

Aggressive Ural owl mothers recruit more offspring

Pekka Kontiainen,^a Hannu Pietiäinen,^a Kalle Huttunen,^a Patrik Karell,^a Heikki Kolunen,^b and Jon E. Brommer^a

^aBird Ecology Unit, Department of Biological and Environmental Sciences, University of Helsinki, PO Box 65 (Viikinkaari 1), 00014 Helsinki, Finland and ^bNikkarinkatu 52, 15500, Lahti, Finland

Animals are thought to adjust their behavior optimally to any given environment. So-called behavioral syndromes, or consistent patterns of behavior across environments, contradict this assumption of unlimited plasticity. We studied nest defense aggressiveness of female Ural owls (244 females with 482 breeding attempts) breeding in a highly variable environment created by fluctuations in the abundance of their main prey (field and bank voles) across years. Ural owls were more aggressive when voles were increasing in density as well as when the Ural owls had large brood sizes and laid early in the season. Aggressive nest defense was highly repeatable between breeding attempts ($r = 0.52 \pm 0.05$ standard error), but individuals also differed in their plasticity (the extent to which they adjusted the level of their aggression to the varying food conditions). Fierce nest defenders produced more recruits to the local breeding population, but a female's survival was not affected by her intensity of nest defense. A path analysis revealed that nest defense aggressiveness, rather than its correlates vole abundance, brood size, or laying date, best explained offspring recruitment. Our findings provide an ultimate explanation for the Ural owl's extremely aggressive nest defense. *Key words:* natural selection, nest defense, personality, *Strix uralensis*, survival, temperament, vole cycle. [*Behav Ecol* 20:789–796 (2009)]

Antipredator behavior in relation to nest or offspring defense is a widely expressed phenomenon in nature. Ricklefs (1969) showed that nest predation is the most important cause for nest failure in birds. During active nest defense, adult birds risk their health, and possibly their life, to protect their offspring. Parents defend older nestlings more than young ones or eggs (Barash 1975). A variety of hypotheses has been brought up to explain this pattern (e.g., Wallin 1987). Some studies have considered clutch or brood size and laying date as proxies for brood value and offspring fitness. According to these arguments, nest defense aggressiveness increases when a brood's value becomes higher (larger brood size and/or earlier laying date; e.g., Wallin 1987; Wiklund 1990; Tolonen and Korpimäki 1995). Alternatively, no relationship has been found between these traits and nest defense behavior (e.g., Galeotti et al. 2000; Carillo and Aparicio 2001). The effects of environment or food availability on behavior have rarely been studied in this context (although see Hakkarainen and Korpimäki 1994; Rytönen et al. 1995; Markman et al. 2002; Rytönen 2002). In particular, most studies have dealt with presumed correlates of offspring fitness. However, we currently lack understanding of the realized fecundity and/or survival consequences of parents showing differential aggressive nest defense over a longer time period. Such studies are essential for gaining insight in the evolutionary dynamics of this behavioral trait.

Behavioral ecologists have traditionally assumed that animal behavior is fully plastic and thus allows an individual, in each given situation, always to act in the optimal way (e.g., Sih et al. 2004; Bell 2007). However, the behavior of individual animals has frequently been found to be relatively inflexible. Animals often exhibit consistent patterns of aggressiveness, boldness,

and activity across environments, and consistent behavioral patterns are termed personality or temperament (Sih et al. 2004; Réale et al. 2007). Temperament traits are individual specific and often genetically determined (e.g., Réale et al. 2000; van Oers et al. 2003; Sih et al. 2004; Dingemanse and Réale 2005; Bell 2005), which implies that animals are relatively fixed in their behavioral response to the environment. On the other hand, the heritability of temperament traits is usually moderate (around 30%, Réale et al. 2000), and non-genetic factors thus potentially have a large effect on such traits (e.g., Bell 2005; Bell and Sih 2007). In particular, animals living in variable environments are expected to be highly plastic in their response to environmental conditions (Roff 2002). Although we may expect plasticity to be important, little is presently known about the plasticity of temperament traits (Sih et al. 2004) or whether individuals differ in their degree of plasticity (individual–environment interaction [IEI], Nussey et al. 2007; Réale et al. 2007).

We studied the nest defense aggressiveness of long-lived and resident Ural owls *Strix uralensis* during visits to nest-boxes to ring the chicks from 1983 to 2006 (excluding 1984 and 1985). Ural owls are medium-sized birds of prey which are known to be very aggressive nest defenders (Cramp 1985). Ural owl females are larger (c. 1000 g) than males (c. 700 g), and the sexes have distinctly different roles in reproduction. Males do most of the hunting providing food for the female and the offspring. Females incubate, feed, brood, and guard the offspring (Cramp 1985). A Ural owl female may take considerable risks while defending her brood. Aggressive females will hit a human intruder with force, and a female may occasionally die because of the impact of the blow (Saurola 1987; Kontiainen P, personal observation). Hence, pronounced aggressive nest defense behavior may be costly.

In Fennoscandia, Ural owls live and breed in a variable environment. This variation is caused by cyclic vole population dynamics (Norrdahl 1995). Voles are the main (and in wintertime only) prey, and to a large extent, vole population dynamics determine Ural owl reproductive success and survival (Brommer, Pietiäinen, and Kolunen 2002). Depending on food supply, Ural owls may lay between 1 and 7 eggs

Address correspondence to P. Kontiainen, who is now at Department of Biological and Environmental Sciences, Bird Ecology Unit, University of Helsinki, PO Box 65 (Viikinkaari 1), FI-00014 Helsinki, Finland. E-mail: pekka.kontiainen@helsinki.fi.

Received 1 August 2008; revised 10 March 2009; accepted 23 March 2009.

(Pietiäinen 1989). Offspring recruitment is affected by vole dynamics such that young hatched in a spring with increasing vole abundance have the highest recruitment probability (Brommer et al. 1998; Brommer, Pietiäinen, and Kokko 2002). In this paper, we analyze the effects of environmental factors (vole dynamics) and main reproductive variables (laying date and brood size) for Ural owl nest defense aggressiveness on the individual level. We estimate the repeatability of nest defense aggressiveness and test whether there is variation in the plasticity of nest defense aggressiveness across individuals. Lastly, using a subset of 12 years of data when Ural owls produced recruits, we explore whether there are any selective benefits of being an aggressive nest defender or whether nest defense aggressiveness is costly in this species.

MATERIALS AND METHODS

Ural owl biology and behavior

Ural owl nest defense aggressiveness was studied in 1983 and in 1986–2006 in southern Finland (Päijät-Häme) in an area of about 1500 km². Ural owls breed in nest-boxes, which are 3–4 km apart from each other. For more details of the study area, see Pietiäinen (1989). The Ural owl is a monogamous and site-tenacious bird of prey (4% move > 5 km; Saurola 1987). The Ural owl is long lived, with an average age at first breeding of 2.9 years and an average breeding life span of 3.3 years (Brommer et al. 1998). Many individuals therefore experience very different environmental conditions during their breeding career. The main prey of Ural owls during winter and prior to laying consist of field voles (*Microtus agrestis*) and bank voles (*Myodes glareolus*; Lundberg 1981; personal observation) although water voles (*Arvicola terrestris*) have a very important role during the nestling and fledgling periods (personal observation). Ural owl females were caught during the laying/incubation period from the nest-box using a hand net that was placed in front of the nest-box opening. Handling did not cause any obvious stress to the females. All the caught females have been ringed as nestlings or at the first capture as adults, thus enabling lifelong individual recognition.

Males play only a minor role in nest defense, and we therefore only use data on females. Nest defense aggressiveness was classified according to the behavior of the female (Table 1) when a human intruder approached and climbed the nest tree and handled the chicks. Nests were visited generally once or twice during incubation/laying and once or twice during brooding. Data used in the analyses are from the period when

the oldest chick in the brood was between 2 and 4 weeks old. Restricting the data to nests with nestlings older than 2 weeks is important because most Ural owl females will stay on their brood for the first 2 weeks of the nestling period. Nest defense aggressiveness cannot be measured from the females staying on their broods because they are caught with a hand net. Hence, nest defense aggressiveness during the early nestling period can only be quantified for a select group of females. In addition, restricting the period for measuring nest defense aggression until the oldest nestling is 4 weeks old ensures that no chicks have fledged. The latter is important because Ural owl females discriminate between fledged offspring and nestlings and will concentrate their defense efforts on fledglings (personal observation). Nest defense behavior was scored following the guidelines of Hakkarainen and Korpimäki (1994), where females were assigned an aggressiveness score according to their highest ranking behavior (Table 1).

Voies and prey delivery

Vole abundance in the study area was estimated by snap-trapping voles biannually in late September/early October and in early June since autumn 1986. We used the small-quadrate method (Myllymäki et al. 1971) where traps ($n = 300$) baited with rye bread were set out for 2 consecutive nights in 25 quadrates (15×15 m) at 3 localities (8, 8, and 9 quadrates per locality), which represented the main components in the landscape (variously aged replantations and mature forest). Three traps were set in every corner of these quadrates approximately 1 m apart from each other. Traps were checked and reset after the first night.

Ural owls do not clean their nest-boxes, and thus, after the breeding season, the prey items delivered to the nest can be collected as a mix of broken pellets and sawdust on the bottom of the box. For a subset of all nests, we counted the number and determined the species of prey on the basis of the unique bones (size and form). The number of prey items were transformed into an estimate of total prey weight delivered using the species-specific average weights (see also Brommer et al. 2003). We used the average prey mass delivered per nestling as an estimate of territory quality in order to analyze a territory-specific effect on female aggression. Territories where more food was delivered per nestling were assumed to be of higher quality. This estimate of territory quality combines, from a female's perspective, the effects of male quality as a hunter and food abundance in the territory because the male is the main provider of food to offspring and female.

Table 1

Scoring was based on frequency of behavior and the threat posed to the intruder

Behavior	Score	Number of attacks or hits	Frequency	Qualitative description
Away, bark	1	0	221	No aggressive behavior
Flyby	2	0	31	Minimal aggressiveness
Attack	3	1–5	99	Moderate, few behaviors
Attack	4	>5	32	Moderate, many behaviors
Hit	5	1–5	86	High, few behaviors
Hit	6	>5	13	High, many behaviors

The higher the score the higher is the level of aggressiveness. A female that was “barking” did not make any approaches toward the intruder but only stayed in the vicinity of the nest-box. A “flyby” was a nonviolent approach (no closer than 3 m) of a female toward the intruder. All the dives that were clearly aggressive and were performed within 3 m radius of the intruder were categorized as “attacks.” All the attacks that made a contact with the intruder were categorized as “hit.”

Statistics

For a number of individuals, aggressive nest defense was observed multiple times per breeding season. In those cases, we averaged the score of these observations to obtain a single yearly score for each individual that was observed multiple times in a given year. The yearly scores of aggressiveness were used in all the analyses. For all the analyses, explanatory variables (whenever continuous) were standardized to zero mean and unit standard deviation in order to make different coefficients comparable.

We analyzed the factors affecting nest defense aggressiveness of 244 individuals with 482 observations. Following Duckworth and Badyaev (2007), we used a linear mixed model (LMM) with restricted maximum likelihood (REML) method. An LMM is robust to unbalanced data which observational data from natural populations often are (Crawley 2002). An LMM also allows adding random effects to correct for multiple observations per individual. Nest defense aggressiveness a of individual i in year y was analyzed as follows:

$$a_{iy} = \mu + \text{ind}_i + \varepsilon_i, \quad (1)$$

where μ is the overall fixed effect mean (see below), ind_i is a random effect, and ε_i is the residual. The LMM estimates variances of the random effect and the residuals, conditional on the fixed effect structure. We considered the effects of overwinter change in vole abundance, brood size, and laying date as fixed effects in our LMM.

In addition to exploring whether there were differences across individuals in their level of nest defense aggressiveness, we also tested whether individuals adjusted their nest defense aggressiveness in a specific manner to external environmental variables. We therefore performed a random regression analysis (Nussey et al. 2007), where we modeled both individual phenotypic deviations from the population mean (elevation) and individual-specific slopes of aggression as a function of an environmental variable. The only significant extrinsic environmental variable was the change in vole abundance (see Results). Hence, we considered the LMM

$$a_{iy} = \mu + \text{ind}_i + b_i \times \text{voles}_y + \varepsilon_i, \quad (2)$$

where μ is the overall fixed effect mean including the effect of the abundance of voles in year y (voles_y). The terms ind_i and b_i are random effects modeling, respectively, the individual-specific deviation from the overall fixed effect mean (elevation, ind_i) and individual-specific change in nest defense aggressiveness as a function of the change in vole abundance (slope, b_i). In the LMM, the variances of the random effects ind_i and b_i as well as their covariance are estimated by REML (e.g., Pinheiro and Bates 2000). A significant variance in slopes would indicate individual-specific plasticity in nest defense aggressiveness in response to the environment (IEI, Nussey et al. 2007). The covariance between elevation and slope is informative of the extent of crossing of the individual-specific nest defense aggressiveness–environment relationships. We did not explore nonlinear individual-specific relationship between nest defense aggressiveness and vole abundance because the overall relationship was rather linear (see Results) and because we lack sufficient repeated records per individual to estimate higher order polynomials.

Statistical significance of each of these random effects was tested with a likelihood ratio test, which is $-2 \times$ difference in the likelihood between hierarchical models tested as a chi-square distribution, with the difference in the number of variance components between the models as the associated degrees of freedom (df). Repeatability (the proportion of among-female variance of the total variance, Falconer and MacKay 1996) of nest defense aggressiveness was analyzed using an LMM approach without correcting for fixed effects and using female identity as a random effect (i.e., following the terminology outlined above: $a_{iy} = \text{ind}_i + \varepsilon_i$). Fixed effects need to be excluded when calculating repeatability because an LMM with such effects included partitions the REML variance after conditioning of the fixed effects in the model rather than the phenotypic variance per se.

In order to study whether territory quality affected female nest defense aggression, we considered the prey mass delivered per nestling as a proxy for territory quality. For this analysis, we could use a subsample where prey delivery was quantified (127 females and 214 breeding attempts from 1994 to 2005). We used prey mass delivered per nestling as a fixed effect and female identity as a random effect in a REML LMM on nest defense aggressiveness. We thus assumed that a better territory allowed the parents to deliver more food per capita to their offspring.

Nest defense aggressiveness and reproductive success

Production of recruits to the study population in relation to nest defense aggressiveness on population level was analyzed using a path analysis. In Ural owl–vole dynamics, laying date, brood size, and nest defense aggressiveness are tightly intertwined. We were interested in the role of nest defense aggressiveness in determining the production of recruits (cause or correlate) and used path analysis to tackle this problem (Mitchell 1992). A path model gives statistical grounds to suggest the most likely causal pathways among the hypothesized relationships. We used the standardized annual mean values of the overwinter change in the vole population index, laying date, brood size, and nest defense aggressiveness to examine their effects on recruitment (yearly number of recruits produced divided by the yearly number of fledglings produced). Hence, we included all the factors that we used in our individual-level analysis in this population-level analysis. The analysis was run using SEM package in R. Hypothesized relationships of our path model are depicted in the path diagram (Figure 1) by the arrows indicating assumed causality. SEM translates the path diagram (Figure 1) into a set of linear equations, which are then solved using multiple regression techniques. With complicated diagrams, path analysis is a powerful tool to explore causal relationships within a set of correlated factors. As these hypothetical relationships were determined a priori, we let them remain in the model although they were not significant (Scheiner et al. 2002).

We included breeding records with known female nest defense aggressiveness in the analysis of local recruitment from 1987 onward. Breeding data before 1987 were not used in this

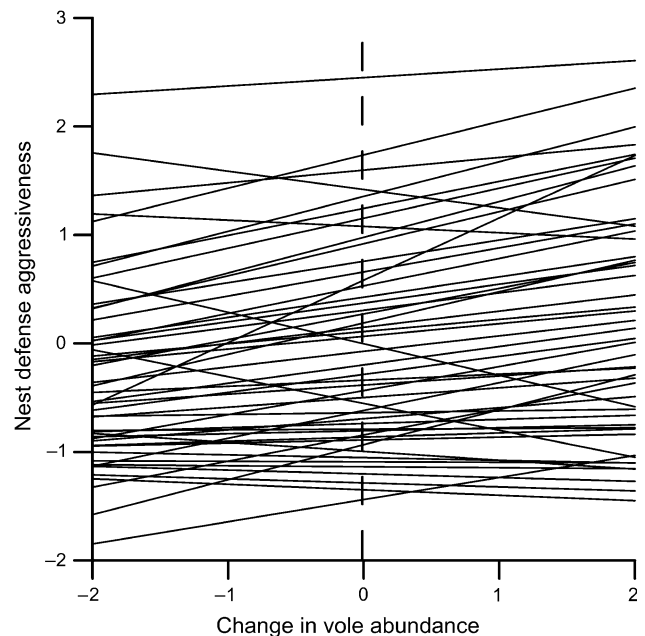


Figure 1

The relationship between nest defense aggressiveness and changes in vole abundance of 50 (out of 244) Ural owl females are depicted here for illustrative purpose. Fifty Ural owl females (every fifth individual including the most and the least aggressive) were chosen on the basis of their nest defense aggressiveness in the average environment (marked with a dashed vertical line). The change in vole abundance is given as standard deviations from the mean. The individual-specific nest defense aggressiveness–vole abundance relationships (thin black lines) are based on the best unbiased predictors (BLUPs) for elevation and slope from the random regression model (Table 2). Correlation between slopes and elevations was 0.5.

analysis because we lacked the vole data from these earlier years. We included data on local recruitment up to and including 2007 in our analysis. We only considered data on nest defense aggressiveness up to and including 2003 because it takes up to 4 years (average age 2.9 years) for Ural owl young to recruit to the reproducing population (Brommer et al. 1998). Hence, the path analysis included information on recruitment, reproductive parameters, and nest defense aggression recorded during 17 years (1987–2003).

Recruitment and survival selection

We analyzed fitness consequences of nest defense aggressiveness on a yearly level, separately in terms of recruitment and survival selection. We constructed a regression model of relative recruitment or relative survival (individual value divided by the yearly mean) against standardized aggression (individual score divided by standard deviation of yearly scores) nested within year. The coefficients of this model are standardized yearly selection gradients, calculated according to Lande and Arnold (1983). Annual quadratic standardized selection gradients were twice the coefficients of squared standardized aggression in a model that also included the linear term (Lande and Arnold 1983). Due to the nature of vole dynamics, every third year, very few Ural owls breed. During these years, very few recruits are produced (Brommer et al. 1998). Recruitment selection cannot be analyzed in years without recruits, and we therefore considered only those years when at least one recruit was produced in the population. There were, in total, 12 such years. For consistency, we also restricted our survival selection analyses to the same years. The results for survival selection did not change when data for all years were included (results not shown).

The significance of recruitment and survival selection in each year was tested with a GLM, assuming Poisson errors for recruitment selection and binomial errors for survival selection. A sign test was used to determine whether there were statistically significant more positive or negative coefficients in the selection analysis. A significant sign test with a positive bias indicates that more aggressive nest defenders consistently produce more recruits.

RESULTS

Nest defense aggressiveness on the individual level

Brood size and overwinter change in vole densities had a positive effect on female nest defense aggressiveness. The effect of laying date was negatively related to nest defense aggressiveness, indicating that individuals which initiated their egg laying later defended their nests less aggressively (Table 2). Individuals differed in their behavior. The repeatability of Ural owl nest defense aggressiveness was $52.3 \pm 5\%$ (standard error) ($df = 1$, $\chi^2 = 36.1$, $P < 0.0001$). Hence, there were consistent differences across individuals in their nest defense aggressiveness. We further found that individuals differentially adjusted their nest defense aggressiveness in response to overwinter changes in vole abundance (IEI). This was indicated by the significant proportion of variance explained by the effect of “ b_i ” (Equation 2, Table 2, Figure 1). The elevation and slope of nest defense aggressiveness were highly correlated. This indicates that more aggressive individuals were more plastic in response to changing food conditions. Individual-specific adjustment of nest defense aggressiveness in response to the overwinter change in voles explained 6.8% of the REML estimated variance in aggression (Table 2, Figure 1).

Table 2

Factors affecting female Ural owl aggressiveness was modeled on 482 observations from 244 individuals with a LMM approach

Fixed effects	Coefficient	\pm SE	F	P	
Laying date	-0.24	0.07	$F_{1,235} = 39.7$	<0.0001	
Brood size	0.32	0.07	$F_{1,235} = 26.0$	<0.0001	
Δ Voles	0.13	0.07	$F_{1,235} = 4.0$	0.047	
Random effects	SD	CI (95%)	df	LRT	P
Ind _{<i>i</i>}	1.14	0.99–1.32	1	$\chi^2 = 84$	<0.0001
b_i	0.41	0.26–0.66	2	$\chi^2 = 6.1$	0.047
Residual	1.00				

Laying date, brood size, and change in vole density (Δ voles) were treated as continuous variables. “ Δ voles” is the difference between the spring vole density and the vole density in previous autumn. Female identity was a random effect to examine potential differences in the level of aggressiveness across individuals (ind_{*i*}, Equation 1). We further explored whether there were individual-specific changes in aggression as a function of Δ voles in a random regression model incorporating individual-specific slopes b_i (Equation 2). Significance of the random effects were tested with likelihood ratio test (LRT) based on chi-square distributions. Explanatory variables were standardized to 0 mean and unit standard deviation (SD). None of the fixed effect interactions were significant. The correlation between elevation (ind_{*i*}) and slope (b_i) was 0.45 ($t_{242} = 7.9$, $P < 0.0001$). SE, standard error; CI, confidence interval.

In a subset of all nests, we could analyze whether the local food supply (estimated by the amount of food delivered to the nest per offspring) affected the nest defense aggressiveness of the female. The estimated amount of food delivered per offspring ranged from 295 to 3220 g, with a mean prey mass of 1272 g and standard deviation of 510 g. The amount of food delivered per nestling was not related to female nest defense aggressiveness ($F_{1,86} = 2.7$, $P = 0.1$).

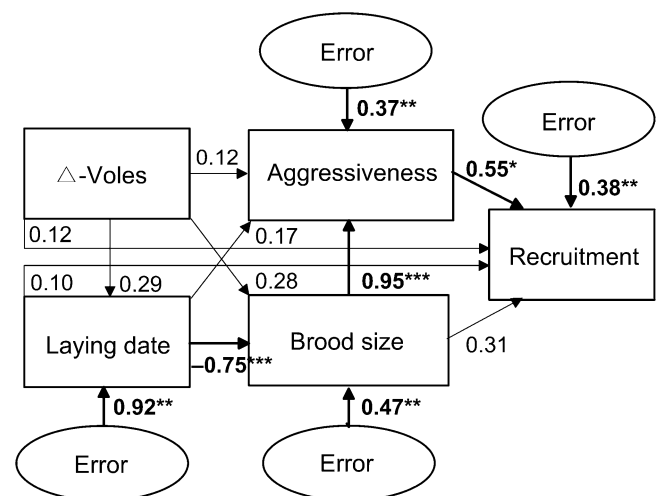


Figure 2

Hypothesized (arrows) and estimated relationships between overwinter change in vole density (Δ voles), laying date, brood size, aggressiveness, and recruitment. Partial regression coefficients from the path model are given with their significance, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. We fit the full model to find statistical grounds to judge differences in the importance of factors affecting recruitment. Thus, model statistics are not meaningful (model $\chi^2 = 0.00$, $df = 1$, $P = 1$) but tell only that model describes data perfectly.

Reproductive success and nest defense aggressiveness on the population level

We analyzed reproductive success on population level using a path model (Mitchell 1992). Hypothesized relationships between factors are depicted with arrows (Figure 2). Our model suggests a causal path laying date–brood size–nest defense aggressiveness–recruitment (thick arrows). That is, nest defense aggressiveness plays an important role in offspring recruitment, independently from the effects of its correlates, reproductive timing (laying date) and reproductive output (brood size). Indeed, recruitment probability of offspring was highest in years with pronounced nest defense aggressiveness ($\tau = 0.58$, $t_{17} = 2.9$, $P = 0.01$; Figure 3).

Selection analysis

We analyzed recruitment and survival selection on nest defense aggressiveness on a yearly level. The annual standardized selection gradients are included in the supplementary materials (Table S1). Analysis of recruitment selection showed that neither year nor the year \times nest defense aggressiveness interaction were significant (year: $F_{11,352} = 0$, $P = 1$; year \times nest defense aggressiveness: $F_{12,352} = 0.95$, $P = 0.49$). Out of a total of 12 years, 10 years had a positive standardized recruitment selection gradient (sign test, $P = 0.04$; Figure 3). Thus, more aggressive individuals consistently produced more recruits. Neither year nor the year \times nest defense aggressiveness interaction had a significant effect on survival (year: $F_{11,352} = 0$, $P = 1$; year \times nest defense aggressiveness: $F_{12,352} = 1.58$, $P = 0.09$). The sign tests on directional standardized survival selection gradients (7 out of 12 positive) and quadratic standardized survival selection gradients (6 out of 12 positive) were not significant ($P = 0.77$ and $P = 1$, respectively; Figure 4). The sign tests thus indicated that there were no consistent patterns in Ural owl female mortality that would relate to nest defense aggressiveness.

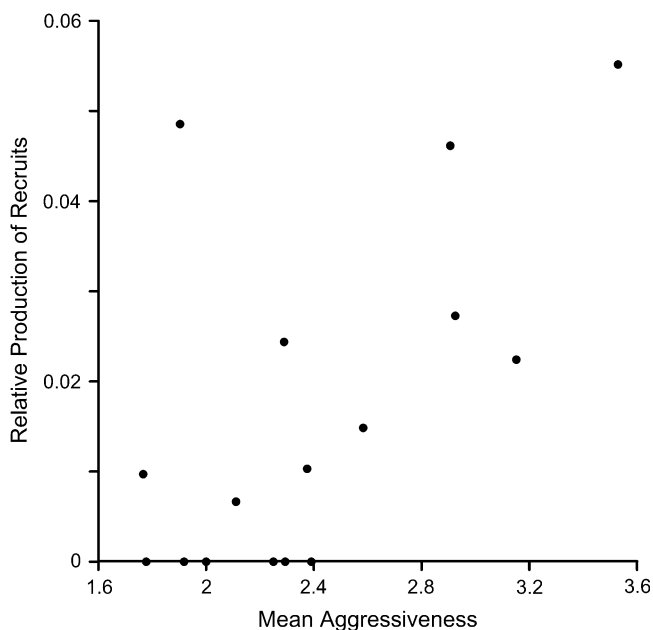


Figure 3 Relative recruit production (number of local recruits produced yearly divided by the number of fledglings produced in that same year) plotted against the mean yearly aggressiveness. Data points are from years 1983 to 2003 (excluding 1984 and 1985; $n = 17$).

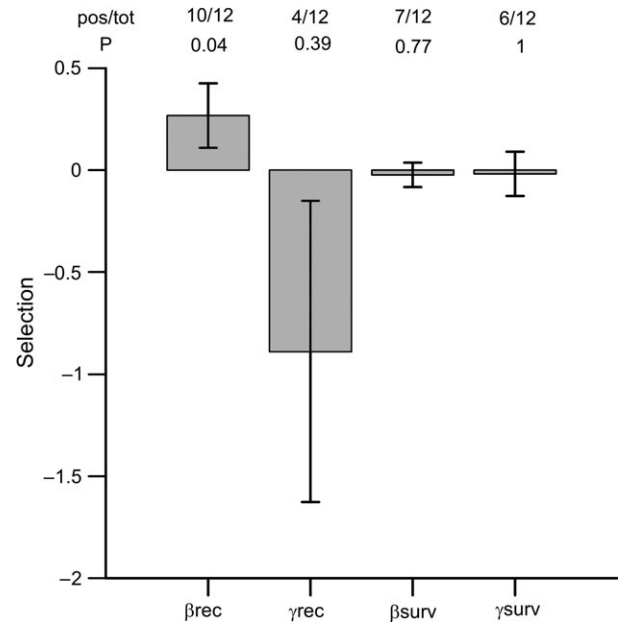


Figure 4 Mean standardized yearly selection gradients ($n = 12$, ± 1 standard error) from the selection model (β_{rec} and β_{surv} for directional selection gradients, and γ_{rec} and γ_{surv} for nonlinear selection gradients). We included only those years in the analysis when population managed to produce recruits. Relative recruit production (rec) and survival (surv) were regressed against standardized aggression nested within a year. On the top of the figure are given number of positive yearly selection gradients out of total number of nonzero selection gradients and P values of associated sign tests.

DISCUSSION

We showed that Ural owl females that laid their eggs early in the season (and consequently had large broods) defended their nests more fiercely than late-laying females (with small broods). In addition, nest defense aggressiveness varied in accordance with vole population dynamics (overwinter change in vole abundance), which represents fluctuations in the Ural owls' main food supply. Individuals differed in their nest defense aggressiveness and in their plastic response of nest defense aggressiveness to overwinter change in the abundance of voles. Lastly, we found evidence that aggressive nest defense on the individual level is under recruitment selection, but not under survival selection. This conclusion is reinforced by our path analysis that reveals nest defense aggressiveness to be the focal trait under recruitment selection in this species, rather than its correlates seasonal reproductive timing and brood size.

Proximate causes for aggressive nest defense behavior—food and reproductive decisions

The Ural owl (predator)–vole (prey) system, which we have been studying, undergoes repeated year-to-year fluctuations in prey abundance. Due to the cyclic nature of vole population dynamics, overwinter changes in vole numbers differ from year to year. Ural owl reproductive decisions are affected strongly by local vole dynamics (Brommer, Pietiäinen, and Kolunen 2002). A long-lived species like the Ural owl allows us to examine the effects of the seasonal change of food supply on nest defense aggressiveness (Table 2). We found that overwinter change in vole density had a significant effect on Ural owl female behavior. Ural owls were more aggressive nest defenders when the vole densities were increasing. Ural owls base their reproductive decisions (e.g., laying date) over long-term

experience of food supply (Brommer, Pietiäinen, and Kolunen 2002), as also illustrated by the finding that current reproductive decisions are affected by experimentally increased food supply in a previous breeding season (Brommer et al. 2004).

In birds of prey, the timing of laying and clutch size are resource limited. Females in good condition initiate laying first (e.g., Meijer et al. 1990; Pietiäinen and Kolunen 1993). Food supply has been identified as a proximate reason determining the timing of laying (Meijer et al. 1990), and laying date has been thought to determine clutch size (Meijer et al. 1990; Brommer, Pietiäinen, and Kokko 2002). Thus, we assumed in our path model that laying date influences clutch size. The evolution of the seasonal decline in clutch size is due to the seasonal decline of the value of the offspring for the parents (e.g., Daan et al. 1990; Brommer, Pietiäinen, and Kokko 2002). Thus, early and large broods are more valuable than late and small broods. It is therefore intuitive that early and large broods are defended more vigorously than late and smaller broods (Wallin 1987; Wiklund 1990; Tolonen and Korpimäki 1995).

Individual variation in the strength of nest defense aggressiveness and in the amount of behavioral plasticity

In our study population, some Ural owl females were consistently more aggressive nest defenders than others, and 52% of the phenotypic variance in nest defense aggressiveness was due to differences across females. This relatively high repeatability suggests that nest defense aggressiveness could be heritable (Falconer and MacKay 1996), and, in general, consistent behavioral patterns do have a moderate heritability (Réale et al. 2007). However, we could not estimate the heritability of nest defense aggressiveness with our current data. Apart from genetic causes, differences across individuals may also be due to differences in territory-level resource availability because Ural owls are highly site tenacious. For example, more aggressive females may be breeding in a territory that is consistently better across years. However, we found that our estimate of territory-level food provisioning did not affect female nest defense aggressiveness, which would suggest that between-individual variation in nest defense aggressiveness is not due to differences in territory quality.

Ural owl females adjusted their nest defense aggressiveness differently to changes in vole abundance. Variation in the plasticity of nest defense aggressiveness across individuals (IEI, Nussey et al. 2007) explained 6.8% of the total variation in nest defense aggressiveness. In general, IEI—when present—explains about 5% of trait variance (Nussey et al. 2007). We found that the variation in plasticity across individuals (individual slopes of the nest defense aggressiveness–vole abundance relationships) was relatively highly correlated with the level of nest defense aggressiveness in the average environment. Hence, generally more aggressive individuals have a stronger positive response to changes in vole abundance. High correlation between slope and elevation means that individual-specific trait–environment relationships form a fanning pattern and, to a large extent, do not cross within the measured range of the environmental variable (Nussey et al. 2007). As a consequence, the ranking of individual nest defense aggressiveness will be in most cases maintained regardless of whether voles are increasing or decreasing in abundance.

Selection on nest defense aggressiveness

Studies of animal temperament displayed by individuals in the wild allow for an explicit evolutionary perspective because the

reproductive success and survival of these individuals can be monitored simultaneously under natural conditions (Arnold 1992; Réale et al. 2000; van Oers et al. 2003; Dingemanse and Réale 2005; Duckworth 2006). Ural owl nest defense aggressiveness was under directional selection, and we find that in almost all years, females with a vigorous nest defense recruited more offspring to the breeding population. In a long-lived species like the Ural owl, truncation of data is a problem when estimating lifetime reproductive success. We therefore analyzed selection on a yearly basis, which avoids serious reduction of the data and allows identification of fluctuating selection pressures across years. Although each estimate of annual selection will, by itself, rarely reach statistical significance because of modest annual sample sizes, it does provide an unbiased estimate of selection (Lande and Arnold 1983). Our overall estimate of the standardized directional selection gradient averaged over all years (0.27) corresponds well with that found in most studies on selection in the wild (typically <0.3 , Kingsolver et al. 2001). By compiling the selection coefficients over 12 years, we find that directional recruitment selection is temporally consistent in favoring more aggressive nest defense.

In general, nest defense aggressiveness is thought to be linked to offspring survival prospects (Hakkarainen and Korpimäki 1994; Rytönen 2002). For instance, Rytönen (2002) conducted a feeding experiment where the nest defense of fed and control groups of great tits were compared. He concluded that higher offspring survival probabilities due to extra feeding led to increased aggressiveness. Tengmalm's owl, a forest owl species that also depends on voles, exhibits the highest nest defense aggressiveness when voles are increasing and when offspring recruitment probabilities are highest, a pattern suggested to be adaptive (Hakkarainen and Korpimäki 1994). Interestingly, our individual-level analysis and path analysis show that the direct effects of seasonal reproductive timing and brood size do strongly affect nest defense aggressiveness, but the analyses show also that it is mainly nest defense aggressiveness that explains recruitment of offspring. This finding suggests that nest defense aggressiveness is the prime target of recruitment selection in the Ural owl. However, we have here taken the approach of quantifying selection in progress, and this finding may thus be influenced by (unknown and unmeasured) variables that we did not consider in our analyses (e.g., Price et al. 1988; Scheiner et al. 2002). Experimental manipulation of nest defense aggressiveness would be required to establish causality.

Assuming that nest defense aggressiveness is the target of natural selection and is indeed heritable, the directional selection, as we documented here, is projected to lead to a response and result in depletion of additive genetic variance for nest defense aggressiveness (e.g., Falconer and MacKay 1996) in case there are no antagonistic selective forces acting on nest defense aggressiveness. We hypothesized that nest defense aggressiveness would be costly because of the obvious risks of attacks. However, female survival was not affected by the degree of nest defense aggressiveness. On the other hand, we have only been able to consider one sex (females) because males seldom show any sign of aggressiveness during our visits to the nests. Nest defense, however, is a kind of trait where, conceivably, the 2 pair members interact (Moore et al. 1997). An Ural owl male is much smaller than a female, and nest defense aggressiveness in males could negatively affect his survival. Potentially, selection on nest defense aggressiveness is sexually antagonistic or subject to sexual conflict (Arnqvist and Rowe 2005; Wilson et al. 2008). Such a scenario would be interesting to explore further and could provide an explanation of the generally low level of male nest defense aggressiveness.

Ural owl females flexibly adjust their nest defense aggressiveness to the prevailing conditions. This plasticity may be maintained by natural selection. We did find significant variation in the extent by which females adjust their nest defense aggression to vole abundance (IEI), and unresponsive females that display a relatively fixed level of nest defense may be less fit than females that readily adjust the level of their aggressive defense to the prevailing environmental conditions. Unfortunately, we have at present insufficient data to explore whether variation in plasticity is under selection because this requires estimates of lifetime fitness (see, e.g., Brommer et al. 2005). We anticipate that, with further accumulation of data, exploration of this level of selection may become possible.

Why does it pay off to be an aggressive nest defender?

The Ural owl defense tactics against a human “predator” (silent dive and hit) show that its physical capabilities and its motivation to attack provide a potentially powerful weapon to fight (nonavian) enemies. Predation of Ural owl offspring in the nest is virtually absent, which could be interpreted as evidence of the efficiency of Ural owl nest defense. On the other hand, we do not know which forces have shaped the nest defense aggressiveness of the Ural owl in its evolutionary past. Ural owls breeding in nest-boxes in modern managed forests may have relatively little to fear from mammalian predators as the current community of mammalian predator species capable of climbing a tree mostly consists of small-bodied species. We therefore believe that the benefits of being an aggressive nest defender in the present day environment are probably related to the protection of offspring from mammalian predators after fledging. A detailed telemetry study on tawny owls *Strix aluco* (a close relative of Ural owl) showed that fledglings were most susceptible to predation by mammals (mostly red fox) during the first days after fledging (Sunde 2005). In total, mammalian predators were responsible for more than half of the fledglings’ deaths prior to independence. Ural owl offspring fledge at about 60% of their adult size and cannot fly (merely glide) while moving considerable distances on or close to the ground. Young are thus highly vulnerable and depend on their parents over the summer months before becoming independent in the early autumn (10–12 weeks after fledging; Cramp 1985). We believe that nest defense aggressiveness toward a human intruder approaching the nest is indicative of the level of aggressive defense toward potential postfledging predators such as, for example, pine marten, *Martes martes*, red fox, *Vulpes vulpes*, and raccoon dog, *Nyctereutes procyonoides*.

A second, nonmutually exclusive, explanation for why aggressive mothers produce more recruits is that a mother’s nest defense aggressiveness may correlate with selectively important behavior (e.g., aggressiveness) of her offspring in other contexts. The current knowledge of animal personalities underlines the key concept of a behavioral syndrome (e.g., Sih et al. 2004), which means that the expression of 2 or more behavioral traits is correlated across contexts. Usually more aggressive individuals are also bolder (e.g., Réale et al. 2000; Dingemanse and Réale 2005) and more active in exploring their surroundings (Hollander et al. 2008). Wild great tits, which defended their nests actively, were also fast in exploring a novel, artificial environment (Hollander et al. 2008). Possibly, the offspring of aggressive nest defenders have a competitive advantage over offspring of nonaggressive ones when finding, assuming, and defending breeding territories. We do not know how individuals obtain a territory, but it seems likely that contest is involved, given that obtaining a territory probably is crucial for a young Ural owl. In the closely related

tawny owl, for example, a young bird without a territory has very slim chances of survival (Southern 1970).

Conclusion

We here describe proximate and ultimate reasons for variation in nest defense aggressiveness of Ural owl females. Our results underline that Ural owl nest defense aggressiveness is highly plastic, mainly in response to food availability, but also correlates with reproductive decisions. We found consistent differences in nest defense aggressiveness across females but also interindividual variation in the plasticity of nest defense aggressiveness. Aggressive nest defenders produce more recruits than nonaggressive ones, thereby providing an explanation for the generally high level of aggression in nest defense in this species.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at <http://www.beheco.oxfordjournals.org/>

FUNDING

Jenny and Antti Wihuri Foundation to P.K.; The Academy of Finland to H.P., J.E.B.; Academy Research Fellow to J.E.B.

We would like to thank all the people who have suffered the Ural owl talons in the course of gathering these data. We would also like to thank the 2 anonymous reviewers for the valuable comments on the earlier versions of the manuscript.

REFERENCES

- Arnold SJ. 1992. Constraints on phenotypic evolution. *Am Nat.* 140: S85–S107.
- Arnqvist G, Rowe L. 2005. *Sexual conflict*. Princeton: Princeton University Press.
- Barash DP. 1975. Evolutionary aspects of parental behavior: distraction behavior of the alpine accentor. *Wilson Bull.* 87:367–373.
- Bell AM. 2005. Behavioural differences between individuals and two populations of stickleback (*Gasterosteus aculeatus*). *J Evol Biol.* 18: 464–473.
- Bell AM. 2007. Future directions in behavioural syndromes research. *Proc R Soc Lond B Biol Sci.* 274:755–761.
- Bell AM, Sih A. 2007. Exposure to predation generates personality in threespined sticklebacks (*Gasterosteus aculeatus*). *Ecol Lett.* 10: 828–834.
- Brommer JE, Karell P, Pietiäinen H. 2004. Supplementary fed Ural owls increase their reproductive output with a one year time lag. *Oecologia.* 139:354–358.
- Brommer JE, Karell P, Pihlaja T, Painter JN, Primmer CR, Pietiäinen H. 2003. Ural owl sex allocation and parental investment under poor food conditions. *Oecologia.* 137:140–147.
- Brommer JE, Pietiäinen H, Kolunen H. 1998. The effect of age at the first breeding on Ural owl lifetime reproductive success and fitness under cyclic food conditions. *J Anim Ecol.* 67:359–369.
- Brommer JE, Pietiäinen H, Kolunen H. 2002. Reproduction and survival in a variable environment: Ural owls *Strix uralensis* and the three-year vole cycle. *Auk.* 119:544–550.
- Brommer JE, Pietiäinen H, Kokko H. 2002. Cyclic variation in seasonal recruitment and the evolution of the seasonal decline in Ural owl clutch size. *Proc R Soc Lond B Biol Sci.* 269:647–654.
- Brommer JE, Sheldon BC, Gustafsson L, Merilä J. 2005. Natural selection and genetic variation for reproductive reaction norms in a wild bird population. *Evolution.* 59:1362–1371.
- Carillo J, Aparicio JM. 2001. Nest defence behaviour of the Eurasian kestrel (*Falco tinnunculus*) against human predators. *Ethology.* 107: 865–875.
- Cramp S. 1985. *Handbook of the birds of Europe, the Middle East and North Africa. Volume 4: The birds of the Western Palearctic: terns to woodpeckers*. Oxford: Oxford University Press.

- Crawley MJ. 2002. Statistical computing, an introduction to data analysis using S-plus. West Sussex (UK): John Wiley & Sons.
- Daan S, Dijkstra C, Tinbergen JM. 1990. Family planning in the kestrel (*Falco tinnunculus*): the ultimate control in covariation of laying date and clutch size. *Behaviour*. 114:83–116.
- Dingemanse NJ, Réale D. 2005. Natural selection and animal personality. *Behaviour*. 142:1159–1184.
- Duckworth RA. 2006. Aggressive behaviour affects selection on morphology by influencing settlement patterns in a passerine bird. *Proc R Soc Lond B Biol Sci*. 273:1789–1795.
- Duckworth RA, Badyaev AV. 2007. Coupling of dispersal and aggression facilitates the rapid range expansion of a passerine bird. *Proc Natl Acad Sci USA*. 104:15017–15022.
- Falconer DS, MacKay TFC. 1996. Introduction to quantitative genetics. 4th ed. Essex (UK): Addison Wesley Longman.
- Galeotti P, Tavecchia G, Bonetti A. 2000. Parental defence in long-eared owl *Asio otus*: effects of breeding stage, parent sex and human persecution. *J Avian Biol*. 31:431–440.
- Hakkarainen H, Korpiimäki E. 1994. Nest defence of Tengmalm's owls reflects offspring survival prospects under fluctuating food conditions. *Anim Behav*. 48:843–849.
- Hollander FA, van Overveld T, Tokka I, Matthysen E. 2008. Personality and nest defence in the great tit (*Parus major*). *Ethology*. 114:405–412.
- Kingsolver JG, Hoekstra HE, Hoekstra JM, Berrigan D, Vignieri SN, Hill CE, Hoang A, Gilbert P, Beerli P. 2001. The strength of phenotypic selection in natural populations. *Am Nat*. 157:245–261.
- Lundberg A. 1981. Population ecology of the Ural owl *Strix uralensis* Pall., in central Sweden. *Ornis Scand*. 12:111–119.
- Lande R, Arnold SJ. 1983. The measurement of selection on correlated characters. *Evolution*. 37:1210–1226.
- Markman S, Pinshow B, Wright J. 2002. The manipulation of food resources reveals sex-specific trade-offs between parental self-feeding and offspring care. *Proc R Soc Lond B Biol Sci*. 269:1931–1938.
- Meijer T, Daan S, Hall M. 1990. Family-planning in the kestrel (*Falco tinnunculus*): the proximate control of covariation of laying date and clutch size. *Behaviour*. 114:117–136.
- Mitchell RJ. 1992. Testing evolutionary and ecological hypotheses using path analysis and structural equation modeling. *Funct Ecol*. 6:123–129.
- Moore AJ, Brodie ED 3rd, Wolf JB. 1997. Interacting phenotypes and the evolutionary process I: direct and indirect genetic effects on social interactions. *Evolution*. 51:1351–1362.
- Myllymäki A, Paasikallio A, Pankakoski E, Kanervo E. 1971. Removal experiments on small quadrates as a means of rapid assessment of the abundance of small mammals. *Ann Zool Fenn*. 8:177–185.
- Norrdahl K. 1995. Population cycles in northern small mammals. *Biol Rev*. 70:621–637.
- Nussey DH, Wilson AJ, Brommer JE. 2007. The evolutionary ecology of individual phenotypic plasticity in wild populations. *J Evol Biol*. 20:831–844.
- Pietiäinen H. 1989. Seasonal and individual variation in the production of offspring in the Ural owl *Strix uralensis*. *J Anim Ecol*. 58:905–920.
- Pietiäinen H, Kolunen H. 1993. Age determination of breeding Ural owls. *Ornis Fenn*. 63:26–27.
- Pinheiro JC, Bates DM. 2000. Mixed-effect Models in S and S-PLUS. Berlin: Springer.
- Price T, Kirkpatrick M, Arnold SJ. 1988. Directional selection and the evolution of breeding date in birds. *Science*. 240:798–799.
- Réale D, Gallant BY, LeBlanc M, Festa-Bianchet M. 2000. Consistency of temperament in bighorn ewes and correlates with behaviour and life history. *Anim Behav*. 60:589–597.
- Réale D, Reader SM, Sol D, McDougall PT, Dingemanse NJ. 2007. Integrating animal temperament within ecology and evolution. *Biol Rev*. 82:291–318.
- Ricklefs RE. 1969. An analysis of nesting mortality in birds. *Smithson Contrib Zool*. 9:1–48.
- Roff DA. 2002. Life History Evolution. Sunderland (MA): Sinauer Associates.
- Rytönen S. 2002. Nest defence in great tits *Parus major*: support for parental investment theory. *Behav Ecol Sociobiol*. 52:379–384.
- Rytönen S, Orell M, Koivula K, Soppela M. 1995. Correlation between two components of parental investment: nest defence intensity and nestling provisioning effort in willow tits. *Oecologia*. 104:386–394.
- Saurola P. 1987. In: Nero RW, Clark RJ, Knapton RJ, Hamre RH, editors. Mate and nest-site fidelity in Ural and tawny owls. Biology and conservation of northern forest owls, Symposium proceedings. Manitoba (Canada): USDA Forest Service General Technical Report RM-142. p. 81–86.
- Scheiner SM, Donohue K, Dorn LA, Mazer SJ, Wolfe LM. 2002. Reducing environmental bias when measuring natural selection. *Evolution*. 56:2156–2167.
- Sih A, Bell A, Johnson C. 2004. Behavioral syndromes: an ecological and evolutionary overview. *Trends Ecol Evol*. 19:372–378.
- Southern HN. 1970. Natural control of a population of tawny owls (*Strix aluco*). *J Zool*. 162:197–285.
- Sunde P. 2005. Predators control post-fledging mortality in tawny owl, *Strix aluco*. *Oikos*. 110:461–472.
- Tolonen P, Korpiimäki E. 1995. Parental effort of kestrels (*Falco tinnunculus*) in nest defence: effects of laying time brood size and varying survival prospects of offspring. *Behav Ecol*. 6:435–441.
- van Oers K, Drent PJ, de Goede P, van Noordwijk AJ. 2003. Realized heritability and repeatability of risk-taking behaviour in relation to avian personalities. *Proc R Soc Lond B Biol Sci*. 271:65–73.
- Wallin K. 1987. Defence as parental care in tawny owls (*Strix aluco*). *Behaviour*. 102:213–230.
- Wiklund CG. 1990. The adaptive significance of nest defence by merlin, *Falco columbarius*, males. *Anim Behav*. 40:244–253.
- Wilson AJ, Gelin U, Perron M-C, Réale D. 2008. Indirect genetic effects and the evolution of aggression in a vertebrate system. *Proc R Soc Lond B Biol Sci*. doi: 10.1098/rspb.2008.1193.