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Sequential polyandry in female Tengmalm's owl (*Aegolius funereus*) during a poor rodent year

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Abstract. In birds of prey, food availability affects the entire breeding process, including reproductive success. Sequential polyandry, sometimes documented in raptors and owls, has been observed occasionally in Tengmalm's owl in years of high food availability. In this study, the effect of food supply on the reproductive strategy of the central European Tengmalm's owl population has been investigated. The availability of the main prey of owls was significantly below average in the study year 2014. This resulted in low breeding density of owls, delayed egg laying, small clutch sizes, and low reproductive success. Nevertheless, successful sequential polyandry of one Tengmalm's owl female was recorded during the breeding season. The polyandrous female laid four eggs in each nests, and 50 % and 75 % of four hatched nestlings left the nest during the first and second breeding, respectively. In both nesting attempts, the two-year old female was of a substandard body mass and she abandoned the fledglings before they left the nests. Prey delivered by males to both nests was comprised mainly of alternative prey (birds and shrews). The results of this study suggest that there are probably some other factors, in addition to food availability, that may play a role in Tengmalm's owl's decisions in matters of parental care.

Key words: boreal owl, polygamy, reproductive success, food abundance, sex ratio, diet structure

Introduction

Multiple breeding in one season is a well-known strategy, especially in songbirds (Clutton-Brock 1991, Reynolds & Székely 1997). Regular social polygyny, where the male partially or entirely deserts his offspring and re-mates in early or sometimes later phases of the breeding cycle is quite common; it occurs in at least 10 % of bird species from at least ten orders (review by Bennett & Owens 2002). Social polyandry, on the other hand, is a type of polygamy where the female deserts her offspring and re-nests in the same breeding season; it is less common among birds, often associated with uniparental care and sex-role reversal (Oring 1986, Owens 2002). Choosing this reproductive strategy results in higher nestling production, but forces the female to abandon the nestlings from each nest earlier, which is reflected in a reduced survival rate in the late nestling and post-fledging stages (Oring 1986, Székely 1996, Eldegard & Sonerud 2009).

Social polyandry is used in only 1 % (Oring 1986), respectively less than 5 % of all bird species (Bennett & Owens 2002) and mostly occurs in precocial species of birds (it is most common in waders; e.g. Amirault et al. 2004, Kosztolanyi et al. 2006). Chicks of precocial species are capable of feeding themselves, so females can choose to desert their broods after clutch completion and leave offspring nurturing to their mates (Oring et al. 1983, Andersson 2005). However, multi-nest sequential polyandry in birds with altricial chicks, where males are either unwilling or physiologically unable to perform the majority of incubation, is sometimes also documented (e.g. lesser spotted woodpecker *Dendrocopos minor*, Wiktander et al. 2000; northern flicker *Colaptes auratus*, Wiebe 2005; barn owl *Tyto alba*, Henry et al. 2013).

In raptors and owls, in which reversed sexual dimorphism is evolved and both sexes have usually distinctly divided parental roles (e.g. Zárybnická & Vojar 2013), polyandry is occasionally observed when food is abundant (Beissinger & Snyder 1987, Carlsson et al. 1987, Korpimäki et al. 2011). In the northern European population of Tengmalm's owl (*Aegolius funereus*) 12 re-mating females from a total of 1135 females were found in years of high vole spring abundance (Korpimäki et al. 2011). Furthermore, Eldegard & Sonerud (2009) revealed that the nest desertion frequency of female Tengmalm's owls increased with both prey availability and an increase the body reserves of parents (especially of the male).

Similarly, in a central European population, the frequency of female offspring desertion occurred more often in years of high food availability and two cases of female re-mating were documented when food was abundant (Zárybnická 2009a). However, there are still only rare examples of female desertion and female re-mating in same season, as well as there is little information regarding the environments in which females are able to re-mate and how the individual nestings of re-nesting females differ from each other (Hipkiss & Hörnfeldt 2004, Korpimäki et al. 2011).

Food abundance is an important factor driving the entire breeding process of Tengmalm's owl, in particular it affects breeding density, laying date, clutch size, reproductive success, and diet structure (Korpimäki & Hakkarainen 2012). In this study, we investigate the effect of food availability on the reproductive strategy of Tengmalm's owls in areas of the Ore Mountains (Krušné hory), Czech Republic, in 2014. We predict that (i) in a year with poor prey availability there will be a low breeding density of Tengmalm's owl nests, owl females will lay small clutches, few fledglings will leave the nests, the timing of nesting will be delayed, and the prey structure will comprise of a high proportion of alternative prey species (i.e. birds and shrews). In contrast, in a year with high prey availability there will be a high breeding density, the owls will raise more fledglings and their diet will be comprised mainly of voles and mice. Simultaneously, we predict that (ii) in a year with poor prey availability, there will be no record of sequential polyandry and, if present, it would only be so as a result of unsuccessful nesting in the first place. Conversely, in a year of rich prey availability sequential polyandry will be more frequent.

Material and Methods

Study area

The study was conducted in the northern part of the Czech Republic (N 50°, E 13°), close to the border with Saxony, in 2014. The study area is situated in forests damaged by industrial air pollution, on plateaus of the Ore Mountains (735-956 m a.s.l.). The habitat at this study site is covered with spruce forest fragments, open areas, and forest clearings (dominated by wood reed *Calamagrostis villosa*), solitary trees (mostly European beech *Fagus sylvatica*) and secondary growth of young trees, mainly blue spruce *Picea pungens*. In this habitat, Tengmalm's owl primarily breeds in nest-boxes (> 90 % nests) as natural cavities can only be found in rare solitary beech trees. Within these habitats, during 1999-2013, the number of deployed nest-boxes varied yearly between 100 and 167 (126.6 ± 26.8). In 2014, 212 nest-boxes for Tengmalm's owl were placed in an area covering 110 km². The boxes were evenly distributed within the study area and were usually placed at the edge of forest patches.

Field procedures

In 2014, data on breeding density (expressed as the number of nesting attempts per 100 nest-boxes available), clutch size, reproductive success (expressed as the number of fledglings that left the nest) and laying date were collected by regular inspection of nest-boxes. All nest-boxes were inspected from late March to late August at intervals of one to three weeks to detect new breeders. All nests found in 2014 were protected against marten predation by a metal cover. To assess owl breeding production in 2014, the data collected were compared with a long-term data set on Tengmalm's owl nesting in the Ore Mountains covering 2000-2013.

Prey abundance

In 2014, the abundances of small mammals were assessed using snap-trap captures. The captures were carried out in the season twice – at the beginning of June and at the beginning of October. The traps were laid out in three trapping squares of 100 × 100 m; spacing of the traps within each square was 10 m, i.e. a total of 121 traps per square. The traps were in place for three days and checked once a day. Trapping squares were situated in open areas and secondary stands of blue spruce where vegetation is dominated by wood reeds. All captured mammals (31 individuals) were identified to the species level. To assess prey availability in 2014, the collected data were compared with a long-term data set on prey availability in the Ore Mountains during 2000-2013 (1117 individuals). Prey availability for that data set was collected by the same methods as in 2014.

Molecular sexing

For molecular sexing, a 50 µl blood sample was taken from each nestling in 2014, via a brachial vein puncture under the wing, approximately 14 days after hatching, following the methods of Hipkiss & Hörnfeldt (2004). Sex determination of the nestlings relied on polymerase chain reaction (PCR) amplification of one intron from the sex chromosome linked *CHD1* gene, which in birds differs in size between the Z

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and W chromosomes (Fridolfsoon & Ellegren 1999); males showed only the shorter Z-fragment, while females were characterised by displaying both a 1.2 kb W-specific and a 0.7 kb Z-specific fragment (Fridolfsoon & Ellegren 1999).

Camera monitoring of polyandrous nests
A camera system embedded in a nest-box (consisting of a computer, two cameras with infrared lighting, a chip reader device, an infrared light barrier, and a 60 Ah 12 V traction battery) was used to determine the prey delivered to the polyandrous nests in 2014. Pictures taken by the nest-box camera system enabled the determination of the presence of individual parents (i.e. male and female) in the nest, and the identification of prey delivered by owl parents as mammals (to the genus or species level) or birds. Only 2.3 % (n = 7 items) of all delivered prey were not determined. Each polyandrous nest was recorded over a mean period of 37.5 ± 20.5 days.

Statistical analyses
Results are reported as mean ± standard deviation. The taxonomic composition of the diet structure between nests was compared using χ^2 tests. All data analyses were processed in the Statistica 6.0 software package (StatSoft Inc. 2010).

Results

Prey availability
In 2014, both spring and autumn prey availability was lower than the long-term yearly mean (1999-2013) and, except for pygmy shrew *Sorex minutus*, none of the prey species reached their 14-year mean abundance (Table 1). Simultaneously, the availability of most small mammal species in 2014 increased from spring to autumn (Table 1).

Basic breeding data
In 2014, there were 10 nesting attempts of Tengmalm's owls and the breeding density was 4.7 nesting attempts per 100 nest-boxes available. Females started egg laying on 13th May ± 31 days. Eight of the nesting attempts were successfully completed and two were deserted by the female before any of the eggs hatched. In successful nests, 3.6 ± 0.5 eggs per clutch were laid and 2.1 ± 1.1 young per nest fledged. The sex ratio of the fledglings in 2014 was female-biased, at 57.3 ± 39.7 %. Breeding density, clutch size, and the number of fledglings in 2014 were all lower than their respective long-term yearly means (2000-2013) and the laying date was delayed (Table 2).

Sequential polyandry
In 2014, one of the ten observed females successfully nested twice during the breeding season. The two-year

Table 1. Spring and autumn small mammal availability in the Ore Mountains, the Czech Republic, estimated by June and October snap-trapping and expressed by the numbers of individuals per 100 trap-nights. Data are shown as yearly mean ± SD in period 2000-2013 (n = 14 years), and in 2014 (n = 3 squares) separately.

Taxa	Spring 2000-2013	2014	Autumn 2000-2013	2014
Microtus agrestis	0.47 ± 0.42	0.09 ± 0.16	0.63 ± 0.69	0.28 ± 0.28
Microtus arvalis	0.05 ± 0.13	0	0.08 ± 0.14	0
Microtus subterraneus	0	0	0.01 ± 0.02	0
Myodes glareolus	0.66 ± 1.10	0	1.69 ± 2.69	0.37 ± 0.16
Apodemus sylvaticus	0.03 ± 0.10	0	0.03 ± 0.04	0
Apodemus flavicollis	1.16 ± 1.74	0.28 ± 0.48	0.94 ± 1.13	0.46 ± 0.80
Sorex araneus	0.21 ± 0.17	0	0.87 ± 1.05	1.19 ± 0.32
Sorex minutus	0.02 ± 0.05	0.09 ± 0.16	0.24 ± 0.53	0.09 ± 0.16
Total	2.45 ± 2.89	0.46 ± 0.42	4.48 ± 4.15	2.39 ± 0.80

Table 2. Data on breeding density, laying date, clutch size and the number of Tengmalm's owl fledglings in the Ore Mountains in the Czech Republic. Data are shown as a yearly mean ± SD in period 2000-2013 (n = 14 years), and in 2014 separately. The breeding density is shown as the number of nesting attempts per 100 nest-boxes available.

	2000-2013	2014
Breeding density	13.3 ± 4.8	4.7 (n = 1 year)
Laying date	April 18 ± 13.4 days	May 13 ± 30.8 days (n = 10 nests)
Clutch size	4.9 ± 1.0	3.6 ± 0.5 (n = 8 nests)
Number of fledglings	3.5 ± 1.4	2.1 ± 1.1 (n = 8 nests)

Table 3. Diet composition of Tengmalm's owls delivered to two sequential nests in the Ore Mountains, the Czech Republic, in 2014.

Taxa	First nest Number of prey items	%	Second nest Number of prey items	%
Apodemus sp.	4	1.5	2	4.7
Microtus sp. and *Myodes glareolus*	63	23.8	13	30.2
Muscardinus avellanarius	1	0.4	0	0.0
Sorex araneus	68	25.7	16	37.2
Sorex minutus	7	2.6	5	11.6
Aves	117	44.1	5	11.6
Unidentified prey	5	1.9	2	4.7
Total	265	100	43	100

old female first nested with a similarly aged male and subsequently nested with a male which was more than three years old. The first egg laying of this female fell on 28th March and the second was on 11th June 2014. The nests were 3.02 km from each other. In the first nesting attempt, the female laid four eggs, all nestlings hatched and only two female-fledglings (i.e. 0 % male sex ratio) left the nest. The female abandoned the first nest when two nestlings were present and the eldest was 22 days old; after this point she did not visit the first nest. The female started egg laying in the second nest 23 days after leaving the first one, with a different male. In the second nest, the female also laid four eggs, all nestlings hatched and three fledglings (two male fledglings and one female fledgling, i.e. 67 % male sex ratio) left the nest. The female abandoned the second nest when three nestlings were present and at the time when the oldest nestling was 20 days old; after this point she visited the second nest once.

During the first nesting, the female weighed 157 g (measured seven days after laying of the first egg) and the male was 92 g (57 days after laying of the first egg). During the second nesting, the same female weighed 145 g (43 days after laying of the first egg) and her new partner weighed 108 g (57 days after laying of the first egg). During the first nesting period, the male delivered 265 prey items within 52 days and during the second nesting the other male delivered 43 prey items within 13 days. There were differences in the taxonomic composition of the diet structure between the first and second nesting ($\chi^2 = 37.2$, df = 6, $P < 0.001$). In the first nesting, bird prey was the dominant diet component (44.1 %); within this, there was a high proportion of songbird nestlings present (44.0 % of all birds collected, in all stages of development). Apart from birds, the most frequent preys were shrews (28.3 %), and voles (23.8 %). In the second nesting, the most common prey components were shrews (48.8 %, mainly common shrew) and voles (30.2 %), while birds only comprised 11.6 % of diet (no bird nestling was present, Table 3).

Discussion

Vole populations tend to be relatively more stable both within and between years in central Europe, compared to northern Europe, where they undergo regular 3-4 year cycles and large multi-annual and intra-seasonal changes in abundance (Hansson & Henttonen 1985, Hanski et al. 1991), which can result in increased nestling mortality and poor reproductive success of northern owl populations (Zárybnická et al. 2015). In this study, a significant effect of food shortage in our central European study site on the breeding processes of Tengmalm's owls has been found. In particular, there was a very low availability of both of the main prey (mice and voles) during spring in the Ore Mountains in 2014; this resulted in low owl breeding density, small clutches, and low reproductive success of owls, expressed as the number of fledglings. All these breeding parameters were significantly lower than their long-term averages. Also a delay of 25 days was found in the mean egg-laying date, in comparison with the 14-year average. Avian predators, and Tengmalm's owl in particular are well known for their ability to adjust their reproductive strategies across space and time, according to the actual food availability (e.g. Hakkarainen et al. 2003, Byholm et al. 2007) and the results presented in this study are in accordance with this (our first prediction).

In contrast to our second prediction, a case of sequential polyandry has been recorded, where a female successfully completed both clutches and broods, and 50 % and 75 % of her fledglings, respectively, left the nests. In both nesting attempts, the female deserted the nests before the fledglings had left the nest, leaving them to be cared for by her mates. The mean body mass of Tengmalm's owl females during the first half of the incubation period reached 181 ± 12.5 g, and during the

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first half of nestling period 168 ± 16.8 g (Korpimäki 1990). Although the polyandrous female was two years old, which could give her advantage for reproductive success (Korpimäki 1988b), she was at a substandard body mass during both nesting attempts (157 g during the first half of incubation period and 145 g during the first half of nestling period, respectively). Due to both the food shortage in the study season and the female's substandard body mass, sequential polyandry was unexpected.

The diet of the owls was composed mostly of alternative prey (birds and shrews were dominant in both nesting attempts; 72.4 % and 60.4 %, respectively, however, the male in the first nesting attempt did provide a higher proportion of birds (44 %) than its successor in the second nest. It has been shown that Tengmalm's owl is a generalist and its prey structure varies depending on prey availability across time and space (Korpimäki 1988a, Hakkarainen et al. 2003, Zárybnická 2009b, Zárybnická et al. 2013). In northern areas of Europe, voles of the genera *Microtus* and *Myodes* form a large part of Tengmalm's owl diet (Korpimäki 1988a, Korpimäki & Hakkarainen 2012), while both voles and mice (genus *Apodemus*) are important prey of owls in central Europe (Zárybnická et al. 2011, 2013). Nevertheless, there is evidence that in both areas, the owls shift to alternative prey (small birds and shrews) during low vole abundance (Korpimäki 1988a, Zárybnická et al. 2013). Korpimäki (1981) highlighted an increase of birds present in the owl's diet from April to June, which is not consistent with our findings. We suggest that the increasing availability of voles and mice in our study area during the course of the season (from spring to autumn 2014), and the different habitat quality of the nesting territories (Norway spruce *Picea abies* forest dominated in first nesting territory, while open areas with secondary stands of blue spruce and European larch *Larix decidua* dominated in the second one) could have resulted in the different prey structure delivered by the individual males to their nests. Moreover, the decreasing availability of songbird nests from spring to late summer could influence the present of bird nestlings in the owl's diet.

Fledglings leaving the first polyandrous nest were female biased (100 %), while fledglings leaving the second nest were male biased (67 %). Since the sex ratio of Tengmalm's owl nestlings do not differ between hatching and fledgling (Hörnfeldt et al. 2000), we can assume the similar sex ratio was present in the hatched nestlings (i.e. brood sex ratio). The sex ratios of broods produced by individual females are not well known (Hipkiss & Hörnfeldt 2004) and thus this study provides valuable findings, indicating that the brood and fledgling sex ratios can differ in sequentially polyandrous females within a season. Moreover, the male breeding with the female in the second nest was older (more than three years old) than the male in the first nest, and in line with this, it also had a higher body mass. Studies have proven that older Tengmalm's owl males produce more fledglings than younger males (Korpimäki 1988b, Laaksonen et al. 2002), which is consistent with our findings.

In conclusion, this study confirms that Tengmalm's owls adjust their reproductive strategies in terms of laying date, breeding density, clutch size, and reproductive success to prey availability. Simultaneously, the study has documented one case of successful sequential polyandry in a year of food scarcity. The two-year-old female with substandard body mass laid four eggs in each clutch, but the number of fledglings and sex ratio of fledglings differed in each nesting attempt. This suggests that not only can food availability drive an owl's decision about parental care, but other factors probably play a role as well.

Acknowledgements

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