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Parents raise higher proportion of high quality recruits from low fledgling production in the local population of tawny owls, *Strix aluco*

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Abstract. The effects of weather and individual attributes of the broods in the local population of tawny owl *Strix aluco* on recruitment were studied in the Duna-Ipoly National Park, Hungary (47º35’ N; 19º02’ E) in 1992–2007. In harsh breeding conditions, with many snowy days, the parents’ body condition was low and they were able to raise only few fledglings. Nevertheless, the few fledglings remaining in this reduced broods left them in better condition and had a greater chance to be recruits than offspring which fledged in mild seasons, with many siblings, from broods raised by the parents in good condition. Parents produced most male recruits in adverse breeding seasons, when one offspring fledged from the broods, but raised most female recruits in mild breeding years, when two offspring left the broods. Sex related differences in the recruitment of a local population of tawny owls are discussed with a focus on environmental effects.

Key words: clutch size, brood size, offspring quality, parental condition, recruitment, weather effect

Introduction

It is generally assumed that natural selection works to optimize total fitness, not the number of offspring (Smith & Fretwell 1974, Brockelman 1975). Thus, the number of recruits to the breeding population, rather than the number of independent nestlings, should be the critical measure of offspring production (Lack 1966, Sibley & Calow 1986). Modelling the bird population dynamic, theoretical biologists have suggested that one of the strongest determinants of variation in the population growth rate is recruitment (Lebreton & Clobert 1991, Caswell 2001). Empirical studies confirm the importance of recruiting offspring in the population dynamics of bird species and showed the effects of environmental factors on recruitment of local populations (Gaillard et al. 2000, Oro & Pradel 2000, Frederiksen & Bregnballe 2001, Crespin et al. 2006).

Some authors suggest that weather may be the most important factor influencing reproduction of raptors (Kostrzewa & Kostrzewa 1990, Dawson & Bortolotti 2000, Krüger 2002, Rodriguez & Bustamante 2003). The spotted owl *Strix occidentalis* has been a preferred subject in population biology investigations of nocturnal raptors (Guttiérez et al. 1995) and annual variations in demographic parameters of this species have been correlated with weather (Franklin et al. 2000, Seamans et al. 2002, LaHaye et al. 2004, Olson et al. 2004). Seamans & Guttiérez (2007) have shown that over a 15 year study period the temperature and precipitation experienced both in the breeding season and during the winter influenced the population growth rate of spotted owls.

Recruitment probability dependent on fledgling condition and body size has been shown for both non-passerines (Westmoreland & Best 1987, Spear et al. 1998, Forero et al. 2002) and passerines (Drent 1984, Lawrence 1987, Lindén et al. 1992). Individual attributes determining the offspring quality vary with pre-fledging factors that affect parental care. Positive relationships were shown between parental condition and the number of recruiting offspring (Tinbergen & Daan 1990, Hakkarainen & Korpimäki 1994, Espie et

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al. 2000), and fledgling survival was inverse related to brood size (Winkler & Wallin 1987, Smith et al. 1989). Our long-term study on the reproductive performance of tawny owls *Strix aluco* revealed weather effects on breeding success and offspring sex-composition as well as relationships between parental condition and offspring quality (Sasvári et al. 2004, Sasvári & Nishiumi 2005, Sasvári & Hegyi 2005). These findings present the opportunity to analyse relationships between factors influencing the pre-fledging condition of offspring, including weather effects, and individual attributes of the broods where owl parents were successful or failed to produce recruits.

The tawny owl is a resident, monogamous, single brooded Palearctic species. Many studies have reported that, throughout Europe, this species relies basically on rodents (Goszczynski 1981, Mikkola 1983, Kirk 1992, Jedrzejewski et al. 1994). Southern & Lowe (1968) suggested that prey availability for tawny owls is determined by ground cover and, when the snow prevents them from preying on small mammals, they change to hunting mainly birds as a secondary, alternative food. Eggs (2–7) are laid, one per day, and the females incubate, beginning with the first egg, for a month. Mothers brood and feed chicks while males bring food for first three weeks. Later both parents hunt, and young leave the nest at 28–30 days. Females are larger and heavier than males and both sexes reach sexual maturity within a year.

During the sixteen year study period we related the number of recruits recorded in each year to the number of clutches laid by females during the previous breeding season. We recorded the weight of parents in early nestling stage, brood size and condition of chicks before they left the nests and distinguished adverse and mild weather effects in winter and the early breeding season. The number of male and female recruits raised per clutch was related to these breeding characteristics and weather conditions.

We focused on three main questions. (1) How is the number of recruits produced per clutch affected by adverse or mild weather when they were raised, and in the breeding season when they reached one year of age? (2) Does the brood size and chick's condition at fledging time influence the recruit production of parents? (3) Are there any differences in the effects of factors influencing recruit production according to whether male or female recruits were raised?

Methods

Study area and sample size

Two hundred and twenty nest-boxes for breeding tawny owls were sited in a mixed oak/hornbeam/beech *Quercus – Carpinus – Fagus* forest, with 40–60 year old trees, in the Duna-Ipoly National Park, 30 km north-west of Budapest (47º35' N; 19º02' E) in 1992–2007. Six to eight nest-boxes were grouped together with 300–600 m between them, the groups were separated by 2–5 km. All nests-boxes were arranged within 18 x 22 km area.

Nest-boxes were checked at 4–8 day intervals from the beginning the end of January. Where clutches were found, nestlings were marked with different combinations of coloured rings for individual identification. Parents were captured during the first week of nestling period by placing a net over the entrance to the box while the birds were inside. These birds were also marked with combinations of coloured rings. Five hundred and two clutches were analysed during the sixteen year study period and 104 fledglings, captured in their first breeding season, were recorded as recruiting offspring. Numbers of recruits were related to all clutches laid in the previous breeding season and number of recruits per clutch was considered as the unit of evaluation of the recruiting production of the parents from the local population. Recruiting males and females were distinguished by body weight and incubation patch.

Predations was recorded when all of the eggs or young disappeared and only remnants of the egg shells, feathers and corpses were found in nests.

Weather effects, parental condition and brood size

We evaluated weather conditions in winter and early breeding seasons using the number of snowy days between 1 January and 31 March for each year. A day was considered snowy if the entire study area was covered with snow. The number of snowy days during this period was averaged for the sixteen study years (mean ± SD: 35.1 ± 14.4 days) and each year were classified as being adverse or mild according to whether there was a greater or lesser number of snowy days than the average. The recruiting production of parents was related to weather conditions recorded in years when recruits were born and when they were one year old.

Parental condition was measured using body weight when their first-hatched young were 2–6 days old and this was related to the number of fledglings raised. The brood size was categorized at fledging time for one, two, three and more than three fledglings and was related to the number of recruits produced per brood in each size category.

Body weights of recruits were measured before fledging, when they were 26–28 days old, and were evaluated according to the number of siblings fledged with the recruits.

Statistical analyses

Statistical tests were carried out using the SPSS statistical package (Norusis 1994). Kruskal-Wallis test was performed on nonparametric data, ANOVA was calculated on parametric data and Chi-square tests were applied for frequency distribution.

Logistic regression was used to model the probabilty of parents in raising recruiting offspring from their clutch, with those offpring breeding the next year in the study area (Cox & Snell 1989). The outcomes were

Study years	2006	2005	1998	2004	2001	1999	1992	1996	2003	1994	1995	2002	2000	1997	1993
Number of snowy days	59	56	52	49	47	43	41	38	31	27	25	24	22	19	14
Number of clutches	31	27	33	29	31	27	25	29	37	41	33	41	37	43	38
Number of recruits next year	8	6	7	6	9	7	6	8	8	9	6	8	4	7	5

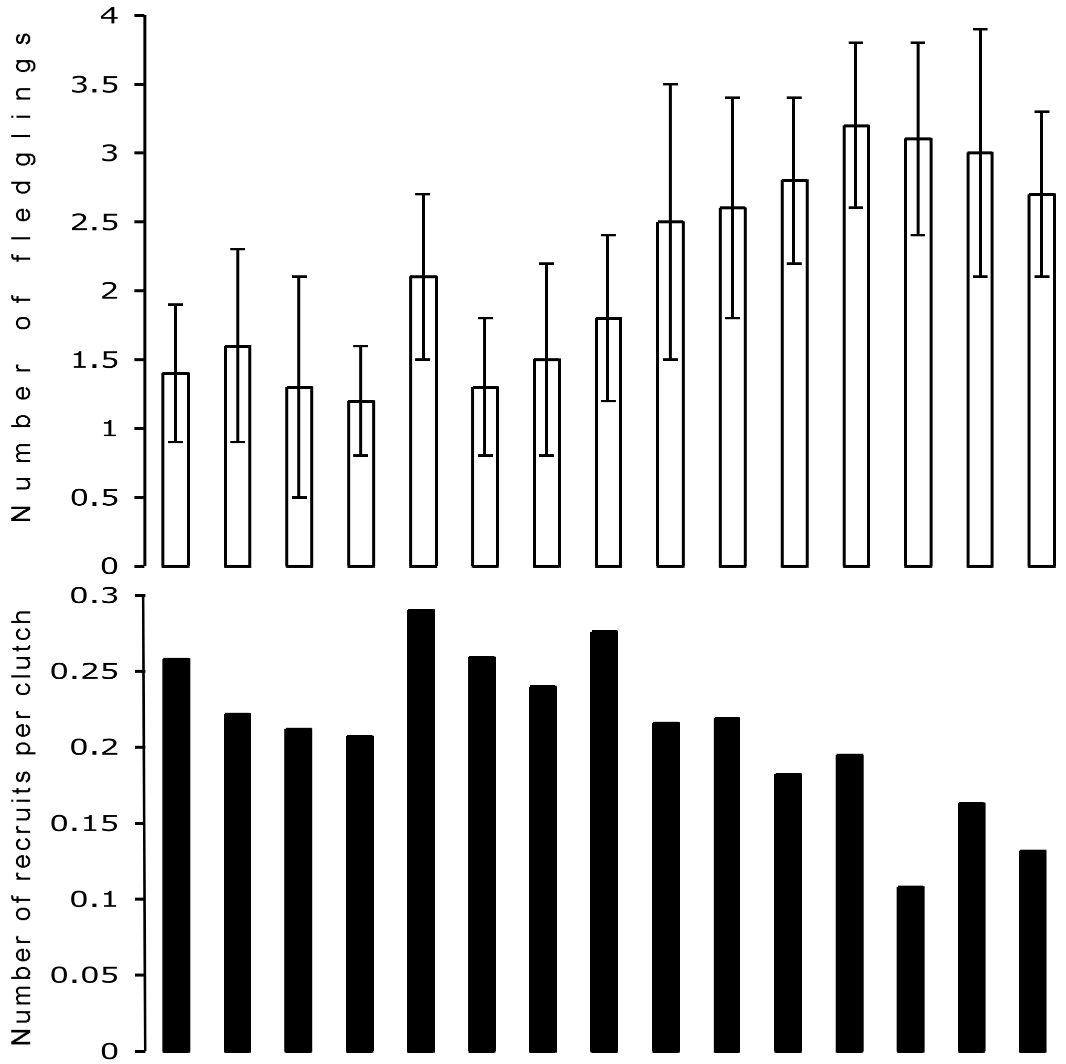

Fig. 1. *Number of clutches, number of fledglings (mean ± SD), and number of recruiting offspring per clutch produced by the pairs arranged in a series according to decreasing number of snowy days during the study years. The number of snowy days was calculated from 1 January – 31 March. Open and black columns indicate the number of fledglings and the number of recruits per clutch. In 2007, when eight recruits which had been born in 2006 were recorded, the number of snowy days was 15.*

treated as binary in the analysis, such that offspring from a clutch either recruited or did not recruit. Multiple logistic regression was used to model the effects of weather condition in year *n* (when recruits were born) and in year *n + 1* (when recruits were one year old) on body weight of fathers and mothers, and brood size at fledging time. The maximized log-likelihood was calculated, multiplied by two for deviance and the differences in deviance were shown with Chi-square tests.

Results

The number of fledglings varied between years, with pairs producing fewer fledglings in years with a high number of snowy days (ANCOVA $F_{14,438} = 2.08$, $P = 0.009$, $b = -0.022$; Fig. 1). The positive correlation showed that the number of recruits per clutch increased with increasing numbers of snowy days in that breeding year ($r = 0.693$, $P < 0.01$, $n = 15$), but the number of recruits per clutch and the number of chicks fledged from the nests were negative correlated ($r = -0.587$, $P < 0.02$, $n = 15$). Number of recruits per clutch increased with a decreasing number of snowy days recorded the next year when offspring were one year old ($r = -0.511$, $P < 0.05$, $n = 15$). No correlation was found between number of recruits breeding in their first year and number of all breeding pairs recorded in the given year in the study area ($r = 0.397$, *ns*, $n = 15$). Distinguishing the gender of recruits, parents produced more male recruits per clutch in adverse breeding seasons (Mann-Whitney U test: $z = 3.43$, $P < 0.001$), but raised more female recruits in mild years ($z = 2.92$, $P = 0.003$; Table 1).

In adverse weather conditions, modal brood size raised by the parents was one fledgling, whereas in mild breeding years it was three nestlings. Number of broods where no offspring fledged and where one offspring fledged in adverse and mild breeding season: 31 and 18; 87 and 14. Number of broods where two, three and more than three chicks fledged in adverse and mild breeding season; 67 and 99; 30 and 114; 17 and 24. (Combined data of all broods: $\chi^2 = 50.2$, $P < 0.001$). The heaviest parents produced the most fledglings and, where only one offspring fledged, both

Table 1. *Number of recruiting males and females per clutch in relation to mild and adverse weather conditions during the winter and early breeding seasons for years when recruits were born. The number of snowy days calculated from 1 January to 31 March during the sixteen study years was averaged, and the adverse or mild years were classified according to whether they had a greater or lesser number of snowy days than the average number of snowy days (35.1 ± 14.4 days), respectively. Number of clutches and number of recruits were combined for the years. In parentheses, number of recruits.*

Weather conditions	Number of clutches in the years of birth	Number of recruits per clutch	
		Males	Females
Adverse	232	0.181 (42)	0.065 (15)
Mild	270	0.056 (15)	0.118 (32)

Table 2. *Number of male and female recruits per brood related to the weight (mean ± SD) of parents and the number of offspring fledged from the nest in birth years. In parentheses, number of recruit.*

Weight of parents		Number of offspring fledged from the nest	Number of broods	Number of recruits per brood		
Fathers	Mothers			All recruits	Males	Females
374.2 ± 27.4	439.0 ± 41.1	One	101	0.297 (30)	0.248 (25)	0.049 (5)
395.0 ± 41.2	453.3 ± 47.2	Two	166	0.241 (40)	0.102 (17)	0.139 (23)
424.3 ± 51.6	479.0 ± 37.7	Three	144	0.187 (27)	0.083 (12)	0.104 (15)
417.7 ± 53.5	486.2 ± 34.8	More than three	42	0.166 (7)	0.071 (3)	0.095 (4)

fathers and mothers had the lowest body weights in the early nestling period (ANOVA males: $F_{3,449} = 4.46$, $P < 0.001$; females: $F_{3,449} = 4.58$, $P < 0.001$; Table 2). However, parents recruited the most males from those broods where one chick fledged, and produced the most females from those broods where two young were fledged (H = 17.3, $P < 0.01$ and H = 9.1, $P < 0.02$). Large differences were found in the distribution of male and female recruits in relation to the size of the brood from which they fledged in the previous year ($\chi^2_3 = 13.8$, $P < 0.01$).

Body weight of both male and female recruits decreased at fledging time with increasing number of siblings fledged with them ($F_{3,53} = 3.74$, $P = 0.019$ and $F_{3,43} = 3.49$, $P = 0.023$; Table 3).

Multiple logistic regression analysis showed that parents in poor body condition raised more probable recruits than parents in good condition, and offspring which fledged from smaller broods were more likely to recruit (Table 4). Although a high number of snowy days in the early breeding season increased the chance that fledglings would be recruits in their first breeding year, fewer snowy days was advantageous for the survival in their first year age. The analysis reflected relationships between the factors influencing the success of parents in recruitment of the local population. In harsh breeding condition, with many snowy days, the parents had relatively low body condition and were able to raise only a few fledglings. Nevertheless those few fledglings left the reduced broods in better condition and had a greater chance to be recruits than offspring which fledged in milder years, when they had many siblings and broods were raised by the parents in good condition.

Discussion

Weather conditions affect prey availability to tawny owl parents and influence both the clutch size and nestling survival in the breeding season (Southern & Lowe 1968, Wendland 1984, Saurola 1995, Solonen

Table 3. *Body weight (g ± SD) of male and female recruits before fledging in relation to the number of siblings that fledged with them.*

	Number of siblings fledged with recruits	Number of recruits	Weight before fledging
Males	No sibling	25	347.5 ± 44.8
	One sibling	17	320.6 ± 39.4
	Two siblings	12	316.7 ± 41.2
	Three siblings or more	3	293.9 ± 26.2
Females	No sibling	5	412.8 ± 51.0
	One sibling	23	398.0 ± 40.2
	Two siblings	15	379.5 ± 38.8
	Three siblings or more	4	362.3 ± 44.5

Table 4. *Logistic regression models for the probability of raising recruits from a clutch: weather effects in year n, when recruits were born and in year n + 1, when recruits were one year old, body weight of fathers and mothers, and brood size at fledging time. Weather effects were calculated using the number of snowy days between 1 January and 31 March for each year. Sample size: 502 clutches.*

Criterion	Chi square	d.f.	*P* value	Regression coefficients (B)	SE of B
Weather effects in year *n*	6.59	1	0.012	0.047	0.018
Weather effects in year *n + 1*	4.22	1	0.039	-0.008	0.026
Body weight of fathers	5.48	1	0.023	0.042	0.017
Body weight of mothers	5.41	1	0.027	0.064	0.021
Brood size at fledging time	6.56	1	0.015	-0.051	0.007

& Karhunen 2002, Solonen 2004, 2005). Hence in this study, we used weather conditions to illustrate the influence of environmental effects on recruitment to the local population of tawny owls. A chick was more likely to become a recruit, as a high quality offspring, if it fledged alone, in good condition, but at the cost of its siblings in the brood that died. The survival only of the strong owlets in such reduced broods is the consequence of harsh weather conditions reducing prey availability and decreasing body weight and condition of the parents.

Raptor fledglings are threatened both by predation and starvation and suffer high mortality after they leave the nest (McFadzen & Marzluff 1996, Rohner & Hunter 1996). Overskaug et al. (1999) carried out telemetry studies on tawny owl fledglings at the northern limit of the range of this species and revealed 61% mortality rate before dispersal. Overskaug et al. (1999) confirmed that fledglings in good condition had more chance of surviving: offspring that died or disappeared during the first ten days after leaving the nest were lighter than those that were still alive at this time. On basis of these findings we imagine that the heavier nestlings were more likely to survive after fledging and represent recruiting offspring in our study area. Nevertheless different factors might affect fitness components during different stages of the post-fledging period. For tawny owls, good fledging condition may not guarantee a higher probability of survival. Sunde (2005, 2008) found during the post-fledging-dependency period that offspring survival was a function of fledging date because of date-dependent predation pressure but unrelated to fledgling condition. However, poor condition might correlate negatively with survivorship if low body weight was associated with late fledging which in return was associated with increased predation pressure.

Sex-related differences that depend on the weather condition in the recruits produced by the tawny owl parents may be explained by two theories. In the sense of the 'brood reduction hypothesis', in order that broods do not suffer total mortality in a poor food environment, only some of the offspring will be raised and parents do not waste effort raising young that will subsequently die (Lack 1954, Slagsvold 1986). Hatching asynchrony causes differences in success in obtaining food by establishing age and size hierarchy between the nestlings. This may result in the death of later-hatching offspring (Gibbons 1987, Magrath 1989). In terms of the sex-allocation theory, in sexually dimorphic birds, the larger sex requires more resources and thus when food is limited, disproportionate mortality of the larger sex produces a bias in fledgling sex ratios (Fisher 1930, Clutton-Brock 1991, Oddie 2000). In several species of raptors that are sexually size dimorphic, when food availability was low, females produced the smaller sex (usually males) more often (Olsen & Cockburn 1991, Wiebe & Bortolotti 1992, Dzus et al. 1996). Appleby et al. (1997) documented an overproduction of females under favourable food conditions in tawny owls in England, whereas more males were produced in territories facing poor food conditions. However Desfor et al. (2007) found, that brood sex ratios were not correlated with the resource abundance during the breeding season in a Danish local population of tawny owls and suggested, that adaptive sex allocation strategies differ across populations.

Our previous studies on tawny owls have shown that in harsh weather conditions when snow cover limits prey availability, less food is delivered to nestlings, which suffer higher mortality than they do in mild weather, without snow cover (Sasvári et al. 2000). In the reduced broods, the chicks that hatched last always died, but all first-hatched chicks survived the nestling period. The primary sex ratio was male-biased, and the secondary sex ratio became even more skewed towards males at fledging time because of the disproportionate mortality of female nestlings (Sasvári & Nishiumi 2005). In mild breeding years, when greater food availability offer the possibility of raising complete broods, sex ratios were female-biased.

The positive relationship between parental condition and the number of recruiting offspring proposed for raptors (Hakkarainen & Korpimäki 1994, Espie et al. 2000), is not supported in the case of male recruits of tawny owls. Male recruits were more likely to have had parents in poor condition than in good condition. The male bias in the reproduction of good quality recruits is linked to scarce food availability in adverse weather conditions and offers two advantages for tawny owls. First, it is less costly to the parents to raise males that will be in good condition at fledging time than to raise females. Second, the male recruits in good condition may be expected to reach higher breeding success than female recruits because they have more chance of occupying high quality territories. By doing this, male recruits elevate their fitness further during their first breeding year.

Selection favours larger female owls for storing energy during period of food shortage and smaller males with shorter wings that are more efficient hunters in dense woodlands (Lundberg 1986, Mueller 1989, Sunde et al. 2003) We found higher mortality in adult tawny owl males than females in harsh winter and confirmed that the smaller size and lower body weight birds are less resistant to starvation (Sasvári & Nishiumi 2005). The increased mortality of adult males and male biased recruit production during severe conditions suggest that the adjustment of sex ratios to the weather conditions has important implications for the demography of the tawny owl breeding population.

During our sixteen year study period the recaptured first year offspring in the study area obviously underestimate the proportion of recruiting fledglings. Hence, our interpretation of the data, with regard to explanatory factors, may relate only the recruits which bred in the study area. Nevertheless, the period between fledging and first breeding is long, and numerous factors may influence offspring survival or the fate and decision of young whether stay within or leave the studied local population. It is unclear, whether those factors which correlate with recruit survival are really important factors influencing fitness. On the other hand, when variable does not apparently influence recruiting processes, a refinement examination linking the given factor may reveal hidden relationships. We did not find density dependent effects on numbers of recruiting offspring in their first reproductive year. Nevertheless, we suspect that a further analysis, focusing on age-related territory occupancy and mate choice in the tawny owl breeding population, may illuminate more detailed demographic effects on recruiting processes.

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