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The effect of female body size on clutch volume of Tengmalm's Owls *Aegolius funereus* in varying food conditions

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Body size may influence offspring quality so that large females produce "fit" offspring. Tengmalm's Owl *Aegolius funereus* is one of the most size-dimorphic birds of prey in the Holarctic region with females larger than males. The contribution of female size to egg size and clutch volume (number of eggs × mean egg volume of a clutch) was studied in western Finland during 1981–1990, when the abundance of the owls' main food (voles) fluctuated in 3-yr cycles. Clutch volume was positively related to female body-weight, independent of laying date, which significantly affected egg size in good vole years. Female age, male age, and territory quality did not affect clutch volume. Clutch volume was not associated with female wing-length, but in the peak phase of the vole cycle, long-winged and heavy females produced significantly larger eggs than did short-winged and light females. The results indicate that females can benefit from large skeletal size only in years of food abundance, and that the nutritional condition of females was essential to reproductive success. Our results also suggest that the largeness of females may not be the main cause of the reversed sexual size dimorphism in Tengmalm's Owls.

1. Introduction

In most birds and mammals, males are larger than females (Selander 1972). However, cases where females are larger than males (reversed sexual size dimorphism, RSD) are not unusual (see also Ralls 1977, Bondrup-Nielsen & Ims 1990). RSD may be due to selection promoting large female size, small male size or both. Also, it is possible that both sexes evolve in the same direction at different rates: in this case, females faster than males. Generally, RSD has been suggested to evolve via selection promoting large female size. For example, egg production and incubation efficiency may increase with increasing body size of females (e.g. Reynolds 1972, Snyder & Wiley 1976, von Schantz & Nilsson 1981). Also, in mammals, Ralls (1976) predicted that big mothers are able to produce more and larger offspring with greater survival chances than small mothers.

Some of the well-known examples of RSD are found in diurnal raptors (Falconiformes) and owls (Strigiformes) (Newton 1979, Mikkola 1983). The degree of RSD is very high in some species, for example, female European Sparrowhawks *Accipiter nisus* are almost twice as heavy as males (Newton 1979, 1986). More than 20 hypotheses have been put forward to explain RSD in birds of prey (see Andersson & Norberg

1981, Lundberg 1986, Mueller 1986, Hakkarainen & Korpimäki 1991 for reviews), but no general consensus on the causes of RSD have emerged.

The body condition of females, as measured by protein and fat reserves, has been shown to play an important role in the early stages of breeding (Hirons 1985). For example, a progressive decline in egg mass, as laying progresses, obviously reflects the nutritional state of the female (Schreiber & Lawrence 1976, Birkhead & Nettleship 1984). Females allocate nutrients to precocial chicks by yolk and albumen that demands both large protein reserves and energy (Robbins 1981, Ojanen 1983). During laying, the protein stores in the female are quickly depleted (e.g. Astheimer & Grau 1985, Alisauskas & Ankney 1985). Investment in building protein and fat stores prior to laying affects both quantity and quality of offspring throughout embryonic growth, hatching success and subsequent survival. For example, egg size is positively related to the survival of Herring Gull *Larus argentatus* chicks (Parsons 1970) and the hatching success of Wandering Albatross *Diomedea exulans* (Croxall et al. 1992).

Our study looks at, whether in Tengmalm's Owl *Aegolius funereus*, which is one of the most size-dimorphic owls in Europe (Mikkola 1983, Korpimäki 1986) and in North America (Mueller 1989), large females produce more voluminous clutches than small females. Females are, on an average, 36% heavier and have 4% longer wings than males (Korpimäki 1990a). Tengmalm's Owls breed in tree cavities and nest-boxes in the coniferous forests of the Holarctic region. Males provide food for the whole family, from the courtship feeding till the end of the breeding season, whereas females incubate eggs and care for the nestlings until they are three weeks old (Korpimäki 1981). We investigated, whether under different food conditions, large females produce more and larger eggs. Female Tengmalm's Owls that lay large eggs produce more young (Hakkarainen & Korpimäki 1993), which, along with clutch size, is a good estimate of lifetime reproductive success of male Tengmalm's owls (Korpimäki 1992). Therefore, both egg and clutch size of Tengmalm's Owl can be considered as fitness-related characteristics.

2. Material and methods

The study was carried out in South Ostrobothnia, western Finland (63°N, 23°E), where about 500 nest-boxes and 30 natural cavities suitable for Tengmalm's Owls were available, in an area of 1300 km^2. Eggs of 268 clutches were measured to the nearest 0.1 mm by sliding calipers during 1981–1990. Female Tengmalm's Owls disperse widely between successive breeding attempts (Korpimäki 1987). Thus, the data included only 28 repeat measurements of the same females. They did not diminish the independence of measurements, because repeatability values of egg ($r = 0.51$; Hakkarainen & Korpimäki 1993) and clutch size ($r = 0.15$; Korpimäki 1991b) of individual female Tengmalm's Owls were quite low. The repeatability (r) value of a characteristic describes the upper limit of heritability (Falconer 1981, Lessells & Boag 1987). In other species, the heritability component of egg size is 60–90% indicating a high degree of genetic determination (e.g. the Great Tit *Parus major*, van Noordwijk et al. 1981, Ojanen 1983; and the Ural Owl *Strix uralensis*, Pietiäinen et al. 1986).

Egg volume was determined by Tatum's (1975) index: $\pi \times$ egg length $\times$ breadth^2/6000. The mean egg volume of a clutch was used in the analyses. Four extremely large volume means were excluded, because they greatly affected statistical tests based on variance components. These outliers deviated statistically significantly ($P < 0.001$) from normality. Breeding success was estimated by the number of eggs produced. Egg volume was independent of clutch size (Hakkarainen & Korpimäki 1993).

Wing-length and body-weight were used as body-size related characteristics of the parent owls. They were trapped during the same stage in the breeding season, 1–2 weeks after hatching, to reduce variation in measurements, especially in female body-weight, which declines during the course of the nestling period (Korpimäki 1981, 1990a). The age of the parents was determined according to the moult pattern of the primary feathers (see Glutz von Blotzheim & Bauer 1980). Three age-classes were differentiated: first-year, second-year, and older owls.

Small mammals, especially voles, are the primary food of Tengmalm's Owls (Korpimäki 1981).

Their abundances were estimated by snap-trapping in May and in September during 1981–1990 (Korpimäki & Norrdahl 1989 and unpubl.). Based on these data, the breeding seasons were divided into three categories. These were: (1) the low phase of the vole cycle (1981, 1984, 1987, 1990) when voles were scarce, (2) the increase phase (1982, 1985, 1988) when vole numbers increased throughout the whole breeding season, from a moderate level in the early spring until they reached a peak in the early breeding season of (3) the peak phase (1983, 1986, 1989). The peak was followed by an abrupt population crash when vole abundance decreased to the low level of the next year. Territory quality was ranked using frequencies of breeding attempts from 1 (one breeding attempt) to 5 (at least 5 breeding attempts) during 1977–1990 (see Korpimäki 1988b for further details).

Statistical analyses were carried out with SYSTAT statistical package (Wilkinson 1988). We used egg size and clutch volume as response variables, and wing-length and body-mass of females as predictor variables. The effects of male and female age, territory quality, and laying date were tested separately against each of the response variables in the low, increase and peak phases of the vole cycle (Tables 1–2). If they significantly (2-tailed, $P < 0.05$) affected the response variables, their effects were controlled in partial correlation analyses. Notably, in Tengmalm's owl, male age affects egg size more than female age (Table 1). This is obviously due to the effects of courtship feeding during which males provide food for females in order for females to build the required protein and fat reserves necessary during the egg laying period.

3. Results

Details of female-wing length, body mass, and egg measurements are presented in Table 3. In the peak phase of the vole cycle, a significant positive relationship was found between egg volume and body-weight of females (Table 4), whereas in the increase phase a similar result was not found after removing the effect of the laying date (Table 4). In the peak phase, long-winged females laid large eggs, whereas in the other phases such a relationship was not found (Table 4). Accordingly, egg size is dependent on body size, but only in years of abundant food.

Table 1. The effects of female age, male age, territory quality and laying date on egg volume of Tengmalm's Owls in the low, increase and peak phases of the vole cycle.

Phase of cycle	df	F-ratio	P
Female age (ANOVA)			
Low	2.25	1.90	0.17
Increase	2.91	0.04	0.96
Peak	2.135	0.05	0.95
Male age (ANOVA)			
Low	1.24	0.19	0.67
Increase	2.89	4.04	0.02
Peak	2.127	3.39	0.04
Territory quality (ANOVA)			
Low	3.22	0.13	0.91
Increase	4.82	0.03	0.88
Peak	4.123	0.85	0.49
Laying date (linear regression)			
Low	26	0.23	0.64
Increase	93	5.48	0.02
Peak	133	0.36	0.55

Table 2. The effects of female age, male age, territory quality and laying date on clutch volume in the low, increase and peak phases of the vole cycle.

Phase of cycle	df	F-ratio	P
Female age (ANOVA)			
Low	2.25	0.35	0.71
Increase	2.91	0.68	0.51
Peak	2.131	0.04	0.96
Male age (ANOVA)			
Low	1.24	3.44	0.08
Increase	2.89	2.50	0.09
Peak	2.124	0.93	0.40
Territory quality (ANOVA)			
Low	3.22	0.05	0.99
Increase	4.82	0.77	0.55
Peak	4.122	1.78	0.14
Laying date (linear regression)			
Low	26	0.64	0.43
Increase	93	6.66	0.01
Peak	132	4.94	0.03

Table 3. Wing-length, body-weight and egg volume of Tengmalm's Owls (CV = coefficient of variation). Pooled data from 1981–1990.

	Mean ± SD	Range	CV	N
Female wing-length (mm)	178.9 ± 3.5	170.0–190.0	0.02	262
Female body-weight (g)	170.7 ± 14.8	129.0–214.0	0.09	257
Mean egg volume (cm^3) of a clutch	12.16 ± 0.9	10.15–14.43	0.07	264

Clutch volume (egg number × mean egg volume in a clutch) was not associated with the wing-length of females in the three phases of the vole cycle (Table 5). In contrast, clutch volume increased with the body mass of females in every phase of the vole cycle (Table 5), indicating that female nutritional reserves are essential to egg production in all kinds of food conditions.

4. Discussion

Long-winged females did not produce clutches of a greater volume than did short-winged ones. In contrast, heavy females produced clutches of a larger volume than light females. Body-weight reflects her nutritional condition, and heavy females lay large clutches (Korpimäki 1986, 1990). The body mass of females varies greatly both within and between the breeding seasons, and depends on extrinsic factors, such as territory quality and availability of voles (Korpimäki 1990). Also, egg formation takes place while the male provides food to the female during the courtship and laying periods (Korpimäki 1981). Accordingly, variations in female body-weight reflect variable nutritional conditions due to differences in food intake. For this reason, the skeletal size of birds of prey is preferably described by wing-length than by body-weight, as it is a much more stable variable than body-weight (see also Mueller 1989, Korpimäki 1990).

In line with the hypothesis that large females may produce large and fit offspring, a significant positive relationship was found between egg volume and wing-length of females in the peak phase of the vole cycle. In contrast, large females were no better at incubating than were small ones, as measured by the hatching success (Hakkarainen & Korpimäki 1991), eventhough Tengmalm's Owl is one of the earliest breeders among Fennoscandian birds (Korpimäki 1986). Most female Tengmalm's Owls begin laying in late March or early April, when the ambient tempera-

Table 4. Correlations between the female body-weight, wing-length and egg volume in the three phases of the vole cycle. The effects of laying date (L) and male age (M) were removed in partial correlation analyses, if they significantly affected egg volume (see table 1).

Phase of cycle	Coefficient (r)	Effects removed	df	P
Body-weight				
Low	–0.02	–	26	0.92
Increase	0.27	M	90	0.01
	0.17	L	93	0.11
Peak	0.20	M	128	0.03
Wing-length				
Low	–0.02	–	26	0.91
Increase	0.11	M, L	80	0.33
Peak	0.23	M	128	0.008

Table 5. Correlations between the female body-weight, wing-length and clutch volume in the different phases of the vole cycle. The effect of laying date (L) was removed, if it affected clutch volume significantly (see table 2).

Phase of cycle	Coefficient (r)	Effects removed	df	P
Body-weight				
Low	0.42	–	26	0.03
Increase	0.28	L	93	0.007
Peak	0.26	L	132	0.003
Wing-length				
Low	0.05	–	26	0.79
Increase	0.06	L	93	0.54
Peak	0.04	L	132	0.63

ture may still fall below −15°C at night (Korpimäki & Hakkarainen 1991).

In many wild birds, there is a positive relationship between egg size and female size (for a review, see Ojanen 1983). However, in most of these studies the effects of the laying date, parental quality, and territory quality remained unknown, though they may partly explain the observed trends. Thus, large egg volume may be due to proximate rather than ultimate factors. This does not result in genes for large size of females becoming prevalent in the population. For instance, large female European Sparrowhawks produce more offspring in their lifetime than do small ones (Newton 1985, 1989). But, despite the long-term data, no genetic selection for the largeness of females was found, because female body size remained stable throughout the 20-year study period (Newton 1989). In the Collared Flycatcher *Ficedula albicollis*, selection for a longer tarsus was due to an environmental deviation (difference between the phenotypic and genotypic characters), and was not due to genetic selection (Alatalo et al. 1990). An environmental deviation reflects differences in the external environment (e.g. variation in food supply), or in the internal environment (random variability in development).

Interspecific comparisons show that reproductive effort decreases with increasing body size, whereas maternal metabolism is higher in larger species (e.g. Peters 1983). Therefore, large females may not be more efficient reproducers than small ones. Also, in energy-limited conditions selection for increased fecundity with maternal size is not common (Shine 1988), which may explain why in this study female size affected egg size mostly in the peak phase of the vole cycle. In Tengmalm's Owl, selection seems to promote small male size, as small males are most successful at breeding in the low phase of the vole cycle (Hakkarainen & Korpimäki 1991). Accordingly, it is possible that selection acts on both sexes; during fat periods large females are favoured and during lean periods small males are favoured.

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Selostus: **Helmipöllönaaraan koon vaikutukset munien tilavuuteen vaihtelevissa ravinto-oloissa**

Tutkimme helmipöllönaaraiden koon vaikutusta keskimääräiseen munakokoon ja pesyeen munien kokonaistilavuuteen (pesyeen munien keskitilavuus × munamäärä) Etelä-Pohjanmaalla, Kauhavan seudulla, vuosina 1981–1990. Tutkimusalueen myyräkantojen vaihtelu voitiin jakaa kolmeen myyräsyklin vaiheeseen: pohja- (1981, 1984, 1987, 1990), nousu- (1982, 1985, 1988) ja huippuvaihe (1983, 1986, 1989). Emot pyydystettiin 1–2 viikkoa poikasten kuoriutumisen jälkeen, jolloin niiden siipi, paino ja ikä määritettiin. Munat mitattiin työntötulkilla 268 pesästä 0.1 mm:n tarkkuudella.

Aluksi testasimme vaikuttavatko erilaiset taustamuuttujat, kuten munintapäivä, reviirin laatu, naaraan ja koiraan ikä (kosioruokinnan kautta) munan keskimääräiseen kokoon ja pesyeen munien kokonaistilavuuteen myyräsyklin eri vaiheissa. Koiraan ikä ja munintapäivä vaikuttivat tilastollisesti merkitsevästi munakokoon myyräkantojen nousu- ja huippuvaiheissa. Munintapäivä vaikutti merkitsevästi myös pesyeen munien kokonaistilavuuteen myyräkantojen nousu- ja huippuvaiheissa. Näiden tekijöiden vaikutukset poistettiin osittaiskorrelaation avulla tutkittaessa naaraan siiven ja painon merkitystä keskimääräiseen munakokoon ja pesyeen munien kokonaistilavuuteen. Pitkäsiipiset naaraat tuottivat suuria munia myyräkantojen huippuvaiheessa. Naaraan siiven pituuden ja pesyeen munien kokonaistilavuuden välillä ei havaittu merkitsevää yhteyttä. Painavat naaraat tuottivat kokonaistilavuudeltaan suurempia pesyeitä kaikissa myyräsyklin vaiheissa kuin kevyet naaraat, samoin suurempia munia myyräsyklin huippuvaiheessa.

Naaraiden ravitsemuksellinen tila vaikuttaa suuresti pesintämenestykseen, kuten tulokset painon ja munien koon suhteesta osoittivat. Siiven pituus on kuitenkin parempi yksilön koon mitta, koska se on lähes muuttumaton yksilön eliniän ajan, kun taas paino vaihtelee suuresti lyhyelläkin aikavälillä kuvastaen lähinnä ravinto-olojen muutoksia. Siten helmipöllönaaraan suuresta koosta siiven pituudella mitattuna oli hyötyä vain myyräkantojen huippuvuosina, jolloin isot naaraat munivat suurimpia munia. Tuloksemme osoittavat, että naaraan koirasta suurempi koko ei ilmeisesti johdu suurten naaraiden kyvystä munia paljon ja suuria munia. Aiemmat tuloksemme sensijaan osoittivat pienten koiraiden tehokkuuden huonoina myyrävuosina, joten koiraiden pieni koko voi olla seurausta koiraiden sopeutumisesta pula-aikoihin pienen koon avulla. Petolintujen sukupuolten välinen kokoero on voinut syntyä siten, että valintapaine suosii ravintopulan aikana pieniä parhaiten selviytyviä koiraita ja runsaan ravinnon aikana puolestaan isoja naaraita.

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