A case of bigyny in the Hawk Owl *Surnia ulula*: spacing of nests and allocation of male feeding effort

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Apparently the first known case of bigyny in the Hawk Owl was observed in the north-boreal zone of SE Norway in 1984. The distance between the primary and secondary nest was 1050 m, and the two females defended separate territories within the single territory of the male. The secondary female started egg laying approximately 26 days later, and laid one egg less than the primary one. The male fed his two females at the same rate until the primary clutch hatched. During the next two weeks the prey consumption rate of the primary nest was lower than the prey capture rate of the male, and the surplus was fed to the secondary female. When this surplus decreased, the secondary female abandoned her clutch. However, she stayed in her territory and begged for food for another two weeks, but did not receive any, and did not renest. The primary brood was successfully raised to fledging.

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Introduction

Among altricial birds polygynous mating occurs most frequently in species with female-biased parental care (Orians 1969, Emlen & Oring 1977, Møller 1986).In birds of prey (Accipitriformes, Falconiformes and Strigiformes) the male usually provides almost all the food for the female during courtship, egg laying, incubation and brooding, as well as most of the food for the nestlings (e.g. Newton 1979, Mikkola 1983). Accordingly, polygyny is rare in most raptors (Newton 1979). However, since it is common in Harriers (*Circus* spp.), factors other than female-biased parental care also select for polygynous mating (Balfour & Cadbury 1979, Newton 1979, Altenburg et al. 1982, Simmons et al. 1986).

In owls (Strigiformes) bigyny is rare and has been recorded only in the Barn Owl *Tyto alba* (Schönfeld & Girbig 1975), Scops Owl *Otus scops* (Koenig 1973), Tawny Owl *Strix aluco* (Glutz von Blotzheim & Bauer 1980), Snowy Owl *Nyctea scandiaca* (Watson 1957, Hagen 1960), and Tengmalm's Owl *Aegolius funereus* (Korpimäki 1983, Solheim 1983, Schwerdtfeger 1984). Bigynous owl males are probably able to successfully rear both the primary and secondary brood only when prey are available in surplus amount. Such conditions may exist during peak years of the fluctuating microtine rodent populations in boreal and arctic areas. The Hawk Owl *Surnia ulula* inhabits boreal and subarctic areas (e.g. Mikkola 1983), and is therefore a candidate for bigynous mating.

Parental care by bigynous males of passerines has been found to be biased towards the primary nest (e.g. Alatalo et al. 1982, Yasukawa & Searcy 1982) or the nest containing the largest brood (Davies 1986). Bigynous male birds of prey have been assumed to favour their primary nestlings when food is in short supply, since the reproductive success of secondary females has been found to be lower than that of the primary ones (e.g. Newton 1979, Altenburg et al. 1982, Solheim 1983, Picozzi 1984). However, only Altenburg et al. (1982) have directly studied how bigynous male raptors allocate their feeding support to their primary and secondary females. Here we report on apparently the first known case of bigyny in the Hawk Owl, and emphasize the allocation of the male's feeding support to the two nests.

Study area and methods

The study was conducted in April–June 1984 in a 20 ha clear-cut and the surrounding mature forest stands situated in the northern boreal zone of SE Norway (60° 56'N 11° 08'E), described by Sonerud (1986).

The behaviour of the Hawk Owls was observed through binoculars and a 25x spotting scope, and recorded using the focal-animal sampling method (Altmann 1974). From a permanent observation hut on a hill in the middle of the clear-cut, the activity of the Hawk Owls was observed in all directions within at least 150 m of the primary nest, and fairly well further west in the area between the two nests. The behaviour of the owls at the secondary nest was not observed in detail. In four cases we saw the male fetch a prey animal stored near the primary nest and carry it to the secondary nest. However, since it is difficult to decide whether or not a flying Hawk Owl carries prey, we assumed that the male fed his secondary female one prey per round-trip visit made from the primary nest to the vicinity of the secondary nest. Prey taken near the secondary nest may have been delivered unnoticed to the secondary female. We were unable to observe to which extent prey was stored around the secondary nest.

We verified that the same male was involved at both nests by observing his travels between them. In order to facilitate this identification the male was ringed and fitted with coloured plastic wing tags on 28 May. Similarly, we were able to tell the primary and secondary female apart as long as they were incubating or brooding by recording which nest box they returned to. In order to avoid confusion when the primary female terminated brooding and resumed hunting, she was ringed and fitted with coloured plastic wing tags on 27 May.

We spent 369 hours in the observation hut recording the owls' activity during 37 days between 20 April–15 June. In addition, the male was fitted with a radio transmitter on 28 May, and tracked during his hunting bouts for 82 hours during 9 days between 29 May–15 June (for equipment and tracking methods see Nybo (1986)). Most of this male tracking was done simultaneously with watching the female's activity from the observation hut, with observers staying in contact using walkie-talkies.

Hawk Owls nesting in the study area almost invariably prey on small mammals, i.e. shrews (Soricidae) and microtine rodents (Nybo 1986, Sonerud 1986). The relative prey density was assessed by snap-trapping in the clear-cut and the surrounding mature forest stands as described by Sonerud (1986). The small mammal populations in the area increased from a low in spring and summer 1982 to a peak in summer and autumn 1984. Their densities were medium during winter 1983–84 and spring 1984, but increased very rapidly during June and July 1984 after our study was terminated (G. A. Sonerud, unpubl.). The snow-cover disappeared unusually early in 1984 (earliest snowmelt recorded in the area during 1977–86) due to little snow-depth all winter and a warm spell during late April. The clear-cut was totally snow-free by 1 May, as opposed to the usual 15 May. Hence, in 1984 the temporarily high availability of vulnerable small mammals in spring between the melt and the growing of new field vegetation (see Sonerud 1986) lasted longer than usual, namely the last week of April and the first three weeks of May.

Results and discussion

Nest spacing

The primary female nested in a box mounted on a pole situated in the middle of the eastern part of the clear-cut. The secondary female nested in a box situated 1050 m west of the primary one, in an open, thinned stand of mature Scots pines *Pinus sylvestris*. Thus, the nesting habitats of both females were typical for Hawk Owls (see Sonerud 1985a).

Within the 1050 m there were 15 nest boxes available for the secondary female — 12 in the clear-cut and three in the open pine forest. The secondary female used the box that was located farthest from the one used by the primary female, but still within view of the male's favourite vantage perches 150 m northwest of the primary nest.

The distance between the primary and secondary nest of the Hawk Owl was of the same order as that recorded for the Tengmalm's Owl (average 1300 m; Korpimäki 1983, Solheim 1983) and the Snowy Owl (1300 m and 1600 m; Watson 1957, Hagen 1960). The minimum distance recorded between two monogamous Hawk Owl nests in our study area is 600 m (B. T. Bækken, pers. comm.).

The Hawk Owl male was monoterritorial. Also, the bigynous Snowy Owl males studied by Watson (1957) and Hagen (1960) were monoterritorial. Based on the fact that the average recorded distance between primary and secondary nests of bigynous males was longer than minimum recorded distance between nests, Solheim (1983) speculated as to whether bigynous Tengmalm's Owl males are polyterritorial. Polyterritoriality, where a polygynous male defends at least two separate territories, has been suggested to be a strategy with which the male can deceive a secondary female — unaware of the existence of the primary female — into mating (Alatalo et al. 1981). However, in hole-nesters at least, the risk of having the nest preyed upon may decrease with increasing distance from other nests being preyed upon (Krebs 1971, Dow & Fredga 1983, Sonerud 1985b). Therefore, polygynous males may space their nests out in order to decrease the risk of having more than one of them taken by nest predators that adopt an area-concentrated search (Winkel & Winkel 1984, Slagsvold & Lifjeld 1986).

Hawk Owls and Tengmalm's Owls are equally exposed to nest predation by the pine marten *Martes martes* (Sonerud 1985a). For both, therefore, spacing the primary and secondary nest more than a certain minimum distance apart may be more important than spacing them in separate territories. Other reasons for maximizing the distance between the primary and secondary nest may be aggression between the two females involved (cf. v. Haartman 1969, Yasukawa & Searcy 1982), and possible depletion of prey around the nests.

Clutch size and the start of egglaying

The primary female was still outside her nest box on 15 April, but was incubating on 20 April. None of her five eggs had hatched on 15 May but three had hatched on 20 May. Assuming an incubation time of 30 days for the first egg laid (Mikkola 1983), laying probably started on 17 April.

The secondary female was incubating her four eggs on 23 and 28 May. Her eggs were cold on 2 June, and were found to contain fetuses. The oldest was judged to be approximately 20 days old, based on Plate V in Ytreberg (1956). Thus, the first egg was probably laid on 13 May.

The calculated difference in times between the primary and secondary clutch of the Hawk Owl (26 days) is within the range found for the Tengmalm's Owl (18–30 days, average 22 days; Korpimäki 1983, Solheim 1983), and somewhat longer than that found for the Snowy Owl (16 and 18 days; Watson 1957, Hagen 1960).

Allocation of male feeding support to the primary and secondary nest

Short-term storing was an important part of the prey handling. When arriving at the vicinity of the primary nest with prey, the male always offered the prey to the female. If she rejected, the male usually stored the prey in a tree within 150 m northwest of the nest. If she accepted, she would usually eat the prey, but occasionally she stored it in the same trees. The male would also regularly offer the female prey taken from these stores. Finally, the female would occasionally take prey directly from these stores, for instance when the male was spending time with the secondary female. The primary female was not observed to capture prey herself until 7 June.

During egg laying and incubation in the primary nest, the male arrived, on average, with almost twice as many prey as the female consumed. The amount of surplus prey temporarily stored was therefore almost equal to the amount of prey consumed by the primary female, as well as to the estimated amount of prey delivered to the secondary female (Fig. 1).

Prey consumption by the primary female and her nestlings gradually increased by a factor of three during the first ten days after hatching. However, the male doubled his prey capture rate during the same period, so that the surplus stayed at approximately the same level as before hatching (Fig. 1).

Following the capture of the male on 28 May (for attachment of the radio transmitter), the amount of surplus prey from the primary nest, and the amount of prey we estimated was fed to the secondary female, dropped to about a half and a third, respectively, of that recorded before the radio transmitter was mounted on the male (Fig. 1). On 2 June the secondary female abandoned her nest and started hunting for herself.

During the first few days after the secondary female had abandoned her nest, prey consumption by the primary female and her nestlings exceeded the prey capture of the male, even if the male increased his capture rate (Fig. 1). At the peak of the nestlings' prey consumption the male's prey capture rate dropped markedly (Fig. 1). This coincided with the resumption of hunting by the female. However, even if the female's prey capture compensated for the drop in the male's capture rate, still fewer prey were captured altogether than consumed by the female and nestlings (Fig. 1). The deficit was taken from prey stored earlier. The oldest young left the nest on 9 June, while the youngest was still in the nest on 15

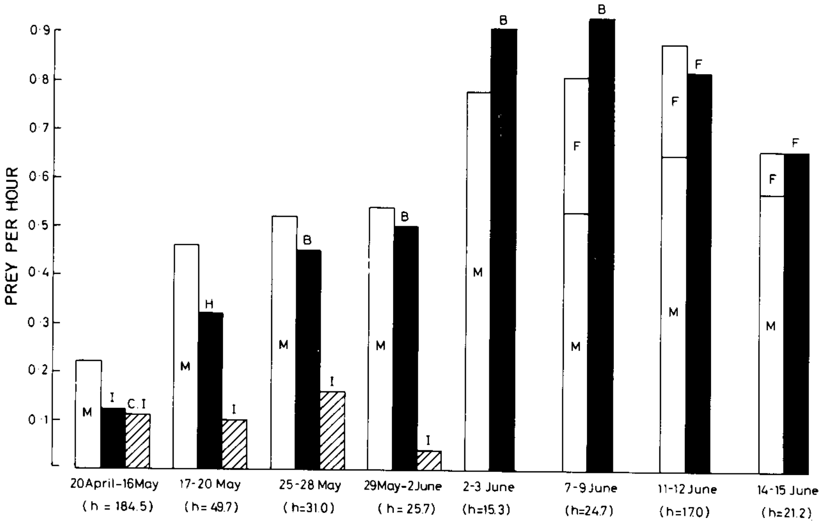

Fig. 1. Rate of prey carried to the primary nest (open bars) by the male (M) and the female (F), compared with the rate of prey consumed by the primary female and her nestlings (black bars), and the rate of prey estimated delivered to the secondary female (hatched bars), during the study. The estimated delivery rate is given as the rate of visits by the male to the secondary nest, subtracted the rate of prey brought back to the primary nest (see text for further explanation). The letters above the bars denote the nesting phase (C=courtship feeding, I=incubation, H=hatching, B=brooding, and F=fledglings). The secondary female abandoned her nest on 2 June. The number of observation hours in each period is given below the bars. Note that prey deficiency during two periods are compensated for by consuming surplus prey stored during previous periods.

June. During the period 11–15 June the balance between prey captured and consumed was restored, mainly due to a reduced consumption by the fledglings (Fig. 1). All the hatched nestlings survived to fledging.

Female Hawk Owls seem unable to raise a brood without feeding support from a male. The male in this study nested monogamously in 1985 (with a third female), 3.0 km north of the nests he had in 1984, and was equipped with a new radio transmitter. During hatching he disappeared, and was found dead 1.2 km from the nest. The female started hunting close to the nest, but was unable to capture enough prey without leaving the newly hatched nestlings unbrooded for too long periods, and a few days later the nest was found abandoned (B. T. Bækken, pers. comm.).

The failure of the Hawk Owl male to provide the secondary female with enough food may have been caused by equipping him with a radio transmitter, since this process implied a prey delivery break of at least 12 hours, and possibly a lowered foraging efficiency afterwards. Bigynous male Marsh Harriers *Circus aeruginosus* also delivered as much prey to their secondary as to their primary female during the incubation period, and favoured their primary nest after hatching (Altenburg et al. 1982).

Behavioural interactions between the three adult owls

The primary female was never seen more than 300 m west of her nest and the secondary female never closer than 350 m to the primary nest, namely, never more than 700 m from her own nest. The two females thus seemed to have separate territories. This was confirmed on 15 June, when the only recorded encounter between the two females took place in the clear-cut exactly at the anticipated border. The hunting primary female was moving from perch to perch towards the border, but turned after meeting the secondary female, watching her at a distance of 20 m for 50 seconds. Thus, aggression between the two females may have caused the spacing between their nests (cf. Yasukawa & Searcy 1982).

During radio-tracking of the Hawk Owl male, the secondary female was observed three times between 6–15 June, from 600–700 m of her former nest; every time uttering begging calls when the male was close by. However, the male was never observed to feed her, and no renesting occurred in the area.

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