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Factors affecting reproduction in the tawny owl *Strix aluco* in southern Finland

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The goal of this study was to evaluate the relative role of some central intrinsic and extrinsic factors affecting reproduction in the tawny owl in southern Finland, near the northern limit of the species' range. The data included 153 successful nestings of pairs of birds in which both mates were identified, sexed, aged, and measured. Brood size was constrained by clutch size that, in turn, could be explained by the positive influence of female age. Female condition was positively influenced by both male condition and female age, while male condition was positively related to the age of male. These intrinsic factors outweighed the effects of extrinsic factors examined. However, these probably prominent extrinsic factors, such as general food supply and winter weather conditions, seemed to be inadequately quantified for use in the present study. Therefore, future studies should proceed by evaluating variables that characterize more accurately those environmental conditions where the studied population lives.

Introduction

The availability of food is inevitably the most prominent factor affecting body condition, survival, and reproduction in various species of birds (Newton 1980, Martin 1987, Meijer *et al.* 1989, Pietiäinen & Kolunen 1993, Brinkhof & Cavé 1997, Wiehn & Korpimäki 1997). A single food type may be decisive for a specialist but it may be of importance for other species as well. So, the high numbers of small voles have significant positive effects on reproduction both in vole specialists and vole-eating generalists (Linkola & Myllymäki 1969, Simmons *et al.* 1986, Pietiäinen 1989, Solonen 2004). In birds of prey, the smaller-sized male is the main provider of food during the early stages of breeding (Newton 1979, Andersson & Norberg 1981, Mikkola 1983, Sunde *et al.* 2003). Thus, during that time females are affected by food supply through their mates, in particular the foraging skills and body condition of males. These characteristics may depend on various other characteristics of individuals, including size, age, and experience (e.g., Andersson & Norberg 1981).

In various species, food supply before the onset of egg-laying governs the determination of clutch size (Drent & Daan 1980, Korpimäki & Hakkarainen 1991, Pietiäinen & Kolunen 1993), and thus sets the upper limit to the potential production of offspring. Food supply and other factors prevailing during the rest of the breeding season determine the final rate of reproduction. In this context, bird age (probably characterizing the experience of the parent birds) seemed to have a particular role, increasing the rate of reproduction (Newton 1989, Sæther 1990, Wunderle 1991, Forslund & Pärt 1995, Martin 1995). Various other factors, such as climate, seem to affect reproduction, largely via food availability (Newton 1978, Dawson & Bortolotti 2000, Hakkarainen *et al*. 2002, Dunn 2006).

The tawny owl *Strix aluco* is a nocturnal bird of prey that has a relatively continuous distribution across most of Europe (Cramp 1985). Tawny owl populations are thus confronted with spatially and temporally widely varying environmental conditions from the Mediterranean through temperate to harsh boreal ones. Populations seem to have prominent differences in their post-glacial origin, as well as in their genetic structure (Brito 2005, 2007). This suggests that the reproduction of different populations is variously affected by different combinations of intrinsic and extrinsic factors. Several studies have demonstrated the prominent effect of food supply on the reproduction of tawny owls in various parts of its range (Linkola & Myllymäki 1969, Southern 1970, Wendland 1984, Ranazzi *et al*. 2000, Solonen & Karhunen 2002, Roulin *et al*. 2003, Kekkonen *et al*. 2008). Food supply affects both the body condition of parent birds and that of their offspring (Hirons 1985). The availability of food is modified by habitat (Petty 1989) and, during different phases of the annual cycle, by various climatic factors (Southern 1970, Solonen 2004, 2005a, 2005b, Sasvári & Nishiumi 2005).

Only few studies have dealt with the consequences of both intrinsic and extrinsic factors on reproduction in the tawny owl (e.g., Wendland 1972, Sasvári *et al*. 2000, Sasvári & Hegyi 2002). An obvious difficulty in this context is to find the relevant variables to describe and quantify the intrinsic and extrinsic factors concerned. Several intrinsic factors, such as sex, size, and age class, are relatively easy to determine, but to find and describe the relevant variables from the multitude of extrinsic factors is not an easy task. Though some of the characteristics of extrinsic factors (such as various weather variables) may be relatively easy to measure, their relevance in the case concerned may be difficult to point out.

The goal of this study was to evaluate the role of some central intrinsic and extrinsic factors affecting reproduction in the tawny owl in southern Finland, near the northern limit of the species' present range (Cramp 1985, Väisänen *et al*. 1998). In earlier studies, the average clutch size and brood size of the population was significantly explained by the general spring vole abundance of the district (Solonen & Karhunen 2002). In the present study, my aim was to quantify the most relevant relationships more comprehensively. Of the intrinsic factors, I expected that an increased age (characterizing growing experience) (Newton 1989, Sæther 1990, Newton & Rothery 1998, McDonald *et al*. 2004) and good body condition (Sydeman *et al*. 1991, Pietiäinen & Kolunen 1993, Sasvári & Hegyi 2001) of mates have positive impacts on reproduction. Due to the characteristics of role division of mates during breeding, I predicted that the effects of male-dependent intrinsic factors on reproductive rate were more pronounced than those of the female-dependent ones. The body condition of mates should be dependent both on hunting skills (experience) of the male and on food availability (both their staple food, voles, and alternative prey). In the harsh environmental conditions of the North, the contribution of extrinsic factors to the reproduction of tawny owls should be particularly pronounced (Linkola & Myllymäki 1969, Solonen 2004, 2005b). I expected that reproduction should be affected negatively not only by low temperatures but also by the recently frequent mild winters, which in certain conditions may lower the abundance of small voles (Solonen 2004, 2006). In any case, the crucial factor governing reproduction in tawny owls, as in birds in general, should be the availability of food, the effect of which will be more or less modified by other factors, including both intrinsic and extrinsic ones (e.g., Newton 1998).

Material and methods

Owls

Data used in the present study were derived from a long-term project for monitoring the population dynamics of the tawny owl near the southern coast of Finland (60°N, 25°E), and covered years 1986–2006 (*see* Solonen & Karhunen

Fig. 1. Observed maximum and minimum body mass values (g) in male and female tawny owls of different sizes (indicated by wing length, 22 and 24 size classes (mm) in males and females, respectively) in a population in southern Finland. Linear regression lines fitted to indicate the approximate minimum (min) levels of body mass (BM) in tawny owls of different size (wing length, WL) are as follows: $BM_{min} = 1.67 \times WL - 45.26$ ($n = 9$) and $BM_{min} = 1.47 \times WL - 64.22$ ($n = 4$), for females and males, respectively.

2002, Solonen & af Ursin 2008). The original data included 200 successful nestings (at least one young fledged) of pairs in which I identified, sexed, aged, and measured (wing length, body mass) both mates. Due to a considerable risk of abandoning eggs or nestlings in earlier stages of breeding, I did not catch the adults before the young were at least about ten days old. After this stage, total nest losses were practically non-existent even from any natural reasons, and, accordingly, only successful breeders were included in the data. Because long-term mate fidelity is common in the tawny owl (Saurola 1987), the same pairs formed a considerable proportion of the successful breeders in successive breeding seasons. So, I captured some of the pairs repeatedly when breeding in different years, which reduced the data set to 146 different combinations of mates.

The nests were visited 3–4 times during the breeding season to determine clutch size and the number of young fledged. Determination of clutch size was based on at least two visits within 2–3 weeks if the stained appearance of the eggs or the beginning of hatching did not reveal that incubation had already lasted at least several days. Because of the considerable risk that tawny owls abandon breeding when disturbed during egg-laying, or in the early phases of incubation, the checking of potential nest sites was commenced relatively late in the season and it was done only in the evenings near the onset of the daily activity period of females. Thus, due to the large annual and seasonal variation in the commencement of egg-laying in the population, information on clutch size was missed in some cases. Accordingly, the number of clutches as well as that of observations included in the present analyses was 153. As an estimate of offspring production, I used the number of nearly fledged (about 3–4 weeks old) young in the nest (Solonen 2005b).

Intrinsic factors

The sexing of individuals was based on the pronounced size differences between mates (Fig. 1) and the prominent incubation patch of the female (Cramp 1985, T. Solonen unpubl. data). I separated three age classes (first year, second year, and third year or older) on the basis of plumage characteristics (Cramp 1985, Ahola & Niiranen 1986). Wing length characterized approximately the body size of owls. By visual inspection of the scatter plots of the body mass *vs*. wing length distribution, I selected sets of a few extreme values to fit ordinary least squares regression lines to characterize the approximate minimum level of body mass values (g) against size categories (indicated by different wing lengths, mm), separately for females and males (Fig. 1). The slopes of these lines proved to be roughly similar with those of the regression lines through the respective total samples. The proportions of the deviations of the observed body mass values from the approximated minimum level indicated the condition of the individual measured: (observed body mass – minimum body mass)/(observed body mass). Contrary to wing length and total body mass, the estimated minimum body mass showed no overlap between the sexes.

Extrinsic factors

The general extrinsic factors predicted to have the most pronounced effects on reproduction in tawny owls were food supply and weather conditions during the preceding winter (Solonen & Karhunen 2002, Solonen 2005b). I characterized the main component of food supply at the beginning of the breeding season by the abundance of small voles (field voles *Microtus agrestis*, bank voles *Clethrionomys glareolus*) in the preceding autumn (October), derived from snap trappings conducted in the vicinity of the study area (P. Ahola & T. Solonen unpubl. data). Vole abundance visualized the general pattern of annual fluctuations in food supply before and during the breeding season of owls. Annual vole indices (individuals/100 trap-nights) were based on 384 trap-nights each. At 64 standard points there were three traps along four trapping lines in two localities for two nights. To enable statistical analysis, I replaced vole densities below the detection limit of the trapping method by a value of 0.001, corresponding to a density of about one half of the minimum detected.

I examined the general role of alternative prey on the basis of the abundance of wintering birds (data derived from winter bird censuses arranged by the Finnish Museum of Natural History, University of Helsinki, provided by R. A. Väisänen), the most probable alternative source of food during the early stages of breeding in tawny owls in Finland (Solonen 2005b). The winter bird index used included small birds up to the size of the feral pigeon *Columba livia* that are suitable prey for the tawny owl (Solonen & Karhunen 2002).

Local weather conditions in mid-winter were characterized by the mean ambient temperature of January, measured at the meteorological station of the Helsinki-Vantaa airport (Finnish Meteorological Institute). Winter temperature seemed to be a useful characterization of general climatic effects on breeding owls and their prey (Solonen & Karhunen 2002, Solonen 2004).

Statistical analyses

Effects of the measured intrinsic and extrinsic factors on tawny owl reproduction were tested using linear mixed-effects models (Pinheiro & Bates 2000). As dependent variables, I tested brood size, clutch size, female owl condition and male owl condition against the following fixed effects: age of the parent bird, body condition of the parent bird (intrinsic factors), food abundance, and winter weather (extrinsic factors). Random effects included in these models were individual and year. All analyses were performed using the nlme library of the R statistical package (R Development Core Team 2008, Venables *et al*. 2008).

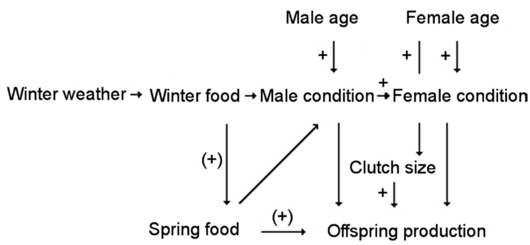

Fig. 2. A path diagram showing the relationships among some central intrinsic and general extrinsic factors hypothesized to have an effect on offspring production in the tawny owl. Arrows in the model indicate the expected direction of causality and pluses show the relationships supported by the data significantly (or, in parentheses, nearly significantly).

Results

Patterns of reproduction in the tawny owl seemed to follow some of the paths expected but there were some discrepancies as well (Fig. 2). Brood size was constrained by clutch size and seemed to be affected by vole abundance, although not statistically significantly so (Table 1). Clutch size was positively influenced by female age but no significant effect was observed for any of the other variables in the model (Table 2). Female body condition was positively influenced by both male condition and female age (Table 3), while male body condition was positively related to the age of male owls (Table 4). None of the extrinsic factors displayed significant relationships with any of the response variables investigated.

Discussion

In line with expectations, increasing age and body condition of parent birds had some positive effect on reproduction in tawny owls. Further-

Table 1. Linear mixed-effects model results on the effects of various intrinsic and extrinsic factors on brood size of the tawny owl. Akaike Information Criterion (AIC) = 426.57.

	Value	SE	df	*t*	*P*
Intercept	–0.093	0.727	133	–0.128	0.898
Clutch size	0.686	0.069	133	9.957	0.000
Female age	0.092	0.085	133	1.080	0.282
Female condition	0.000	0.001	133	0.120	0.905
Male age	0.126	0.104	133	1.210	0.229
Male condition	–1.652	1.275	133	–1.295	0.197
Preceding vole abundance	0.021	0.010	11	2.120	0.058
Winter bird abundance	0.000	0.000	11	0.425	0.679
Mid-winter temperature	–0.002	0.027	11	–0.073	0.943

Table 2. Linear mixed-effects model results on the effects of various intrinsic and extrinsic factors on clutch size of the tawny owl. AIC = 453.22.

	Value	SE	df	*t*	*P*
Intercept	3.249	0.856	134	3.798	0.000
Female age	0.270	0.092	134	2.930	0.004
Female condition	0.001	0.001	134	0.773	0.441
Male age	–0.046	0.113	134	–0.411	0.682
Male condition	–1.889	1.376	134	–1.373	0.172
Preceding vole abundance	0.002	0.025	11	0.068	0.947
Winter bird abundance	–0.000	0.000	11	–0.457	0.657
Mid-winter temperature	0.067	0.066	11	1.019	0.330

Table 3. Linear mixed-effects model results on the effects of various intrinsic and extrinsic factors on the condition of tawny owl females. AIC = 1628.49.

	Value	SE	df	*t*	*P*
Intercept	476.437	24.557	135	19.401	0.000
Female age	21.237	5.179	135	4.101	0.000
Male age	–4.897	6.724	135	–0.728	0.468
Male condition	377.093	75.898	135	4.968	0.000
Preceding vole abundance	–0.303	0.836	11	–0.362	0.724
Winter bird abundance	0.000	0.000	11	0.722	0.485
Mid-winter temperature	0.807	2.286	11	0.353	0.731

Table 4. Linear mixed-effects model results on the effects of various intrinsic and extrinsic factors on the condition of tawny owl males. AIC = –377.75.

	Value	SE	df	*t*	*P*
Intercept	0.065	0.023	137	2.858	0.005
Male age	0.033	0.007	137	4.845	0.000
Preceding vole abundance	0.001	0.001	11	1.240	0.241
Winter bird abundance	0.000	0.000	11	0.083	0.935
Mid-winter temperature	0.002	0.002	11	1.075	0.305

more, the roles of the sexes were as expected. Contrary to expectation, the extrinsic factors examined showed no significant relationships to reproduction in the tawny owl. Discrepancies between predicted and observed results might be largely due to some indirect effects and the inability of the general large-scale extrinsic variables used to characterize local conditions adequately.

Intrinsic factors

Age seemed to have an effect on breeding performance in the tawny owl, as has also been observed in many other birds of prey species (Simmons *et al*. 1986, Newton & Rothery 1997, Brommer *et al*. 1998, Kenward *et al*. 1999, Arroyo *et al*. 2007). In a Hungarian population of tawny owls, sex-related age differences affected the breeding performance of the parents in their first and second known breeding year: egg number and hatching success were influenced by the age of females, while fledging success was influenced by the age of males (Sasvári & Hegyi 2002, 2005). Within-pair age differences did not affect the breeding performance at their third known breeding year. Age-related differences in breeding performance may appear if there is a lower efficiency in resource gathering (mates, food, nests) in young birds (Forslund & Pärt 1995). They may also appear through an optimization of reproductive effort (the relative amount of resources allocated to reproduction), which should increase as the residual reproductive value decreases (Schaffer 1974, Newton & Rothery 1997). Greater productivity of older birds in comparison to younger ones suggested in this study has also been observed in other bird species, including various birds of prey (Mearns & Newton 1988, Newton & Rothery 1998, Espie *et al*. 2000, McDonald *et al*. 2004, Arroyo *et al*. 2007). This indicates that older birds provide more effective parental care (Forslund & Pärt 1995). In most cases, breeding performance improves with age in the early years of life and reaches a maximum level at the middle age (Newton 1989, Laaksonen *et al*. 2002).

The importance of body size and condition for reproductive investment and success in birds is debated (Blums *et al*. 2002). Some workers report a positive correlation between female size or condition and clutch size (Pietiäinen & Kolunen 1993, Barbraud *et al*. 1999), but others have not found these relationships (Winkler & Allen 1996, and this study). Nutrient storage and use may be influenced by body size, but the interplay of body size and condition in reproductive effort and success is uncertain (Alisauskas & Ankney 1990), and has not been fully evaluated (Barbraud *et al*. 1999, Blums *et al*. 2002). Larger individuals may be heavier, and those with better condition may have greater breeding success than smaller, light-weight individuals because they may be able to retain larger nutrient reserves (Lundberg 1986, Overskaug *et al*. 1997). Body condition and clutch size seem to be traits that are intimately linked in many bird species, especially birds of prey: pairs of better quality (whether defined by age, condition, or territory quality) usually lay more eggs than others (Newton & Marquiss 1981, Daan *et al*. 1990, Korpimäki & Hakkarainen 1991). A crucial point is that a possible relationship between condition and reproduction depends on when condition is measured. The body condition of birds may be highly variable between pre-laying, incubation, brooding, and chick feeding. In the present study, all measurements were made within a week or two during the last half of the nestling period, suggesting that they were well comparable between individuals.

Effects of extrinsic factors

Based on results from this study, the effects of extrinsic factors on tawny owl reproduction were minor. Earlier, larger-scale studies have revealed significant relationships both with food supply and weather conditions (Solonen 2004, 2005a, 2005b). Local and regional responses may differ, for instance, due to some prominent differences between habitats (e.g., Solonen & af Ursin 2008). Thus, such general indices of vole abundance used here outline a general picture of the annual fluctuations in vole numbers but they do not necessarily tell much about local variations in food supply of the owls. Similarly, midwinter temperature may provide an inadequate characterization of relevant weather conditions.

Food supply and age may have interactive effects (Boeckelheide & Ainley 1989, Sydeman *et al*. 1991, Ratcliffe *et al*. 1998, Arroyo *et al*. 2007). For example, if the costs of reproduction increase with decreasing food conditions, and age-related breeding patterns are related to reproductive constraints, we should expect that the breeding performance and the probability of whether to breed or not under different conditions change with age: young females should produce less and they should more frequently be non-breeders during low food conditions. In particular, if differences in breeding performance arise due to young birds being less skilled, this should be particularly noticeable when resources are scarce and/or more difficult to gather. Regardless, differences between age groups should be more marked during poor food conditions.

Methodological aspects

The present data included only successful nestings (at least one nestling fledged). Occasional impacts of total brood losses by predation were not considered here. In tawny owls, nest losses mainly occur during the early stages (egg-laying, incubation) of breeding (T. Solonen unpubl. data), and predation upon young mainly occur after fledging (Overskaug *et al*. 1999, Sunde 2005). Successful breeders probably were, in general, older, more experienced birds, and they probably were in better condition than the unsuccessful ones, and, in particular, those birds that did not breed at all. Unsuccessful breeders and non-breeding individuals were, however, out of reach of the catching methods used here.

The reliability of the results depends largely on the accuracy by which the measurements and indicators used describe the variables concerned. The results obtained describe the relationships between the measurements and indicators that characterize, more or less, the general variables in question. In the present case, only the sex and age classes of individuals, as well as clutch size and brood size, can be considered strictly reliable. However, even the age classes do not necessarily reliably reflect the breeding experience of birds, because tawny owls of each age category used may be first-time breeders (*see* Sasvári & Hegyi 2002).

Conclusions

The present results demonstrate prominent effects of some intrinsic factors on reproduction in the tawny owl in southern Finland. The contributions of extrinsic factors were, however, left inadequately characterized. In general, extrinsic factors are more difficult to measure or describe quantitatively than intrinsic factors. Thus, their exact roles may be much harder to characterize than those of some intrinsic factors. Future studies should proceed by searching for more accurate variables, characterizing those food and weather conditions where the populations studied live and focus on their effects. The relevant features of territories and the total spectrum of food supply they provide for the generalist tawny owl should be characterized in detail. Furthermore, in a more detailed approach the relevant characteristics and competence of individuals should be quantified more comprehensively.

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