

## EFFECTS OF BREEDING EXPERIENCE ON NEST-SITE CHOICE AND THE REPRODUCTIVE PERFORMANCE OF TAWNY OWLS (*STRIX ALUCO*)

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**ABSTRACT.**—Nest boxes for breeding Tawny Owls (*Strix aluco*) were located in a mixed oak-hornbeam-beech (*Quercus—Carpinus—Fagus*) forest located in the Duna-Ipoly National Park, 30 km northwest of Budapest, Hungary, during the period 1992–2004. We marked the parents individually in the first known breeding year of the females and recorded their reproductive performances through 5 subsequent breeding years. Reproductive performance of females increased with increasing breeding experience; they laid more eggs and reared more fledglings with subsequent breeding years. However, no significant differences were found in reproductive performance between the third and fifth breeding years. Fledging success was higher when the males were older than the females, but hatching success was not influenced by the age of the males. Parents achieved higher hatching and fledging success in years without snow cover than those with snow cover. Fledging success was higher than hatching success in the females' first and second breeding years, but hatching success was higher in third, fourth, and fifth breeding years, which indicates age-dependent change in offspring production limitation by parents. Pairs changed nest sites and moved to lower altitudes in years with snow. As a consequence, the majority of older parents bred at low elevations. Based on the greater mass loss by females than males in adverse weather conditions, we concluded that males reduced the amount of prey brought to their mates to ensure their own survival in conditions in which food was scarce. Females raised lighter fledglings in snow years than in years without snow cover during their first and second breeding season, but the influence of snow cover on fledglings' condition was not present in the broods of experienced parents.

**KEY WORDS:** *Tawny Owls; Strix aluco; fledging success; hatching success; parental age; parental condition; weather condition.*

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### EFFECTOS DE LA EXPERIENCIA REPRODUCTIVA SOBRE LA ELECCIÓN DE SITIOS DE NIDIFICACIÓN Y EL DESEMPEÑO REPRODUCTIVO DE *STRIX ALUCO*

**RESUMEN.**—Se instalaron cajas de nidificación para *Strix aluco* en un bosque mixto de *Quercus*, *Carpinus*, y *Fagus* localizado en el Parque Nacional Duna-Ipoly, 30 km al norte de Budapest, Hungría, entre 1992 y 2004. Marcamos individualmente a las parejas durante el primer año reproductivo de las hembras y registramos su desempeño reproductivo durante los 5 años siguientes. El desempeño reproductivo de las hembras aumentó con el aumento de la experiencia reproductiva: éstas pusieron más huevos y criaron un mayor número de polluelos en los años posteriores. Sin embargo, no se encontraron diferencias significativas entre el cuarto y el quinto año reproductivo. El éxito de emplumamiento fue mayor cuando los machos fueron más viejos que las hembras, pero el éxito de eclosión no fue influenciado por la edad de los machos. Las parejas alcanzaron un mayor éxito de eclosión y de emplumamiento en los años sin cobertura de nieve que en los años con cobertura de nieve. El éxito de emplumamiento fue mayor que el éxito de eclosión durante el primer y segundo año reproductivo de las hembras, pero el éxito de eclosión fue mayor durante el tercer, cuarto y quinto año reproductivo, lo que indica un cambio dependiente de la edad en la limitación de la producción de progenie por parte de los padres. En los años con nieve, las parejas cambiaron de sitio de nidificación y se desplazaron hacia sitios de menor altitud. Consecuentemente, la mayoría de los padres de mayor edad nidificaron en elevaciones bajas. Con base en la mayor pérdida de peso en las hembras que en los machos en condiciones de

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clima adverso, concluimos que los machos redujeron la cantidad de presas llevadas a sus parejas para asegurar su propia sobrevivencia en condiciones en las cuales el alimento fue escaso. Durante el primer y segundo año reproductivo, las hembras criaron volantones de menor peso en los años con nieve que en los años sin nieve, pero la influencia de la cobertura de nieve sobre la condición de los volantones no se observó en las nidadas de parejas experimentadas.

[Traducción del equipo editorial]

Both theoretical papers and empirical evidence indicate that young birds invest less in reproduction than do older birds (Williams 1966, Pianka 1976), which may be due to the young birds' poorer condition (Coulson 1968, Pugsek and Diem 1983, Weimerskirch 1992) or their inexperience in foraging and knowledge of the habitat (Orians 1969, DeSteven 1978). Long-term studies on owls have also shown the effects of age on breeding performance (Recher and Recher 1969, Korpimäki 1988, Gehlbach 1989, Saurola 1989). We have shown in a previous study the effect of age composition on breeding success of Tawny Owls (*Strix aluco*) and found sex-related influences on number of eggs, hatching and fledging success in first, second, and third breeding years of the pairs (Sasvári and Hegyi 2002). The aim of our recent study was to examine age-dependent reproductive performance through five consecutive breeding years of owl parents and the effect of weather both on breeding success and nest-site choice of the pairs.

Southern and Lowe (1968) suggested that prey availability for Tawny Owls is determined by ground cover, and when snow prevents them preying on small mammals, they switch to hunting mainly birds. Many papers have reported that throughout Europe, this species relies mostly on rodents, but will feed on birds as a secondary, alternative food (Southern and Lowe 1968, Goszczynski 1981, Mikkola 1983, Kirk 1992, Jedrzejewski et al. 1994). We thus examined the breeding performance achieved by the pairs in snow years and in years when snow did not cover the ground during the incubation and early nestling periods. In addition, we recorded the distribution of nest sites at different elevations and changes in nest-site choice depending on snow condition.

The Tawny Owl is a resident, strongly monogamous owl in central Europe that can be attracted to artificial nest boxes. We marked individual parents and determined the age (Petty 1992) of the pairs in the first known breeding years of the females. In order to evaluate the condition of the owls, we measured the body mass of parents and

both body mass and length of tarsus on nestlings before fledging.

On the basis of the sexual dimorphism in Tawny Owls, we hypothesized that the lighter male offspring, which demand less parental investment, survive better than heavier female offspring during food shortages (e.g., Olsen and Cockburn 1991, Wiebe and Bortolotti 1992, Dzus et al. 1996). If the different sex offspring require varying amounts of care, the young that demands more parental effort should be fewer in a poor-food environment reducing the total reproductive cost to the parents (Slagsvold 1990, Clutton-Brock 1991, Weatherhead and Teather 1991). To examine the reduction of reproductive cost by elimination of heavier offspring, we related the body condition of nestlings before fledging to the number of breeding seasons that females were present and to the weather.

#### METHODS

We placed 220 nest boxes for breeding Tawny Owls in a mixed oak-hornbeam-beech (*Quercus—Carpinus—Fagus*) forest, with 40–60-yr old trees, in the Duna-Ipoly National Park, 30 km northwest of Budapest (47°35'N; 19°02'E) during the period 1992–2004. Six to eight nest boxes were grouped together with 300–600 m between them, the groups being separated by 2–5 km. Nest boxes were checked at 4–8 d intervals beginning at the end of January.

We captured 157 females and 141 males during the nestling period by placing a net over the entrance of the boxes while the birds were inside. The birds were marked with different combinations of colored rings for individual identification. We identified 44 females that bred through three successive breeding seasons and 26 females that bred through four seasons, and 17 females that bred through five seasons. Owls changed mates on nine occasions, but none lost their nests through predation. Age of females was determined by the pattern of the primaries and secondaries (Petty 1992) in their first known breeding year and their mates were categorized as (1) of same age or younger, or (2) older. The 44 females in their first known breeding year consisted of 15 1-yr old, 23 2-yr old, and six 3-yr old birds. Body mass of parents were measured when their first hatched-young were 3 d old, and fledgling masses were recorded when they were 25–28 d old.

As a consequence of the 550 m altitude range of the study area (130–680 m), snow covered the ground longer in the higher-elevational nest areas than the lower ones.

Table 1. Mean reproductive performance measures ( $\pm$ SD) of female Tawny Owls over five successive breeding seasons in relation to the age of their mates and snow condition around the nest. Numbers in parentheses indicate number of females.

BREEDING YEARS OF FEMALES	AGE OF MALES RELATED TO FEMALES	SNOW COVER		NUMBER OF EGGS	HATCHING SUCCESS	FLEDGING SUCCESS	NUMBER OF FLEDGLINGS
		ON THE GROUND					
First	Younger or same	Yes (9)		2.22 $\pm$ 0.72	0.65 $\pm$ 0.12	0.85 $\pm$ 0.04	1.22 $\pm$ 0.60
		No (15)		2.33 $\pm$ 0.87	0.71 $\pm$ 0.10	0.92 $\pm$ 0.03	1.53 $\pm$ 0.38
	Older	Yes (7)		2.00 $\pm$ 1.00	0.64 $\pm$ 0.08	0.88 $\pm$ 0.05	1.14 $\pm$ 0.48
		No (13)		2.54 $\pm$ 0.97	0.73 $\pm$ 0.07	0.92 $\pm$ 0.04	1.69 $\pm$ 0.60
Second	Younger or same	Yes (7)		2.14 $\pm$ 0.48	0.67 $\pm$ 0.11	0.90 $\pm$ 0.05	1.29 $\pm$ 0.49
		No (16)		2.81 $\pm$ 1.07	0.77 $\pm$ 0.07	0.91 $\pm$ 0.04	2.00 $\pm$ 0.71
	Older	Yes (9)		2.33 $\pm$ 0.75	0.71 $\pm$ 0.03	0.93 $\pm$ 0.08	1.56 $\pm$ 0.62
		No (12)		2.92 $\pm$ 0.73	0.78 $\pm$ 0.04	0.93 $\pm$ 0.02	2.08 $\pm$ 0.73
Third	Younger or same	Yes (10)		2.90 $\pm$ 1.06	0.90 $\pm$ 0.04	0.73 $\pm$ 0.06	1.90 $\pm$ 0.77
		No (14)		3.00 $\pm$ 0.69	0.93 $\pm$ 0.05	0.77 $\pm$ 0.03	2.44 $\pm$ 0.74
	Older	Yes (8)		2.88 $\pm$ 0.89	0.91 $\pm$ 0.03	0.81 $\pm$ 0.07	2.43 $\pm$ 0.71
		No (12)		3.33 $\pm$ 0.77	0.93 $\pm$ 0.01	0.83 $\pm$ 0.04	2.58 $\pm$ 0.60
Fourth	Younger or same	Yes (6)		3.17 $\pm$ 0.54	0.84 $\pm$ 0.03	0.79 $\pm$ 0.10	2.15 $\pm$ 0.74
		No (8)		3.00 $\pm$ 1.33	0.88 $\pm$ 0.05	0.76 $\pm$ 0.03	2.00 $\pm$ 0.50
	Older	Yes (5)		3.60 $\pm$ 0.77	0.87 $\pm$ 0.08	0.75 $\pm$ 0.05	2.40 $\pm$ 0.70
		No (7)		3.43 $\pm$ 1.15	0.92 $\pm$ 0.06	0.81 $\pm$ 0.04	2.57 $\pm$ 0.84
Fifth	Younger or same	Yes (4)		3.25 $\pm$ 0.50	0.93 $\pm$ 0.04	0.75 $\pm$ 0.09	2.25 $\pm$ 1.00
		No (2)		4.00 $\pm$ 0.00	1.00 $\pm$ 0.00	0.62 $\pm$ 0.06	2.50 $\pm$ 0.66
	Older	Yes (5)		3.80 $\pm$ 0.33	0.89 $\pm$ 0.07	0.71 $\pm$ 0.06	2.40 $\pm$ 0.70
		No (6)		3.50 $\pm$ 0.70	0.90 $\pm$ 0.03	0.74 $\pm$ 0.09	2.33 $\pm$ 0.67

A year when snow completely covered the ground for a radius of 1 km from the owl nest during the incubation and early nestling period (until 10 d after hatching of the last young) was considered as a snow breeding year for any given pair. The elevations between 130–680 m were separated into three categories: <300 m, 300–500 m, and >500 m, which included 64, 85, and 71 nest boxes for the owls, respectively. The number of nests occupied by the pairs in each of the three altitudinal ranges was related to the number of breeding years of the females and snow condition of the given year.

Statistical analyses were carried out using the SPSS statistical package (Norusis 1977). Hatching success and fledging success were calculated by number of eggs hatched per number of eggs laid and number of nestlings fledged per number of nestlings hatched, respectively. Percent data were arcsine transformed for parametric analysis.

## RESULTS

**Reproductive Performance.** We found no significant relationships between the breeding year of the female and male age for number of eggs and hatching success, but in all breeding years, broods with older males than the females experienced higher fledging success (Tables 1, 2). Snow conditions affected all categories of reproductive performance of females. Male age did not influence

the effects of snow on clutch size and hatching success. However, broods of older males experienced higher fledging success and produced more nestlings both in snow years and in years without snow cover.

Females laid more eggs and fledged more nestlings as they aged (combined data on age of males, ANOVA:  $F_{4,170} = 3.77$ ,  $P = 0.005$ ;  $F_{4,170} = 5.31$ ,  $P < 0.001$ ; respectively), but there were no significant differences in reproductive performances of females between their third and fifth breeding seasons ( $F_{2,84} = 2.97$ ,  $P = 0.063$ ;  $F_{2,84} = 3.07$ ,  $P < 0.072$ ). Hatching success was not influenced by the age of male related to female age ( $F_{1,173} = 3.16$ ,  $P = 0.077$ ); however, fledging success was higher when the males were older than the females ( $F_{1,173} = 9.17$ ,  $P < 0.001$ ; respectively). Parents achieved both higher hatching success and fledging success in years without snow cover than those with snow cover during the incubation and early nestling period ( $F_{1,173} = 8.96$ ,  $P < 0.001$ ;  $F_{1,173} = 9.03$ ,  $P < 0.001$ ; respectively). Higher fledging success than hatching success was recorded in first and second breeding years of the females ( $F_{1,42} = 8.94$ ,  $P =$

Table 2. Three-way ANOVA for the relationship between reproductive performance of female Tawny Owls and breeding years, age of males, and snow effects. Categories for the variations: first, second, third, fourth, and fifth known breeding season of females; males of the same age or younger males than their mates, compared with males older than their mates; snow cover versus no snow cover during the incubation and early nesting period.  $N = 131$  females.

SOURCE OF VARIATION	RESPONSE VARIABLES	df	<i>F</i>	<i>P</i>
Breeding years of females $\times$ age of males	Number of eggs	4	2.28	0.074
	Hatching failure	4	2.17	0.081
	Nestling mortality	4	2.87	0.027
	Number of fledglings	4	2.73	0.034
Breeding years of females $\times$ snow	Number of eggs	4	3.87	0.006
	Hatching failure	4	4.62	0.003
	Nestling mortality	4	4.97	<0.001
	Number of fledglings	4	5.12	<0.001
Age of males $\times$ snow	Number of eggs	1	2.94	0.084
	Hatching failure	1	3.43	0.069
	Nestling mortality	1	6.97	0.003
	Number of fledglings	1	4.80	0.029
Breeding years of females $\times$ age of males $\times$ snow	Number of eggs	4	2.57	0.043
	Hatching failure	4	3.01	0.022
	Nestling mortality	4	4.61	0.002
	Number of fledglings	4	3.79	0.007

0.003;  $F_{1,42} = 9.37$ ,  $P < 0.001$ ; respectively), but hatching success exceeded fledging success in the third, fourth, and fifth breeding years of the females ( $F_{1,42} = 11.52$ ,  $P < 0.001$ ;  $F_{1,24} = 11.20$ ,  $P < 0.001$ ; and  $F_{1,15} = 8.92$ ,  $P = 0.002$ ).

**Body Mass.** Body mass of both females and males increased as the number of breeding years increased (female:  $F_{4,170} = 2.93$ ,  $P = 0.021$ , male:  $F_{4,170} = 3.10$ ,  $P < 0.017$ ; Fig. 1) but there were no significant differences in body mass between the third and fifth breeding seasons (female:  $F_{2,84} = 2.52$ ,  $P = 0.087$ , male:  $F_{2,84} = 2.69$ ,  $P = 0.073$ ). Female body mass was lower in years with snow than in years without snow cover in the first, second, and third breeding seasons, although the  $P$  values declined from the first to the third breeding years ( $t_{43} = 4.52$ ,  $P < 0.001$ ;  $t_{43} = 3.47$ ,  $P < 0.01$ ;  $t_{43} = 2.40$ ,  $P < 0.05$ ; respectively) and there was no significant difference in fourth and fifth breeding year ( $t_{25} = 1.47$ , NS and  $t_{16} = 1.30$ ,  $P > 0.005$ ). A similar tendency was recorded for male body mass, but the differences were lower than those of females in first and second breeding years ( $t_{43} = 2.62$ ,  $P < 0.02$ ;  $t_{43} = 2.28$ ,  $P < 0.05$ ; respectively) and disappeared in third, fourth, and fifth breeding seasons ( $t_{43} = 1.44$ ,  $t_{25} = 1.16$ ,  $t_{16} = 1.30$ , respectively;  $P > 0.05$ ). If the differences in mass loss

between the females and males are presented as percentage mass loss in snow years in relation to mass in years without snow cover, the smaller decrease for males than females is notable (Fig. 2).

**Between-year Shift in Nest Sites.** Distribution of selected nest sites between the three altitude ranges showed significant differences for the five successive breeding seasons of the females ( $\chi^2_8 = 24.72$ ,  $P < 0.01$ ; Fig. 3). In the first and second breeding years, nest sites were chosen mainly between 300–500 m elevation, and a high proportion of the owls nested above the 500 m, but in third, fourth, and fifth breeding seasons the majority of the females nested below 300 m. The increase in the proportion of breeders in the lowest altitude range was greatest between second and third breeding years of the females, and the highest proportion was recorded in fourth breeding season ( $\chi^2_8 = 24.38$ ,  $P < 0.001$ ).

The movement between the altitude ranges was related to snow conditions and the age of breeding females (Table 3). A large number of females changed elevation in their second breeding year in relation to the previous breeding season, but only a few females did so if there was no snow cover in the early breeding season ( $\chi^2_1 = 6.31$ ,  $P < 0.02$ ). Movement of females between the three altitude

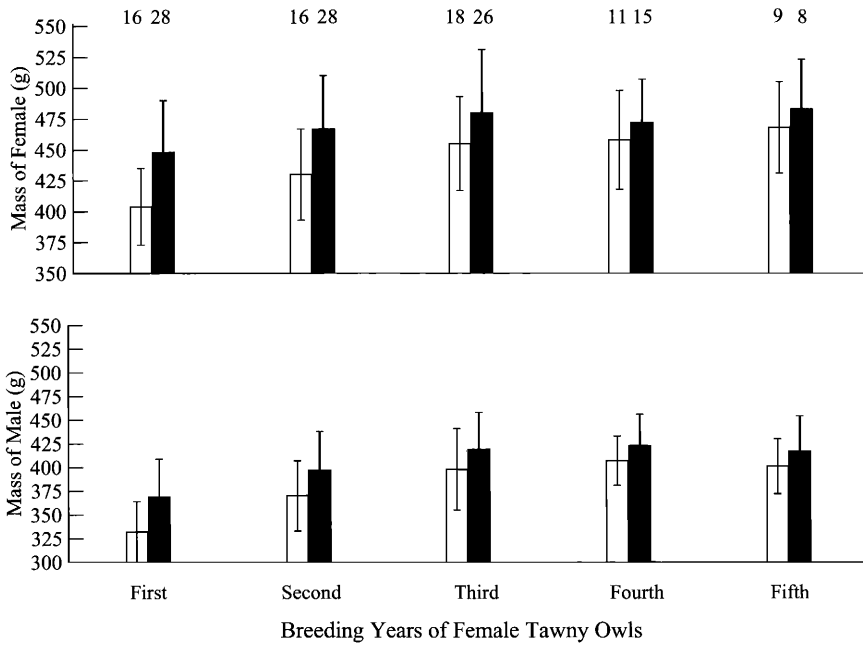


Figure 1. Body mass of Tawny Owl parents in five successive breeding years when snow covered and did not cover the ground during the incubation and early nestling period. Open bars indicate masses in snow years and black bars indicate masses in years without snow cover. Error lines indicate SD. Numbers above the bars indicate number of parents.

ranges was also found to be more common in snow years in their third breeding season ( $\chi^2_1 = 4.08, P < 0.05$ ). However, snow conditions did not influence changes between elevations in the fourth and fifth breeding years ( $\chi^2_1 = 0.13$  and  $\chi^2_1 = 0.15$ , respectively;  $P > 0.05$ ). In most cases females moved from higher to lower elevations (25 of 35 changes; 71.4%,  $\chi^2_1 = 12.91, P < 0.001$ ).

**Body Mass and Length of Tarsus before Fledging.** Mean body mass and mean tarsal length per brood of the nestlings before fledging increased in subsequent breeding years ( $F_{4,170} = 3.69, P = 0.005$ ;  $F_{4,170} = 2.87, P = 0.021$ ; respectively; Fig. 4), but differences were not recorded between the third and fifth breeding seasons ( $F_{2,84} = 3.01, P = 0.069$  and  $F_{2,84} = 3.09, P = 0.062$ ; respectively). Nestlings were heavier with longer tarsal length in years without snow cover than in snow years in the females' first ( $t_{43} = 2.46, P < 0.02$ ;  $t_{43} = 3.88, P < 0.001$ ; respectively) and second breeding years ( $t_{43} = 2.33, P < 0.05$ ;  $t_{43} = 4.04, P < 0.001$ ; respectively). In the females' third, fourth, and fifth breeding years, nestlings did not differ either in body mass or tarsal length according to snow con-

dition ( $t_{43} = 1.59, t_{25} = 2.17, t_{16} = 1.19$ ;  $P > 0.05$  in all occasions).

DISCUSSION

**Hatching Success Versus Fledging Success.** The relatively low fecundity of young females compared to older females has been documented both in passerines (Perrins 1979, Dhondt 1989) and non-passerines (Newton 1989, Saether 1990, Sydeman et al. 1991). Thus, the small clutch size with low hatching success of Tawny Owl females may also be due to low fecundity in their first and second breeding years. Male owls feed their mates during the incubation period, but egg survival was not influenced by male age. Nevertheless, in the females' first and second breeding years the reduction in number of offspring occurred in the incubation period rather than the nestling period because fledging success was higher than hatching success. For birds with more breeding experience, during their third, fourth, and fifth breeding years, the relationship between hatching success and fledging success was reversed: lower fledging success

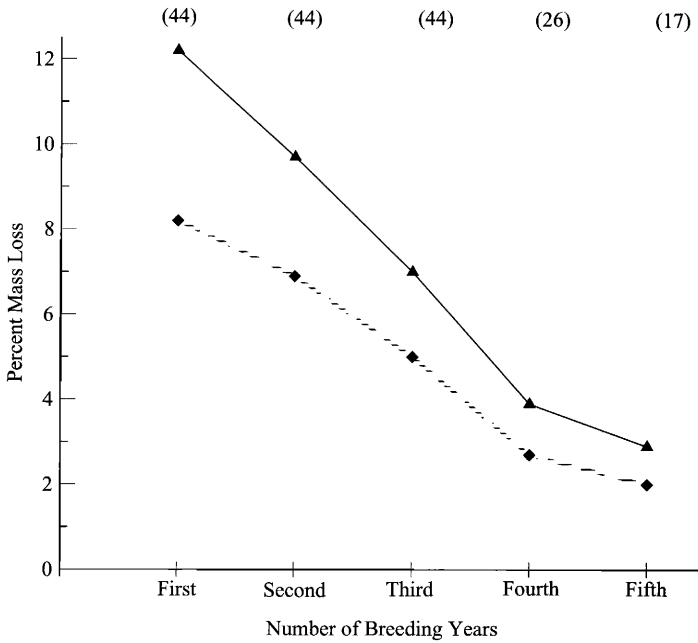


Figure 2. Percent mass loss in snow years related to body mass recorded in years without snow cover in female and male Tawny Owls in five successive breeding years. Solid line and broken line indicate percent mass loss of females and males, respectively. Mass losses were calculated using body mass recorded in snow years and in years without snow cover. Numbers above indicate the number of females and males.

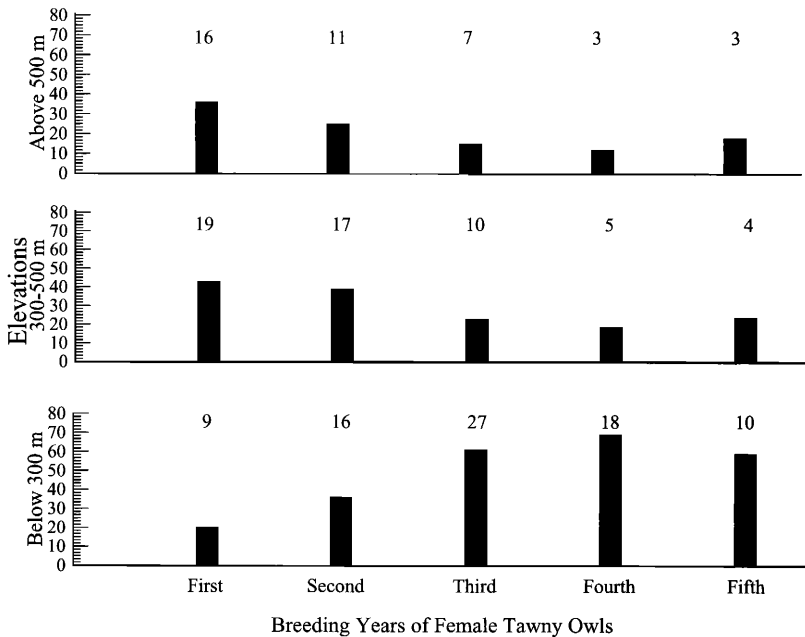


Figure 3. Percentage distribution of nest sites among the three altitude ranges in five successive breeding seasons of female Tawny Owls. The number of nests are presented above the bars.

Table 3. Percentage distribution of females that changed or retained nest sites between the three altitude ranges (<300 m, 300–500 m, >500 m) in relation to snow cover and successive breeding seasons. The changes and retentions are related to the nest sites in previous breeding season. The number of pairs are presented in parentheses.

BREEDING YEAR OF FEMALES	SNOW COVER	NEST SITE CHANGED	NEST SITE RETAINED
Second	Yes	43.8 (7)	53.3 (9)
	No	10.7 (3)	89.3 (25)
Third	Yes	61.1 (11)	38.9 (7)
	No	19.2 (5)	80.8 (21)
Fourth	Yes	18.2 (2)	81.8 (9)
	No	13.3 (2)	86.7 (13)
Fifth	Yes	33.3 (3)	66.7 (6)
	No	25.0 (2)	75.0 (6)

limited the number of offspring produced rather than hatching success.

Both females and nestlings depend upon food supplied by the males during the brooding period, thus the differences in fledging success and number of fledglings probably reflected male age.

Compared to pairs where the males were the same age or younger than their mates, pairs where the males were older than the females raised more offspring with higher fledging success.

Longitudinal studies on bird species have shown that clutch size and fledging success increased with age to a plateau and decreased among the oldest breeders (Newton et al. 1983, Thomas 1983, Nisbet et al. 1984, Newton 1989, Pugsek and Wood 1992). We have not yet conducted the prolonged studies of the Tawny Owl that would allow us to examine the possible effects of senescence. Nevertheless, we believe that the present study was long enough to demonstrate that the females reached a plateau in their breeding success, because females showed no differences in reproductive performances after their third breeding years.

**Numerical Responses of Tawny Owls to Snow Cover.** Predators may respond to fluctuations in the abundance of prey in different ways (Solomon 1949). Numerical responses involve changes in reproductive success, survival, and immigration/emigration rate, whereas functional responses reflect changes in prey composition (Andersson and Erlinge 1977). Long-term studies on nocturnal raptors have shown both numerical and functional re-

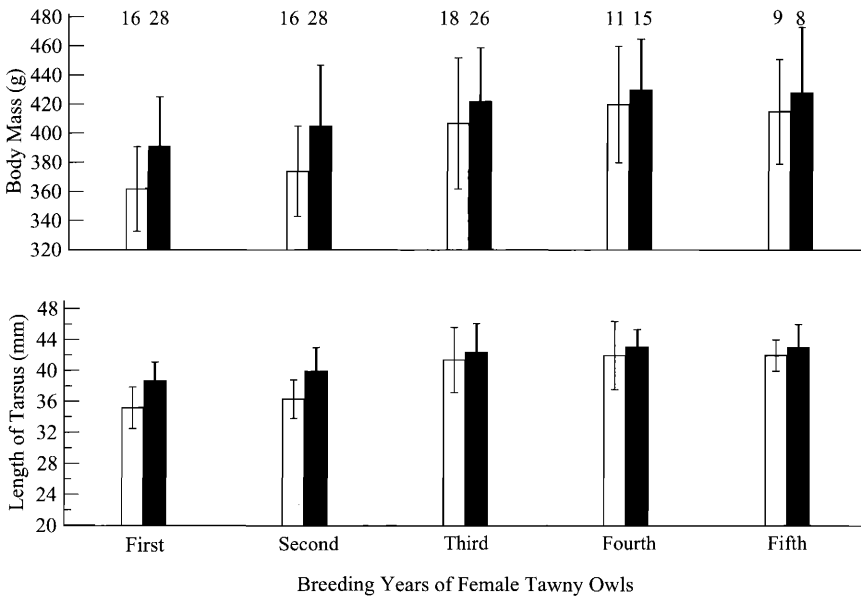


Figure 4. Mean body mass and length of tarsus of Tawny Owl nestlings per brood before fledging in five breeding years with and without snow cover during the incubation and early nestling period. Open and black bars indicate mass and length of tarsus in snow years and in years without snow cover, respectively. Error lines indicate SD. Numbers above the columns indicate number of broods.

sponses to fluctuations in prey abundance, both in boreal and temperate regions in northern latitudes (Southern and Lowe 1868, Adamcik et al. 1978, 1979, Korpimäki 1986, 1987, Piñtiäinen et al. 1986, Korpimäki and Norrdahl 1991). The reproductive performance of Tawny Owls increased with increasing breeding experience, but the change in productivity also reflected numerical responses of owls to snow cover.

We found that even pairs with considerable breeding experience achieved lower reproductive success in adverse weather conditions with snow cover. Analysis of diet showed that, when the availability of small mammals was low because of snow cover, the males delivered more birds to females and their offspring (Sasvári et al. 2000), and older males were better than young males at providing alternative prey. However, we suggest that in snow years both the young and old males delivered fewer food items with lower total food mass than in years without snow cover and neither the inexperienced nor experienced males were able to compensate fully for the loss of the primary prey. We found lower fledging success in snow years than in years without snow cover even in fourth and fifth breeding seasons of the parents.

**Higher Mass Loss for Females than Males in Years with Snow Cover.** When the snow effects resulted in a change in prey availability, inexperienced parents suffered not only a greater reduction in breeding performance, but also a larger decline in body condition. Reflecting the dependence of the females on food supplied by the males during the incubation and brooding period, the differences in the mass between the snow years and years without snow cover were considerably higher for females than males. Hence, we suggest that male owls reduce prey provided to their mates during incubation and early nestling period to ensure their own survival. In successive breeding years increased breeding experience meant that the males were better equipped to exploit the secondary food resources in adverse weather conditions and did not suffer loss of mass.

**Nest Site Switching by Experienced Breeding Pairs.** The Tawny Owl parents shifted nest sites and relocated to new breeding territories at lower elevations in snow years. As a consequence of these changes, the majority of parents in their third breeding season and following years nested at low elevations. We suggest that leaving the higher elevations and the apparent benefit for older parents

of moving, in terms of their increased reproductive performance, is due to the higher frequency of secondary prey available at lower elevations during adverse-weather periods.

In our previous study on the effect of Tawny Owls' predation on songbirds (Sasvári and Hegyi 1998), we estimated the abundance of birds around the owl nests in snow years (1993 and 1996) and in years without snow cover (1995 and 1997). We recorded number of birds over a period of 30 min in a radius of 150–200 m of the nests during the incubation period. The surveys were carried at low, middle, and high altitude ranges between 130–680 m at 24, 31, and 29 sites in snow years and 33, 38 and 32 sites in years without snow cover. The mean number of birds recorded from the low to high altitude range was  $15.3 \pm 8.7$ ,  $9.5 \pm 7.6$ , and  $3.4 \pm 3.2$  ( $F_{2,81} = 5.91$ ,  $P = 0.004$ ) in snow years, and  $13.6 \pm 6.0$ ,  $11.7 \pm 5.1$ , and  $8.6 \pm 4.7$  ( $F_{2,100} = 3.86$ ,  $P = 0.027$ ) in years without snow cover. These data show that possible prey species of birds were most abundant at low elevations in all years, but their numbers were highest at the lowest altitude range in years with snow, when numbers were noticeably reduced at the highest altitude range.

The birds, both the prey and predators, were more protected from the effect of adverse weather in valleys than on the steep slopes of the hills. Also, villages and other man-made objects are found in valleys and the birds may also be able to find food related from human activity to aid winter survival.

**Lower Body Mass and Tarsal Length and Differential Gender Survival.** In terms of sexual dimorphism in raptors, dimorphism in size and body mass is nearly as pronounced at the time of fledging, as in adulthood (Newton and Marquiss 1979, Fiala 1981, Richter 1983, Bortolotti 1986). Adult female Tawny Owls were heavier and larger than the adult males, hence the differences in body mass and tarsal length measured on nestlings, before fledging, reflected the sexual dimorphism of offspring. If one sex requires more food than the other, this sex should experience increased mortality when food resources are scarce, skewing the sex ratio toward the less costly sex (Slagsvold 1990, Weatherhead and Teather 1991, Clutton-Brock 1991). We did not identify the sex of the owlets, but on the basis of body mass and tarsal length, we presumed that the sex ratio in the broods of Tawny Owls was biased in favor of the "cheaper" male during difficult feeding conditions.



The lower mean body mass and mean shorter tarsi of the nestlings in a brood raised in snow years may be due to the shortage of food and the better survival of the sex requiring less investment. Nevertheless, we found no differences in body mass and length of tarsus of nestlings before fledging related to snow cover in the third, fourth, and fifth breeding seasons. The condition of fledglings raised in these years did not differ between the successive seasons. The influence of snow cover on fledglings' condition was not apparent in the broods of experienced parents.

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#### LITERATURE CITED

- ADAMCIK, R.S., A.W. TODD, AND L.B. KEITH. 1978. Demographic and dietary responses of Great Horned Owls during a snowshoe hare cycle. *Can. Field-Nat.* 92:156-166.
- , ———, AND ———. 1979. Demographic and dietary responses of Red-tailed Hawks during a snowshoe hare fluctuation. *Can. Field-Nat.* 93:15-27.
- ANDERSSON, M. AND S. ERLINGE. 1977. Influence of predation on rodent populations. *Oikos* 29:591-597.
- BORTOLOTTI, G.R. 1986. Influence of sibling competition on nestling sex ratios of sexually dimorphic birds. *Am. Nat.* 127:495-507.
- CLUTTON-BROCK, T.H. 1991. The evolution of parental care. Princeton Univ. Press, Princeton, NJ U.S.A.
- COULSON, J.G. 1968. Differences in the quality of birds nesting in the centre and on the edges of a colony. *Nature* 217:478-479.
- DESTEVEN, D. 1978. Clutch size, breeding success, and parental survival in the Tree Sparrow (*Iridoprocne bicolor*). *Evolution* 34:278-291.
- DZUS, E.H., G.R. BORTOLOTTI, AND J.M. GERRARD. 1996. Does sex-biased hatching order in Bald Eagles vary with food resources? *Ecoscience* 3:252-258.
- DHONDT, A.A. 1989. The effect of old age on the reproduction of Great Tits *Parus major* and Blue Tits *P. caeruleus*. *Ibis* 131:268-280.
- FIALA, K.L. 1981. Reproductive costs and the sex ratio in Red-winged Blackbirds. Pages 198-214 in R.D. Alexander and D.W. Tinkle [EDS.], Natural selection and social behavior. Chiron Press, New York, NY U.S.A.
- GEHLBACH, F.R. 1989. Screech-Owl. Pages 315-326 in I. Newton, [ED.], Lifetime reproduction in birds. Academic Press, London, U.K.
- GOSZCZYNSKI, J. 1981. Comparative analysis of food of owls in agrocenosis. *Ekol. Pol.* 29:431-439.
- JEDRZEJEWSKI, W., B. JEDRZEJEWSKA, K. ZUB, A.I. RUPRECHT, AND C. BYSTROWSKI. 1994. Resource use by Tawny Owls *Strix aluco* in relation to rodent fluctuation in Białowieża National Park, Poland. *J. Avian Biol.* 25:308-318.
- KIRK, D.A. 1992. Diet changes in breeding Tawny Owls (*Strix aluco*). *J. Raptor Res.* 26:239-242.
- KORPIMÄKI, E. 1986. Gradients in population fluctuation of Tengmalm's Owl *Aegolius funereus* in Europe. *Oecologia (Berlin)* 69:195-201.
- . 1987. Dietary shifts, niche relationships, and reproductive output of coexisting kestrels and Long-eared Owls. *Oecologia (Berlin)* 74:277-285.
- . 1988. Effects of age on breeding performance of Tengmalm's Owl *Aegolius funereus* in western Finland. *Ornis Scand.* 19:21-26.
- AND K. NORRDAHL. 1991. Numerical and functional responses of kestrels, Short-eared Owls, and Long-eared Owls to vole densities. *Ecology* 72:814-826.
- MIKKOLA, H. 1983. Owls of Europe. Poyser, Staffordshire, U.K.
- NEWTON, I. 1989: Lifetime reproduction in birds. Academic Press, London, U.K.
- AND M. MARQUISS. 1979. Sex ratio among nestlings of the European Sparrow Hawk. *Am. Nat.* 113:309-315.
- , ———, AND P. ROTHERY. 1983. Age structure and survival in a sparrowhawk population. *J. Anim. Ecol.* 52:591-602.
- NISBET, I.C., J.M. WINCHELL, AND A.E. HEISE. 1984. Influence of age on the breeding biology of Common Terns. *Colon. Waterbirds.* 7:117-126.
- NORUSIS, M.J. 1977. SPSS/PC+ advanced statistics 4.0. SPSS, Gorinchem, U.K.
- OLSEN, P.D. AND A. COCKBURN. 1991. Female-biased sex allocation in Peregrine Falcons and other raptors. *Behav. Ecol. Sociobiol.* 28:417-423.
- ORIANI, G.H. 1969. Age and hunting success in the Brown Pelican (*Pelecanus occidentalis*). *Anim. Behav.* 17:316-319.
- PERRINS, C.M. 1979. British tits. Collins, London, U.K.
- PETTY, S.J. 1992. A guide to age determination of Tawny Owl *Strix aluco*. Pages 89-91 in C.A. Galbraicht, J.R. Taylor, and S. Perceival [EDS.], The ecology and conservation of European owls. Joint Nature Conservation Committee, Peterborough, U.K.
- PIANKA, E.R. 1976. Natural selection of optimal reproduction tactics. *Am. Zool.* 16:775-784.
- PIÉTIÄINEN, H., P. SAUROILA, AND R.A. VÄISÄNEN. 1986. Parental investment in clutch size and egg size in the Ural Owl *Strix uralensis*. *Ornis Scand.* 17:309-325.
- PUGESEK, B.H. AND K.L. DIEM. 1983. A multivariate study of the relationship of parental age to reproductive success in California Gulls. *Ecology* 64:829-839.

- AND P. WOOD. 1992. Alternative reproductive strategies in the California Gull. *Evol. Ecol.* 6:279–295.
- RECHER, H.F. AND J.A. RECHER. 1969. Comparative foraging efficiency of adult and immature Little Blue Herons (*Florida caerulea*). *Anim. Behav.* 17:320–322.
- RICHTER, W. 1983. Balanced sex ratios in dimorphic altricial birds: the contribution of sex-specific growth dynamics. *Am. Nat.* 121:158–171.
- SAETHER, B.E. 1990. Age-specific variation in reproductive performance of birds. *Current Ornithology* 7:251–283.
- SASVÁRI, L. AND Z. HEGYI. 1998. Bird predation by Tawny Owls (*Strix aluco* L.) and its effect on the reproductive performance of tits. *Acta Oecol.* 19:483–490.
- AND ———. 2002. Effects of age composition of pairs and weather condition on the breeding performance of Tawny Owls, *Strix aluco*. *Folia Zool.* 51:113–120.
- , ———, T. CSÖRGÖ, AND I. HAHN. 2000. Age-related diet change, parental care, and reproductive cost in Tawny Owls *Strix aluco* L. *Acta Oecol.* 21:267–275.
- SAUROLA, P. 1989. Ural Owl. Pages 327–345 in I. Newton [Ed.], *Lifetime reproduction in birds*. Academic Press, London, U.K.
- SLAGSVOLD, T. 1990. Fisher's sex-ratio theory may explain hatching patterns in birds. *Evolution* 44:1009–1017.
- SOLOMON, M.E. 1949. The natural control of animal population. *J. Anim. Ecol.* 18:1–35.
- SOUTHERN, H.N. AND V.P.W. LOWE. 1968. The pattern of distribution of prey and predation in Tawny Owl territories. *J. Anim. Ecol.* 37:75–97.
- SYDEMAN, W.J., J.F. PENNIMAN, T.M. PENNIMAN, P. PYLE, AND D.G. ANLEY. 1991. Breeding performance in the Western Gull: effects of parental age, timing of breeding and year in relation to food availability. *J. Anim. Ecol.* 60:135–149.
- THOMAS, C.S. 1983. The relationship between breeding experience, egg volume, and reproductive success of the Kittiwake *Rissa tridactyla*. *Ibis* 125:567–574.
- WEATHERHEAD, P.J. AND K.L. TEATHER. 1991. Are skewed fledgling sex-ratios in sexually dimorphic birds adaptive? *Am. Nat.* 138:1159–1172.
- WEIMERSKIRCH, H. 1992. Reproductive effort in long-lived birds: age specific patterns of condition, reproduction and survival in the Wandering Albatross. *Oikos* 64:464–473.
- WIEBE, K.L. AND G.R. BORTOLOTTI. 1992. Facultative sex ratio manipulation in American Kestrels. *Behav. Ecol. Sociobiol.* 30:379–386.
- WILLIAMS, G.C. 1966. Natural selection, the cost of reproduction, and a refinement of Lack's Principle. *Am. Nat.* 100:687–690.

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