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Effects of age composition of pairs and weather condition on the breeding performance of tawny owls, *Strix aluco*

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Abstract. Nest boxes for breeding tawny owls *Strix aluco* were sited in a mixed oak/hornbeam/beech forest located in the Pilis Biosphere Reserve, 30 km northwest of Budapest, Hungary, during the period 1992–2000. We hypothesized that both within-pair differences in age composition and weather conditions affect the breeding success of the parents. To test our hypothesis, we marked the owl parents in their first known breeding year and related their reproductive performance was to within-pair age composition through three subsequent breeding seasons. Sex-related age differences affected the breeding performance of the parents in their first and second known breeding year: number of eggs and hatching success were influenced by the age of females, while fledging success was influenced by the age of males. Within-pair age differences did not affect the breeding performance at their third known breeding year. Reproductive performance was lower in snowy years than in years without snow cover in all of their three subsequent breeding seasons. On basis of the lower mean body mass and shorter mean tarsi of the nestlings before fledging recorded in adverse weather conditions, we suggest that parents favour the sex that demands less investment in care. As a consequence, the sex-ratio becomes skewed towards the male in a poor food environment.

Key words: fledging success, hatching success, owl, parental age, reproductive performance, *Strix*, weather condition

Introduction

Studies of lifetime reproductive success on long-lived bird species have shown that young parents have a lower breeding performance than older birds (Ollason & Dunnet 1988, Scott 1988, Bradley et al. 1989, Newton & Rothery 1997). Young parents invest less in reproduction than do more mature birds, which may be due to the young birds' poorer condition or their inexperience in foraging and knowledge of the habitat (Orians 1969, Recher & Recher 1969, Pugesek & Diem 1983, Thomas & Coulson 1988, Weimerskirch 1992). Long-term studies on owls have also revealed age dependent effects on breeding performance (Korpimäki 1988, Gehlbach 1989, Saurola 1989).

The aim of our recent study was to examine the age dependent reproductive success of tawny owls *Strix aluco* which maintained their pair bond in subsequent breeding periods. Tawny owl is a resident strongly monogamous owl species that can be attracted to artificial nest boxes. We marked individual parents and determined the age composition of the pairs in their first known breeding years. We focused our study on the question: do within-pair age differences influence the breeding performance of the parents? Nevertheless we also hypothesized that weather conditions affect the reproductive success of all pairs whether young or old. Southern & Lowe (1968) suggested that food availability for owl species preying on small mammals is determined by ground cover and papers have reported that owls changed to secondary foods, when snow prevents them from hunting rodents (Goszczynski 1981, Mikkola 1983, Kirk 1992). We thus examined the breeding performance achieved by the pairs in snowy years and in years when snow did not cover the ground during the incubation and early nestling periods. In addition, we recorded the body mass and length of tarsus of nestlings before fledging and related these measures to the number of breeding seasons of the parents and weather effects.

It has been suggested that, if the different sex of offspring require different care in a brood, the young which demand more parental effort should be limited in a poor food environment in order to reduce the total reproductive cost to the parents (Slagsvold 1990, Clutton – Brock 1991, Weatherhead & Teather 1991). On the basis of the sexual dimorphism in tawny owls we presumed that the lighter offspring, which demand less parental investment, survive better during brood reduction. In order to examine the reduction of reproductive cost by elimination of heavier offspring, we measured the body mass of nestlings before fledging and related this to hatching order.

Methods

One hundred and eighty nest-boxes for breeding tawny owls were sited in a mixed oak/hornbeam/beech forest, with 40–60 year old trees, in the Pilis Biosphere Reserve, 30 km north-west of Budapest (47°35'N; 19°02'E) during the period 1992–2000. 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 day intervals from the first week in February.

Ninety-eight females and 85 males were captured during the nestling period by placing a net over the entrance of the boxes while the birds were inside, and the birds were marked with different combinations of coloured rings to ensure individual identification. From these, 39 pairs were identified which bred through three subsequent breeding seasons, which did not divorce in the following breeding season, and did not lose their nests through predation. These pairs were chosen for our study of the relationship between the reproductive performance, parental age composition and weather conditions. Age determination was based on the pattern of the primaries and secondaries (Petty 1992), and four categories were distinguished for the age composition of the pairs in their first known breeding season: (1) parents were two years old or less; (2) male was more than two years old, female was two years old or less; (3) female was more than two years old, male was two years old or less; (4) parents were more than two years old.

As a consequence of the 500 m altitude range of the study area (from 200–700 m), snow covered the ground longer in the higher nest areas than the lower ones. A year when snow completely covered the ground for a radius of 1km from the owl nest during the incubation and early nestling period (until the 10 days after the hatching of the last young) was considered as a snowy breeding year for any given pair.

Statistical analyses were carried out using the SPSS statistical package. Multiple comparisons calculated by GT2-method were used for testing the relationships between breeding performance and within-pair age composition of the parents. 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.

Results

Breeding performance of the pairs of various age composition

Within-pair age differences influenced both the number of eggs and hatching success in the first and second breeding seasons of the parents (first: $F_{3,35} = 4.22$, $P = 0.013$ and $F_{3,35} = 3.36$, $P = 0.027$; second: $F_{3,35} = 3.94$, $P = 0.020$ and $F_{3,35} = 3.69$, $P = 0.029$; Table 1.) but effects were not found in their third breeding season ($F_{3,35} = 2.34$, $P = 0.082$ and $F_{3,35} = 2.09$, $P = 0.215$). Multiple comparisons showed that pairs where females were more than two years old produced more eggs with higher hatching success than pairs where females were two years old or less in their first and second known breeding year (Table 2). Within-pair age differences also influenced fledging success in the first and second breeding season (first: $F_{3,35} = 6.24$, $P < 0.001$; second: $F_{3,35} = 3.36$, $P < 0.001$), but effects were not recorded in the third breeding season ($F_{3,35} = 2.07$, $P = 0.229$). Multiple comparisons supported the idea that pairs where males were more than two years old reached higher fledging success than pairs where males were two years old or younger.

More fledglings were raised by the pairs where males were more than two years old in the first and second breeding year ($F_{3,35} = 4.89$, $P < 0.001$ and $F_{3,35} = 5.23$, $P = 0.002$), but no differences were recorded between pairs according to their within-pair age composition in their third breeding season ($F_{3,35} = 2.66$, $P = 0.072$). Parents produced more fledglings in their second known breeding year than in their first ($t = 2.89$, $P < 0.01$) and raised more young in their third breeding year than in their second ($t = 3.16$, $P < 0.01$).

Relationships between the age composition and weather condition influencing the breeding performance

Parents laid fewer eggs in years when snow covered the ground than in years when snow did not cover the ground in their first ($t = 4.53$, $P < 0.001$), second ($t = 3.28$, $P < 0.01$) and third breeding season ($t = 2.18$, $P < 0.05$), but differences were not recorded for hatching success

Table 1. Number of eggs, hatching success, fledging success and number of fledglings produced by owl parents of various age composition in their first second and third breeding years. In parentheses, number of pairs.

Age composition	Breeding Years	Number of eggs	Hatching success	Fledging success	Number of fledglings
Parents two years old or less than two years old (13)	First	2.15±0.60	0.79±0.06	0.64±0.11	1.08±0.46
	Second	2.77±0.71	0.83±0.08	0.73±0.05	1.69±0.45
	Third	3.31±0.85	0.91±0.12	0.87±0.08	2.61±0.66
Male more than two years old, female two years old or less (9)	First	2.34±0.63	0.80±0.07	0.93±0.09	1.89±0.83
	Second	3.22±0.41	0.81±0.09	0.95±0.04	2.44±0.92
	Third	3.56±0.76	0.90±0.09	0.92±0.11	2.89±0.83
Female more than two years old, male two years old or less (9)	First	2.89±0.34	0.95±0.05	0.55±0.13	1.56±0.46
	Second	3.33±0.44	0.96±0.06	0.62±0.08	2.00±0.76
	Third	3.44±0.93	0.93±0.10	0.88±0.10	2.89±0.83
Parents older than two years old (8)	First	3.13±0.60	0.96±0.06	0.86±0.06	2.63±0.49
	Second	3.75±0.88	0.92±0.08	0.87±0.09	3.00±0.48
	Third	3.88±0.75	0.93±0.07	0.90±0.07	3.25±0.96

Table 2. Multiple comparisons (GT2-method) among the number of eggs, hatching success and fledging success produced by pairs of various age composition. Numbers in parentheses indicate the four classes of age composition. Upper numbers denote the number of eggs, hatching success and fledging success in the first, lower numbers denote the number of eggs, hatching success and fledging success in the third breeding year. Asterisks indicate significant differences at the 0.05 level. Values calculated for second breeding year are not presented because the significant differences showed the same relationships in first and second breeding seasons.

			Minimal significant differences (MSD)											
			Number of eggs				Hatching success				Fledging success			
			(1)	(2)	(3)	(4)	(1)	(2)	(3)	(4)	(1)	(2)	(3)	(4)
Differences in absolute value between the groups	Parents two years old or less than two years old	(1)	--	0.45	0.61	0.77	--	0.07	0.06	0.08	--	0.15	0.13	0.11
			--	0.19	0.03	0.25	--	0.03	0.04	0.06	--	0.06	0.04	0.07
	Male more than two years old, female two years old or less	(2)	0.34	--	0.29	0.45	0.05	--	0.04	0.06	0.21*	--	0.22	0.09
			0.15	--	0.18	0.11	0.01	--	0.04	0.06	0.04	--	0.07	0.01
	Female more than two years old, male two years old or less	(3)	0.75*	0.39*	--	0.26	0.14*	0.07*	--	0.04	0.11	0.30*	--	0.17
			0.01	0.14	--	0.29	0.01	0.01	--	0.07	0.01	0.05	--	0.07
	Parents older than two years old	(4)	0.94*	0.58*	0.19	--	0.16*	0.09*	0.02	--	0.15*	0.05	0.27*	--
			0.20	0.06	0.20	--	0.04	0.04	0.03	--	0.04	0.02	0.03	--

Table 3. Number of eggs, hatching success, fledging success and number of fledglings produced in snowy years and in years without snow cover. In parentheses, number of breeding pairs.

Breeding years	Snow cover on the ground	Number of eggs	Hatching success	Fledging success	Number of fledglings
First	Yes (16)	1.94±0.71	0.87±0.07	0.70±0.06	1.19±0.75
	No (23)	3.00±0.74	0.88±0.10	0.78±0.04	2.04±0.88
Second	Yes (12)	2.67±0.68	0.91±0.08	0.71±0.09	1.75±0.75
	No (27)	3.41±0.59	0.92±0.06	0.85±0.05	2.70±0.88
Third	Yes (14)	3.36±0.42	0.94±0.05	0.84±0.04	2.64±0.39
	No (25)	3.60±0.36	0.92±0.07	0.91±0.05	3.00±0.46

($t = 0.16$, $t = 0.54$, $t = 0.10$, n.s. in all occasions; Table 3). Pairs achieved lower fledging success and fledged fewer nestlings in snowy years than in years without snow cover in all breeding seasons (first: $t = 2.87$, $P < 0.01$ and $t = 3.24$, $P < 0.01$; second: $t = 3.70$, $P < 0.001$ and $t = 2.45$, $P < 0.01$; third: $t = 2.70$, $P < 0.02$ and $t = 2.59$, $P < 0.02$).

Three-way ANOVA shows significant differences in the breeding performance for the relationships between within-pair age composition and breeding years (Table 4). Within-pair age composition affected the number of eggs, hatching and fledging success in the first and second breeding seasons, but did not influence the performance of the parents in later breeding years. Significant differences in breeding performance were found for the relationships between within-pair age composition and weather effects, except during the incubation. i.e. pairs laid fewer eggs and achieved lower fledging success in all age categories when snow covered the ground but hatching success was not influenced by the

Table 4. Three-way ANOVA for the relationships between the breeding performance and within-pair age composition, number of breeding years and weather effects. Within-pair age composition was distinguished into four categories: (1) parents two years old or less; (2) male more than two years old, female two years old or less; (3) female more than two years old, male two years old or less; (4) parents more than two years old. Breeding years were categorized for three subsequent breeding seasons. Weather effects were distinguished into two categories: snow covered the ground and snow did not cover the ground during the incubation period and early nestling period (until the age of 10 days old of last-hatched nestlings). Sample size: 117 broods.

Source of variation		d.f.	F	P
Within-pair age composition x Breeding years	Number of eggs	6	3.79	<0.001
	Hatching success	6	3.52	<0.001
	Fledging success	6	2.63	0.022
Within-pair age composition x Weather effects	Number of eggs	3	2.80	0.032
	Hatching success	3	2.21	0.083
	Fledging success	3	3.07	0.027
Breeding years x Weather effects	Number of eggs	2	4.70	0.013
	Hatching success	2	2.74	0.065
	Fledging success	2	5.13	0.007
Within-pair age composition x Breeding years x Weather effects	Number of eggs	6	2.90	0.012
	Hatching success	6	2.31	0.038
	Fledging success	6	2.79	0.015

Table 5. Mean body mass (g±SD) and mean length of tarsus (mm±SD) of nestlings before fledging per brood. n = number of broods.

Number of breeding years	Snow cover	n	Body mass	Length of tarsus
First	Yes	16	372.5±24.1	38.0±2.5
	No	23	395.7±21.6	39.8±3.1
Second	Yes	12	383.0±17.8	38.4±2.1
	No	27	411.8±24.7	41.2±2.3
Third	Yes	14	380.6±17.2	39.0±2.8
	No	25	422.1±18.2	42.3±2.7

relationship between weather and within-pair age differences. Also, differences in numbers of eggs and fledging success were recorded for the relationships between breeding years and weather effects. Pairs achieved higher performance in their third than in their first and second breeding years, but lower performance in snowy years than in years without snow cover in all breeding seasons. These relationships did not affect hatching success.

Body mass and length of tarsus of nestlings before fledging

We recorded 137 nestlings before fledging and 42 nestlings which died in 61 broods. Mean body mass of nestlings per brood was heavier and mean tarsal length of nestling per brood was longer in the second broods of the parents than in the first ($t = 2.45$, $P < 0.02$ and $t = 2.64$, $P < 0.02$) and nestlings were heavier with longer tarsal lengths in the third than in second breeding years ($t = 2.20$, $P < 0.05$ and $t = 2.76$, $P < 0.02$; Table 5). Parents fledged nestlings with higher mean body mass and longer mean tarsal length per brood in years without snow cover than in snowy years both in their first (t = 2.90, P < 0.01 and t = 2.60, P < 0.02), second (t = 3.97, P<0.001 and t = 4.02, P < 0.001) and third breeding seasons (t =5.37, P<0.001 and t = 3.39, P < 0.01).

Discussion

Our findings on the relationships between parental age and reproductive performance may be summarized as follows.
(1) Reproductive performance of pairs increased through successive breeding years.
(2) Sex-related age-differences influenced the breeding performance of pairs in the first and second known breeding years, the within-pair age differences did not affect in the third breeding season.
(3) Age of females affected the number of eggs and hatching success (older females laid more eggs with higher hatching success) while age of the males affected fledging success (older males were associated with higher fledging success).

Low fecundity of young females compared to older females has been documented both in passerines (Perrins 1979, Dhondt 1989, Newton 1989) and non-passerines (Newton 1989, Saether 1990, Sydeman et al. 1991), and the small clutch size with low hatching success of tawny owl females may be due also to a low fecundity in their first and second breeding years. Male owls feed the females during the incubation period, but surprisingly egg survival was not influenced by male age.

The high rate of nestling mortality recorded in the ten days after hatching suggests that nestlings are most at risk during the brooding season. Both females and nestlings are supplied with food by the males during the brooding period and the higher fledging success achieved by older males in their first and second breeding year is due to their more efficient food provision. The differences in number of offspring fledged reflected also the effects of age of the males: pairs raised more offspring where the males were old than pairs where the males were young.

Longitudinal studies on bird species have shown that clutch size, hatching success 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, Pugesek & Wood 1992). We have not yet conducted such long term studies of the tawny owl that we can examine the possible effects of senescence, and we followed only the period of their life span where success rates are increasing. It has been found both in passerines (Harvey et al. 1988) and non-passerines (Scott 1988) that experience of breeding, irrespective of age, increased breeding success, and we suggest that maintainance of the pair-bond between females and males and the breeding experience acquired together lead the parents of various ages to the highest level of the reproductive performance after the same number of breeding years. When the common breeding experience resulted in high reproductive success in their third breeding season, the effects of within-pair age differences ceased for breeding.

Predators may respond to fluctuations in the abundance of prey numerically or functionally (Solomon 1949). The numerical responses are due to reproductive success, survival and immigration/emigration rate, whereas the functional responses are reflected in a change in prey composition (Andersson & Erlinge 1977). Studies have shown numerical responses in nocturnal raptors: the productivity of owls increased in a rich food environment but decreased when the prey declined both in boreal and temperate regions in northern latitudes (Adamcik et al. 1978, 1979, Korpimäki & Norrdahl 1991, Jedrzejewski et al. 1994). In this study we also found that pairs even with common breeding experience of many years achieved lower reproductive success in adverse weather conditions. The analyses of diet composition of tawny owls showed that males delivered more birds for the females and their offspring when the availability of small mammals was low because of snow cover (S a s v á r i et al. 2000). The older males were better than young males at providing alternative prey. However, both the young and old males delivered fewer food items with lower food mass during the incubation and early nestling period in snowy years than in years when snow did not cover the ground. Neither the inexperienced nor experienced males were able to fully compensate by secondary prey types for the loss of primary food.

The lower mean body mass and mean shorter tarsi of the nestlings in a brood raised in snowy years may be due to the food shortage and the preference of the parents which favours the sex requiring less investment. Adult females are heavier and larger than adult males in tawny owls, and on the basis of the findings that, by the time of fledging, dimorphism in size and body mass is usually as pronounced as adulthood (N e w t o n & M a r q u i s 1979, F i a l a 1981, R i c h t e r 1983, B o r t o l o t t i 1986). Hence we may suppose that the differences in body mass and tarsal length measured on nestlings before fledging reflected the dimorphism of offspring. If one sex requires proportionally more food than the other then, when food resources are scarce, this sex should experience increased mortality and the sex-ratio becomes skewed towards the less costly sex (S l a g s v o l d 1990, W e a t h e r h e a d & T e a t h e r 1991, C l u t t o n - B r o c k 1991). We did not identify the sex of the owlets but, on basis of body mass and length of tarsi, we may assume the sex ratio to be biased in favour of the cheaper male. The reduction in effort maintains the parents in better condition and promotes their survival and future reproductive performance.

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LITERATURE

ADAMCIK, R. S., TODD, A. W. & KEITH, L. B., 1978: Demographic and dietary responses of Great Horned Owls during a snowshoe hare fluctuation. *Can. Field Nat., 92: 156–166.*

ADAMCIK, R. S., TODD, A. W. & KEITH, L. B., 1979: Demographic and dietary responses of Red-tailed Hawks during a snowshoe hare fluctuation. *Can. Field Nat., 93: 15–27.*

ANDERSSON, M. & ERLINGE, S., 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.*

BRADLEY, J. S., WOOLLER, R. D., SHIRA, I. J. & SERVENTY, D. L., 1989: Age-dependent survival of breeding Short-tailed Shearwaters *Puffinus tenuirostris. J. Anim. Ecol., 58: 175–188.*

CLUTTON-BROCK, T. H., 1991: The evolution of parental care. *Princeton University Press, Princeton.*

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. In: Alexander, R.D. & Tinkle, D.W. (eds), Natural Selection and Social Behavior. *Chiron Press, New York: 198–214.*

GEHLBACH, F. R., 1989: Screech-Owl. In: Newton, I. (ed.), Lifetime reproduction in birds. *Academic Press, London: 315–326.*

GOSZCZYNSKI, J., 1981: Comparative analysis of food of owls in agrocenoses. *Ekol. Pol., 29: 431–439.*

HARVEY, P. H., STENNING, M. J. & CAMPBELL, B., 1988: Factors influencing reproductive success in the Pied Flycatcher. In: Clutton-Brock, T. H. (ed.), Reproductive success. *Chicago University Press, Illinois, USA: 189–200.*

JEDRZEJEWSKI, W., JEDRZEJEWSKA, B., ZUB, K., RUPRECHT A. I. & BYSTROWSKI, C., 1994: Resource use by Tawny Owls *Strix aluco* in relation to rodent fluctuation in Bialowieza National Park, Poland. *J. Avian Biol., 25: 308–318.*

KIRK, D. A., 1992: Diet change in breeding tawny owls *(Strix aluco). J. Raptor. Res., 26: 239–242.*

KORPIMÄKI, E., 1988: Effects of age on breeding performance of Tengmalm's Owl *Aegolius funereus* in western Finland. *Ornis Scand., 19: 21–26.*

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.*

MIKKOLA, H., 1983: Owls of Europe. *T. & A. D. Poyser, Calton.*

NEWTON, I. 1989: Lifetime reproduction in birds. *Academic Press, London.*

NEWTON, I. & MARQUISS, M., 1979: Sex ratio among nestlings of the European sparrow-hawk. *Am. Nat., 113: 309–315.*

NEWTON, I., MARQUISS, M. & ROTHERY P., 1983: Age structure and survival in a Sparrowhawk population. *J. Anim. Ecol., 52: 591–602.*

NEWTON, I. & ROTHERY, P., 1997: Senescence and reproductive value in sparrowhawks. *Ecology, 78: 1000–1008.*

NISBET, I. C., WINCHELL, J. M. & HEISE, A. E., 1984: Influence of age on the breeding biology of Common Terns. *Colon. Waterb., 7: 117–126.*

OLLASON, J. C. & DUNNETT, G. M., 1988: Variations in breeding success in Fulmars. In: Clutton-Brock, T. H. (ed.), Reproductive success. *Chicago University Press, Chicago, Illinois, USA: 263–278.*

ORIANS, 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, England.*

PETTY, S. J., 1992: A guide to age determination of Tawny Owl *Strix aluco*. In Galbraith, C., Taylor, A. I. R. & Percival, S. (eds), The ecological and conservation of European owls. *Joint Nature Conservation Committee, Peterborough: 89–91.*

PUGESEK, B. H. & DIEM, K. L., 1983: A multivariate study of the relationship of parental age to reproductive success in California gulls. *Ecology, 64: 829–839.*

PUGESEK, B. H. & WOOD, P., 1992: Alternative reproductive strategies in the California Gull. *Evolut. Ecol., 6: 279–295.*

RECHER, H.F. & RECHER, J. A., 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., HEGYI, Z., CSÖRGŐ, T. & HAHN, I., 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. In: Newton, I. (ed.), Lifetime reproduction in birds. *Academic Press, London: 327–345.*

SCOTT, D. H., 1988: Reproductive success in Bewick's Swans. In: Clutton-Brock, T. H. (ed.), Reproductive success. *Chicago University Press, Chicago, Illinois, USA: 220–236.*

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. & LOWE, V. P. W., 1968: The pattern of distribution of prey and predation in tawny owl territories. *J. Anim. Ecol., 37: 75–97.*

SYDEMAN, W. J., PENNIMAN, J. F., PENNIMAN, T. M., PYLE, P. & AINLEY, D. G., 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.*

THOMAS, C. S. & COULSON, J. C., 1988: Reproductive success of Kittiwake *Rissa tridactyla*. In: Clutton-Brock, T. H. (ed.), Reproductive success. *Chicago University Press, Chicago, Illinois, USA: 251–262.*

WEATHERHEAD, P. J. & TEATHER, K. L., 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.*