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DIET CHANGES IN BREEDING TAWNY OWLS (*Strix aluco*)

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ABSTRACT.—I examined the contents of Tawny Owl (*Strix aluco sylvatica*) pellets, between April 1977 and February 1978, in mixed woodland and gardens in northeast Suffolk, England. Six mammal, 14 bird and 5 invertebrate species were recorded in a sample of 105 pellets. Overall, the Wood Mouse (*Apodemus sylvaticus*) was the most frequently taken mammal prey and the House Sparrow (*Passer domesticus*) was the most frequently identified bird prey. Two types of seasonal diet change were found; first, a shift from mammal prey in winter to bird prey in the breeding season, and second, a shift from small prey in the winter to medium-sized (>30 g) prey in the breeding season. Contrary to some findings elsewhere in England, birds, rather than mammals, contributed significantly to Tawny Owl diet during the breeding season.

Cambios en la dieta de búhos de la especie *Strix aluco* durante el período de reproducción

EXTRACTO.—He examinado el contenido de egagrópilas del búho de la especie *Strix aluco sylvatica,* entre abril de 1977 y febrero de 1978, en florestas y huertos del noreste de Suffolk, Inglaterra. Seis mamíferos, catorce aves y cinco especies invertebradas fueron registrados en una muestra de 105 egagrópilas. En el total, entre los mamíferos, el roedor *Apodemus sylvaticus* fue el que con más frecuencia fue presa de estos búhos; y entre las aves, la presa identificada con más frecuencia fue el gorrión *Passer domesticus.* Dos tipos de cambio en la dieta estacional fueron observados: primero, un cambio de clase de presa: de mamíferos en invierno a la de aves en la estación reproductora; y segundo, un cambio en el tamaño de las presas: de pequeñas en el invierno a medianas (>30 g) en la estación reproductora. En contraste con hallazgos realizados en otras partes de Inglaterra, las aves, en vez de los mamíferos, contribuyeron significativamente a la dieta del *Strix aluco sylvatica* durante las estación reproductora.
[Traducción de Eudoxio Paredes-Ruiz]

The diet of many owl species is influenced by habitat and season (e.g., Marti 1974, Yalden 1985, Mikkola 1983). Among sedentary "generalist" species, Tawny Owls (*Strix aluco sylvatica*) inhabiting deciduous woodland in England preyed on Bank Voles (*Clethrionomys glareolus*) and Wood Mice (*Apodemus sylvaticus*) in winter, but switched to Moles (*Talpidae*), young Rabbits (*Oryctolagus cuniculus*), Cockchafers (*Melolontha melolontha*) and earthworms (*Lumbricina*) in summer (Southern 1954, 1969). In urban or other open habitats, birds may form important components of Tawny Owl diet (e.g., Harrison 1960, Beven 1965, Yalden and Jones 1971, Glue 1972), but these have generally been aggregated in analyses so that the seasonal importance of different species or size classes cannot be investigated.

Few data exist with regard to Tawny Owl diet in discontinuous woodland habitats, where prey species and hunting techniques may differ from that of owls inhabiting larger forest tracts (Nilsson 1978). In this paper, I report on seasonal variation in the diet of Tawny Owls from a site in south-eastern England in relation to breeding and possible changes in prey selection or availability. Because Tawny Owls disgorge pellets before roosting (Guérin 1932), pellets are scattered throughout territories, making them difficult to find. However, in this study sufficient numbers of pellets were found by intensive searching and knowledge of roost sites of individual owls.

STUDY AREA AND METHODS

This study was carried out between April 1977 and February 1978 at Herringfleet, north-east Suffolk, in a 0.06 km^2 woodland dominated by Scots Pine (*Pinus sylvestris*), with mixed woods of birch (*Betula pendula*), oak (*Quercus robur*), rowan (*Sorbus aucuparia*), maple (*Acer platanoides*) and ash (*Fraxinus excelsior*), interspersed with large gardens. Marshes used for grazing and reedbeds (*Phragmites australis*) occur along a river to the west and

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Table 1. Total numbers and percentage contribution by weight of prey species recovered in Tawny Owl pellets, during and outside the breeding season (April–August; non-breeding season September–February).

	Breeding Season			Winter Season		
Prey Species	No.	Weight (g)	% Weight	No.	Weight (g)	% Weight
Common Shrew *Sorex araneus*	0	0	0	1	8	0.3
Wood Mouse *Apodemus sylvaticus*	4	72	4.4	34	612	20.7
Field Vole *Microtus agrestis*	0	0	0	14	294	10.0
Bank Vole *Clethrionomys glareolus*	1	16	1.0	29	464	15.7
Rabbit *Oryctolagus cuniculus*	1	100	6.1	0	0	0
Norway Rat *Rattus norvegicus*	3	180	10.9	4	240	8.1
Kestrel *Falco tinnunculus*	1	220	13.3	0	0	0
Wren *Troglodytes troglodytes*	0	0	0	1	8	0.3
Dunnock/Robin *Prunella modularis/Erithacus rubecula*	1	20	1.2	1	20	0.7
Blackbird/Song Thrush *Turdus merula/T. philomelos*	7	599	36.3	3	257	8.7
Redwing/Starling *Turdus iliacus/Sturnus vulgaris*	0	0	0	5	368	12.5
Coal Tit/Blue Tit *Parus ater/P. caeruleus*	0	0	0	4	48	1.6
Jay *Garrulus glandarius*	1	161	9.8	0	0	0
Starling *Sturnus vulgaris*	2	164	9.9	0	0	0
House Sparrow *Passer domesticus*	0	0	0	12	294	10.0
Chaffinch *Fringilla coelobs*	0	0	0	2	49	1.7
Greenfinch *Carduelis chloris*	0	0	0	2	52	1.8
Small bird (unidentified)	5	100	6.1	10	200	6.8
Dor beetle *Geotrupes stercocarius*	0	0	0	30	30	1.0
Dung Beetle *Typhaeus typhoeus*	13	13	0.8	6	6	0.2
Cockchafer *Melolontha melolontha*	4	4	0.2	0	0	0
Beetles Carabidae	0	0	0	4	0.4	0.01
Earthworms Lumbricidae	1	0	0	34	0	0
Total	43[a]	1649		162[a]	2950	

[a] Excluding earthworms.

farmland to the east. Exotic shrubs such as rhododenron (*Rhododendron* spp.) and laurel (*Prunus laurocerasus*) provide roosts for small birds during winter.

I collected pellets at weekly intervals at roosts in 2–3 ha of mature Scots Pine in two large wooded gardens. Of the 105 pellets, 77% were collected during the first 5 mo, the remaining 23% were collected between September and February. One pair of Tawny Owls nested in a nestbox, approximately 300 m from the roost sites used for pellet collection. However, few pellets were found beneath the nestbox. The principal source of pellets was from this pair of owls but due to territorial infringements some pellets might have been from other individuals (territories in discontinuous woodland in Wytham averaged 22 ha; Hirons 1985). I collected up to 16 pellets per week from October–February (21% of pellets cast by owls, assuming 1.27 pellets/day are produced in winter; Lowe 1980), but between April and September relatively few pellets (1–6 per week) were found (6% of pellets cast, assuming 1.03 pellets/day are produced in summer) for the reasons described by Southern and Lowe (1968).

Mammal remains were identified to species by dental and cranial features (Yalden 1977), while birds were identified by comparing skulls or bills with reference skeletons collected locally. Other remains used to identify birds were feet, pelvises, gizzard size and feathers in the pellet matrix. The number of individuals represented was determined by counts of skulls, jaws or pelvises for mammals, and skulls, mandibles and long bones for birds as suggested by experiments with Tawny and other owl species (Short and Drew 1962, Raczyński and Ruprecht 1974).

Coleoptera were identified by elytra striations and chitinous remains. Earthworms were identified by chaetae and I estimated earthworm numbers by the proportion of fibrous material and sand in pellets (Southern 1954). Estimates of earthworms were excluded from table totals because they were not comparable with counts of other prey. Average weights of bird species were calculated by the length of humeri recovered in pellets using the regression equation; log weight = (2.706 × log humerus length) − 2.062 (Yalden 1977) or by using average weights in Hickling (1983, Appendix 12). I used data in Yalden (1977, 1985) for weights of small mammals and Coleoptera.

Results and Discussion

I recorded 6 mammal, 14 bird and 5 invertebrate species in the 105 pellets examined (Table 1). Of a total of 204 prey items recovered from pellets (ex-

cluding earthworms), 45% by number were mammals. Wood Mice predominated (19%), followed by Bank Voles (15%) and Field Voles (7%). Birds comprised 28% of total prey; birds smaller than 30 g estimated body weight contributed 19%. Of the species identified, House Sparrows (6%) and thrushes (*Turdus* spp. 5%) were most important. Numerically, Coleoptera represented 30% of total diet. By weight, mammals formed 43% and birds 56%, respectively. European Blackbirds and Song Thrushes were most important by weight (19%), followed by Wood Mice (15%), Bank Voles (10%) and Norway Rats (9%). The contribution of Coleoptera by weight was negligible.

Significantly more birds than mammals were taken between April–August than between September–February ($G = 8.08$, $P < 0.005$), suggesting a switch from small rodents to birds during the breeding period. Also, significantly more medium-sized than small vertebrate prey were taken by owls during the breeding season than in autumn and winter when the converse was true ($G = 24.29$, $P < 0.001$; Table 2). Similar results were found when bird prey were considered separately ($G = 8.57$, $P < 0.005$), although the total biomass intake of small and medium-sized birds was similar between the breeding and non-breeding season (Table 2). The weight of vertebrate prey was significantly higher in the breeding than the non-breeding season (breeding season $\bar{x} = 62.8$ g, SE = 9.7, $N = 26$; non-breeding $\bar{x} = 23.9$ g, SE = 1.5, $N = 122$; Mann Whitney U test, $Z = 4.473$, $P < 0.001$), but no difference was found when invertebrates were included.

During the breeding season, thrushes, European Starlings, Jay, and Eurasian Kestrel together contributed 69% of the diet by weight. Wood Mice and Bank Voles comprised only 5%. In winter, Wood Mice, Bank Voles, Field Voles and Common Shrews accounted for 47% of the diet by weight. Small birds (e.g., House Sparrows) comprised 23% of the winter diet by weight (Tables 1 and 2). Earthworms were taken mostly in the non-breeding season, particularly in October and December, probably due to the wet conditions in these months resulting in increased availability of earthworms. The importance of earthworms was probably greatly underestimated since I did not weigh the granular content of pellets as recommended by Yalden (1985). Two species of dung beetles (*Geotrupes stercocarius* and *Typhaeus typhoeus*) were also taken in large numbers. *Geotrupes* occurred in pellets most frequently in autumn and winter, showing that Tawny Owls foraged over marshes where there were cattle. *Typhaeus* was most commonly taken in the summer (Table 1). Cockchafer beetles were found in pellets from June and July, the period of emergence for this species.

Table 2. The contribution of different-sized prey in Tawny Owl diet during and outside the breeding season (percentage figures refer to weight of prey items in grams).

	Breeding Season (24 Pellets)		Winter Season (81 Pellets)	
	No.	% Weight (g)	No.	% Weight (g)
Small mammals	5	5.3	78	46.7
Medium-sized mammals	4	17.0	4	8.1
Small birds	6	7.3	32	22.7
Medium-sized birds	11	69.4	8	21.2
Invertebrates[a]	18	1.0	44	1.2
Total number	43		166	
Total weight		1649		2950

[a] Excluding earthworms.

A shift from small to larger (mammal) prey in Tawny Owl diet during the breeding season was also found in Derbyshire, England, but in contrast to my study bird prey was most important in the 'winter' season (Yalden 1985, Table 2). Increased weight of prey taken by Tawny Owls during the breeding season was suggested by Nilsson (1984) in Sweden, and by Southern (1954) in Oxfordshire, England. However, in the latter study owls apparently did not prey on abundant fledgling passerines.

The increase in medium-sized (often fledgling) bird prey in this study during the breeding season suggested that Tawny Owls might selectively take larger prey when they have chicks, as noted by Mikkola (1983, Table 26) and as documented in some Common Barn Owl (*Tyto alba*) pairs (Buckley and Goldsmith 1975). Southern (1969) also recorded diet changes in Wytham owls when their young were half-grown and no longer brooded. Tawny Owls are sexually dimorphic, and the larger size of females (26% heavier than males; Hardy et al. 1981) might allow them to select larger prey than the male (for other owl species see Earhart and Johnson 1970, Mikkola 1983), especially when they have limited hunting time due to demands from their chicks. Also, individual Tawny Owls can specialize on particular prey types, so perhaps the female owl in this study selectively took large bird prey at this time. Conversely, more small birds were found in winter pel-

lets probably as a result of owls feeding on communally roosting birds as occurs in Long-eared Owls (*Asio otus*; Glue and Hammond 1974).

Prey availability for Tawny Owls is determined by ground cover (Southern and Lowe 1968) which may account for seasonal change in the diet of Tawny Owls at Herringfleet. Dense vegetation cover (especially Bracken *Pteridium aquilinum*) in summer could prevent owls from locating small mammal prey. Conversely, dieback of vegetation in autumn may mean that small rodents are more vulnerable to owl predation. Rodents might make more noise moving through leaf litter on the ground in autumn and winter and thus be more easily located by foraging owls. The fact that a major prey species, the Wood Mouse, spends less time foraging outside the nest in winter on moonlit nights (Wolton 1983) also indicates that small mammals are more vulnerable to Tawny Owl predation in the winter season. Thus, changes in vegetation cover could account for the abundance of small rodents in Tawny Owl diet at Herringfleet during the winter season.

My results suggest one, or a combination of factors in the apparent diet shift; 1) small mammals were more vulnerable to owl predation outside the breeding season; 2) owls switched, opportunistically, to fledgling birds during the breeding season because they were easier to catch or 3) medium-sized birds were taken selectively by owls because they were more 'profitable' prey (with a higher nutrient intake per handling time) than rodents, during the period when owls had dependent young.

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