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Brief report

Post-fledgling parental success by widowers in the Tawny Owl *Strix aluco*

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1. Introduction

The evolution of monogamy has been explained by a need for bi-parental care in rearing young (Emlen & Oring 1977, Wittenberger & Tilson 1980). However, in passerines, such as Eastern Bluebirds (*Siala sialis*) (Gowaty 1983) and Tree Swallows (*Tachycineta bicolor*) (Dunn & Hannon 1992), it is shown that widows are able to raise offspring with success (Whittingham *et al.* 1994, Whittingham & Dunn 1998). On the other hand, in Ptarmigans (*Lagopus lagopus*) single males were less successful than pairs or single females (Pedersen & Andersen 1982, Martin & Cooke 1987). In Florida Snail Kite (*Rostrhamus sociabilis*), a neotropical hawk which nests in loose colonies, males and females deserted with nearly equal frequency, but this did not affect offspring survival (Beissinger & Snyder 1987).

Observations of the success of widowed breeding adults can contribute to our understanding of the significance of bi-parental fledgling care versus single adults provisioning capacity (e.g. Martin 1987, Cezilly *et al.* 2000). The deaths of two females in our telemetry studies on Tawny Owl (*Strix aluco*) families in Norway in 1997 provided such an opportunity. Tawny owls are strictly monogamous and the young have a long period of dependence on their parents (Southern 1970). Bi-parental care is therefore assumed to be important for raising fledglings. Yet, studies in other owls have shown that when the females abandoned, the males continued to raise the young. For example, in Great Grey Owls (*Strix nebulosa*), Bull and Duncan (1993) described how females abandoned 3–6 weeks after fledging, but the males continued to feed the young for an additional 6 weeks. Likewise, Long-eared Owl (*Asio otus*) females may desert when the fledglings are 6–10 weeks old, but the males continue feeding for an additional 2–3 weeks (Marks *et al.* 1994). In the Southern Boobook (*Ninox novaeseelandiae*), a small owl species that breeds in Australia, females stopped feeding young 2–4 weeks after fledging but the male continued for another three weeks (Olsen & Trost 1997).

Our observations, where the Tawny Owl fledglings were radio-tagged, provide an opportunity to observe and evaluate the response in the males and the survival of the young. We sum up

some aspects of our observations versus the monogamous lifestyle in the species using the theory of evolutionary stable strategies (ESS) (Maynard Smith 1977) as an explanatory tool.

2. Methods

This study was conducted in a spruce- and agriculture dominated landscape < 100 m above sea level near the city of Trondheim, central Norway (63°20´N, 10° 45´E). Here, the Tawny Owl is at the northern limit of its range (Cramp 1985). During 1995–97, females were captured when incubating in nest-boxes and tagged with backpack radios (20 g) (< 5% of body mass), and their young were marked with leg-hold tags (3.5 g) (< 5% of body mass) (Biotrack Ltd., Dorset, UK) a few days before their nest departure. After fledging, the birds were radio-located and directly observed every third day (Overskaug *et al.* 1999).

The males were not radio tagged, but from repeated observations of the size, color, and behavior of the males, we assume that only the remaining male was guarding and feeding the fledglings (e.g. Wendland 1972). Furthermore, to our knowledge neither replacement of dead mates nor polyandry has been reported in Tawny Owls (Southern 1970, Cramp 1985).

3. Results

In 1997, 32 fledglings (12 broods) were radio-tagged, including the two families in which the females died. Due to starvation and predation, only 14 (44%) of the fledglings survived to disperse, and five of them were those that had lost their mothers early in the fledgling period. Average brood size in 1997 was 2.6 at the beginning of the fledgling period. In the two widowed families, the respective two females died shortly after nest departure.

In case 1, four eggs were laid around 24 March 1997. Three hatched around 23 April. Three young survived to leave the nest at an estimated age of 31 days between 23 and 24 May. On 5 June, when the young had been outside the nest for 11–12 days, the female was killed by a Goshawk (*Accipiter gentilis*). We visited the study-area and radio-located and directly observed the three young every third day until their dispersal from their natal territory later on in the summer. The last one dispersed from the study area about 110 days after fledging.

In case 2, four eggs were laid around 18 April 1997. Two hatched around 16 May. The two young survived to leave the nest at an estimated age of 32 days between 17 and 18 June. On 23 June, when the young had been outside the nest for 4–5 days, the female was killed in a collision with a power line. We visited the study-area and radio-located and directly observed the two young every third day until their dispersal from the natal territory later on in the summer. Both dispersed from the nesting territory about 80 days after fledging.

Dispersal was reflected by a change in range use, and moving outside the natal territory (*see* also Greenwood & Harvey 1982, Sonerud *et al.* 1988). Aircraft were used in the tracking until late fall when radio-contact was lost, but at least one young in case 1 survived to the next spring when it was found newly dead about 30 km away after a collision with a building.

4. Discussion

Male birds rarely care for young alone (Dawkins & Carlisle 1976), and bi-parental care seems to be an evolutionary stable strategy (Maynard Smith 1977, Møller & Cuervo 2000). In avian top-predators, for whom the prey base can be unstable and limited, one may expect the need of both parents for successful breeding — such as in the Tawny Owl where it is normal to observe both adults feeding the fledglings. Nevertheless, we would like to propose some ecological aspects, and sex-specific Tawny Owl morphological and behavioural factors, that under special circumstances can explain a widower's capacity for successful raising of fledged young.

First, as in most owls, male Tawny Owls feed the female during incubation (Mikkola 1983), and are often the main providers to the fledglings as they increasingly beg for food (Southern *et al.* 1954). The males in our study had already invested

considerably in the offspring when their mates died, and their active hunting role probably continued as long as their young was capable to eat the food they bring. Hence, the age of the fledglings, and their ability to be somewhat self-sufficient, probably represent much of the key to the widower's success.

In addition, some more factors may also play a role. For example, Trivers (1972) surmised that parental investment depresses the parent's ability to survive, but widowers that raise broods may derive a fitness advantage, depending on their future breeding potential (Grafen & Sibley 1978). Even though Tawny Owls reach an age of > 10 years, life expectancy of 1-year-old individuals is only 2–3 years (Olsson 1958, Southern 1970). Consequently, continued investment in raising young may pay a fitness advantage if rearing some young is possible.

Furthermore, Tawny Owls display reversed sexual size dimorphism, as do other raptors (Earhart & Johnson 1970). One hypothesis behind the phenomenon is that there is selection for small males (efficient hunters) and large females (good incubators) (Mueller 1986). Male Tawny Owls in our study area do have a broader diet than females (Overskaug *et al.* 1995), and if males are more efficient hunters, then the female's presence may be less important during the post-fledgling period. Telemetry studies of Tawny Owl females in the study area (Sunde *et al.* 2001) indicate in fact that several females roosted away from the fledglings relatively early in the summer. Later in the autumn they can stay permanently outside the summer-territory, and do not return to the vicinity of the nest-box until the onset of the next breeding season. During this period the females build up large fat-deposits (Overskaug *et al.* 1997, Overskaug & Bolstad 1998), which favor their future incubation effort (Overskaug 1998). Data may therefore support that Tawny Owl females, at least in our Nordic study area, sometimes can be of less importance in raising fledglings. A female strategy where she gives priority to self-restoration may also be favorable to the male in monogamous species.

We sum up this using the theory of evolutionary stable strategies (ESS) (Maynard Smith 1977) as an explanatory tool. Suppose that the presence of both sexes (V_2) is necessary for success in the nesting period, the female incubates and later on warms chicks, whereas the male hunts and provisions for the family. Success, p, is zero if one of the adults dies or deserts during this period, and a monogamous lifestyle may secure the best p (*see also* Møller & Birkhead 1993, Schwagmeyer *et al.* 1999). For the period after fledging, suppose that paternal care (V_1) is enough for raising young. A female that deserts after the young nest departure may therefore still have a chance of reproductive success. Furthermore, after brooding it may pay for a female to prepare for winter-survival and the next breeding season. The challenge is a balance between participating in the care for the young, and self-restoration. Since the fitness of a monogamous male also depends upon an experienced female that must survive the winter and be ready for another breeding attempt next spring, such a role division may favor him, too. Therefore, under some circumstances one may have the situation; $p > 0$ if $V_1 \geq V_2$.

However, widowers success may be possible only under special conditions, for example when fledglings have reach an age where they can eat the prey that the male bring. Since single male raising of fledglings is not reported in Tawny Owls, and less in other related species, we also suggest that there is a high cost to this behavior. Yet, when our widowers still continue to provision, this may be linked to the possible short lifespan in our northern study area. Even at high cost, single males that continue to raise young may favor their lifetime reproductive success if high adult mortality excludes future breeding opportunities.

Our observations may glimpse into some parts of the sexual roles in the breeding cycle of Tawny Owls. This aspect may also be relevant for the understanding of the reversed sexual size dimorphism in the species. Complete life-history studies on individuals and pairs, for example by the help of banding and telemetry, may be the key to further investigations, and a natural next step in those studies.

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Sammanfattning: **Framgångsrik unguppfostran hos ensamma kattuglehanar *Strix aluco***

Under en telemetristudie på beteende och överlevnad hos kattuglefamiljer *Strix aluco* i Norge, uppstod två situationer då de vuxna honfåglarna dog cirka 4–5 och 11–12 dagar efter att deras ungar hade lämnat boet. Dödsorsaken hos de vuxna honorna var i ett tillfälle kollision med strömledning och i ett annat tillfälle predation från duvhøk *Accipiter gentilis*. I den ena familjen var det två kvarvarande ungar, och i den andra tre kvarvarande ungar. Även om bägge föräldrarnas närvaro antas vara viktig för framgångsrik unguppfostran hos denna monogama toppredator, klarade i bägge fallen de ensamma hanarna att uppfostra ungarna. Vi föreslår att mycket av denna success kan förklaras av att ungarna hade uppnått en ålder då de på egen hand kunde tillgodogöra sig de bytesdjur som hanen inskaffade, men att morfologiska och beteendemässiga karaktärer knytna till artens omvända storlekskillnad, där honfågeln är betydligt större än hanfågeln, också gör hanen särskilt ägnad som unguppfostrare.

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