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Source: Ardea, 97(4) : 635-644

Published By: Netherlands Ornithologists' Union

URL: https://doi.org/10.5253/078.097.0433

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How owls select their prey: a study of Barn Owls *Tyto alba* and their small mammal prey

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Taylor I.R. 2009. How owls select their prey: a study of Barn Owls *Tyto alba* and their small mammal prey. In: Johnson D.H., Van Nieuwenhuyse D. & Duncan J.R. (eds) Proc. Fourth World Owl Conf. Oct–Nov 2007, Groningen, The Netherlands. Ardea 97(4): 635–644.



Male Barn Owls *Tyto alba* delivered significantly more male than female Field Voles *Microtus agrestis* to their mates and nestlings in spring. The male bias was evident both in the prey stored at the nest and in the skeletal remains of prey in pellets taken from the nest. The sex ratio in voles caught by trapping showed a slight female bias. Analysis of pellets produced by the male barn owls at their roosts at the same time, showed the same biased sex ratio of voles, demonstrating that selection of male voles occurred at capture and was not a result of differences between prey delivered to the nest and those consumed by the males. The mean weights of trapped male and female voles in spring were 23.4 g (SE 0.5) and 18.5 g (SE 0.4) respectively. During winter when voles were not breeding the sex ratio in pellets of male and female owls was close to unity. This suggests that the increased aggressiveness and/or activity levels of male voles associated with territorial behaviour and breeding in spring led to an increase in their detection rate by owls hunting by use of auditory cues. Thus the selection for male voles was the result of an increased encounter rate rather than optimal foraging based on the greater body mass of male voles. In spring the owls caught significantly more Field Voles than Wood Mice *Apodemus sylvaticus* than predicted from the relative abundances of the two species in the field. It is suggested this was the result of the greater ability of Wood Mice to detect the owls and their greater agility in evading capture.

Key words: prey selection, optimal foraging, *Tyto alba, Microtus agrestis, Apodemus sylvaticus*

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INTRODUCTION

Optimal foraging theory proposes that predators such as owls should forage efficiently (Stephens & Krebs 1986). Individuals that maximise their energy intake rates while at the same time minimising their predation or injury risk should produce more offspring and survive better and hence be selected for. There is empirical and experimental evidence for several species of owls that their productivity and survival are limited by food supply. Annual variations in both have been shown to be related to variations in prey density, especially among species that depend on cyclic small mammal as prey (Korpimäki & Norrdahl 1989, Taylor 1994). Experimental addition of food has increased productivity and also advanced laying dates, which significantly affects the probability of young being recruited to the breeding population (Korpimäki 1987, Korpimäki & Lagerström 1988, Taylor 1994). This suggests that individuals that can forage more efficiently and increase their food intake rates should be selected for.

Foraging efficiency can be defined as the net rate of energy or nutrient intake divided by search time plus handling time. For most owls energy intake is equivalent to the body mass of their prey. Prey body mass should therefore be an important factor in foraging decision making. In general terms, body mass of prey has been shown to be positively related to predator body mass among a wide range of terrestrial predators (Vezina 1985) and among different species of diurnal

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raptors (Schoener 1968). Among different subspecies of Barn Owls there is also a positive relationship between bird body mass and mean prey mass (Taylor 1994). The simplest interpretation of such relationships is that there is an optimum prey mass for each species in terms of foraging efficiency, related to its own body mass. Additionally, there may be a risk of injury to owls that attempt to capture and subdue exceptionally large prey.

The time taken in prey handling for owls is minimal in most species but search time is usually significant. Search time, the time spent searching between the captures of successive prey, is influenced by the rate at which prey are encountered and the rate at which encountered prey are captured successfully. Thus, factors that affect encounter rates and capture success should both have a strong effect on search times. Most owls are nocturnal and although most probably use visual cues to some extent during hunting they depend mainly on auditory cues from their prey, first to locate them and then to capture them (Payne 1971, Knudsen & Konishi 1979). Also, many species take prey from within long grass or in some cases under snow where they also must depend on auditory cues. Auditory cues can take the form of prey vocalisation or noises produced during eating or movement. Clearly if owls are to make foraging decisions based on auditory cues they must be able to relate noises produced by prey to specific characteristics of those prey such as species, body mass or age. In laboratory trials Barn Owls have been shown to be capable of distinguishing between closely similar and complex noise spectra and to be able to memorise these differences (Quine & Konishi 1974, Konishi & Kenuk 1975). However, there have been no attempts to relate these abilities specifically to the selection of specific prey in the field. This is important as the extent to which they are able to make appropriate and efficient foraging decisions depends on the ability of their sensory capacities to do so. Capture success may also depend upon the ability of prey to detect and avoid attacking owls and may be affected by the availability of cover into which prey can move.

In summary, four major factors may be involved in the optimal foraging decisions made by owls:

(1) Prey size and sex (or prey body mass).

(2) Prey vocalisation and activity rates.

(3) Prey ability to detect predators and agility to evade predators.

(4) Prey access to cover.

There is evidence in the literature that each of these may be important, perhaps operating to different extents in different species or in different circumstances (Kulczycki 1964, Saint-Girons 1965, Southern & Lowe 1968, Dean 1972, Bishop & Hartley 1976, Goszcynski 1977, Lagerström & Häkkinen 1978, Marti & Hogue 1979, Morris 1979, Korpimäki 1981, Colvin 1984, Janes & Barss 1985, Longland & Jenkins 1987, Derting & Cranford 1989, Mappes *et al.* 1993, Kotler *et al.* 1988, 1991, Bellocq 1998, Dickman *et al.* 1991, Koivunen *et al.* 1996a,b, 1998a,b, Norrdahl & Korpimäki 1998, Christe *et al.* 2006).

This paper explores prey selection in the Barn Owl *Tyto alba*, within and among its small mammal prey species. It examines selection for sex and size in the Field Vole *Microtus agrestis* in spring. Barn Owls might select male Field Voles because they are heavier than females or because they are easier to locate. In the breeding season male Field Voles are strongly territorial and aggressive with high vocalisation and activity rates (Clarke 1956, Myllymäki 1977, Viitala 1977). Male bias in predation rates has been recorded in several owl species and for several prey species (e.g. Southern & Lowe 1968, Korpimäki 1985, Taylor 1994, Koivunen *et al.* 1996a,b). However, the evidence has been based mostly on prey stored at the nest. Owls are single prey loaders and during central place foraging such as when feeding females on the nest during incubation or while feeding chicks, the possibility that birds may select heavier items to take to the nest and consume smaller items themselves has generally been little tested (Houston & McNamara 1985, Sodhi1992, Sonerud 1992). Thus for most studies it is not known if bias in the sex of prey stored at the nest is equivalent to bias in prey actually caught. This paper tests for such bias in the Barn Owl by comparing prey delivered by males and stored at the nest in spring with remains in pellets at the nest and with prey consumed by the males. Pairs of owls were selected in which males roosted separately from the nest enabling their prey consumption to be assessed from pellets at their roosts.

Optimal foraging theory predicts that as the preferred prey becomes less abundant the birds should switch to less profitable prey (Houston & McNamara 1985). Field voles were strongly cyclic in the study area (Taylor 1994). Thus if selection for male voles was based only on their greater body mass it might be predicted that more females should be taken during vole crash years. This was tested by examining the sex of prey taken by all pairs of Barn Owls in the study area over several vole cycles. Also, if selection was based on the higher vocalisation rates of males in spring, the selection should be less evident in winter when the aggressiveness of male voles is less. This was tested by collecting pellets at winter roost sites and comparing

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the sex ratio of vole remains in them with that in pellets collected in spring.

In addition to examining preferences within species an assessment was made of the relative predation rates by Barn Owls on two species, Field Vole and Wood Mouse *Apodemus sylvaticus*, where they occurred in the same habitat, by comparing the proportions of each species available with the proportions taken by the owls. Wood Mice have much better developed visual and auditory senses than Field Voles and are also much more agile. They should be better able to detect hunting Barn Owls and to take more effective evasive action when attacked and so would be predicted to have a lower susceptibility to predation by the owls.

METHODS

Study area

The study was conducted within the catchments of the Rivers Esk and Liddle (1600 km^2) in southern Scotland (55°05'N, 3°10'W). At lower altitudes pastoral farming for dairy and sheep production predominated while at higher altitudes land use was either open range sheep farming on rough upland pastures or forestry plantations of exotic conifers, especially of Sitka Spruce Picea sitchensis. Even-aged plantations typically covered many thousands of hectare blocks on former sheep rangeland. Exclusion of livestock and fertiliser application resulted in essentially a long grassland habitat until the trees reached the age of about 6–8 years, providing excellent habitat for small mammals. The lower altitude farmland characteristically had small fields of pasture, silage and hay bounded by hedges or fence lines, and many small woodlands. Suitable small mammal habitat was restricted mainly to field edges, especially between fence lines and woodlands.

Throughout the study area Barn Owls nested and roosted in the many disused farm buildings throughout the study area that had been abandoned following farm amalgamations to achieve greater economic efficiency during the 1960s and early 1970s and during the afforestation of upland areas.

Sex and size of voles taken in spring

The study was done in two extensive areas of 2–4 year old plantations of Sitka Spruce over periods of 3–4 weeks in spring when the female owls were brooding small chicks and all of the food for females and young was provided by the males. Six pairs of Barn Owls were studied in 1982 and four pairs in 1984, all of which nested in abandoned farm buildings. Pairs were selected for which previous study had demonstrated that males roosted consistently on roof beams at sites in buildings away from the nest site. These sites were not used by the females during the study period. At the start of the study all old pellets were removed from the males' roost sites to ensure that only pellets produced during the study period were included in the analysis. Roosts were visited every five days to collect pellets. Nest were visited every four days in the early morning and all stored prey were identified, sexed and weighed, and all fresh (wet or moist) pellets collected. Stored prey were fur-clipped to avoid counting the same individuals twice.

Sampling of Field Vole populations was conducted during the same period over which stored prey and pellets at nests were examined. In each of the two study areas, grids of traps measuring 30 x 50 m were set up. Two traps were set at each trapping station at intervals of 10 m across the grid such that the entire grid contained 48 traps. Traps were metal snap traps painted matte black and modified with a metal plate measuring 6 x 5 cm to operate the release mechanism and adjusted so that it could be triggered by weights down to about 6–7 g running across the treadle. The traps were laid across vole runways so that the treadle plate lay at the level of the runway floor. At each trapping station the two traps were laid randomly within a 2 m radius of the central point of the station. The grids were visited daily and all trapped voles removed. Trapping continued until no new voles had been caught for two days so that trapping usually lasted for six or seven days.

Vole remains in pellets collected from nests in spring were sexed using marked differences in the shapes of male and female pelvic bones (Clevedon Brown & Twigg 1969, a method also used by Longland & Jenkins (1987) to analyse Great Horned Owl *Bubo virginianus* pellets.

Relationships between dentary lengths and body mass of trapped voles were quantified to enable the body mass of voles to be estimated from dentaries in pellets.

To test if any sex bias in the prey taken by the owls varied in relation to the density of voles available pellets were collected from nests of all breeding pairs in the study area in spring and early summer each year between 1980 and 1993 and compared with an index of vole abundance obtained by trapping each year (Taylor 1994).

Sex of voles taken in winter

Pellets were collected from roosts in disused farm buildings and haysheds during December and January over several years. Old pellets were cleared from sample

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sites at which both males and females of pairs roosted, or separate sites if they roosted apart, before the start of December to ensure that those collected and analysed were winter pellets. The sex of voles was determined from their pelvic bones.

Temporal patterns of prey deliveries

The temporal pattern of delivery of prey items to the nest could be important in understanding any selectivity shown by the owls. In the study area breeding Barn Owls started hunting up to four hours before sunset and at most nests there was a peak of delivery of prey to nests in the two hours before sunset. Thus it was possible to observe the male owls hunting and quantify whether they consumed prey themselves or took it to the nest. During spring and summer of 1984, five male owls in farmland habitat were fitted with tail-mounted transmitters. They were tracked from leaving their roosts to begin hunting for the evening and for complete foraging trips and delivery back to the nest. Each male was followed for an average of 3–4 hours each evening, using 2–3 observers with receivers in cars and moving around a good network of farm tracks over the area. Mostly the birds could be kept under direct observation except for brief periods of a few minutes when they flew across woods to forage on the other side. They tended to be quite predictable in their foraging areas so that after preliminary observations such movements could be anticipated and observers were stationed to almost eliminate periods when owls were out of view.

Selection for prey species

A comparison of preference between Field Voles and Wood Mice was done in an area of enclosed farmland supporting five breeding pairs of Barn Owls in the spring of 1984. In this habitat the owls hunted almost exclusively along field edges and the study pairs had been radio-tracked the previous year to establish preferred feeding areas for each (Taylor 1994). For each pair of owls a section of the field edge that was used most for hunting was selected for small mammal trapping. In all cases the edges were 4–5 m wide and consisted of grassland mostly 15–100 cm tall, separated from adjacent pastures by fences and with either Norway Spruce *Picea abies* or mixed conifer/deciduous woodland on the other side. Comparing the abundances of different small mammal species by trapping may present difficulties as species may have different susceptibilities to be caught. To reduce such errors and improve the validity of estimates the removal method described by Zippen (1956, 1958) was used and compared with the totals actually trapped. Lines of treadle-operated traps were set along the edges with 20 trapping stations 10 m apart and two traps set within 2 m of each other at each station. Traps were baited with rolled oats and two days of pre-baiting were used before setting the traps. Traps were operated for seven nights and all trapped animals removed each morning. During the 10 days prior to trapping at each site all fresh pellets at the nests and male roosts were collected by visits every third day.

RESULTS

Selection for sex and size of voles

In spring, the sex ratio of prey stored at the nest differed significantly from the sex ratio of voles caught by trapping, showing a strong male bias in both years (1982, $\chi^2_1 = 26.8$, $P < 0.001$; 1984, $\chi^2_1 = 50.0$, $P < 0.001$), as did that in pellets taken from the nest in 1984 ($\chi^2_1 = 79.1$, $P < 0.001$). In both years about 90% of voles stored at the nest were males, whereas there was a slight female bias in trapped voles (Fig. 1). The sex ratio of voles in pellets at the nest in 1984 did not differ significantly from that of stored voles ($\chi^2_1 = 0.15$, ns) and also the ratio in pellets taken from male roosts did not differ from that in pellets taken from the nests ($\chi^2_1 = 0.46$, ns, Fig. 2). Combining data for trapping from both years, the mean weights of male voles trapped was 23.4 ± 0.5 g ($n = 58$) and of females was 18.5 ± 0.4 g ($n = 70$).

In both years the body masses of male voles taken by the owls and delivered to the nest were significantly greater than those of voles taken in the traps (1982: owls, mean 28.3 ± 0.5 g, $n = 52$; traps, mean 21.9 ± 0.6 g, $n = 21$, $F_{1,76} = 53.1$, $P < 0.001$; 1984: owls, mean 29.7 ± 0.3 g, $n = 116$; traps, mean 24.3 ± 0.8 g, $n = 37$, $F_{1,151} = 63.1$, $P < 0.001$, Fig. 3). Trapped voles ranged down to 16 g whereas the minimum delivered to nests was 24 g. The mean weights of male voles from pellets at male roosts in 1984, estimated from dentary lengths, did not differ significantly from those in pellets at nests (male roosts: 29.1 ± 0.7 g, $n = 106$; nests, 29.6 ± 0.2 g, $n = 227$).

In winter the sex ratio of voles in pellets at male and female Barn Owl roost sites did not show the strong male bias that was evident in spring (Table 1).

Between 1980 and 1993 there were four complete vole cycles in the study area. Over this period the proportion of male voles in prey stored at the nests for all owl pairs in the study area combined did not vary in relation to vole abundance in the field ($R^2 = 0.10$, $P = 0.30$, $n_{\text{years}} = 13$, $n_{\text{prey items}} = 3729$).

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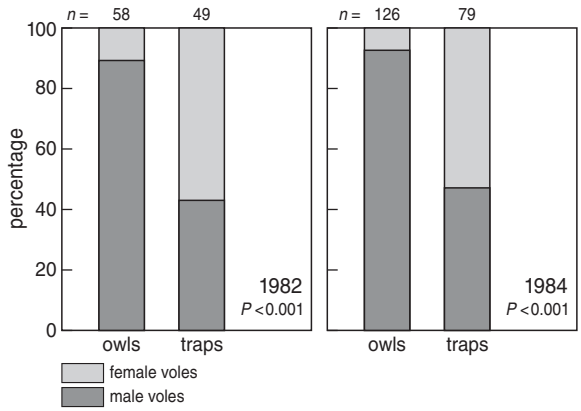


Figure 1. The sex ratio of Field Voles stored at the nests of Barn Owls during spring compared with the ratio among trapped voles. Sample sizes given above columns.

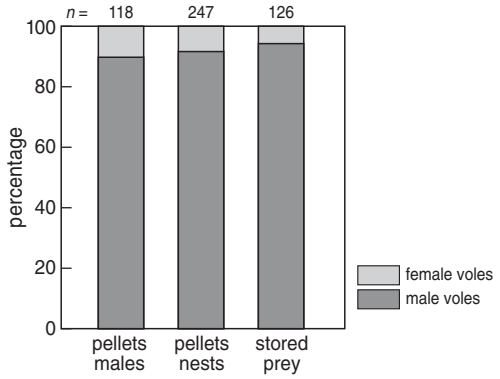


Figure 2. Comparison of the sex ratio of Field Voles from prey stored at Barn Owl nests, among pellets collected from nests and among pellet, collected at roost sites of males. Sample sizes given above columns.

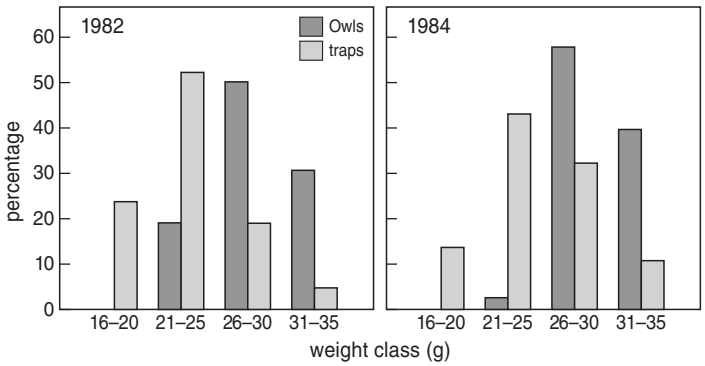


Figure 3. The distribution of weights of male Field Voles among prey stored at nests compared with that of trapped male voles.

Table 1. Comparison of the sex ratio of Field Voles in pellets collected at nests and roosts of Barn Owls in spring (April–May) and in winter (December–February).

Season	Percent male voles	Percent female voles	Number of years sampled	Number of items sampled	Number of owl pairs sampled
Spring	89.6	10.4	14	3729	293
Winter	52.4	47.6	5	1568	28

Diurnal patterns of prey deliveries

When providing food for their mates and young chicks the radio-tracked male Barn Owls took all of the first 7–8 prey they caught to the nest. Only after this did they consume some of the items themselves. There tended to be a short period when males consumed 1–3 prey items themselves, followed by a resumption of delivery to the nest but at a lower rate than earlier in the evening (Fig. 4).

Selection for prey species

The extrapolated population sizes for Field Voles and Wood Mice estimated from the removal method (Zippen 1958) did not differ significantly from the total cumulative numbers of animals captured. There may have been two reasons for this. The proportion of traps released by small mammals was low (15.2% over the whole trapping period, 255 animals trapped from 1680 trap nights) suggesting that individuals were not

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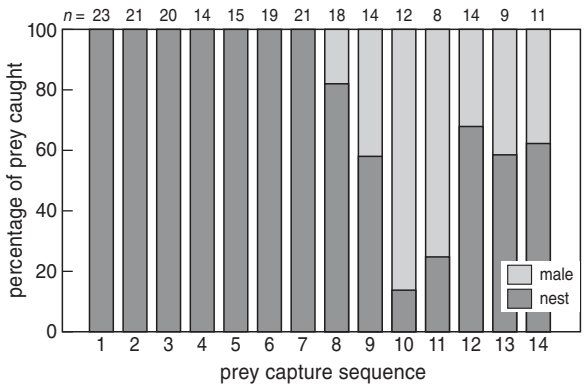


Figure 4. The sequence of foraging decisions made by breeding male Barn Owls during the evening's hunting in spring and early summer. The graph shows the fate of prey items caught by the owls from the start of hunting until darkness prevented further observations. Items were either taken to females and chicks in the nest or eaten by the males.

excluded because of trap saturation. Also very few animals were caught after the fourth day of trapping suggesting that the population was close to being trapped out. For simplicity, the actual proportions of the two species trapped rather than the estimated numbers from the removal method were therefore used for statistical comparison with the proportions taken by the owls. Koivunen *et al.* (1991b) also concluded for similar reasons that the numbers of different species trapped were an adequate representation of their relative abundance in the field.

For each pair of owls the proportions of voles and mice caught by the owls, assessed from prey remains in pellets, differed significantly from the proportions available in the field assessed by trapping (paired *t*-test, $t = 7.93$, $P = 0.001$, Table 2). All pairs showed a strong preference for Field Voles compared with Wood Mice.

Table 2. Comparison of the ratio of Field Voles to Wood Mice in pellets collected at the nests and roosts of five pairs of Barn Owls in spring with the ratio among animals trapped over the same period.

Pair	Prey remains	*n*	Traps	*n*
1	1.72	98	0.36	42
2	1.38	112	0.61	58
3	1.81	135	0.51	37
4	2.0	78	0.27	47
5	2.14	116	0.45	29

DISCUSSION

It is usually difficult to assess the true sex ratio in populations of small mammals as trapping frequently results in an excess of males, which is often attributed to their greater mobility and home range size compared with females (Myllymäki *et al.* 1971, Korpimäki 1981, Bujalska 1989, Koivunen *et al.* 1996a, b). The sex ratio of Field Voles trapped in this study was closer to unity. This may have been caused by several factors. At the time of the study females had only just started breeding so may not have had such a strong reduction in their activity. Compared with most previous studies the density of traps was higher and on all trapping days far exceeded the number of animals caught, and the number of days of trapping was longer, all of which would have increased the chances of females being caught. Nevertheless, regardless of the difficulties of establishing the sex ratio of animals at risk to be captured, the bias towards male voles in stored prey and in pellet remains compared with trapped animals was too extreme to be accounted for by errors in sampling the natural populations.

The male bias in Field Voles stored at nests did not result from differential selection of prey delivered to the nest compared with those consumed directly by foraging male Barn Owls during central place foraging but was an accurate representation of the prey caught by the males. It is possible that the body mass difference between male and female voles was not great enough for such differentiation; previous studies have shown that male birds of prey tend to consume only very small prey themselves (Sonerud 1992). However, the prey delivery behaviour, in which there was a partial separation of periods of hunting for chick provisioning from periods when the males consumed prey themselves, would have masked any potential detection of prey segregation. The behaviour of the males in taking all prey caught during the first 7–8 successful hunts of each evening directly back to the nest may simply have been a prioritisation of chick provisioning but it might also have been a deliberate strategy to enhance their foraging efficiency. Had they consumed prey themselves at the start of the evening's hunting they would have increased their body mass by about 9% for each vole eaten which may have reduced their flight efficiency and agility in prey capture.

The very high percentage of male voles in prey caught by Barn Owls could have resulted from optimal foraging behaviour; selecting males because they were heavier on average than females. Had this been the only explanation it was predicted that selection for

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males should have decreased when vole populations crashed and the abundance of the preferred prey (male voles) was reduced. However, selection for male voles was independent of overall vole densities during all stages of the vole cycle. This suggests that the selection for male voles was most likely a result of a greater encounter rate compared with female voles rather than the difference in body mass. Male Field Voles are strongly territorial in spring with associated higher vocalisation rates and greater mobility than female voles (Clarke 1956, Myllymäki 1977, Viitala 1977, Norrhahl & Korpimäki 1998). For a species such as the Barn Owl that hunts mainly using acoustic cues, prey vocalisation and mobility rates could both contribute to encounter rates and in reality it is impossible to distinguish between them. The absence of selection for male voles during winter when the voles were not breeding and aggression levels of males lower also supports the suggestion that the size difference between males and female voles was not the main reason for the biased sex ratio in the prey taken in spring. A shift from male-biased predation during the breeding season to an absence of such bias during the non-breeding season has also been recorded in Kangaroo Rats *Dipodomys merriami* (Daly *et al.* 1990).

Within the male voles taken by the Barn Owls in spring there was also a strong selection for larger males. Again it is unlikely this selection was based on size *per se*. Large male voles are much more likely to be territory owners and to be involved in more noisy territorial conflicts during the breeding season than are smaller males (Turner & Iverson 1973).

The lack of male bias among voles taken during winter raises some interesting questions about the efficiency of the owls' foraging in winter. If, as is suggested here, the mobility and noise produced by voles is important in determining the rates at which Barn Owls encounter prey, it follows that their encounter rates and hence their foraging efficiency should be lower during winter. This could be an important contributor to the higher mortality rates the owls experience during winter (Taylor 1994).

Taylor (1994) suggested the higher predation rate on male voles was a cost of territory defence and associated greater noise production and activity in males, a suggestion repeated by Christe *et al.* (2006) using a wider range of examples. However both of these studies relied on the untested assumption that prey remains stored at nests were representative of the total prey caught. The present study has established that such prey remains are indeed representative of the prey caught by Barn Owls and confirms the suggestion that avian predators are a cause of selective mortality of male small mammals. Christe *et al.* (2006) suggested that such sex-biased predation by avian predators may explain the shorter life span of many male animals. However, in doing so they failed to take into account the much higher predation rates on female small mammals caused by mammalian predators such as Least Weasels *Mustela n. nivali* which hunt mainly by sight and scent and can capture female voles in nests and burrows (Norrdahl & Korpimäki 1998).

The bias towards male Field Voles taken by Barn Owls in this study was considerably greater than that found in Field Voles taken by Tengmalm's Owls (Koivunen *et al.* 1996a) and in other small rodents taken by Tawny Owls *Strix aluco* (Southern & Lowe 1968, Christe *et al.* 2006). Also, the strong bias towards larger males did not occur in Tengmalm's Owls, which on average caught individuals that were smaller than those taken by trapping. These differences may reflect the different hunting techniques and habitats of the different owls. Tengmalm's Owls and Tawny Owls hunt almost exclusively from low perches in forested or treed habitats (Southern 1954, Southern & Lowe 1968, Norberg 1970), whereas in the present study area Barn Owls hunted mainly in flight, taking prey from long grassland habitats (Taylor 1994). It seems likely that the amount of noise or movement made by the prey would be particularly important in prey detection by flight hunters, especially when prey are hidden in long grassland. In such circumstances predation might be concentrated especially strongly on the most vocal component of the vole population: the large territorial males. This idea is perhaps supported by the much lower bias towards males shown by Barn Owls when capturing Common Voles, *M. arvalis*, a species that occurs more often in short grass habitats (Christe *et al.* 2006). Owls hunting from perches should be able to detect more subtle cues from potential prey and may thus be less dependent on the high noise production of male small mammals. The susceptibility of male small mammals to avian predation may vary depending on the hunting methods of the predator and the general habitat type (forest vs. grassland) and on the species of species of mammal and its specific habitat preferences, especially in relation to vegetative cover.

Barn Owls in farmland showed a strong preference for Field Voles compared with Wood Mice. This was not based on the relative profitability of the two species in terms of body mass as their mean masses did not differ significantly. Nor was it based on habitat differences between the species as the owls hunted almost exclusively in long grassland field margins (Taylor 1994),

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the habitat in which the relative abundances of the two species were assessed in this study. Similar preferences for voles compared with mice of various species have been shown in several studies and seems to be a widespread phenomenon (Marti 1974, Colvin 1984, Nishimura & Abe 1988, Derting & Cranford 1989). However in all of these studies the body mass of the voles was about twice that of the mice so that the relative profitability based on body mass of the different species covaried with any morphological and behavioural differences that might have affected their relative predation risk. This was not the case in the present study as the body masses of the two prey species were similar, and the low predation risk experienced by Wood Mice was probably attributable to differences in their sensory capabilities and mobility. Compared with Field Voles they have larger eyes and ear pinnae so are probably better able to detect the approach of owls and their longer, more powerful hind legs enable them to jump to avoid predators. It is not known if Barn Owls are capable of distinguishing between the vocalisations of Wood Mice and Field Voles and if the low predation on the mice occurred because Barn Owls avoided attacking them once detected or if when attacked mice were simply better able to avoid capture. It seems likely that Barn Owls should be able to distinguish between prey species as they can learn to distinguish between closely similar sound frequencies and between complex noise spectra in the laboratory (Quine & Konishsi 1974, Konishi & Kenuk 1975). However, this remains to be tested and it would also be interesting to learn if they can distinguish between sexes and age classes within species.

Conclusion

The selection of large male voles by Barn Owls in spring is unlikely to have represented an optimal foraging strategy based on the difference in prey mass between male and female voles. Rather, it probably represented a difference in encounter rates resulting from the greater activity and/or noise made by large male voles compared with females and smaller males. By contrast, the interspecific preference shown for Field Voles compared with Wood Mice was most probably a result of a greater ability of the mice to detect the approach of the owls or a greater agility which enabled a more effective escape response. It is not known if attack rates towards mice were less than those towards voles based on experience of expected capture success.

ACKNOWLEDGEMENTS

This work was funded by grants from the Natural Environment Research Council, World Wide Fund for Nature and The University of Edinburgh. I am grateful to those who helped in the field and the laboratory, especially Tom Irving, Aleem Chaudhary, Peter Bell, Mairi Osborne, Fiona Slack, Ian Langford and Donna Kreft. I would like to thank David H. Johnson for his valuable comments on the draft.

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SAMENVATTING

In het onderhavige onderzoek is de geslachtsverhouding bepaald van Veldmuizen *Microtus agrestis* die Kerkuilen *Tyto alba* vingen. Mannetjes Kerkuilen brachten meer mannetjes dan vrouwtjes Veldmuizen naar het nest om hun partner en kleine jongen te voeren. Dit verschil bleek zowel uit de prooien die bij het nest lagen als uit de skeletresten in braakballen die uit het nest waren verzameld. Een zelfde verschil was zichtbaar in de braakballen die op de slaapplaats van de mannetjes waren verzameld. Dit laat zien dat de verschillen al optraden op het moment van vangen en dat ze niet het gevolg waren van selectie door mannetjes van wat ze zelf opaten en wat naar het nest werd gebracht. In tegenstelling tot de vangsten door de uilen liet de verhouding van de seksen bij de Veldmuizen die in het veld met vallen werden gevangen juist een licht overschot aan vrouwtjes zien. Het gemiddelde gewicht van met vallen gevangen Veldmuizen was 23,4 (SE 0,5) g (mannetjes) en 18,5 (SE

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0,4) g (vrouwtjes). Gedurende de winter werden evenveel mannetjes als vrouwtjes Veldmuizen gevangen. Deze waarnemingen zijn een aanwijzing dat mannetjes Veldmuizen door een verhoging van hun agressie of activiteit in verband met territoriaal- en voortplantingsgedrag dan gemakkelijker te pakken zijn door uilen. Dit zou betekenen dat de selectie voor mannetjes Veldmuizen het gevolg was van een betere vangbaarheid van de mannetjes en niet van een hogere aantrekkelijkheid door hun hoger gewicht. In het voorjaar vingen de uilen meer Veldmuizen dan Bosmuizen *Apodemus sylvaticus* dan te verwachten op grond van het relatieve voorkomen van de twee soorten in het veld. Er wordt verondersteld dat dit voortkwam uit het beter vermogen van de Bosmuis om uilen op te merken en een snellere wendbaarheid om uit de klauwen van uilen te blijven.

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World Owl Conference Special

Editors – David H. Johnson, Dries Van Nieuwenhuyse and James R. Duncan, in cooperation with Jouke Prop and Rob G. Bijlsma

Technical editor – Jouke Prop

Dutch summaries – Arie L. Spaans, Dries Van Nieuwenhuyse, Jouke Prop, Rob G. Bijlsma, or authors

Graphs and layout – Dick Visser

Drawings – Jos Zwarts

Cover photos - Serge Sorbi
front – Snowy Owl
back – Snowy Owl, Great Grey Owl and young Tengmalm's Owl

Production – Hein Bloem, Johan de Jong and Arnold van den Burg

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Printed by Van Denderen, Groningen, The Netherlands, December 2009

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