abruptly during the winter of 1984/1985), 1987, and 1988 and was low in the spring of 1983 and 1986 (Tables 1 and 2).

Results

Occurrence of polygyny and sex ratio in autumn

In the vole peak years of 1984 and 1985, 33% and 7%, respectively, of the observed number of males were bigynous (Table 1). Thus, in 1984, 50%, and in 1985, 12% of the nestlings included a bigynous male (Table 1). In 1984, one male was found to have a secondary female breeding outside the study area. As indicated by singing data, a second male was also suspected of having a secondary female outside the area in 1984. In 1987, this male was found to sing and later to breed in a nest box outside the study area 3 km from the 1984 primary nest. The numbers of singing males in 1984 and 1985 were 17 and 23, respectively (nonbreeding males singing only once were excluded). Only one breeding male (7%) was not recorded as singing in 1984. In contrast, the corresponding number was 13 males (41%) in 1985.

Sex ratio among owls trapped in autumn differed between years (Table 2). The proportion of females among the owls trapped was positively correlated with vole abundance ($r_s = 1.00$, $n = 4$, $P < 0.05$, one-tailed).

Table 1. Number of nests and number of ringed males and females in relation to vole abundance (no. of voles per 100 trap nights) in 1984 and 1985

Year	No. of nests			No. of breeding (ringed) owls							Vole abundance (index)	
	monog	bigyn	total	Males			Females				previous autumn	spring
				monog	bigyn	total	monog	primary	secondary	total		
1984	10	10	20	9	5	14	10	5	5	20	2.4	1.9
1985	30	4	34	11	1	12	29	2	2	33	10.7	1.3

Table 2. Total number of trapped owls, number of sexed owls, and number of trapping nights in autumn in relation to vole abundance (no. of voles per 100 trap nights)

Year	Total no. of trapped owls	No. of identified owls		No. of trapping nights	Vole abundance in autumn
		Males	Females		
1984	89	10	8	17	10.7
1985	4	0	0	2	1.1
1986	26	10	0	14	2.3
1987	32	4	2	11	5.2
1988	59	7	3	8	4.2

Singing activity and age of early and late singing males

In 1984, males began singing successively during the study period (Fig. 1). Only about half of the breeding males were recorded singing before first laying date of the season (Fig. 1a). In 1984, 53% of tape recorded males (9 out of 17 males) were singing before the first breeding started (4 April), but in 1985 this figure was 83% (19 out of 23 males), which was significantly higher ($X^2 = 4.10$, $df = 1$, $P < 0.05$; Fig. 1). In 1984, all breeding males singing before the first laying date of the season (before 4 April) were ≥ 2 years old (7 males). In contrast, among the males that began to sing later (after 4 April), 2 males were 1 year old and 5 males were ≥ 2 years old. Age composition differed significantly between early and late singing males (Mann-Whitney U -test, $P < 0.05$).

Among those males that started to breed after the median laying date in 1984, none ($N = 6$; out of which one was never heard) was observed singing before the earliest laying date. In 1985, the corresponding number was 8 out of 15 (= 53%; 4 were never heard). The proportion of early singers among late-nesting males differed significantly between these years ($P = 0.03$, Fisher Exact Test). In 1985, 8 males that started breeding before the median laying date were not heard to sing at all during the study period.

On two occasions in 1984, I observed males occupying nest boxes within existing or newly abandoned home ranges of other males. I interpreted these observations as examples of new arrivals to the area. One male (Fig. 1a; no. 16) started to sing at a box on 14 May. This box was situated between the primary and secondary boxes of a bigynous male (no. 8) that had sung at

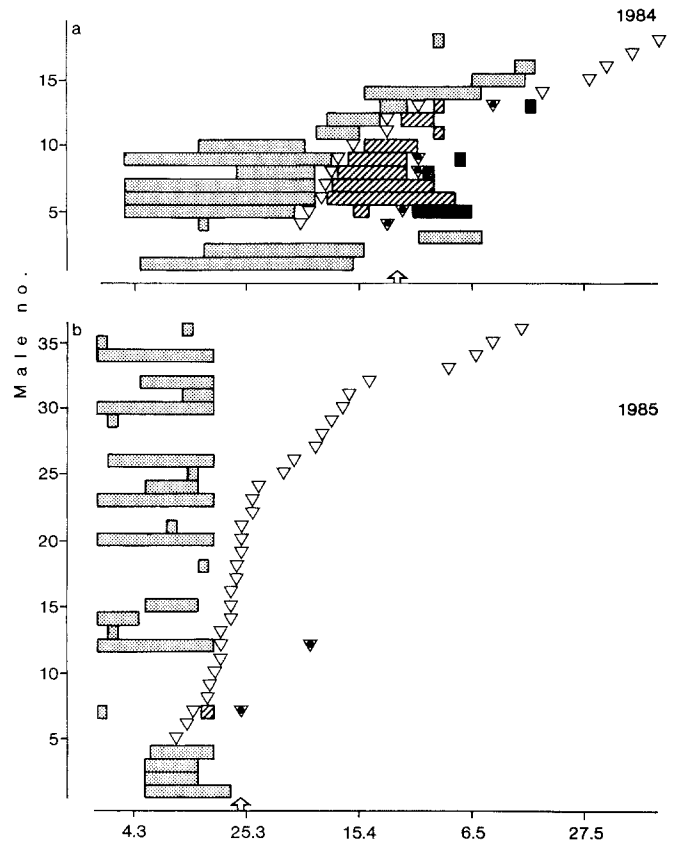


Fig. 1 a, b. Singing activity at primary (shaded), secondary (ruled) and tertiary (black) nest holes of individual males in relation to advancement of two different seasons, **a** 1984 and **b** 1985. First egg laying dates for primary (▽) and secondary (▽) females and median laying date (arrow) are marked for each year. In 1985 singing activity was not recorded after 22 March

this box about one month earlier. Another male (no. 2) was singing intensively at four neighboring nest boxes (maximum distance between boxes, 1250 m) between 17 March and 3 April. Two days later, he began to sing in a new area 4.5 km from the previous one. On 9 April a new male (no. 12) started singing at the same boxes that had recently been abandoned by the previous male.

Polyterritorial behavior

Before breeding, males were singing at up to five different nest boxes. They sung most frequently at what be-

came the primary breeding box and with a decreasing frequency at more distant boxes within their home ranges (Fig. 2a). In 1984, all of those males paired with females that started laying before 1 May (67% of total number of males; Fig. 1a, males no. 4–13), continued to sing after their “primary” female had started laying. However, they did not sing at boxes closer than 300 m from the primary nest (where they sang before the primary clutch was initiated; Fig. 2b). The difference in male singing positions before and after initiation of the primary clutch is statistically significant ($X^2 = 12.65$, $df = 6$, $P < 0.05$). The longest distance recorded between two singing sites of a resident male was 3.2 km. One male had his secondary female outside the study area, and the distance between his two nests was 4.2 km. In 1984, four bigynous males (nos. 5, 8, 9, 13 in Fig. 1a) continued to sing at a tertiary nest hole, but they did not succeed in attracting a third female.

In 1984, a male (no. 16) that I assumed was a late arrival occupied a box situated between the boxes of a bigynous male (no. 8), only 200 m from the secondary nest of the latter male. The bigynous male (equipped with a radio transmitter) once passed within 50 m of the new singing male. The first (bigynous) male was irritated and uttered the skew call (terminology from Bondrup-Nielsen 1984), but no fighting occurred. The new intruding male did not stop singing.

Mating options available to settling females

There were no indications that females could discriminate between mated and unmated males. Supposing that (1) final female mate choice was made 1 week before laying date, (2) they could choose between all available males within my study area, and (3) these males were available up to 1 week before laying, only 9 females (out of 20, Fig. 1a) had both unpaired and paired singing males to choose between. Five of these 9 females made their final choice among already mated males, which were the most common category (mean no. of singing males: 5.6 mated vs 2.4 unmated). However, 4 females chose unmated males although, in three cases, these were in a minority (mean of these three latter cases: 3.3 singing unmated males vs 6.0 singing mated males).

Three out of the five females that became secondary in 1984 would probably have had a higher reproductive output by mating unmated males that were singing at the same time. One secondary female (to male no. 13; Fig. 1a) laid seven eggs, but only three of her owlets fledged. Only 1 km away an alternative male (no. 18) was singing at the same time as male no. 13. This male attracted a female 3 weeks later, which laid five eggs and reared five fledglings. Another female also mated with an already mated male (no. 8) although an unpaired, future bigynous male (no. 13) was singing 1 km away. She laid six eggs and raised two fledglings, while the primary female of male no. 13 also laid six eggs but raised three fledglings. Also the third female mated with an already paired male (no. 4), although an unpaired, future monogamous male (no. 11) was singing 2 km

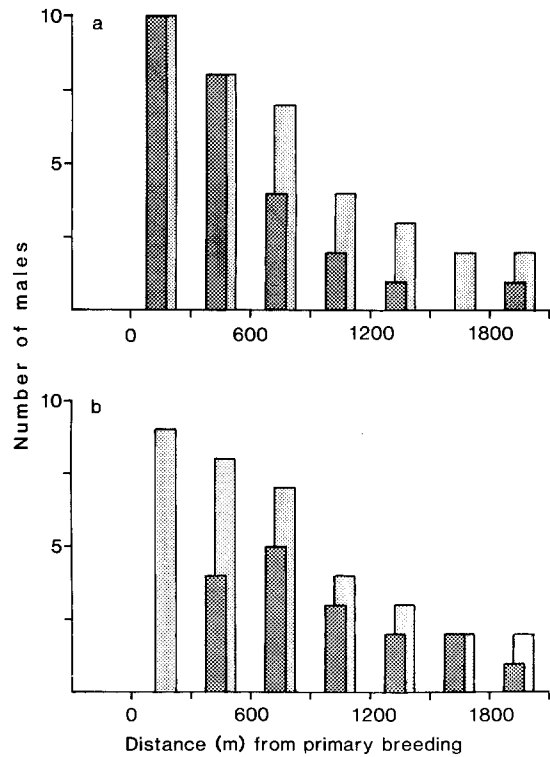


Fig. 2a, b. Data for 10 males' singing positions (dark bars) in relation to their primary nest boxes (0 m) before **a** and after **b** initiation of primary breeding. Light bars indicate number of males with ≥ 1 free nest box at each distance interval (based on mapping of home ranges by males' singing activity)

away. This third female laid five eggs and raised two fledglings, while the future monogamous female laid eight eggs and raised six fledglings. The other two secondary females within the study area could only choose between paired males singing at secondary nest holes and one and two unmated males, respectively, but they did not succeed in raising any fledglings that season.

Courtship display and possible cues for female mate choice

The number of nest holes defended within the home range of a singing male may be an important cue for the female to judge the quality of a prospective mate. Among those males that were heard singing at least 5 nights, non-breeders sang at 3.7 holes (three males), monogamous males sang at 4.7 nest holes (average of six males) and bigynous ones sang at 6.5 holes (four males). Among the three males that were not successful in attracting any female, two sang at two nest holes and the third at five holes.

Observations of male singing behavior indicated that females visited different males. The highly characteristic shifts in male song (from staccato song to prolonged staccato song, Bondrup-Nielsen 1984) when a female approached him made it possible for me to “track” (by listening) a female's visits to different neighboring males. If a female remained in the neighbourhood of a male, the male started a courtship display. He then flew be-

tween the defended nest holes while singing intensively; then the female visited his different holes. This display lasted for several hours, and the matings seemed to be performed in the boxes.

Discussion

Recruitment of mates and male singing activity in the 2 vole peak years

Deteriorating abundance of voles before a cyclic low seemed to stimulate adult females and juveniles to leave the old breeding areas (Löfgren et al. 1986). Adult males are often site tenacious (Löfgren et al. 1986; Korpimäki et al. 1987; Sonerud et al. 1988). During the first peak year (1984), some old and probably site tenacious males were singing in early March. However, new (and partly young) singing males were successively observed during a long breeding season in this year. As the breeding season progressed in 1984, the number of bigynous nestings decreased, which suggests that all males would have gained a higher reproductive output by singing early. Therefore, the delayed singing of late breeding males (as opposed to those in 1985), indicates that these males arrived in the area shortly before they started to sing in 1984. Observations of males occupying nest boxes within existing or newly abandoned home ranges of other males are in line with this conclusion. Favorable food conditions likely "convinced" the owls to stay in the area from 1984 to 1985, and a great majority of the singing males, including those breeding late, were heard singing before the first breeding started in 1985.

In adult females, the degree of site tenacity is low, especially over cyclic lows of vole abundance, and female nomadism is likely common (e.g., Wallin and Andersson 1981; Löfgren et al. 1986; Korpimäki et al. 1987; Sonerud et al. 1988). The absence of trapped females during the cyclic low in the autumn of 1986 is in line with this nomadic behavior. I assume that the successive appearance of breeding females in the nest boxes in 1984 was a result of successively immigrating owls (see also Carlsson et al. 1987). This successive appearance of females provided a source of mates to late singing males, which consisted of both mated (singing secondarily) and unmated males. A high availability of females was also indicated late in the 1984 season by the presence of (at least two) polyandrous females.

In 1985, most of the breeding females had likely been in the area since the previous year. This may have led to the formation of some pairbounds before the studies started in spring (perhaps from previous autumn). This assumption is supported by the fact that eight early breeding males were never heard singing earlier in spring. Indications of polygynous breeding attempts were few, and only one male was found to sing secondarily. It seems reasonable to conclude that polygyny was rarer in the second year of this study. One reason for this may have been a deficiency of late, unmated females (cf. Carlsson et al. 1987). However, the deteriorating

food conditions at this time may also have been causative.

Many of the immigrating owls may have originated from Finland, where the vole abundance fluctuated asynchronously with that within my study area. The vole abundance in South Ostrobothnia, western Finland, was declining in 1983 with a low in 1984 (Korpimäki and Norrdahl 1989); i.e., it lagged 1 year behind that in my study area. One of my breeding females was previously caught and ringed in the autumn of 1984 on the island of Valsörarna (Finland), situated between Sweden and Finland in the Gulf of Bothnia. This indicates an exchange of birds over vast areas (see also Löfgren et al. 1986).

In Tengmalm's owl, sometimes foreign breedings have been noticed to occur between primary and secondary nests (cf. Carlsson et al. 1987). I showed here that primary nests and secondary singing sites are situated far away from each other; boxes closer than 300 m from the primary female's nest were never used for secondary singing, although these were often used before the primary breeding was started.

Models for male polyterritoriality

Different factors may have contributed to the evolution of polyterritorial behavior in birds. These include (1) access to alternative nest holes if the breeding female is disturbed and leaves the first nest (cf. Slagsvold and Lifjeld 1986), (2) increased male mating success if the female uses number and quality of nest holes for decision making (cf. Alatalo et al. 1986), (3) possibility of polygyny by deception (Alatalo et al. 1981), (4) advantages to the male at polygynous breedings such as (a) reduced future predation risk by the long distance between his breeding females (Sonerud 1985), (b) energetic profits from separate hunting areas of primary and secondary breedings (cf. Korpimäki 1987), or (c) reduced aggression between females of a polygynous male (Breihagen and Slagsvold 1988).

Slagsvold and Lifjeld (1988) included the benefits just listed in a general model for male polyterritoriality, termed the Resource Competition Hypothesis. They proposed that three conditions are important for male polyterritoriality: (1) territories are small and easy to defend, (2) male competition is weak, and (3) the duration of male resource holding is short. Tengmalm's owl males only defend the nest holes and their immediate surroundings (König 1969). Further, the incidence of polyterritoriality was lower during the year (1985) with high densities of singing males as indicated by my singing data. However, males are often site tenacious between years and, therefore, the duration of male resource holding is long. This factor may be compensated for by reduced costs for resource holding because of the small body size of males (cf. Slagsvold and Lifjeld 1988; Korpimäki 1988) and the energy-rich and abundant prey (voles) that release time for activities other than hunting during vole peak years when competition between males is increased.

Different mating options for secondary females

Newton (1979) suggested that secondary females of polygynous harriers, *Circus* spp., may have accepted polygyny because it was the only alternative for them to non-breeding. Also, when future secondary wood warbler (*Phylloscopus sibilatrix*) females arrived at the breeding areas, most of the singing males were already paired (Temrin 1989). The few unpaired ones often defended territories in inferior habitats. In Tengmalm's owl, there were also mostly paired males singing at the time when late females mated. However, in 1984, all secondary females had an opportunity to choose between simultaneously singing paired and unpaired males, and three (out of five) of these females likely would have raised more fledglings by mating with unpaired males (see also Korpimäki 1990). Therefore, females did not seem to be able to discriminate between singing mated and unmated males, and their choice seemed to be influenced by the relative frequency of the mate options. In Tengmalm's owl, it is important for a singing male not to show that he is already paired because secondary females raise significantly fewer fledglings than do primary and simultaneous monogamous females (see also Carlson et al. 1987; Korpimäki 1989). Korpimäki (1990) noticed that secondary and tertiary females would gain a better breeding success, in terms of number and weight of fledglings produced, by pairing with available unmated males. However, he did not identify the alternative singing males, and thereby data on the breeding success of these males is uncertain. Different males may occupy the same nest hole during different times of the same breeding season (this paper).

Is male deception efficient?

In Tengmalm's owl, one important reason for polyterritoriality is obviously the possibility of polygynous breeding by deception. In relation to alternatives, males gain in fitness by mating polygynously, while females lose by becoming secondary (Carlsson et al. 1987; Korpimäki 1988). These conditions imply a strong selective force for polyterritorial behavior and deception by the male.

In pied flycatchers and wood warblers (*Phylloscopus sibilatrix*), paired males left their territories more often than did unpaired males (Stenmark et al. 1988; Temrin 1989). This behavior could act as a cue for females to assess a male's pairing status. Stenmark et al. (1988) claimed that deception of females is not an evolutionary stable strategy because an observant female would soon discover a male's status. They proposed that the high costs of searching for a new mate make it more profitable for a secondary female to be faithful to her mate in spite of her knowledge of his status and prospects of reduced breeding success (cf. Slagsvold et al. 1988; Alatalo et al. 1988). In Tengmalm's owl, paired males often sing and also attract secondary females during the laying period of the primary female. During laying the females need a lot of food, and the male often leaves the secondary territory to catch prey for the primary female (Carlsson, unpublished data). The presence of

relatively unsuccessful secondary females and of available, alternative mating options, represented by singing unmated males in the vicinity, indicate that male deception is efficient. Also, there appeared to be no difference in the amount of food in nests of primary and secondary females during egg laying (Carlsson et al. 1987; Korpimäki 1990).

Aggressions between females of bigynous males?

Many passerine females have a lower fitness when their males have secondary mates (e.g., Yasukawa and Searcy 1982; Breihagen and Slagsvold 1988; Temrin 1989). Therefore, primary females should actively prevent their mates from doing so. In pied flycatchers monogamous females were found to be highly aggressive towards other females within their territories and also at the secondary territory of the male (Breihagen and Slagsvold 1988). These authors proposed that female-female aggression may be the reason for male polyterritoriality. In Tengmalm's owl, it is reasonable to suspect that a primary female is aware of her mate's singing at a secondary nest hole because the song is often heard at distances of 2–3 km by humans. However, the primary female does not seem to react to male's secondary singing, and I have never observed aggression between females during many hours of studies (by a videocamera and a microphone mounted in the nest box) during the prelaying and laying period. The primary females were given priority by the males, and they produced more fledglings than the secondary females (Carlsson et al. 1987; Korpimäki 1989). The primary female seems to be provided with the prey she needs for herself and for her nestlings and, therefore, has nothing to win by spending time and energy chasing and fighting potential rivals. In addition, Tengmalm's owls often breed during periods of low night temperatures (below freezing), and females cannot leave the eggs for long periods (Korpimäki 1989).

Which cues of male and/or territory quality do females use?

I assume that a female primarily chose her breeding area according to available food supply. However, the observation that females made short visits to different males indicates that at least these females also chose between different males. In this study, males often defended more nest holes than actually were used for subsequent breeding in. In addition, the different holes were thoroughly exhibited for the female during the courtship. Thus, within a good feeding area, females likely chose among different males by assessing males' quality as reflected by the number of defended nest holes. One factor that may affect this choice is the quality of the defended nest holes. Sonnerud (1985) found that females preferred to nest in new holes because nests in older holes were more exposed to predation.

In natural situations nest holes are in short supply (Lundberg 1979). The observations of owner shifts of boxes in this study indicate that competition for nest holes may occur among males. I suggest that the number

of good nest holes defended by a male and the quality of his feeding area are highly correlated with male quality with respect to food provisioning ability. A female choosing a high quality male early in the breeding season (when the risk of being secondary is small) would have a high prospect of a successful breeding.

Conclusion

During the first peak year of a vole cycle, successively appearing females increased the number of mates available to already-paired, site tenacious males singing at secondary nest holes. In contrast, during the second peak year the deficiency of late, unmated females reduced prospects of bigynous breedings, and only one male sang secondarily in that year. Prospects of bigynous breedings were also reduced by deteriorating food conditions. Male polyterritoriality in Tengmalm's owl seems best explained by the general model termed Resource Competition Hypothesis where the possibility of polygynous breeding by deception seems to be the most important component. The females seemed unable to discriminate between paired and unpaired males, but other cues of male and/or territory quality may still have been important in mate choice. The male defense of more nest holes than needed for their breedings and the exhibition of these holes during courtship suggest these cues to be important to females in assessing the male's quality before mating.

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