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Clutch size and breeding success in relation to nest-box size in Tengmalm's owl Aegolius funereus

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Clutch size and breeding success was related to nest-box size in 215 nests of Tengmalm's owl in the Kauhava region, western Finland in 1966–82. In vole peak years, but not in other years, mean clutch size was positively correlated with the bottom area of the nest-box, increasing on average by 0.005 eggs cm^{-2}. In successful nests there were fewer nestlings in small and medium-sized than in large boxes. Breeding was most successful in thick-walled boxes with a small entrance diameter. The optimal box for Tengmalm's owl has the following dimensions: bottom area 20 × 20 cm, entrance diameter 8 cm, and wall thickness at least 3 cm.
Hypotheses suggested to explain the "area effect" based on breeding data of hole-nesting passerines do not hold good for Tengmalm's owl. Since there were more stored prey animals in medium-sized and large boxes than in small boxes, I suggest that the "area effect" is related to food availability, which may determine how sensitive the species is to different bottom areas of the boxes, at least in areas with cyclic food (e.g. northern Europe).

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1. Introduction

The breeding biology of hole-nesting passerine birds has been extensively studied in nest-boxes during the last decades. Variations in clutch size have been investigated in detail and found to be influenced by population density, age of the female, habitat (e.g. in the great tit *Parus major,* Lack 1958, Perrins 1963, 1965, Orell 1983), date of egg-laying (e.g. pied flycatcher *Ficedula hypoleuca,* von Haartman 1967), the order in which the female laid eggs in the population (e.g. starling *Sturnus vulgaris,* von Haartman 1982), and temperature during the egg-laying period (e.g. starling, Korpimäki 1978). In addition to these factors, there is a general tendency for an increase in mean clutch size with increasing bottom area of the nest-boxes (great tit: Graczyk 1967, Löhrl 1973, Johansson 1974, Nilsson 1975, Karlsson and Nilsson 1977; willow tit *Parus montanus* and marsh tit *P. palustris:* Ludescher 1973; pied flycatcher: Johansson 1974, Nilsson 1975, Karlsson and Nilsson 1977; but not in the starling: Karlsson 1983).

Three different hypotheses have been offered as explanations of the "area-effect" in hole-nesting passerines: (1) a larger clutch can be produced in larger nest-boxes due to the better insulation of the eggs (by a thicker layer of nest material; Löhrl 1973); (2) in a large box the nestlings can spread out on hot days and avoid hyperthermia (Löhrl 1973); (3) the amount of energy lost from a brood will be affected by the proportion of the nest-box bottom area, which the brood occupies. So the size of the species in relation to the size of the nest cavity may determine how sensitive the species is to variations in the bottom area (for further discussions see Karlsson and Nilsson 1977).

In the present paper I analyse clutch size and breeding success in relation to nest-box size in Tengmalm's owl *Aegolius funereus,* which is a non-passerine, raptorial species which does not build a nest. I also explore whether or not the above-mentioned hypotheses for the "area-effect" are valid in Tengmalm's owl.

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2. Study area, material and methods

Data on population fluctuations and breeding biology of Tengmalm's owl were collected between 1966 and 1982 in the Kauhava region (63°N, 23°E), western Finland (see Korpimäki 1981a, 1981b, 1982, 1983). The owls nested mainly in nest-boxes (90% of all nest finds, n = 287). Because clutch size is smaller and breeding success lower in natural cavities than in boxes (Korpimäki 1984), I only used material from nest-boxes when analysing breeding data in relation to nest-hole size. Breeding data for "good" food years (i.e. 1966, 1969, 1973, 1977, and 1982, here identified by having a mean clutch larger than six) were separated from the other years in order to explore the "area-effect" under different food conditions.

The study area is about 1 000 km² and contained from 35 (in 1966) to 450 (in 1982) boxes and holes suitable for Tengmalm's owl. Most boxes were made of darkened board and had square-shaped bottoms. Their inner width ranged between 15 and 25 cm and their height between 45 and 60 cm. Wall thickness varied from 0.5 to 10 cm and the diameter of the entrance hole was 5–18 cm. All the above-mentioned dimensions varied independently of each other among nest-boxes. The roof of the boxes could be opened to facilitate observations. See Korpimäki (1981a) for additional details on material and methods.

3. Results

3.1. Breeding success in relation to bottom area of the nest-box

Mean clutch size and bottom area of the nest-box correlated positively in the peak years (Fig. 1, $r = 0.313$, $p < 0.01$), clutch size increasing on average by 0.005 egg cm^{-2} increase in bottom area. In the other years no such relation was found.

Mean clutch size was significantly larger in medium-sized nest-boxes than in small ones ($p < 0.01$, Tab. 1). The difference was significant between medium-sized and large boxes too, both in the whole material and in the "good" years only ($p < 0.05$), but not in the other years only. However, in the latter years the difference was significant between small and medium-sized boxes ($p < 0.05$).

The clutch size of Tengmalm's owl is larger in early than in late nests (Korpimäki 1981a). The great tit prefers large boxes, when a choice is possible (e.g. Henze 1966, Löhrl 1970). Therefore the correlation between bottom area of the nest-box and clutch size might be explained by the decrease in clutch size with laying date (Klomp 1970). But this "calendar effect" does not cause the "area-effect" in Tengmalm's owl, because the median dates for egg-laying did not differ significantly between boxes of three different size classes (Tab. 1).

Hatching success seemed to be greater in small boxes than in medium-sized and large nest-boxes (for the whole material, $p < 0.1$, Tab. 1). The mean number of fledglings in successful nests was significantly smaller in small and medium-sized than in large boxes, both in the peak years and in the whole material ($p < 0.01$). The bottom area of the nest-box affected the number of fledglings in vole peak years only.

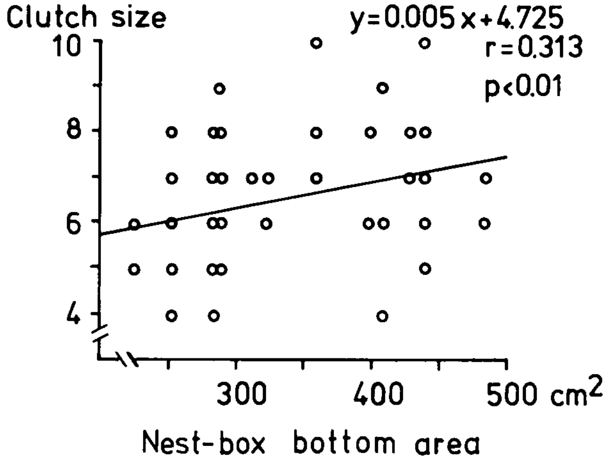

Fig. 1. Correlation between bottom area of the nest-box and clutch size in Tengmalm's owl. Data from vole peak years (1966, 1969, 1973, 1977 and 1982).

3.2. Breeding success in relation to entrance diameter and wall thickness of the nest-box

There was a higher proportion of totally destroyed nests in boxes with medium-sized and large entrance holes than in those with small ones (diameter from 5 to 8 cm, Tab. 2). The wall thickness of the nest-box did not have any effect on clutch size and number of fledglings, but there were significantly more unhatched eggs in boxes with thin walls (0.5–3.0 cm) than in boxes with thick walls (t-test, $p < 0.05$, Tab. 3). So the incubation was most successful in boxes with thick walls, especially in good vole years.

4. Discussion

4.1. Relation between breeding success and nest-box size in Tengmalm's owl

Most Tengmalm's owls start nesting in the latter half of March in good vole years (Korpimäki 1981a). Consequently, this owl is one of the earliest breeders among birds in northern Europe, and begins to lay eggs at the same time as in Germany (Schelper 1972) despite the latitudinal difference of 10°. In Finland night temperatures in March may be as low as −20°C, so thermoregulation in the female requires much energy. The better insulation provided by the thick-walled nest-boxes may make them energetically more advantageous than the thin-walled ones, especially during incubation.

Tab. 1. Breeding data for Tengmalm's owl in nest-boxes with different bottom area. A = in vole peak years (1966, 1969, 1973, 1977 and 1982), B = in other years (1967, 1970–71, 1974–76, 1978–81), and C = all years combined. Significance levels refer to tests of the difference between adjacent size classes: * = $p < 0.05$, ** = $p < 0.01$ and *** = $p < 0.001$ (t-test). Number of studied nests within parentheses.

		Size of box (bottom area)					
		Small (15–17 × 15–17 cm)		Medium (18–20 × 18–20 cm)		Large (21–25 × 21–25 cm)	
Median date for egg-laying	A	26 March	(20)	28 March	(48)	25 March	(26)
	B	13 April	(26)	6 April	(55)	8 April	(28)
	C	5 April	(46)	4 April	(103)	2 April	(54)
Mean clutch size (x̄±S.D.)	A	5.65±1.08	(31)***	6.48±0.89	(42)*	7.15±1.41	(26)
	B	4.81±1.23	(26)*	5.44±1.02	(64)	5.46±0.86	(26)
	C	5.26±1.23	(57)**	5.85±1.10	(106)*	6.31±1.44	(52)
% of eggs hatching	A	91.7	(17)	86.6	(40)	88.1	(20)
	B	92.5	(14)	87.6	(46)	88.9	(18)
	C	92.0	(31)	86.9	(86)	88.3	(38)
Mean number of fledglings in successfull nests (x̄±S.D.)	A	3.85±1.66	(26)	4.09±1.50	(41)**	5.57±1.48	(21)
	B	2.80±1.28	(20)	3.23±1.60	(53)	3.13±1.45	(23)
	C	3.39±1.57	(46)	3.61±1.61	(94)**	4.30±1.89	(44)

Tab. 2. Breeding data for Tengmalm's owl in nest-boxes with different entrance diameter. In parentheses are given the number of clutches observed in each category.

	Entrance diameter (cm)					
	5–8		9–11		12–18	
Mean clutch size ± S.D.	5.82±1.08	(11)	5.74±1.30	(145)	6.06±1.23	(49)
% of eggs hatching	86.6	(9)	87.3	(105)	91.6	(38)
Mean number of fledglings ± S.D.	3.36±2.16	(11)	3.05±2.04	(149)	3.38±2.19	(48)
Percentage of totally destroyed nests	0.0	(0)	16.8	(25)	16.7	(8)

Food abundance is the main factor regulating the clutch size and breeding success of Tengmalm's owl, which lays very large clutches at peak densities of field vole *Microtus agrestis* and common vole *M. arvalis* ($\bar{x}$ = 6.4, n = 70 in my study area, Korpimäki 1981a). There was regularly a store of prey animals in the boxes, especially during egg-laying, incubation and hatching as well as at the beginning of the nestling period. The prey animals were kept at the edges of the nest and were eaten in the order in which they were brought to the box. The maximum number of stored prey individuals recorded simultaneously in a nest was 35 (total weight about 800 g; Korpimäki 1981a). A large clutch and numerous prey animals occupy much bottom area in the box. This may underlie the positive correlation between bottom area and clutch size, because there were signifi-

Tab. 3. Breeding data for Tengmalm's Owl in nest-boxes with different wall thickness. For additional explanations, see Tab. 1.

		Wall thickness (cm)					
		0.5–1.5		2.0–3.0		3.5–10.0	
Mean clutch size ± S.D.	A	6.25±1.04	(8)	6.52±1.11	(65)	6.38±1.50	(21)
	B	4.71±1.98	(7)	5.43±0.95	(83)	5.07±1.07	(27)
	C	5.53±1.68	(15)	5.91±1.15	(148)	5.65±1.42	(48)
% of eggs hatching	A	88.0	(4)	86.0	(55)	94.2	(19)
	B	91.5	(5)	86.7	(57)	92.5	(16)
	C	89.9	(9)	86.3	(112)	93.5	(35)
Mean number of fledglings in successfull nests ± S.D.	A	4.17±1.94	(6)	4.24±1.54	(58)	4.94±1.87	(19)
	B	3.00±2.14	(7)	3.14±1.59	(66)	3.14±1.35	(21)
	C	3.54±2.03	(13)	3.65±1.65	(124)	4.00±1.84	(40)

Tab. 4. Mean numbers of stored prey animals ± S.D. (average values from all inspection visits to the nests) in nest-boxes with different bottom area. A = in vole peak years, B = in other years, and C = in the whole material. Number of inspection visits in parentheses. See Tab. 1 for additional explanations.

	Size of box (bottom area)			
	Small (15–17×15–17 cm)		Medium and large (18–25×18–25 cm)	
A	4.59±3.88	(41)*	6.50±6.73	(107)
B	2.91±2.22	(74)***	5.72±6.36	(156)
C	3.50±3.01	(115)***	6.04±6.51	(263)

cantly more stored prey individuals in boxes with medium sized and large bottoms than in boxes with small bottoms ($p < 0.05$, Tab. 4).

The energy costs for thermoregulation during incubation increase in large boxes as compared with small boxes; this may explain the lower hatching percentage in large and medium-sized boxes than in small boxes. On the other hand the energy loss is partly compensated for by the larger size of Finnish than of German Tengmalm's owls (Korpimäki 1981a). The degree of sexual size dimorphism of this owl is the highest among Finnish owls, females being 49% heavier than males (Korpimäki 1981a), and a great female can incubate effectively even in large boxes when the availability of food is good.

The maximum number of fledglings recorded in my study area was eight (Korpimäki 1981a and unpubl.). Since the female broods the young and also cuts up the prey for the nestlings inside the box during the first three weeks of the nestling period, there may be a keen need for room in the nest during this critical period, when the mortality among nestlings is highest (see Korpimäki 1981a). A small box size may also increase the amount of cannibalism among large young near the end of the nestling period, thus reducing the production of fledglings.

Temperatures can be high at the end of the nestling period. In large boxes the nestlings can spread out on hot days and avoid hyperthermia. Mertens (1969), van Balen and Cáve (1970) and O'Connor(1975) also showed that there is a decrease in thermoregulatory costs of nestlings of great tit, blue tit *Parus caeruleus* and house sparrow *Passer montanus* in normal compared with small broods, and that large broods may suffer from hyperthermia at high temperatures. Hyperthermia is quite rare in northern Europe, however, where the weather is cold. When voles are scarce, Tengmalm's owl begins to lay as late as in April or May (Korpimäki 1981a). Then the temperature is about 10°C higher than in March, and the insulation provided by the box walls is no longer as important as in early nests. Clutch size and the number of nestlings are small, and fewer prey animals are stored. Consequently, medium sized boxes may be energetically more advantageous than large boxes in these late years.

4.2. What is the optimal size of the nest-box for Tengmalm's owl?

All data collected so far indicate that the square-shaped bottom area of a nest-box most suitable for Tengmalm's owl must be at least 18 × 18 cm, preferably 20 × 20 cm, because stored prey, eggs, female and nestlings need much room in vole peak years (Tab. 1). Therefore, natural nesting cavities with circular bottoms (e.g. holes of black woodpecker *Dryocopus martius* with an average diameter of 20.1 cm, Rudat et al. 1979) and commonly used nest-boxes (e.g. Haapanen and Vaarna 1971) are not optimal for Tengmalm's owl in the vole peak years.

The insulation of nest-boxes may be important in

Tab. 5. The relation between clutch size and bottom area of the nest-cavity in some hole-nesting bird species. Weights for passerines from von Haartman et al. (1963–72) and for Tengmalm's owl from Korpimäki (1981a).

Species	No. of studies	Mean of the slopes (egg cm^{-2})	Signif. of the correlation coefficient	Range of bottom area (cm^2)	Mean weight of females (g)	Weight of female ×100/bottom area of the box (cm^2) (%)	Source
Marsh tit	1	0.117	p<0.001	25–65	11.0	24.4	Ludescher (1973)
Willow tit	1	0.072	p<0.001	25–65	11.2	24.9	Ludescher (1973)
Great tit	4	0.023	p<0.001	57–125	17.0	18.7	Johansson (1974), Nilsson (1975), Karlsson and Nilsson (1977)
Pied fly-catcher	5	0.009	p<0.01, in two studies only	57–110	12.6	13.8	Johansson (1974), Nilsson (1975), Karlsson and Nilsson (1977)
Starling	3	0.001		120–225	73.6	21.3	Karlsson (1983)
Tengmalm's owl	1	0.005	p<0.01, in vole peak years only	225–484	170.3	48.0	Present study

northern Europe, where the weather is cold during breeding. The thickness of the walls and bottom must be at least 3 cm and a 5–10 cm thick layer of sawdust, turf or other softening material must be put on the bottom of the box.

The preferable diameter of the entrance hole is 8 cm, because it prevents larger hole-nesting owls (e.g. tawny owl *Strix aluco* and Ural owl *S. uralensis*) from competing for the box. In addition to this resource competition, the above mentioned species are aggressive towards smaller owls and can even kill Tengmalm's owls (i.e. interference competition; for additional details, see Mikkola 1976, 1982). The main predator of Tengmalm's owl in my study area is pine marten *Martes martes* (Korpimäki 1981a). It uses boxes with large entrance holes (average diameter more than 10 cm) as nesting (Ahola and Terhivuo 1982) and daytime roosting places (Nyholm 1972), but it is reluctant to enter a small hole (Nyholm 1972). In all probability pine martens find the nest of Tengmalm's owls in boxes with large entrance holes more frequently than in those with small ones. Consequently, a box with small entrance hole is a quite safe nesting place for Tengmalm's owl due to the reduced predation.

4.3. The "area-effect" hypotheses applied to Tengmalm's owl

The hypotheses presented by Löhrl (1973) do not hold good for Tengmalm's owl, because this species does not build a nest, and hyperthermia is very rare due to the early breeding in northern Europe. In Tab. 4 I analyse the suggestion of Karlsson and Nilsson (1977). The results indicate that the weight of the species in relation to the bottom area of the box does not correlate with the degree of "area-effect" (with the slope of the regression line) among the studied hole-nesting birds. So we need a new explanation for the response documented in this paper.

According to Cody (1966) clutch size of birds is determined by a balance of allocations of limited resources to competition, predator avoidance and reproduction. Food availability is the most important factor regulating clutch size and breeding success in Tengmalm's owl. Consequently, food availability may determine how sensitive the species is to variations in the bottom area of the nest-box, at least in areas with cyclic food production (e.g. in northern Europe). On the other hand, in a relatively stable environment (for example in Central Europe), food availability is more constant between different breeding seasons and the species should react less strongly to the different bottom areas of the boxes. However, further investigations from different hole-nesting bird species, geographical areas and breeding seasons will be needed in order to explain the inter- and intraspecific differences in "area-effect" solidly.

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