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Source: *Folia Zoologica*, 60(3) : 221-227

Published By: Institute of Vertebrate Biology, Czech Academy of Sciences

URL: <https://doi.org/10.25225/fozo.v60.i3.a6.2011>

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# Age-related territory occupation and fledgling production of males in a Central-European local population of tawny owls, *Strix aluco*

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Received 9 November 2010; Accepted 19 May 2011

**Abstract.** Nest boxes for breeding tawny owls (*Strix aluco*) were located in a mixed oak-hornbeam-beech (*Quercus-Carpinus-Fagus*) forest in the Duna-Ipoly National Park, 30 km northwest of Budapest, Hungary during the period 1992–2010. The 550 m altitude range (120–680 m) of the study area was divided into low and high elevations: < 400 m, and > 400 m, each containing 88 nest-boxes. We marked 77 males in their first breeding year and evaluated the lifetime territory occupation and reproductive performance for individuals which reached five, six, seven, eight or nine years old. The fledgling production of tawny owl males increased in their first, second and third years, reached a high level in years four and five, but declined once they were six years old. The relative low reproductive performance in the early and late years of the males' lives may be attributed to the fact that the majority of males were unable to occupy high quality territories, and the rate at which individuals skipped breeding was high. We suggest that both the reduced ability to acquire high quality territories and declining fledging production in late years of males reflect senescence patterns in tawny owls.

**Key words:** age-related breeding success, lifetime reproduction, males' quality, nocturnal raptors, senescence, territory quality

## Introduction

The life history of an individual includes its age specific patterns of growth, reproduction and survival (Roff 1992, Stearns 1992), and understanding how reproduction varies with age is an important area for development in life-history theory. Effects of parental age on breeding success have been studied for many long-lived birds. Generally, reproductive performance improves with age during the early years of life (sparrowhawk *Accipiter nisus*: Newton 1989; western gull *Larus occidentalis*: Pyle et al. 1991) and reaches a maximum level in middle age (western gull *Larus occidentalis*: Sydeman et al. 1991; barnacle goose *Branta leucopsis*: Forslund & Larsson 1992) with some studies showed a decline during later years, attributed to senescence (sparrowhawk *Accipiter nisus*: Newton & Rothery 1998; red-billed chough *Pyrrhocorax pyrrhocorax*: Reid et al. 2003).

Three theories, which are not mutually exclusive, are suggested to explain the age-related patterns in breeding performance. The differential mortality theory (Smith 1981, Nol & Smith 1987) propose progressive appearance or disappearance of different-quality individuals within an age-cohort in a population, while the restraint hypothesis (Williams 1966, Pianka & Parker 1975, Clutton-Brock 1988) and constraint theory (Curio 1983, Komdeur 1996, Pärt 2001) suggest changes between breeding attempts of the individuals in relation to their ages. The constraint theory predicts that increased breeding experience with increased age brings, for example, better foraging efficiency and improved breeding performance with increasing age (Wheelwright & Schultz 1994, De Forest & Gaston 1996, Ratcliffe et al. 1998, Catry & Furness 1999). We have shown increasing reproductive performance

on tawny owls (*Strix aluco*) between their first and third breeding years, but breeding success did not alter between the third and fifth breeding years (Sasvári et al. 2000, Sasvári & Hegyi 2002, 2005). To test the constraints hypothesis, we analysed the relationships between the age-related territory occupation and reproductive success in our recent studies on tawny owls.

The tawny owl is a resident, sexually dimorphic, monogamous, single-brooded species in the Palearctic region and reaches sexual maturity within a year (Glutz von Blotzheim et al. 1977, Mikkola 1983). Males occupy and defend territory where the resources determine the breeding success, and they supply food to incubating females and feed both the females and nestlings in brooding period (Mikkola 1983). Hence previous breeding experience of males presumably plays a bigger role than that of females in habitat choice: a breeding attempt will result in high fledgling production provided the males occupy high quality territories. Studies have documented, that in species where males provide food for their mate and brood, male age is expected to be more important than female age in determining breeding success (sparrowhawk *Accipiter nisus*: Newton 1979; barn owl *Tyto alba*: Taylor 1994; kestrel *Falco tinnunculus*: Korpimäki & Wiehn 1998; great skua *Stercorarius skua*: Ratcliffe et al. 1998; Tengmalm's owl *Aegolius funereus*: Laaksonen et al. 2002).

We carried out a 19 year study (1992-2010) on tawny owls and followed the breeding success of long-lived males (seven, eight, and nine years old). In this study we focused our examinations upon two main questions. 1) Are there any differences in territory choice between the young and old males and do these differences reflect territory quality? 2) Do the relationships between territory choice and fledgling production show senescence patterns in old male tawny owls?

## Methods

Twenty two nest-box colonies for breeding tawny owls were sited in a mixed oak/hornbeam/beechness *Quercus-Carpinus-Fagus* forest with 40-60 year old trees in the Duna-Ipoly National Park, 30 km north-west of Budapest, Hungary (47°35' N; 19°02' E) from 1992-2010. Colonies of eight nest-boxes, spaced at 300-600 m, were separated by 2-5 km. All nest-boxes (176) were arranged within an 18 × 23 km area.

Nest-boxes were checked from the end of January. Where we found clutches in a nest, we followed the events of the breeding process by checking at 4-8 day intervals. If first egg-laying, or any other event

within the clutch and brood, occurred during the period between two checks, the day half-way between visits was recorded. Males and females in their first breeding year were captured by placing a net over the entrance of the nest-box while the birds were inside. They were marked with different combinations of coloured rings to ensure individual identification throughout the subsequent breeding years. Parental age was determined by the pattern of the primaries and secondaries (Petty 1992).

In a previous study we found that male tawny owls supplied the females and chicks with more preys and produced more fledglings in those broods reared at lower altitudes (Sasvári et al. 2009). This higher breeding success was attributed to the fact that the main alternative prey species, the birds, were more abundant around the owl nests at low than high elevations (Sasvári & Hegyi 2005). We suggest that the different territory quality influences male age-related breeding performance, hence the 550 m altitude range (120-680 m) of the study area was divided into low and high elevations: < 400 m, and > 400 m, each containing 11 nest-box colonies with 88 nest-boxes.

In previous studies we have analysed the breeding performance of tawny owls in the early and middle years of their lives (Sasvári et al. 2000, Sasvári & Hegyi 2002, 2005), in this study we focus on the later years of this species. As we evaluated the reproductive success of males in consecutive breeding years, repeated data from same tawny owls were used in our examinations. We marked 77 males in their first breeding year. Of these, 24 bred in the study aged five, 19 went on to breed again aged six, 15 at age seven, 13 at age eight and, of the original 77 birds marked, 6 bred at age nine. Our evaluation was based on three main points. 1) We recorded the number of territories acquired by males of the same age in the high or low altitude ranges and related these to all territories occupied by males of the same age. 2) We separated all males of the same age into those which bred that year and those which did not breed in that breeding season (the skipping individuals) and related this to all males of that age. 3) We evaluated the age-specific fledging production of males. To account for between-year variation, we standardized fledging success data by subtracting the annual population-wide mean performance (calculated from all observed breeding pairs, not solely known-age breeders) from each observed value, and dividing by the population-wide standard deviation (Zar 1999). These evaluations included breeding attempts where the males suffered total brood mortality. Males which did not breed in a given breeding season were omitted

from the calculations taken for the age-related fledgling production.

The changes in the distribution of territories between high and low altitude range, the rate of skipping males, and fledgling production were evaluated throughout the life-span of tawny owls. For our calculations we distinguished three age classes (1-3, 4-6 and 7-9 years old males), for comparisons of fledgling productions between the high and low altitude range, and when the age of females was related to age of males in the breeding performance of the pairs. ANOVA was used to evaluate of between-year fledgling production, and Chi-square tests were applied for goodness of fit to a null model of constant frequency in the comparisons between the high and low elevations. Statistical analysis were carried out using the SPSS statistical package (Norusis 1994).

## Results

Yearly data, including the distribution of breeding attempts between the high and low altitude range and the number of fledglings raised by the males in high and low elevations are presented in Table 1. As

the same males which changed territories between breeding seasons also changed altitude range, the rate of males which changed elevations in relation to the previous breeding year is also presented in Table 1.

Younger males, in their first, second and third years, were more likely to occupy territories at high than low altitude. Males between four and six years old occupied more territories at lower altitude, while most males aged seven, eight or nine, bred at high elevations ( $\chi^2_8 = 64.9, P < 0.001$ ; Fig. 1). Large differences were found in the numbers of males that did not breed as their age increased (Fig. 2). The number of skipping males declined between the age of one-and five-years old, but increased notably for seven, eight and nine years old ( $\chi^2_8 = 16.5, P < 0.05$ ). Combined data showed that more males skipped breeding at high than at low altitudes (42 and 21 males in relation to 253 and 244 breeding attempts;  $\chi^2_1 = 7.3, P < 0.01$ ).

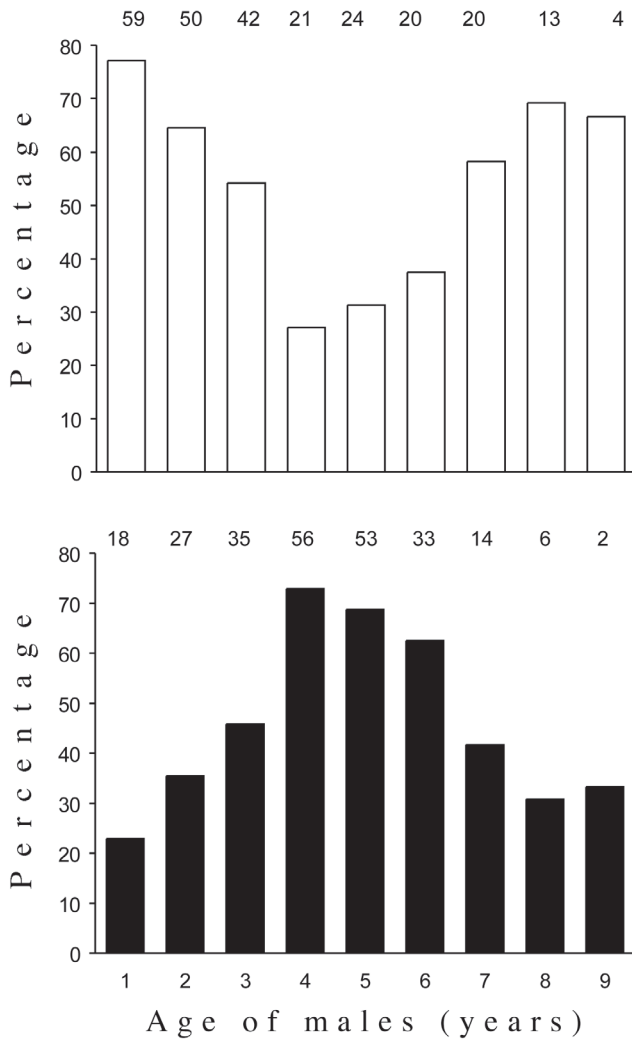
The number of fledglings raised by the males increased from when they were one year old to reach a peak when they were four or five years old, but then declined notably from they were six years old ( $F_{8, 425} = 2.87, P < 0.001$ ; Fig. 3). Fledgling production declined

**Table 1.** Yearly basic data recorded on breeding attempts of male tawny owls during the study period 1992-2010.

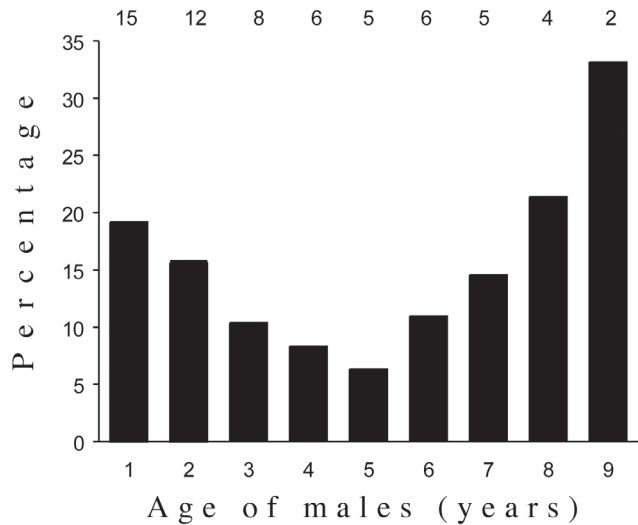
Study years	Number of males studied	Proportions in two altitude ranges (%)		Rate of skipping males (%)	Number of fledglings raised in two altitude ranges (mean $\pm$ SD)		Rate of males changing altitudes (%)
		high	low		high	low	
1992	22	72.7	27.3	13.6	2.18 $\pm$ 0.71	2.97 $\pm$ 0.92	-
1993	24	58.3	41.7	16.7	2.34 $\pm$ 1.02	3.17 $\pm$ 1.17	8.3
1994	25	48.0	52.0	8.0	1.88 $\pm$ 0.66	2.50 $\pm$ 1.20	8.0
1995	29	55.2	44.8	13.8	2.04 $\pm$ 0.84	2.63 $\pm$ 0.97	6.9
1996	26	50.0	50.0	11.5	1.97 $\pm$ 1.12	3.28 $\pm$ 0.88	11.5
1997	31	48.4	51.6	9.7	2.71 $\pm$ 0.73	3.40 $\pm$ 1.22	16.1
1998	23	52.5	47.8	17.4	2.08 $\pm$ 1.37	3.03 $\pm$ 0.94	17.4
1999	22	31.8	68.2	4.5	1.86 $\pm$ 0.73	2.49 $\pm$ 1.30	18.2
2000	22	50.0	50.0	13.6	2.55 $\pm$ 0.90	2.96 $\pm$ 1.05	13.6
2001	30	43.3	56.7	10.0	2.40 $\pm$ 1.22	3.31 $\pm$ 1.34	16.7
2002	26	34.6	65.4	3.8	1.95 $\pm$ 0.86	2.90 $\pm$ 0.95	15.4
2003	23	39.1	60.9	4.3	2.27 $\pm$ 1.24	3.03 $\pm$ 1.36	8.7
2004	24	29.2	70.8	8.3	1.90 $\pm$ 0.70	3.20 $\pm$ 1.12	17.7
2005	27	59.3	40.7	14.8	2.19 $\pm$ 0.98	3.32 $\pm$ 1.09	18.5
2006	31	64.5	35.5	19.4	1.83 $\pm$ 1.06	3.04 $\pm$ 1.26	12.9
2007	24	41.7	58.3	12.5	2.10 $\pm$ 1.52	3.18 $\pm$ 1.08	20.8
2008	26	61.5	38.5	19.2	2.27 $\pm$ 1.17	2.98 $\pm$ 0.93	19.2
2009	33	63.6	36.4	18.2	2.36 $\pm$ 1.24	2.92 $\pm$ 1.13	9.1
2010	29	55.2	44.8	17.2	1.96 $\pm$ 0.86	3.21 $\pm$ 0.97	10.3

with increasing proportions of males breeding at high elevations ( $r = 0.804$ ,  $P < 0.001$ ,  $n = 8$ ). The negative correlation reflected lower territory quality at high altitude, where males achieved lower reproductive success in their early and late years. All three age classes (1-3, 4-6 and 7-9 years old) bred more successfully at lower altitudes ( $F_{1,229} = 6.63$ ,  $P = 0.009$ ;  $F_{1,205} = 5.20$ ,  $P = 0.024$ ;  $F_{1,57} = 9.20$ ,  $P = 0.003$ ; Fig. 4).

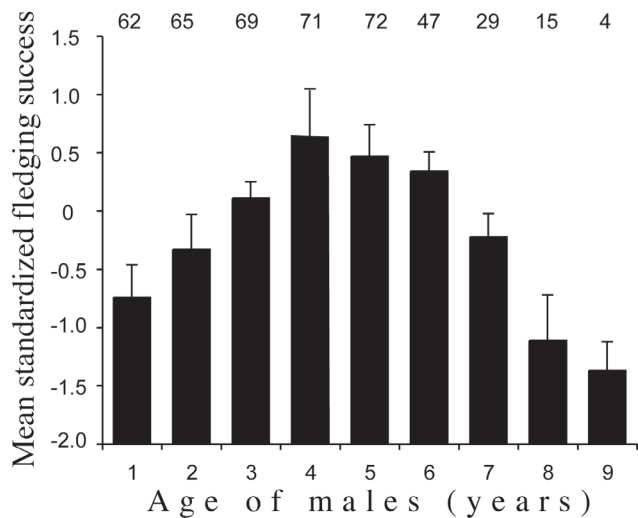
Females' age influenced fledgling production when male birds were in the early and mid age classes (Fig. 5). Young and middle-aged males mating with older females raised more offspring than if their mates were the same age (young:  $F_{2,229} = 7.37$  and middle-aged:  $F_{2,205} = 7.07$ ,  $P < 0.001$  in both occasions). Female age had no effect on fledgling production for the oldest class of males ( $F_{2,57} = 4.23$ ,  $P = 0.074$ ). Frequency distribution of females' age in relation to males' age



**Fig. 1.** Percentage distribution of territories occupied by tawny owl males in high (open columns) and low (black columns) altitudes as their age increased. Numbers above the columns denote numbers of territories.



**Fig. 2.** Rate (%) of territories where males did not breed as their age increased. Numbers above the columns indicate numbers of territories where males did not breed.

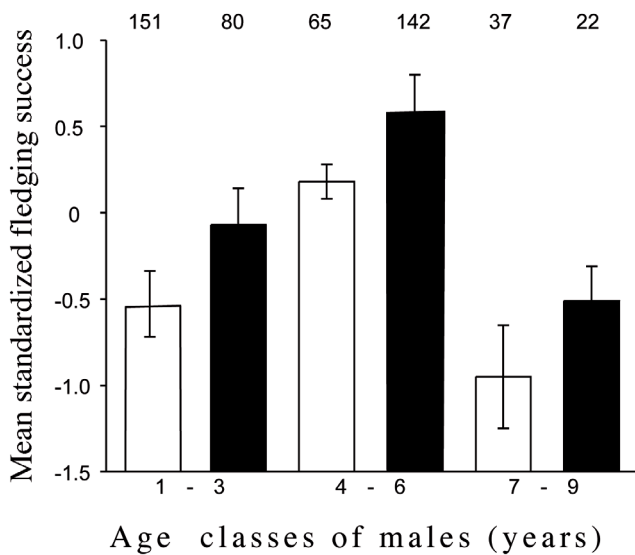


**Fig. 3.** Mean standardized fledging success of males as their age increased. Bars denote SD. Numbers above the columns indicate numbers of males.

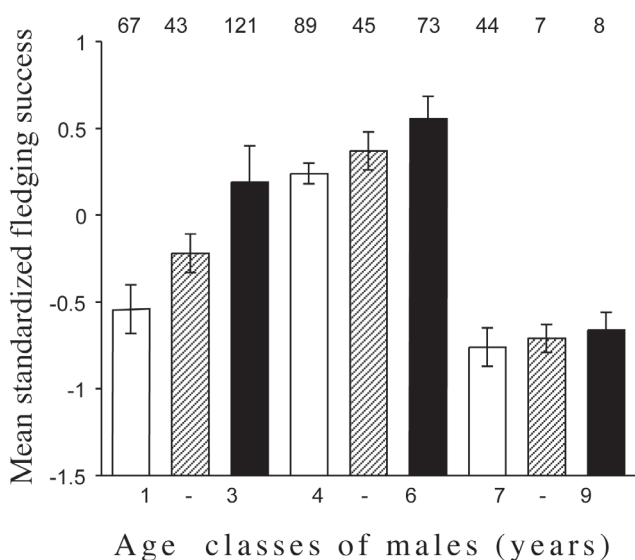
showed that the majority of males in the youngest age group mated with older females, but middle-aged and old males mostly paired with younger females, including all pairing when parents changed pairs after divorce ( $\chi^2_4 = 23.5$   $P < 0.001$ ).

## Discussion

Tawny owl settlement patterns correspond to the ideal despotic model (Fretwell & Lucas 1970, Zimmerman et al. 2003) in which the best quality individuals monopolize the best quality sites. Territorial behaviour regulates access to these high quality sites, and lower quality individuals are relegated to progressively



**Fig. 4.** Mean standardized fledging success in three age classes for males breeding at high and low altitudes. Open and black columns indicate males at high and low elevations. Bars denote SD. Numbers above the columns indicate numbers of males.



**Fig. 5.** Mean standardized fledging success in three age classes of males, when the females were younger, same age, or older than their mates. Open, hatched and black columns indicate younger, same age and older females. Bars denote SD. Numbers above the columns indicate numbers of broods.

inferior territories. Studies documented that tawny owl males occupy territories of various quality in terms of prey availability (Redpath 1995, Ranazzi et al. 2000, Francis & Saurola 2004, Solonen 2005).

In previous studies we have shown with three relevant relationships that the different territory qualities might be separated by their altitude range in the breeding area

of the tawny owls. 1) We found that the main alternative prey species, the songbirds and woodpeckers, which are particular important for the owls when snow cover the ground in incubation and brooding period, were more abundant around the owl nests in low rather than high elevations (Sasvári & Hegyi 1998, 2005). 2) Males delivered more prey items with higher mass of prey to females and chicks and produced more fledglings in the broods reared at lower altitudes (Sasvári et al. 2009). 3) Since superior habitats are the most desirable, territory quality may be measured by the occupancy rate of the breeding area (review: Sergio & Newton 2003). The higher settlement densities reflected better territory quality in low elevations for tawny owls in our study area (Sasvári & Hegyi 2005, Sasvári et al. 2009).

Most of males in their first three years, as befitted their relatively low quality, occupied territories in high elevations, where they raised fewer offspring than those males which bred at low elevations. The high number of skipping males recorded at high elevations also indicates lower quality males. The increased reproductive performance in middle age was attributed to an improved ability to acquire good territories at low elevations. In later years most males were no longer able to acquire territories at lower altitudes and as a result the rate of skipping males increased and fledgling production of those males that bred declined.

Age-dependent maternal condition influences clutch size (Korpimäki & Wiehn 1998, Espie et al. 2000, Laaksonen et al. 2002, Solonen 2009) and low fecundity of young females compared to high fecundity of older females has been documented both in passerines (Perrins 1979, Dhondt 1989) and non-passerines (Newton 1989, Sydeman et al. 1991). Male tawny owls mating with females older than themselves was more advantageous for those males in the young and middle-aged their classes because they raised more fledglings than males which paired with females younger than themselves. There was no influence of females age on male fledgling production for the oldest males. The youngest males benefited most by mating with older females.

In terms of the three main hypotheses' ability to explain the patterns of age-dependent reproduction, we did not examine either the differential mortality or restraint hypothesis. The former predicts that individuals of different phenotypic quality differ in age of first reproduction or survival probability (Smith 1981, Nol & Smith 1987), while the latter assumes a trade-off between present breeding effort and future reproduction whereby younger individuals put less effort into breeding because increased parental effort

increases mortality (Williams 1966, Pugsek & Diem 1983). In the context of constraint hypothesis (Curio 1983, Komdeur 1996, Pärt 2001) we detected a within-individual increase in reproductive performance in young (1-3 year old) male tawny owls, which reaches the high levels in middle age, and found a significant decline fledgling production in later years. Breeding success could, initially, improve with age as the older males acquired higher quality territories where they were successful in mating with females and did not skip breeding years. We suggest that the decrease of fledgling production of older males can be attributed to a decline in their ability to acquire or retain good territories. Finally, we conclude that the differences in territory choice between the high and low altitude range reflected territory quality, with males achieving higher reproductive success at lower elevations. Males in their early years occupied poorer quality territories and produced few fledglings, but their breeding success increased in the mid-stage of their life, because they

were able occupy higher quality territories at low altitudes. However the decreased ability to occupy higher quality territories and the decline in fledgling production in later life reflect senescence patterns in male tawny owls.

### Acknowledgements

*We are indebted to anonymous referees for their constructive comments and suggestions. Linguistic revision of this article was taken by Publisher Services of American Journal Experts. This work was supported by the Department of Zoology, Eszterházy Károly College of Education, Leányka u. 6., H-3300, Eger, Hungary, and Hungarian National Foundation for Scientific Research (project number: T 67669). We are also grateful to the Frank M. Chapman Memorial Fund, The American Museum of Natural History, for financial support. All research was carried out in accordance with the legal and ethical standards of the country in which the work was performed.*

### Literature

- Catry P. & Furness R.W. 1999: The influence of adult age on territorial attendance by breeding great skuas (*Catharacta skua*): an experimental study. *J. Avian Biol.* 30: 399–406.
- Clutton-Brock T.H. 1988: Reproductive success. *University of Chicago Press, Chicago and London.*
- Curio E. 1983: Why do young birds reproduce less well? *Ibis* 125: 400–404.
- De Forest L.N. & Gaston A.J. 1996: The effect of age on timing of breeding and reproductive success in the thick-billed murre. *Ecology* 77: 1501–1511.
- 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.
- Espie R.H.M., Oliphant L.W., James P.C., Warkentin I.G. & Lieske D.J. 2000: Age-dependent breeding performance in merlins (*Falco columbarius*). *Ecology* 81: 3404–3415.
- Forslund P. & Larsson K. 1992: Age-related reproductive success in the barnacle goose. *J. Anim. Ecol.* 61: 195–204.
- Francis C.M. & Saurola P. 2004: Estimating components of variance in demographic parameters of tawny owls *Strix aluco*. *Anim. Biodiv. Conserv.* 27: 489–502.
- Fretwell S.D. & Lucas H.L. 1970: On territorial behaviour and other factors influencing habitat distribution in birds. *Acta Biotheor.* 19: 16–36.
- Glutz von Blotzheim U., Bauer L. & Bezzel E. 1977: Handbuch der Vögel Mitteleuropas. *Academie Verlag, Wiesbaden, Germany.*
- Komdeur J. 1996: Influence of age on reproductive performance in the Seychelles warbler. *Behav. Ecol.* 7: 417–425.
- Korpimäki E. & Wiehn J. 1998: Clutch size of kestrels: seasonal decline and experimental evidence for food limitation under fluctuating food conditions. *Oikos* 83: 259–272.
- Laaksonen T., Korpimäki E. & Hakkarainen H. 2002: Interactive effects of parental age and environmental variation on the breeding performance of Tengmalm's owls. *J. Anim. Ecol.* 71: 23–31.
- Mikkola H. 1983: Owls of Europe. *T. & A.D. Poyser, Calton. UK.*
- Newton I. 1979: Population ecology of raptors. *Poyser, Berkhamsted, UK.*
- Newton I. 1989: Lifetime reproduction in birds. *Academic Press, London.*
- Newton I. & Rothery P. 1998: Age-related trends in the breeding success of individual female sparrowhawks (*Accipiter nisus*). *Ardea* 86: 21–31.
- Nol E. & Smith J.N.M. 1987: Effects of age and breeding experience on the seasonal reproductive success in

- the song sparrow. *J. Anim. Ecol.* 56: 301–313.
- Norusis M. 1994: SPSS Advanced statistics 6.1. *SPSS Chicago*.
- Pärt T. 2001: Experimental evidence of environmental effects on age-specific reproductive success: the importance of resource quality. *Proc. R. Soc. Lond. B* 268: 2267–2271.
- Perrins C.M. 1979: British tits. *Collins, London, England*.
- Petty S.J. 1992: A guide to age determination of tawny owl *Strix aluco*. In: Galbraicht C.A., Taylor I.R. & Percival S. (eds.), The ecology and conservation of European owls. *Joint Nature Conservation Committee, Peterborough, UK*: 89–91.
- Pianka E.R. & Parker W.S. 1975: Age-specific reproductive tactics. *Am. Nat.* 360: 113–117.
- 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.
- Pyle P., Spear L.B., Sydeman W.J. & Ainley D.G. 1991: The effects of experience and age on the breeding performance of western gulls. *Auk* 108: 25–33.
- Ranazzi L., Manganaro A. & Salvati L. 2000: The breeding success of the tawny owls *Strix aluco* in a mediterranean area: a long-term study in Rome, Italy. *J. Raptor Res.* 34: 322–326.
- Ratcliffe N., Furness R.W. & Hamer K.C. 1998: The interactive effects of age and food supply on the breeding ecology of great skuas. *J. Anim. Ecol.* 67: 853–862.
- Redpath S.M. 1995: Habitat fragmentation and the individual: tawny owls *Strix aluco* in woodland patches. *J. Anim. Ecol.* 64: 652–661.
- Reid J.M., Bignal E.M., Bignal S., McCracken D.I. & Monaghan P. 2003: Age-specific reproductive performance in red-billed choughs *Pyrrhocorax pyrrhocorax*: patterns and processes in a natural population. *J. Anim. Ecol.* 72: 765–776.
- Roff D.A. 1992: The evolution of life histories: theory and analysis. *Chapman & Hall, New York*.
- Sasvári L. & Hegyi Z. 1998: Bird predation by tawny owls (*Strix aluco* L.) and its effect on the reproductive performance of tits. *Acta Oecol.* 19: 483–490.
- Sasvári L. & Hegyi Z. 2002: Effects of age composition of pairs and weather condition on the breeding performance of tawny owls, *Strix aluco*. *Folia Zool.* 51: 113–120.
- Sasvári L. & Hegyi Z. 2005: Effects of breeding experience on nest-site choice and the reproductive performance of tawny owls (*Strix aluco*). *J. Raptor Res.* 39: 26–35.
- Sasvári L., Hegyi Z., Csörgő T. & Hahn I. 2000: Age-dependent diet change, parental care and reproductive cost in tawny owls *Strix aluco*. *Acta Oecol.* 21: 267–275.
- Sasvári L., Péczely P. & Hegyi Z. 2009: Plasma testosterone profile of male tawny owls *Strix aluco* in relation to breeding density, breeding experience, and offspring provision. *Acta Ornithol.* 44: 59–68.
- Sergio F. & Newton I. 2003: Occupancy as a measure of territory quality. *J. Anim. Ecol.* 72: 857–865.
- Smith J.N.M. 1981: Does high fecundity reduce survival in song sparrows? *Evolution* 35: 1142–1148.
- Solonen T. 2005: Breeding of the tawny owl *Strix aluco* in Finland: responses of a southern colonist to the highly variable environment of the North. *Ornis Fenn.* 82: 97–106.
- Solonen T. 2009: Factors affecting reproduction in the tawny owl *Strix aluco* in southern Finland. *Ann. Zool. Fennici* 46: 302–310.
- Stearns S.C. 1992: The evolution of life histories. *Oxford University Press, Oxford*.
- 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.
- Taylor I. 1994: Barn owls. Predator-prey relationships and conservation. *Cambridge University Press, Cambridge*.
- Zimmerman G.S., LaHaye W.S. & Gutiérrez R.J. 2003: Empirical support for a despotic distribution in a California spotted owl population. *Behav. Ecol.* 14: 433–437.
- Wheelwright N.T. & Schultz C.B. 1994. Age and reproduction in savannah sparrows and tree swallows. *J. Anim. Ecol.* 63: 686–702.
- Williams G.C. 1966: Natural selection, the costs of reproduction, and a refinement of ack's principle. *Am. Nat.* 100: 687–690.
- Zar J.H. 1999: Biostatistical analysis. *Prentice Hall, New Jersey*.