

Does variation of sex ratio enhance reproductive success of offspring in tawny owls (*Strix aluco*)?

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SUMMARY

Tawny owls, *Strix aluco*, laid female-biased clutches on territories with more abundant prey (field voles) in June, the month that chicks fledge. This appeared to enhance the subsequent reproductive success of fledglings, as in 1995 there was a significant correlation between the number of chicks fledged by adult females and the June vole abundance in the territory on which they were reared as chicks. This relationship did not hold for males. Since tawny owls lay eggs in March, these results indicate that owls are able to predict the June vole numbers on their territory, and respond by producing more of the sex most likely to gain a long-term benefit when resources are good.

1. INTRODUCTION

Where the fitness returns of each sex differ, parents are expected to divide their investment between sons and daughters to maximize their own lifetime reproductive success. Where the reproductive success of one sex is more dependent on the amount of parental resources it receives, parents should produce more of this sex when resources are plentiful (Trivers & Willard 1973).

Recent studies on bird species have shown skewed sex ratios of offspring corresponding with the resources available to parents. For example, broods of American kestrels *Falco sparverius* were more likely to be male biased in years of poor food availability, or when the parents were in poor condition (Wiebe & Bortolotti 1992). In addition, yellow-headed blackbird *Xanthocephalus xanthocephalus* broods laid by primary females, which received more paternal care and therefore had higher resource availability, were more likely to be male biased (Paterson *et al.* 1980). The fitness gain to the parents of producing different sex offspring in conditions of different resource availability has, however, seldom been investigated. A recent exception is the discovery that Seychelles warblers produced more female offspring on high-quality territories (Komdeur 1996; Komdeur *et al.* 1997) which appears to increase the fitness of parents, as females are the helping sex, and helpers are beneficial when food is abundant.

In this paper we present the results of a study on sex ratios from a population of tawny owls, which indicate that parent owls produce more female chicks on

territories with higher numbers of their major prey, field voles *Microtus agrestis*, at the time the young are fledging. This is adaptive because females but not males appear to enjoy a subsequent reproductive advantage from being reared under good food conditions.

2. METHODS

(a) Study population

We studied tawny owls at Kielder Forest, Northumberland, UK. Tawny owls have been monitored by S.J.P. at this site since 1980. Because most of the recruits into the breeding population were ringed and reared in the study area, the natal territory and breeding history of nearly all adults were known. All pairs in the study area bred in nest boxes, and most of the adults were caught and identified at each breeding attempt. All chicks were ringed each year. In 1994 and 1995, blood samples were collected from chicks, under licence, by brachial vein puncture in order to determine their sex. Blood could be taken from chicks the day after hatching, and no ill effects of taking blood were found. Nests were sampled in an order determined by convenience of location, and the age that blood samples were first taken from chicks varied between 0 and 21 days in both years, with a mean sampling age of 8.7 days in 1994 and 8.9 days in 1995. This difference was not significant (Mann-Whitney $U = 3611$, $p = 0.99$, $N_1 = 113$, $N_2 = 64$).

As we were interested in the primary sex ratio of owl broods, we included in the analysis only nests where all eggs hatched and all chicks were sexed. Sex-biased mortality can cause the sex ratio of broods remaining complete after major mortality to be different to that of the population as a whole (Fiala 1980). We had no evidence that sex-biased mortality was occurring in nestling tawny owls. Altogether 14 of 83

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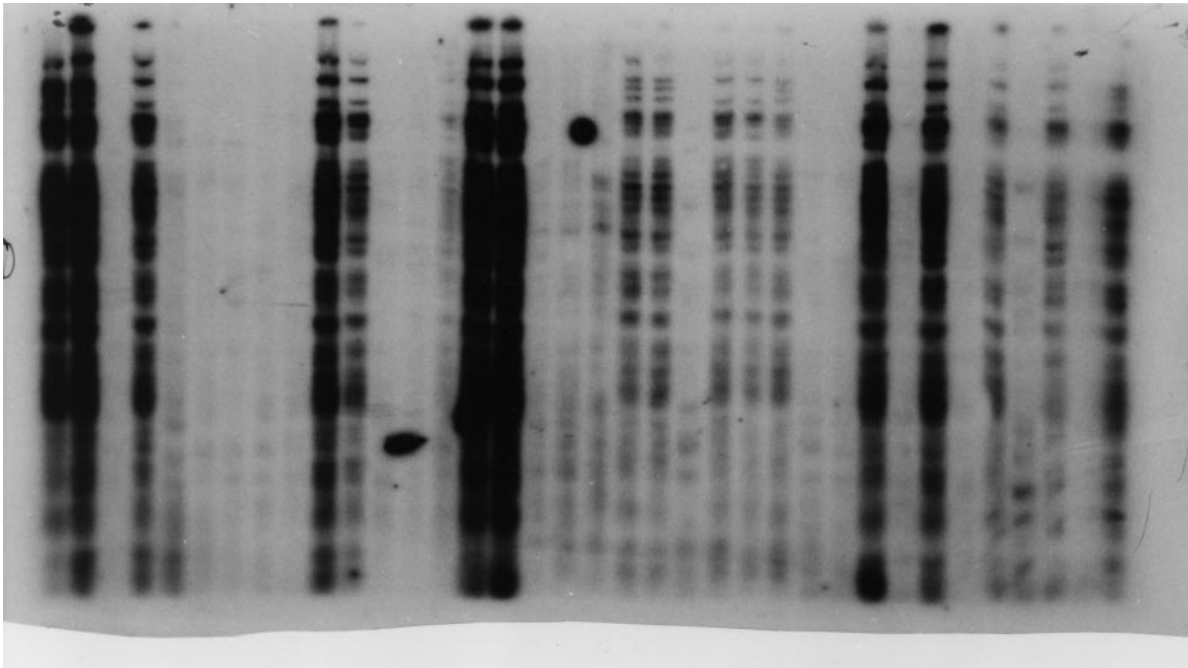


Figure 1. Example of sex identification in tawny owls using characteristic female-specific minisatellite DNA.

female chicks and ten of 81 male chicks died after sexing. This difference was not significant ($\chi^2 = 0.24$, degrees of freedom (d.f.) = 1, $p = 0.63$ with Yate's correction). In addition, the majority of chicks that died had already been sexed (63% $N = 38$), so it was unlikely that the small unsexed portion would have influenced overall sex-specific mortality rates. Nests excluded due to mortality were usually those visited late due to their location and there was no difference in the June vole index of territories that were included or excluded from the analysis (t -tests; 1994: $t = -1.91$, $p = 0.37$, $N = 42$, 1995: $t = -1.3$, $p = 0.22$, $N = 21$). Therefore, we were confident that we were dealing with the primary sex ratio of a random sample of nests in the population.

(b) Sexing technique

To determine the sex of nestlings, we used female-specific minisatellite fragments identified by DNA fingerprinting in owls (J.K.B. & B.M.A., unpublished data). Genomic DNA was isolated from blood by proteinase K digestion, purified by salt extraction (Miller *et al.* 1988) and recovered by ethanol precipitation. Purified DNA was digested with restriction enzyme HaeIII (BRL) according to the manufacturers' instructions. Equal amounts ($\sim 4 \mu\text{g}$) of each sample digested were electrophoresed through 0.9% agarose gels until fragments $< 1 \text{ kb}$ had migrated off the bottom of the gel. DNA fragments were then transferred by Southern blotting onto Zetaprobe GN Nylon membrane (Bio-Rad Ltd) and cross-linked by baking at 80°C for 1 hour.

Membranes were first probed with human minisatellite probe 33.15 (Jeffreys *et al.* 1985), which hybridizes to female-specific minisatellites giving a series of characteristic bands in females but not in males. Blots were then stripped and re-probed with HaeIII digested tawny owl genomic DNA, as a control for differences in DNA concentration between samples. DNA probes were radiolabelled with ^{32}P -dATP by random priming (Feinberg & Vogelstein 1984) to a specific activity $> 109 \text{ cpm mg}^{-1}$. Probe hybridization conditions followed Westneat *et al.* (1988). Filters were then washed at 65°C to a stringency of $1\times\text{SSC}$, until blank control filters had only background radiation levels. Minisatellite loci hybridizing to the probe were visualized by autoradiography.

Female owls show a characteristic invariant suite of eight major minisatellite bands in the range 2–12 kb, whereas males have no band hybridizing at all (figure 1). Over forty owls that were sexed using this method had their sex confirmed by either chromosome squashes or recapturing birds as adults. Of these, 100% were correctly sexed. A small number of samples did not have sufficient DNA of good quality for restriction digestion; these were sexed by a polymerase chain reaction-based method (Griffiths *et al.* 1996) developed subsequently.

(c) Estimates of prey indexes

In Kielder Forest, field voles comprised the main prey of tawny owls (Petty 1987, 1989). Field voles consisted of 72% of 2429 prey items found in pellets collected during 1980–1989, and 66% of 991 prey items collected from owl nests at Kielder during this same period (Petty 1992). The abundance of field voles in Kielder Forest fluctuates with a regular 3–4 year cycle, but with some spatial asynchrony (Petty 1992). This means vole abundance can be increasing in some parts of the forest while declining in others.

In each year of the study, the abundance of voles was assessed at 20 sites in March and June. At each site, a 25 cm^2 quadrat was thrown 25 times along a similar route, and the presence or absence of fresh (green) grass clippings in vole runs was recorded. Thus calculated, the vole sign index (VSI) for each site ranged from 0 to 25. The accuracy of this method was checked by trapping voles on one vole sign assessment site, at the same time that the VSI was done during 1984–1990, to provide a vole trapping index (VTI). Each trapping session comprises 576 trap nights. There were significant seasonal relationships between the VSI and the VTI, and linear relationships were then used to seasonally adjust the VSIs. (March $\text{VTI} = 1.88 + 0.81 \times \text{VSI}$, $n = 6$, $R^2 = 0.72$; June $\text{VTI} = 0.93 + 1.83 \times \text{VSI}$, $N = 7$, $R^2 = 0.72$). In this analysis, we use these seasonally adjusted VSIs. An individual measure of vole abundance was assigned to each owl territory from the nearest vole sign assessment site. This was considered to be a reasonable estimate of vole numbers on a territory as vole densities change only gradually between areas.

(d) Statistical analysis

Brood sex ratios were analysed by logistic regression with the GLIM package (Version 4, Royal Statistical Society, 1992) by specifying a binomial error distribution and a logit link. The number of males in a brood was used as the dependent variable and brood size as the binomial denominator. This circumvents the problems of non-normal and non-constant variances inherent in proportional data (Crawley 1993). The statistical significance of fitting a predictor variable (vole abundance) to the null model was measured as the change in deviance (ΔD) of the fit of the model on inclusion of the predictor; this is distributed approximately as χ^2 with the change in degrees of freedom ($\Delta d.f.$) on fitting the predictor to the null model (Armitage & Berry 1987) giving two-tailed p values.

3. RESULTS*(a) Sex ratio in relation to food-supply*

1994 was a year of generally increasing vole abundance, and only 17 out of 116 (14.5%) chicks died between hatching and fledging. In contrast, 1995 was a year of generally decreasing vole abundance and 22 out of 70 (31.4%) chicks died before fledging. In both years brood sizes ranged between 1–4, with a mean of 2.8 chicks in 1994 and 2.5 chicks in 1995.

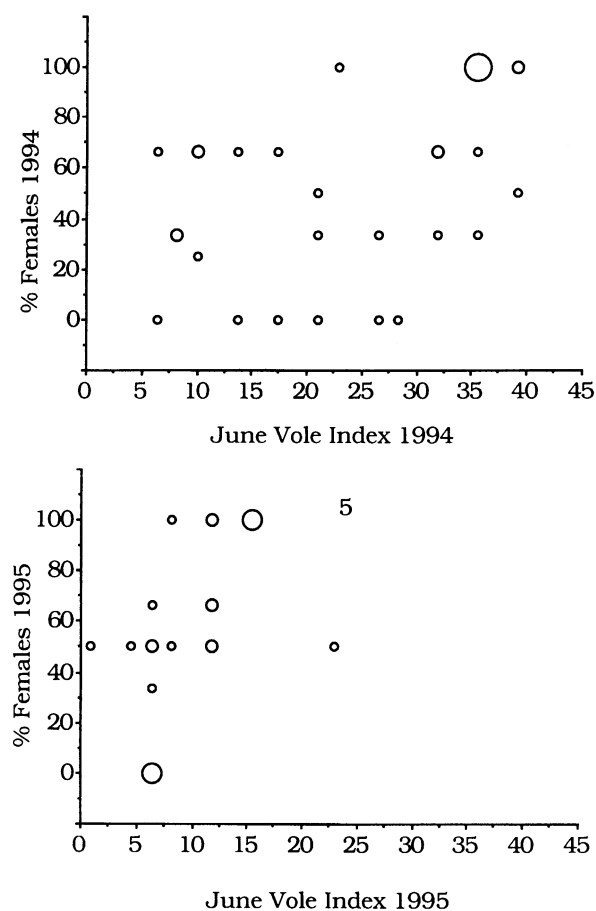


Figure 2. The percentage of females in clutches of eggs laid by tawny owls in Kielder Forest in 1994 and 1995 plotted against the June vole index on the territory that year. Only broods where all eggs laid hatched and all chicks were sexed are included. Circles of increasing size indicate 1, 2, 3 and 4 data points respectively.

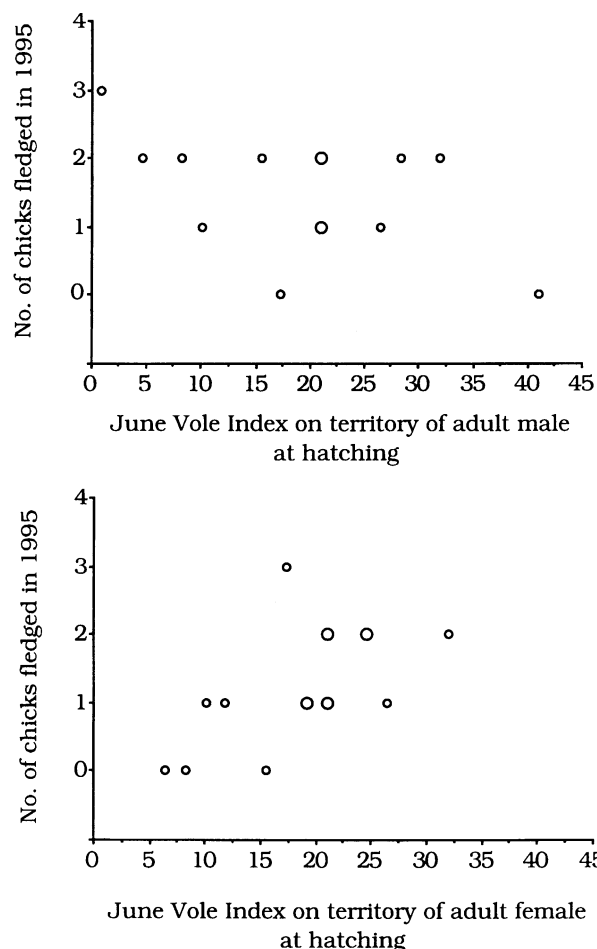


Figure 3. The number of tawny owl chicks fledged on a territory in 1995 plotted against the June vole index on the natal territory of the adult male and female in the year that they hatched. Smaller circles indicate one data point, larger circles indicate two data points.

There was a significantly different nestling mortality rate between years ($\chi^2 = 3.96$, $d.f. = 1$, $p = 0.046$ with Yates' correction).

In both 1994 and 1995 the proportion of female chicks within a brood increased significantly with the June vole index (1994: $\Delta D = 6.557$, $\Delta d.f. = 1$, $p < 0.05$, $N = 30$ broods. 1995: $\Delta D = 4.954$, $\Delta d.f. = 1$, $p < 0.05$, $N = 21$ broods) (figure 2). No such relationship was found with the March vole index (1994: $\Delta D = 1.250$, $\Delta d.f. = 1$, $p > 0.25$, $N = 30$ broods. 1995: $\Delta D = 1.619$, $\Delta d.f. = 1$, $p > 0.1$, $N = 19$ broods). As only nests where all eggs hatched and all chicks were sexed were included in this analysis, this result could not be attributed to sex-biased mortality in eggs or nestlings. Neither was this relationship the result of the same female adults producing more female offspring in both years, as there was no correlation between the proportion of female chicks in the broods of the same females in 1994 and 1995 ($r_s = -0.06$, $N = 24$, $p = 0.85$). There was also no correlation between the June vole index on the same territories in 1994 and 1995 ($r_s = -0.11$, $N = 24$, $p = 0.62$). Producing more female chicks appears to be a flexible response to the prevailing food-supply on the territory in that year.

Female owls lay eggs in March and April, and as the vole index in June did not correlate with the vole index

in March (1994: $r_s = -0.14$, $N = 20$, $p = 0.3$. 1995: $r_s = -0.27$, $N = 20$, $p = 0.1$) there must be some cue other than vole numbers used by the female owls to 'predict' future vole abundance.

(b) Reproductive success of adults in relation to vole abundance on natal territories

To assess whether there was a relationship between food-supply available to fledglings and their subsequent breeding success as adults, the number of chicks fledged by adults breeding in 1994 and 1995 was compared to the June vole index on their natal territories in the year they hatched (natal vole index). In 1994 there was no significant correlation between the number of chicks fledged and the natal vole index of either the male or female parent (females $r_s = 0.09$, $N = 26$, $p = 0.65$; males $r_s = 0.02$, $N = 25$, $p = 0.92$). In 1995 there was a significant correlation between the number of chicks fledged and the natal vole index of the mother ($r_s = 0.61$, $N = 16$, $p = 0.01$), but there was no significant correlation for fathers ($r_s = -0.38$, $N = 14$, $p = 0.18$) (figure 3). The relationship between the number of chicks fledged by females and their natal vole index was still significant after controlling for the June vole index on females' territories in 1995 ($r_s = 0.59$, d.f. = 13, $p = 0.02$). There was, however, no significant relationship between the number of chicks that females fledged and the June vole index on their territories in 1995 after controlling for the natal vole index of females ($r_s = -0.11$, d.f. = 13, $p = 0.35$). This implies that in 1995 the vole index on the natal territories of females was a more important factor in determining their breeding success than the vole index on their territories while they were raising the chicks.

To determine what stage in the 1995 breeding cycle accounted for the differences in productivity between females with different natal vole abundances, the number of eggs laid, the number of unhatched eggs, the number of hatched eggs and the number of chicks that died in the nest was compared to natal vole abundance. After controlling for March vole index there was a non-significant positive correlation between the number of chicks laid in 1995 and natal vole index ($r_s = 0.47$, d.f. = 13, $p = 0.08$) and a significant negative correlation between natal vole index and the number of unhatched eggs ($r_s = -0.58$, d.f. = 13, $p = 0.02$). This resulted in a highly significant correlation between natal vole index and the number of chicks hatched ($r_s = 0.68$, d.f. = 13, $p = 0.005$). There was no correlation between the number of chicks that died in the nest and natal vole index of the female ($r_s = 0.15$, d.f. = 13, $p = 0.60$). Thus females reared on territories with high vole abundance appeared to lay slightly more eggs, which had a significantly higher hatching success.

The age of females breeding in 1995 for which the natal vole index was known varied between two and 14 years with a mean of 6.6 in 1995. The relationship between the natal vole index and the number of chicks fledged by females in 1995 was still significant after controlling for both female age and June vole index on their territories ($r_s = -0.68$, $N = 11$, $p = 0.01$).

4. DISCUSSION

Our results indicate that tawny owls lay female-biased clutches on territories that have high vole numbers in June. The mechanism by which the sex of eggs might be determined during laying has yet to be elucidated. There are several bird species where the sex of the progeny differs according to the position of the egg in the laying sequence (Ryder 1983; Bortolotti 1986; Dijkstra *et al.* 1990; Bednarz & Hayden 1991; Wiebe & Bortolotti 1992; Leroux & Bretagnolle 1996). This implies there might be non-random shedding of Z- and W-bearing ova by the mother. Krackow (1995) suggested this effect could occur if sex chromosomes interfere with the gonadotropic-dependent regulation of follicle maturation; however no data exist to support this suggestion.

Tawny owls fledge around mid-May, but remain on their parent's territory until mid-August, so summer vole numbers on natal territories will determine the food available to chicks for their first few months of life. There is little information on the effect of rearing conditions on subsequent reproductive success of adults in bird species. Haywood and Perrins (1992) found that female zebra finches *Poephila guttata* that received higher amounts of food as chicks laid larger clutches as adults, thus indicating that rearing conditions might have long-term effects on the reproductive success of female birds. The increased hatching success of eggs of female owls that had been reared under conditions of good food availability could have been due to more effective incubation of eggs. Alternatively, they might have been able to invest more body reserves in eggs leading to more eggs with lower foetal mortality. Female zebra finches given a higher-quality prebreeding diet laid eggs with a higher hatching success than control birds (Selman & Houson 1996), and body reserves of protein and fat are known to be important in the formation of eggs (Houston *et al.* 1995 *a, b, c*).

From our results, tawny owls appear to be 'predicting' vole abundance on their territories in June, although vole abundance during laying in March did not appear to indicate future vole abundance. Previous studies have suggested that predators might be able to predict future food-supply in conditions of cycling prey density. Clutch size (Korpimäki & Hakkarainen 1991), egg size (Hakkarainen & Korpimäki 1994*a*) and nest defence intensity (Hakkarainen & Korpimäki 1994*b*) of the Tengmalm's owl were higher in the increasing than the peak phase of the vole cycle in Finland, although vole density was higher in the peak phase. Korpimäki & Hakkarainen (1991) hypothesized that increasing proportions of pregnant and lactating females and young individuals in the increase phase were used by owls as an indicator of high future prey numbers. It is also possible that the size of voles may give owls an indication of future numbers. Body size of voles is larger in the increase phase of multiannual cycles than in the decline phase (Chitty & Chitty 1962). Alternatively the change in vole availability with time may give owls a cue as to future numbers. Mammals also appear able to predict changes in vole abundance. Lindström (1988), found that in the red

fox *Vulpes vulpes* the ovulation rate of females in February corresponded with vole numbers two months later in May. He proposed that foxes can respond to the reproductive hormones in voles.

If female owls were able to predict food-supply later in the summer, they should be able to adjust clutch size accordingly. However, the mean number of eggs laid by tawny owls in Kielder Forest correlated with the March, not the June vole index (Petty 1992). This could be because the number of eggs females lay is influenced by their body condition before laying. A relationship between the number of eggs laid and food-supply before or during laying has been found in zebra finches (Selman & Houston 1996), domestic fowl *Gallus domesticus* (Romanoff & Romanoff 1949), house martins *Delichon Urbica* (Bryant 1973), short-eared owls *Asio flammeus* (Lack 1954) and Tengmalm's owls *Aegolius funereus* (Korpimäki 1988). That tawny owls are limited by food in the number of eggs they can lay is supported by the fact that the probability of relaying after desertion is positively correlated with the March vole index (Petty 1992).

It is interesting that the correlation between the natal vole index and number of chicks fledged by females was only significant in 1995. This could be because high vole numbers in 1994 allowed even poorer individuals to breed successfully. Thus, differences in quality between birds might only be apparent in years of low vole numbers when only higher-quality individuals breed successfully.

No study of a wild bird population has previously demonstrated that resource availability to chicks during rearing can influence the reproductive success of adult birds. Our results indicate that vole abundance on the territories of female tawny owls during rearing can influence their reproductive success up to 11 years later, and that under conditions of good food-supply tawny owls produce more female chicks that accrue a greater long-term benefit. Tawny owls appear to be able to predict food-supply in order to produce this skewed sex ratio.

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