**ORIGINAL ARTICLE**

# Poor reproductive success of polygynously mated female birds with obligatory bi-parental care: a result of deceptive behaviour of males?

Inga Kujala[1] · Hannu Pöysä[1] · Erkki Korpimäki[2]

## Abstract

Social polygyny usually benefits males by increasing the number of offspring, whereas it is detrimental for females as they must share the resources provided by their mate. An intersexual conflict may exist in animals with obligatory bi-parental care, such as birds of prey, in which females incubate and brood, whereas males provision food for their families. Long-term ringing data from Eurasian kestrels (*Falco tinnunculus*) breeding in nest-boxes and data on density indices of main prey animals (voles) were collected during 1985–2013 in western Finland to study polygynous behaviour. Of 1294 males, 54 (4.2%) were encountered at two (53) or three (1) nests during the same breeding season. Polygyny occurred more frequently during years of high vole abundance. The distances between nests of corresponding primary and secondary females were greater (median 1010 m) than the distances from nests of primary females to the nearest vacant nest-box (median 455 m). Twenty-eight (53%) of 53 secondary females had nearest available monogamous male within 2 km from their nest-boxes, indicating that mating options were available. Secondary females produced 30% less fledged offspring than simultaneously laying monogamously paired females. The abundance of prey animals is apparently alleviating the effort of males mating with multiple females. Spacing out the nests of primary and secondary females implies deceptive behaviour in the nest-site selection of polygynous males. Contradicting the polygyny threshold model, reproductive success of secondary females was significantly reduced in comparison to monogamous females laying simultaneously. These results show that secondary kestrel females apparently made a maladaptive choice, likely because they were deceived to accept polygynous mating status during the courtship feeding period.

## Significance statement

As dedicated parental effort of both the male and the female is vital to ensure the offspring survival amongst animals with obligatory bi-parental care, polygyny should be inherently a maladaptive mating strategy for females. However, regular social polygyny has been documented in at least 10% of bird species from ten orders. Previous studies on breeding success of polygynous birds of prey indicate reduced offspring production of secondary female partners with no apparent cause for females to choose polygynous males over other mating options. We showed that polygyny in Eurasian kestrels is frequent when food is abundant facilitating males to provision their two or more females during courtship feeding. Polygynous males space out their two nests thus attempting to hide their mating status from their secondary partners which suffer from their mate choice in form of poor reproductive success. Therefore, amongst the "cost of polygyny to females" hypotheses, the deceptive behaviour of males during courtship feeding appeared to be an apparent explanation for maladaptive mate choice of secondary females.

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✉ Inga Kujala
ingaku@uef.fi

1   Department of Environmental and Biological Sciences, University of Eastern Finland, Joensuu, Finland

2   Section of Ecology, Department of Biology, University of Turku, N20014 Turku, Finland

## Introduction

Animals display a remarkable variety of mating systems, induced by the intricate battle of sexes and the diverse ecological niches they occupy. Whilst avian mating systems are flexible in both ecological and evolutionary time, social monogamy is the predominant mating system of bird species with obligatory bi-parental care (Johnson and Burley 1998). However, many individual-level population studies have revealed that regular social polygyny occurs in at least 10% of bird species from ten orders (review by Bennett and Owens 2002). In general, polygyny benefits males by increasing the number of offspring with little effort, whereas it is detrimental for females as they must share the resources provided by their mate (e.g. Orians 1969; Davies 1997; Emlen and Oring 1977). Therefore, in order for a polygynous mating system to evolve, the conflict between the sexes should be settled: females must either benefit in some other way from accepting their status as a secondary partner, be coerced into it by having no better options or enter it unknowingly.

Several hypotheses that can be divided in two categories have been put forward to explain female acceptance to polygyny depending on whether females face a cost of polygyny (review in, e.g. Davies 1997; Cézilly and Danchin 2008). In resource defence polygyny, males possess some resource critical to females and, therefore, have control over females as well (Emlen and Oring 1977). If resources are distributed unevenly amongst males, a female must choose her mate based both on the quality of males themselves and the resources they are defending, such as territory quality. Considering hypotheses that assume no ultimate costs of polygyny to females, the polygyny threshold model has received much attention. This model states that females accept the status of a secondary mate of a male with a high-quality territory despite his reduced contribution to parental care when it is more profitable than pairing with a monogamous male possessing a poor-quality territory (Verner 1964; Verner and Willson 1966). Female choice based on territory quality is possible with or without their knowledge of mating status of polygynous males. The "sexy son" hypothesis, in turn, says that a female chooses an attractive mate in order to maximise the reproductive success of her male offspring inheriting attractive characteristics from his father (Weatherhead and Robertson 1979). If "sexy sons" type of selection was in effect, females should choose polygynous males over unmated males even though their immediate reproductive success would be reduced, as their sons would later reap the benefits of multiple pairings (Weatherhead and Robertson 1979; Heisler 1981). However, for a species to exhibit true "sexy son" selection, polygynous marital status should be highly heritable (Alatalo et al. 1981). There are two hypotheses that assume a cost (immediate and long-term) of

polygyny to females: first, the deception hypothesis states that already-mated males can appear as bachelors during courtship by possessing multiple territories, letting females to choose solely on the basis of territory and/or male quality whilst unaware of the premise of sharing the male (Alatalo et al. 1981). Second, the "no better option" hypothesis states that a lack of alternative mating options could mean the only alternative to polygyny is not breeding (Newton 1979). Later this idea has been extended to passerines (e.g. Stenmark et al. 1988).

An intersexual conflict may exist in animals with obligatory bi-parental care, such as birds of prey, in which females incubate and brood, whereas males provision food for their families. Despite the rigid roles in parental care based on sex and the responsibility for food provisioning for offspring belonging almost solely to male parents, polygynous mating has been observed in multiple bird of prey species (e.g. Balfour and Cadbury 1979; Altenburg et al. 1982; Simmons et al. 1986a; Korpimäki 1989; review in Korpimäki 1988). For predatory birds, the prevalence of polygyny appears to be determined by the availability of food during the time of breeding (Simmons et al. 1986a; Korpimäki 1988, 1991). Likewise, the environmental conditions associated with the breeding success have been proposed to affect the frequency of polygyny in songbird populations (Santoro et al. 2022). Therefore, the abundance of prey animals is expected to influence the ease of attaining a mate and the likelihood of successfully courting and mating with multiple females (Newton 1979; Korpimäki 1988).

Eurasian kestrels (*Falco tinnunculus*; hereafter kestrels) display a distinct division of labour between the sexes like most birds of prey (Masman et al. 1998). Males deliver prey to females during pair formation and courtship feeding and during the egg-laying period and proceed to forage in increasing intensity from incubation to hatching and nestling periods to sufficiently feed female parents and their brood. Female parents are responsible for egg laying, incubation and brooding of the chicks until they are 2–3 weeks old. Therefore, the kestrel family is predominantly dependent on food provisioning by the male parent (Masman et al. 1988; Tolonen and Korpimäki 1994; Jönsson et al. 1996). During courtship, the female typically ceases foraging altogether and instead waits for the male at the prospective nest-site, begging for food deliveries (Masman et al. 1988; Palokangas et al. 1992). As courtship feeding is extremely time-consuming for males, maintaining necessary provision rates for a clutch of nestlings and a secondary mate simultaneously appears unlikely without a generous supply of food (Korpimäki 1988; Masman et al 1988).

Voles of the genera *Microtus* and *Myodes* are the predominant food source of kestrels, comprising over a half of their diet (Village 1982a; Korpimäki 1985b; Masman et al. 1988). Consequently, fluctuations in vole abundance largely

modify the dispersal, breeding density and reproductive success of kestrels (Village 1982b; Korpimäki 1984; Korpimäki and Norrdahl 1991; Korpimäki and Wiehn 1998; Vasko et al. 2011). Breeding male kestrels forage at a range of under 2 km from their nest, with their hunting territories overlapping with neighbouring pairs (Village 1983). Kestrels do not exhibit extreme territorial behaviour; both female and male kestrels defend their territories predominantly in the immediate vicinity of their nests, and neighbouring pairs are usually tolerated during good vole years in particular, as breeding pairs appear in higher densities when voles are available in plenty (Village 1983; Korpimäki 1984; Wiklund and Village 1992).

In polygynous setting, males appear to favour their first brood over any other: differences between primary and secondary females and monogamous females in terms of food provisioning by males and reproductive success have been observed in, for example, pied flycatchers (*Ficedula hypoleuca*) (Alatalo et al. 1981), Eurasian marsh harriers (*Circus aeruginosus*) (Altenburg et al. 1982), northern harriers (*Circus hudsonius*) (Simmons et al. 1986b) and Tengmalm's owls (*Aegolius funereus*) (Korpimäki 1991). Favouring of primary females over the secondary one in a bigynous mating setting has also been documented in the red kite (*Milvus milvus*) (Kleef and Bustamante 1999) and in the flammulated owl (*Psiloscops flammeolus*) (Linkart et al. 2008). For the kestrel, the few existing observations from food provisioning of bigynous males indicate that the males favour their primary females (Wang et al. 2019) and that secondary females produce only 52% of the fledglings of simultaneously laying monogamous females (Korpimäki 1988).

As the acceptance of polygyny by secondary females appears, at least in terms of immediate breeding success, to be maladaptive amongst many bird of prey species including kestrels, the "costs to female" hypotheses are seemingly most probable explanations for acceptance of harem position by females and for successful mating of males with more than one female. However, these hypotheses—the deception hypothesis and the "no better option" hypothesis—have not yet been tested with long-term data including kestrels. Therefore, the aim of this study is to attempt to answer to the following questions: (1) do polygynous pairings of kestrels occur more frequently during high abundance of main prey animals, (2) are the polygynous males attempting to conceal their mating status when pairing with their secondary mate by spacing out their two or more nests, (3) are monogamous mating options available for secondary females when they accept harem position, (4) are the secondary females disadvantaged compared to primary females or females in monogamous pairs laying simultaneously in terms of offspring production, and (5) are birds of certain age and size more susceptible to become secondary partners or polygamists? Finally, we will discuss our results in the light of the four abovementioned main hypotheses put forward to explain polygyny.

## Materials and methods

### Study area and data collection

The data was collected from a study area of 1300 km² in the Kauhava region, South Ostrobothnia, western Finland, in years 1985–2013. The area is comprised of two subregions, one of which is located in the valley of Lapua river (Alajoki field plain) and has a largely homogenous landscape with vast fields in agricultural use (area 100 km²), whilst the other is located in the municipality of Kauhava and consists of smaller (1–10 km²) fields alongside with plots of coniferous forest and clear-cut areas. Data obtained from large fields (Alajoki field plain) and small fields in Kauhava region were analysed separately when analysing the relationship between polygyny and vole abundance, as landscape heterogeneity has been found to affect the reproductive success in kestrels, especially in tandem with fluctuations in food availability (Sumasgutner et al. 2019).

Breeding adult kestrels were captured from their nest boxes with swing-door traps during the mid-nestling period, when the females are stationed at their nests almost invariably and males can be encountered on occasional visits (see Vasko et al. 2011; Terraube et al. 2015 for further details on methods). DNA-fingerprinting showed that the frequency of extra-pair paternity was low and thus males captured at nestboxes were genetic fathers of their offspring (Korpimäki et al. 1996). Captured birds were sexed and aged based on their plumage (2nd-year and older individuals; Forsman 1999), ringed or identified by a pre-existing ring, and their body mass, wing length and tail length were measured. Nests were visited routinely to determine the date of first egg-laying, clutch size and the number of hatchlings and fledglings (see Korpimäki and Wiehn 1998 for further details). It was not possible to record data blind because our study involved focal animals in the field.

For estimating local vole densities, small mammals were trapped with snap traps in both agricultural field and forest habitats at 3 to 5 different sites in both subregions for 200–600 trap nights per site (Korpimäki et al. 2005). Annual vole trappings were conducted in spring (mid-May), reflecting the food availability during the egg-laying and incubation periods of kestrels. Vole indices were calculated as the number of voles caught per hundred trap nights. Of all mammal species captured, voles of the genera *Microtus* and *Myodes* were included in determining the vole indices, because they are the main prey species of kestrels in the study area (Korpimäki 1985a, b). The other encountered species, harvest mouse (*Micromys minutus*), house mouse

(*Mus musculus*) and Eurasian shrew (*Sorex araneus*), were excluded from calculations because they are only alternative prey for kestrels (Korpimäki 1985a, b).

## Statistical methods

We used Wilcoxon matched-pairs signed ranks test for comparing the breeding success and parental characteristics (wing length, tail length, body mass and age) of primary and secondary females of polygynous males to each other and to monogamously paired females of simultaneous timing in the initiation of egg laying. Similarly, Wilcoxon matched-pairs signed ranks test was used to test differences in body size and age between monogamous and polygynous males. For choosing comparable monogamous birds, females in same subregion with the closest laying date during the same breeding season were selected as matched pairs for primary and secondary females, whereas in males, the laying date of either the sole mated female (in monogamous males) or the primary female (in polygynous males) was used to form matched pairs of monogamous and polygynous males within the same subregion.

For determining the association between vole abundance and the frequency of polygynous males, Spearman's rank correlation coefficient ($r_s$) was calculated between the vole index and the percentage of polygynous males for each year, separately for large and small fields (see above).

Linear distances between the nests of primary females and their respective secondary female, as well as the distance from the nest of primary females to their closest vacant nest box, were calculated in ArcMap using the Point Distance tool. Wilcoxon matched-pairs signed ranks test was used to test the significance of differences between primary female nest–secondary female nest and primary female nest–closest empty nest box distances. For the purpose of determining the distance from secondary nests to the nearest available monogamous mating option, the nearest available monogamous mating option was defined as the nearest monogamous

female with a later laying date, as laying date has been shown to closely correlate with the order of females choosing their mate in kestrels in Scotland (Village 1985) and in the present study area (Palokangas et al. 1992).

All statistical analyses were conducted in RStudio operating on R version 4.0.3 (RStudio Team 2020). In addition to RStudio's built-in commands, packages *dplyr*, *ggpubr* and *ggplot2* were used either in analyses or in creating figures.

## Results

### Vole abundance and the frequency of polygyny

Of all 1294 males captured from nest boxes, 54 were encountered at two (53) or three (1) different nests during the same breeding season and hence identified as polygynous (proportion of polygynous males 4.2%, Table S1). For one polygynous male, the female status could not be assessed due to indetermined laying dates, and the two females were therefore omitted from analyses. Likewise, the sole tertiary female was not included in the analyses. The relative frequency of polygynous males increased with vole abundance both at the study site of large fields ($r_s = 0.69$, $p < 0.001$) and at small fields ($r_s = 0.57$, $p < 0.01$, Fig. 1).

### Inter-nest distances

Of the 53 secondary females, only 11 occupied the vacant nest box closest to their corresponding primary females. Median distance between nests of primary females and their nearest unoccupied nest box was 455 m (mean = 515 m, $SD = 327$ m, range 58–1780 m) whilst median distance between nests of primary and secondary females sharing a polygynous male was 1010 m (mean = 1 410 m, $SD = 1380$ m, range 252–6170 m) (Wilcoxon matched-pairs signed ranks test, two-tailed, z = 5.64, $p < 0.001$, Fig. S1).

**Fig. 1** Relationship between the local abundance index of voles and the percentage of polygynous males of all males caught for large fields (left panel) and small fields (right panel). Each individual dot represents 1 year (1985–2013, *N* = 29)
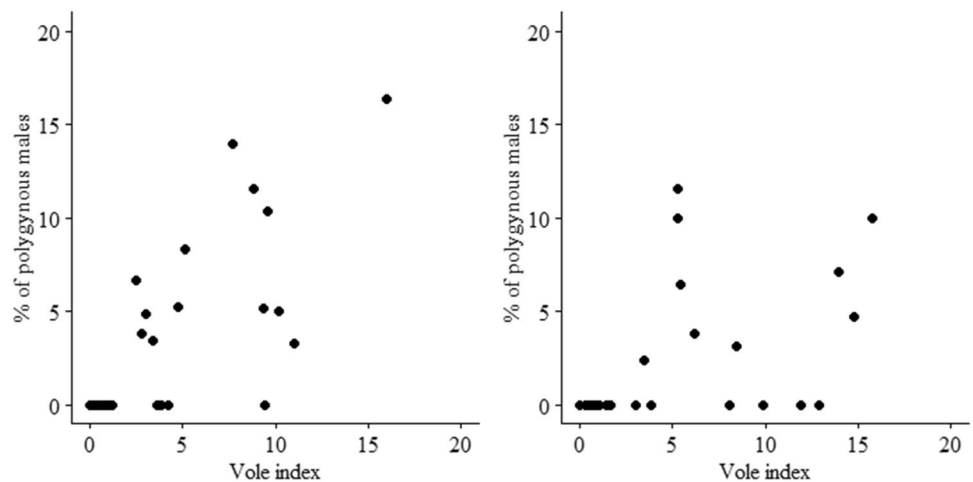
Twenty-eight (53%) of 53 secondary females had nearest available monogamous mating option within 2 km from their nest boxes when pairing with polygynous male (Fig. S2). Half of secondary females had the nearest available monogamous male option within the distance of 1690 m (mean 3000 m, *SD* = 3160 m, range 266–13,400 m).

## Breeding success

Concerning breeding success, 53 polygynous primary females and 53 polygynous secondary females were compared with each other and with monogamous females of similar timing of egg laying (Fig. 2). Primary females laid larger clutches than secondary females (Wilcoxon signed-rank test, two-tailed, z = 3.2, *p* < 0.01) and produced a higher number of fledglings (Wilcoxon signed-rank test, two-tailed, z = 3.3, *p* < 0.001). Contrarily, the difference in the number of hatchlings between primary and secondary females was not statistically significant (Wilcoxon signed-rank test, two-tailed, z = 1.8, *p* = 0.07).

In comparison to simultaneous females in monogamous pairings, secondary females produced a smaller number of fledglings (Wilcoxon signed-rank test, two-tailed, z = 3.1, *p* < 0.01). In fact, secondary females performed poorly in terms of number

of fledglings, because they produced 30% less fledged offspring than simultaneously laying monogamously paired females. No obvious difference was found in terms of clutch size (Wilcoxon signed-rank test, two-tailed, z = 0.54, *p* = 0.59) or number of hatchlings (Wilcoxon signed-rank test, two-tailed, z = 1.6, *p* = 0.11) between secondary and monogamous females.

## Parental characteristics

Amongst all groups of females with different mating status, no differences in wing length, tail length, or body mass were found (Tables 1, 2 and 3). Yearlings (second calendar year; hereafter 2 cy) appeared to be more numerous amongst secondary females than amongst primary females, but the difference was not statistically significant. Secondary females of polygynous males initiated egg laying on average 14 days later than primary females (see Table S2 for range and variation of laying date).

Polygynous and monogamous males appeared to be similar in regard to wing length, tail length, and body mass (Tables 4 and 5). In comparison to monogamous males, polygynous males were more likely to be older (third or greater calendar year; hereafter + 2 cy) birds (Table 5).



**Fig. 2** Mean values of clutch size, number of hatchlings and number of fledglings shown for females of different mating statuses. The error bars represent standard deviation values. The sample size of each group is represented above bars
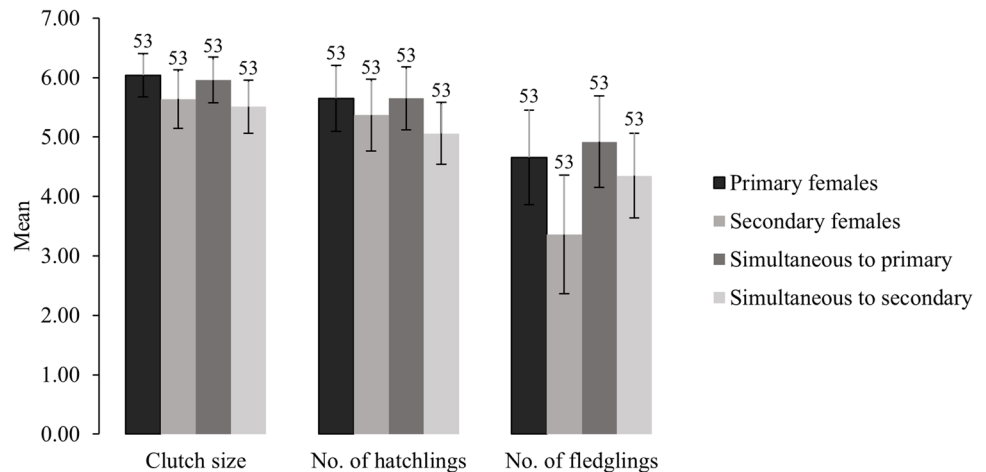
**Table 1** Comparison of wing length, tail length, body mass, and laying date of primary and secondary females of polygynous males, and females of monogamous males with similar timing of laying in Eurasian kestrel

| | Polygynous | | | | | | Monogamous | | | | | |
| | Primary females | | | Secondary females | | | Simultaneous to primary | | | Simultaneous to secondary | | |
| | Mean | SD | N | Mean | SD | N | Mean | SD | N | Mean | SD | N |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Wing length (mm) | 257 | 6.66 | 53 | 256 | 5.37 | 53 | 257 | 7.69 | 53 | 257 | 6.56 | 53 |
| Tail length (mm) | 168 | 9.93 | 53 | 168 | 6.75 | 53 | 169 | 6.52 | 53 | 167 | 7.53 | 53 |
| Body mass (g) | 214 | 20.5 | 53 | 208 | 18.4 | 53 | 215 | 18.2 | 53 | 211 | 17.9 | 53 |
| Laying date | 30.6 | 8.36 | 53 | 44.5 | 8.54 | 53 | 30.7 | 7.88 | 53 | 44.2 | 8.36 | 53 |

**Table 2** Comparison of age class (in calendar years, with 2 cy meaning a bird hatched in the previous year and + 2 cy a bird hatched before the previous year) distribution of primary and secondary females of polygynous males, and females of monogamous males with similar timing of laying

| Age | Polygynous | | Monogamous | | Total |
| | Primary females | Secondary females | Simultaneous to primary | Simultaneous to secondary | |
|---|---|---|---|---|---|
| 2 cy | 7 | 15 | 8 | 13 | 43 |
| % | 13.2% | 28.3% | 15.1% | 24.5% | 20.3% |
| + 2 cy | 43 | 36 | 41 | 36 | 156 |
| % | 81.1% | 67.9% | 77.4% | 67.9% | 73.6% |
| Unknown | 3 | 2 | 4 | 4 | 13 |
| % | 5.7% | 3.8% | 7.5% | 7.5% | 6.1% |

**Table 3** Statistical comparisons of wing length, tail length, body mass, laying date, and age class (in calendar years, with 2 cy meaning a bird hatched in the previous year and + 2 cy a bird hatched before the previous year) distribution between females of different mating statuses using Wilcoxon signed-rank test (two tailed). Statistically significant $p$-values ($p < 0.05$) are marked with an asterisk (*)

| Wilcoxon test (two-tailed) | Polygynous primary and polygynous secondary | | Polygynous primary and simultaneous monogamous | | Polygynous secondary and simultaneous monogamous | |
| | z | p | z | p | z | p |
|---|---|---|---|---|---|---|
| Wing length (mm) | 0.55 | 0.6 | 0.37 | 0.7 | 0.028 | 1 |
| Tail length (mm) | 0.96 | 0.3 | 0.19 | 0.9 | 0.73 | 0.5 |
| Body mass (g) | 1.3 | 0.2 | 0.65 | 0.5 | 0.79 | 0.4 |
| Laying date | 6.3 | <0.001* | 0.66 | 0.5 | 0.82 | 0.4 |
| Age (2 cy or + 2 cy) | 1.6 | 0.1 | 0 | 1 | 0.70 | 0.5 |

**Table 4** Comparison of wing length, tail length and body mass of polygynous males and monogamous males similar in timing to the primary pairing of the polygynous male

| | Polygynous males | | | Monogamous males | | |
| | Mean | SD | N | Mean | SD | N |
|---|---|---|---|---|---|---|
| Wing length (mm) | 249 | 6.37 | 54 | 248 | 6.25 | 54 |
| Tail length (mm) | 164 | 7.42 | 54 | 164 | 5.51 | 54 |
| Body mass (g) | 175 | 12.5 | 54 | 172 | 12.2 | 54 |

**Table 5** Comparison of age class (in calendar years, with 2 cy meaning a bird hatched in the previous year and + 2 cy a bird hatched before the previous year) distribution of polygynous males and monogamous males similar in timing to the primary pairing of the polygynous male, and statistical comparisons of wing length, tail length, body mass, and age class distribution between the two male groups using Wilcoxon signed-rank test (two tailed). Statistically significant $p$-values ($p < 0.05$) are marked with an asterisk (*)

| Age | Polygynous males | Monogamous males | Total | Wilcoxon test (two-tailed) | z | p |
|---|---|---|---|---|---|---|
| 2 cy | 0 | 6 | 6 | Wing length (mm) | 0.80 | 0.4 |
| % | 0 | 11.1% | 5.6% | Tail length (mm) | 0.37 | 0.7 |
| + 2 cy | 54 | 48 | 102 | Body mass (g) | 0.52 | 0.6 |
| % | 100% | 88.9% | 94.4% | Age (2 cy or + 2 cy) | 2.3 | <0.05* |

## Discussion

The following main findings emerged in this study. (i) Polygynous pairings appeared to be more frequent during years of high vole abundance. (ii) The distances between the nests of corresponding primary and secondary females were greater than the distances from nests of primary females to the nearest vacant nest box. (iii) More than a half of secondary females had nearest available monogamous mating option within 2 km from their nest-boxes when pairing with polygynous male. (iv) The secondary females of polygynous males started egg laying on average 14 days later and produced less fledglings than the primary females. (v) Secondary females performed poorly in terms of number of fledglings, as they

produced a 30% smaller number of fledglings than simultaneously laying monogamously paired females, although there was no obvious difference in the number of eggs and hatched chicks. This indicates that there is a cost of polygyny to secondary females, and that the "deceptive behaviour" hypothesis rather than the "no better option" hypothesis could explain the poor choice of harem females.

### Polygyny and food availability

Male kestrels were more likely to attract multiple females during seasons when main prey animals (voles) were available in plenty. This result appears to be consistent with the suggestion that with reliable opportunities to acquire food, a secondary territory and nest-site are easier to maintain, and the male is more likely to succeed in mating with two subsequent females and in feeding his females so that they can lay eggs (Korpimäki 1988). Heterogeneity of the breeding environment does not appear to increase the prevalence of polygyny, even though the correlation between vole abundance and breeding success of kestrels has been found to be stronger in areas of more variable territory characteristics (Sumasgutner et al. 2019). In previous studies, a similar relationship between abundance of main foods (voles) and frequency on polygyny has been also found in northern harriers (Hamerstrom et al. 1985; Simmons et al. 1986a) and Tengmalm's owls (Korpimäki 1991).

The outmost importance of food abundance during early stages of breeding in attaining polygyny is further highlighted by the following facts. The mean time interval between the start of egg laying in primary and secondary nests was only 14 days indicating that the fertile periods (beginning approximately 10 days before and ending 8–10 days after the first egg is laid for a 6-egg clutch) of two females of bigynous males somewhat overlapped (Korpimäki et al. 1996). After pair formation, male kestrels must trade-off between attracting additional mates and investing in paternity assurance by frequent within-pair copulations (207–230 per clutch; Korpimäki et al. 1996) and courtship feeding at the primary nest. After successful attraction of a secondary female, a bigynous male has to copulate frequently with her and guard and feed two mates > 1 km apart. Despite these constraints, DNA-fingerprinting showed that polygynous males did not lose genetic paternity of their two broods (Korpimäki et al. 1996). Polygynous males may thus be high-quality hunters and have a territory with abundant food supply so that they can simultaneously assure their paternity and feed their two mates prior to and during egg laying.

### Spacing out of nests of polygynous males

Polygynous males preferred to attract their secondary females to distant nest boxes instead of vacant nest boxes near their primary females' nest. Hunting territories of breeding male kestrels appear to extend to a radius of under 2 km from the nest in Scotland, with the distance between nearest neighbouring nests being usually within 500 m and noticeably less during good vole years (Village 1983). Therefore, the remote locations of secondary nests in relation to primary nests of polygynous males are unlikely to be indicative of inherent nest density distribution of kestrels, particularly when considering that in most cases, there were unoccupied nest boxes available in a closer distance. It would be reasonable to assume that the male choice for remote secondary nest-sites would be costly in terms of time and resources allocated to mate guarding, copulation and courtship feeding at primary nests (see above). Nevertheless, separating primary and secondary nests to distant locations would be advantageous to polygynous males when attempting to hide the fact that they have already mated. Accordingly, the existence of deceptive behaviour in polygynous mating amongst kestrels would be at the very least a partial explanation for why females would accept the disadvantageous position as a secondary mate.

In comparison to previously studied characteristics of polygyny in birds of prey, the behaviour recorded from polygynous kestrels seems to be parallel with polygynous Tengmalm's owl males in terms of spacing out their two or more nests (Korpimäki 1991). Whereas Tengmalm's owl is a nocturnal species inhabiting forests, the diurnally active open-country kestrels may not be able to hide their mating status with as little effort. Nevertheless, the average distance between nests of polygynous males is only slightly smaller amongst Tengmalm's owls (mean 1 351 m [Korpimäki 1991] vs. 1 410 m in this study). Conversely, amongst the open-habitat breeding northern harriers, non-primary harem females prefer nesting close to their corresponding primary females, with an average of 458 m distance between intra-harem nests, rendering the notion of hidden marital status impossible (Simmons 1988).

### "Cost of polygyny to females" hypotheses

More than a half of secondary females had nearest available monogamous mating option within 2 km from their nest-boxes when pairing with polygynous male, indicating that mating options were available within the average hunting range of breeding kestrels (Village 1983). Whilst late-arriving females have been suggested (e.g. Stenmark et al. 1988) to choose a polygamous mate because settling for a mated male would be less costly than keeping on searching for an unmated one, unpaired male kestrels should not be difficult to find, as kestrels are open-country raptors and the males perform visible display flights over their nest-sites (Piechocki 1982; Village 1990). Therefore, our results do not appear to support the "no better option" hypothesis (Newton 1979).

In comparison to simultaneously breeding females mated with monogamous males, secondary females of polygynous males produce 30% less offspring surviving into fledgling age, although there was no obvious difference in the number of eggs and hatched chicks. This poor offspring production is inconsistent with the prediction of the polygyny threshold model (Verner 1964; Verner and Willson 1966). The amount of food provided by males prior to and during the egg-laying period directly determines clutch size in kestrels and other birds of prey, with plentiful feeding resulting in larger clutches (Simmons 1988; Korpimäki and Wiehn 1998). Therefore, during the egg-laying and incubation periods, polygynous male kestrels feed their secondary mates as often as monogamous males pairing simultaneously, but evidently appear to favour their primary broods in food provisioning during the nestling period. Food provisioning rates of male kestrels during the egg-laying period are usually closely correlated with provisioning rates during the nestling period (Palokangas et al. 1992, 1994). Therefore, our interpretation for the poor offspring production of secondary females is that polygamous males likely imitate provisioning rates of unpaired males during the courtship feeding and egg-laying periods but decline their parental effort at secondary nests when chicks of primary females hatch. As "deceptive" courtship feeding rates during pair-formation have been observed in polygamous northern harrier and Tengmalm's owl males, it could potentially explain the discrepancy between the number of laid eggs and fledged chicks of secondary kestrel females as well (Simmons 1988; Korpimäki 1991).

Amongst polygynous males, older males were found to be significantly more frequent than in monogamous males, which has been observed amongst other instances of polygyny in birds of prey (Korpimäki 1991). As older kestrels are likely to rear more surviving offspring than inexperienced parents, females might be disposed to select a mate with the physical characteristics of an older male if they were to choose their mate based on immediate cues (Village 1985, 1986). Since birds that arrive and begin breeding later in the season are mostly comprised of young individuals, it would be expected of late-arriving females to choose an already-mated male over the younger bachelor males of similar arrival timing (Village 1985).

Monogamously paired female kestrels are partially able to compensate reduced food provisioning rates of their mates during the late nestling period (Tolonen and Korpimäki 1994), but female parents cannot leave their newly hatched chicks without brooding and start to hunt at a distance in the early phase of the nestling period under harsh weather conditions of our study area. Similar results have been obtained in northern harriers in Canada (Simmons et al. 1986b): harem females were not able to compensate for lowered food provisioning rates of polygynous males. Decreased investment in food provisioning by polygynous males has been documented in hen harrier harems, but secondary hen harrier females are somewhat able to compensate the

losses in male provisioning by capturing larger prey items themselves, performing only slightly poorer than their corresponding primary females (Redpath et al. 2006). This result contrasts with the marked cutback in offspring production of secondary female kestrels and northern harriers. One potential reason for secondary female kestrels being unable to compensate is that in northern, less productive environments, they have scarcity of larger prey items (Korpimäki 1985a, b), whereas hen harriers have abundance of larger prey species (for example, red grouses *Lagopus lagopus scoticus*, and meadow pipits *Anthus pratensis*) in Scottish moors (Redpath and Thirgood 1999; Redpath et al. 2006). Hen harriers might be better able to shift to larger animals to upkeep sufficient food provisioning, in addition to polygynous hen harrier males potentially possessing higher grade territories yielding more prey biomass for secondary harem females as well (Redpath et al. 2006). As these differences in the ability to compensate for the losses in male provisioning would be rooted in ecological and environmental variation between the study populations, this reasoning would be in line with the hypothesis of available breeding resources influencing the costs of polygyny (Santoro et al. 2022).

As we did not examine the lifetime reproductive output or long-term fitness of secondary females, we cannot rule out the possibility of "no cost of polygyny" hypotheses explaining female acceptance in kestrels. The "sexy son" hypothesis would be a feasible explanation to female acceptance of polygyny if secondary females would surpass monogamous ones in fitness over multiple generations, requiring a considerable increase in the reproductive success of their male offspring in order to cover the mothers' losses (Heisler 1981). However, because the prevalence of polygyny in kestrels appeared to be closely associated with food availability and being essentially non-existent during years of low vole abundance, polygynous behaviour is likely to be more influenced by environmental than genetic factors. Nonetheless, a proper test of "sexy son" hypothesis would have required comparing numbers of surviving grandchildren between monogamous and non-monogamous females, which is impossible in a restricted study area, considering the tendency of long-distance dispersal amongst juveniles of both sexes and adult female kestrels (Vasko et al. 2011). Finally, individual variation in male quality may importantly affect the indirect benefits of secondary and primary females relative to monogamous females and should be considered when testing the "sexy son" hypothesis (Santoro 2020).

## Conclusions

Amongst "cost of polygyny to females" hypotheses, the deception hypothesis appears as the most plausible explanation behind female acceptance amongst kestrels. As secondary females had poor offspring production, it is reasonable

to assume that they did not choose harem position willingly. Additionally, the deception hypothesis would be plausibly supported by the findings on the effect of food availability on the occurrence of polygyny: it should be demanding for already-mated males to convincingly present themselves as unmated without high prey availability fuelling their provisioning and copulation rates during courtship feeding of their mates.

Whilst primary females appear to be largely unaffected by the premise of polygyny, secondary females suffer from markedly reduced reproductive output compared to other females who chose their monogamous mate from the same pool of males. As raising a brood would be a considerable investment for any female kestrels, producing 30% less fledged offspring compared to monogamous females of similar timing in laying is a notable fitness loss for the secondary females. Since voluntarily accepting these conditions would not yield a preferable outcome for females, deceptive behaviour of polygynous males could be an enabling factor for successive mating from the viewpoint of reproductive success as well.

In regard to the future direction of research on polygynous behaviour in kestrels and other birds with obligatory bi-parental care, the behaviour related to the deception hypothesis could be explored further. Additional research could be done on topics such as mate searching behaviour of secondary females before they accept harem status, and time and resources allocated by polygynous males to primary and secondary nests during the fertility period of their two or more mates. In order to paint the full picture of polygyny in kestrels, the prospect of uneven operative sex ratios would be sensible to examine as well, considering the differing dispersal behaviour of the sexes which could affect the local density of female kestrels, who are more likely to disperse following prey population fluctuations (Vasko et al 2011). Also, long-term longitudinal studies are much needed so that variation in individual quality could be taken into account when assessing different hypotheses to explain mating decisions of females (Santoro 2020). In any case, male kestrels appear to win the battle between sexes, because polygynous males gain in mating with multiple partners, whereas secondary females lose when choosing harem position.

**Data availability** All data generated or analysed during this study are included in this published article and its supplementary information files.

## Declarations

**Competing interests** The authors declare no competing interests.

**Ethical approval** Trapping and ringing of kestrel parents were executed in accordance to Finnish and EU Laws and regulations and under the ringing licence (no. 524 to EK) by Ringing Centre of the Finnish Museum of the Natural History. Ethical approval from ethics committee for involving animals in this study was not required. All applicable international, national and/or institutional guidelines for the use of animals were followed.

## References

Alatalo RV, Carlson A, Lundberg A, Ulfstrand S (1981) The conflict between male polygamy and female monogamy: the case of the pied flycatcher Ficedula hypoleuca. Am Nat 117:738–753

Altenburg W, Daan S, Starkenburg J, Zijlstra M (1982) Polygamy in the marsh harrier, Circus aeruginosus: individual variation in hunting performance and number of mates. Behaviour 79:272–312

Balfour E, Cadbury CJ (1979) Polygyny, spacing and sex ratio among hen harriers Circus cyaneus in Orkney, Scotland. Ornis Scand 10:133–141

Bennett PM, Owens IPF (2002) Evolutionary ecology of birds life histories, mating systems and extinction, 1st edn. Oxford University Press, Oxford

Cézilly F, Danchin E (2008) Mating systems and parental care. In: Danchin E, Giraldeu LA, Cézilly F (eds) Behavioural ecology. Oxford University Press, Oxford, pp 429–465

Davies NB (1997) Mating systems. In: Krebs JR, Davies NB (eds) Behavioural ecology: an evolutionary approach. Blackwell Science, Oxford, pp 263–294

Emlen ST, Oring LW (1977) Ecology, sexual selection and the evolution of mating systems. Science 197:215–223

Forsman D (1999) The raptors of Europe and the Middle East: a handbook of field identification. Poyser, London

Hamerstrom F, Hamerstrom FN, Burke CJ (1985) Effect of voles on mating system in a central Wisconsin population of harriers. Wilson Bull 97:332–346

Heisler IL (1981) Offspring quality and the polygyny threshold: a new model for the "sexy son" hypothesis. Am Nat 117:316–328

Johnson K, Burley NT (1998) Mating tactics and mating systems of birds. Ornithol Monogr 49:21–60

Jönsson KI, Korpimäki E, Pen I, Tolonen P (1996) Daily energy expenditure and short-term reproductive costs in free ranging Eurasian Kestrels (Falco tinnunculus). Funct Ecol 10:475–482

Kleef HV, Bustamante J (1999) First recorded polygynous mating in the red kite (Milvus milvus). J Raptor Res 33:254–257

Korpimäki E (1984) Population dynamics of birds of prey in relation to fluctuations in small mammal populations in western Finland. Ann Zool Fenn 21:287–293

Korpimäki E (1985a) Prey choice strategies of the kestrel Falco tinnunculus in relation to available small mammals and other Finnish birds of prey. Ann Zool Fenn 22:91–104

Korpimäki E (1985b) Diet of the kestrel Falco tinnunculus in the breeding season. Ornis Fenn 62:130–137

Korpimäki E (1988) Factors promoting polygyny in European birds of prey – a hypothesis. Oecologia 77:278–285

Korpimäki E (1989) Mating system and mate choice of Tengmalm's owls Aegolius funereus. Ibis 131:41–50

Korpimäki E (1991) Poor reproductive success of polygynously mated female Tengmalm's owls: are better options available? Anim Behav 41:37–47

Korpimäki E, Norrdahl K (1991) Numerical and functional responses of kestrels, short-eared owls, and long-eared owls to vole densities. Ecology 72:814–826

Korpimäki E, Wiehn J (1998) Clutch size of kestrels: seasonal decline and experimental evidence for food limitation under fluctuating food conditions. Oikos 83:259–272

Korpimäki E, Lahti K, May CA, Parkin DT, Powell GP, Tolonen P, Wetton JH (1996) Copulatory behaviour and paternity determined by DNA fingerprinting in kestrels: effects of cyclic food abundance. Anim Behav 51:945–955

Korpimäki E, Norrdahl K, Huitu O, Klemola T (2005) Predator-induced synchrony in population oscillations of co-existing small mammal species. Proc R Soc Lond B 272:193–202

Linkhart BD, Evers EM, Megler JD, Palm EC, Salipante CM, Yanco SW (2008) First observed instance of polygyny in flammulated owls. Wilson J Ornithol 120:645–648

Masman D, Daan S, Dijkstra C (1988) Time allocation in the kestrel (Falco tinnunculus), and the principle of energy minimization. J Anim Ecol 57:411–432

Newton I (1979) Population ecology of raptors. T & AD Poyser, Berwick-upon-Tweed

Orians GH (1969) On the evolution of mating systems in birds and mammals. Am Nat 103:589–603

Palokangas P, Alatalo RV, Korpimäki E (1992) Female choice in the kestrel under different availability of mating options. Anim Behav 43:659–665

Palokangas P, Korpimäki E, Hakkarainen H, Huhta E, Tolonen P, Alatalo RV (1994) Female kestrels gain reproductive success by choosing brightly ornamented males. Anim Behav 47:443–448

Piechocki R (1982) Der Turmfalke. A Ziemsen Verlag, Wittenberg Lutherstadt, Die Neue Brehm-Bücherei

Redpath SM, Thirgood SJ (1999) Numerical and functional responses in generalist predators: hen harriers and peregrines on Scottish grouse moors. J Anim Ecol 68:879–892

Redpath SM, Leckie FM, Arroyo B, Amar A, Thirgood SJ (2006) Compensating for the costs of polygyny in hen harriers Circus cyaneus. Behav Ecol Sociobiol 60:386–391

RStudio Team (2020) RStudio: integrated development environment for R. RStudio, PBC, Boston, MA, http://www.rstudio.com/

Santoro S (2020) The neglected role of individual variation in the sexy son hypothesis. Evol Ecol 34:1–9

Santoro S, Fernández-Díaz P, Canal D, Camacho C, Garamszegi LZ, Martínez-Padilla J, Potti J (2022) High frequency of social polygyny reveals little costs for females in a songbird. Sci Rep 12:277

Simmons RE (1988) Food and the deceptive acquisition of mates by polygynous male harriers. Behav Ecol Sociobiol 23:83–92

Simmons RE, Barnard P, MacWhirter B, Hansen GL (1986a) The influence of microtines on polygyny, productivity, age, and provisioning of breeding hen harriers: a 5-year study. Can J Zool 64:2447–2456

Simmons RE, Smith PC, MacWhirter RB (1986b) Hierarchies among northern harrier (Circus cyaneus) harems and the cost of polygyny. J Anim Ecol 55:755–771

Stenmark G, Slagsvold T, Lifjeld JT (1988) Polygyny in the pied flycatcher, Ficedula hypoleuca: a test of the deception hypothesis. Anim Behav 36:1646–1657

Sumasgutner P, Terraube J, Coulon A, Villers A, Chakarov N, Kruckenhauser L, Korpimäki E (2019) Landscape homogenization due to agricultural intensification disrupts the relationship between reproductive success and main prey abundance in an avian predator. Front Zool 16:31

Terraube J, Vasko V, Korpimäki E (2015) Mechanisms and reproductive consequences of breeding dispersal in a specialist predator under temporally varying food conditions. Oikos 124:762–771

Tolonen P, Korpimäki E (1994) Determinants of parental effort: a behavioural study in the Eurasian kestrel, Falco tinnunculus. Behav Ecol Sociobiol 35:355–362

Vasko V, Laaksonen T, Valkama J, Korpimäki E (2011) Breeding dispersal of Eurasian kestrels (Falco tinnunculus) under temporally fluctuating food abundance. J Avian Biol 42:552–563

Verner J (1964) Evolution of polygamy in the long-billed marsh wren. Evolution 18:252–261

Verner J, Willson MF (1966) The influence of habitats on mating systems of North American passerine birds. Ecology 47:143–147

Village A (1982a) The diet of kestrels in relation to vole abundance. Bird Study 29:129–138

Village A (1982b) The home range and density of kestrels in relation to vole abundance. J Anim Ecol 51:413–428

Village A (1983) The role of nest-site availability and territorial behaviour in limiting the breeding density of kestrels. J Anim Ecol 52:635–645

Village A (1985) Spring arrival times and assortative mating of kestrels in south Scotland. J Anim Ecol 54:857–868

Village A (1986) Breeding performance of kestrels at Eskdalemuir, South Scotland. J Zool 208:367–378

Village A (1990) The kestrel. Poyser, London

Wang Y, Liu H, Wang H, Wang Y, Ma L, Yi G (2019) Polygyny in the Eurasian kestrel (Falco tinnunculus): behavior, morphology, age, heterozygosity, and relatedness. J Raptor Res 53:202–206

Weatherhead PJ, Robertson RJ (1979) Offspring quality and the polygyny threshold: "The sexy son hypothesis." Am Nat 113:01–208

Wiklund CG, Village A (1992) Sexual and seasonal variation in territorial behaviour of kestrels, Falco tinnunculus. Anim Behav 43:823–830