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The impact of predation by birds on bat populations in the British Isles

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ABSTRACT

The role played by predation of birds in the mortality of British bats is assessed. A review of dietary studies and anecdotal accounts revealed eleven species of bird which occasionally feed on bats—Herring Gull *Larus argentatus*, Black-headed Gull *Larus ridibundus*, Rook *Corvus frugilegus*, Carrion Crow *Corvus corone*, Little Owl *Athene noctua*, Short-eared Owl *Asio flammeus*, Kestrel *Falco tinnunculus*, Hobby *Falco subbuteo*, Merlin *Falco columbarius*, Peregrine *Falco peregrinus* and Sparrowhawk *Accipiter nisus*. A further three species feed more frequently on bats—Barn Owl *Tyto alba*, Tawny Owl *Strix aluco* and Long-eared Owl *Asio otus*. Rates of predation were very low accounting for only 0·0034% of items taken by small hawks and falcons (*n* items = 29 519) but 0·035% of prey taken by owls (*n* items = 99 479). By multiplying together the average annual prey capture rates of the predators, assessed from their energetic food requirements and direct observations of prey intake rates, the British populations of the predators and the contribution to the diet made by bats, the annual number of bats which die each year as a result of predation was estimated. The total losses of bats to predation might amount to about 201 400 bats/annum. The most significant predators are Tawny Owl (*c.* 168 850 bats/annum), Barn Owl (*c.* 8800 bats/annum), Long-eared Owl (*c.* 10 200 bats/annum) and Kestrels (*c.* 8400 bats/annum). This predation by avian predators would account for about 11% of the annual mortality of British bats. An assessment of the biases involved in this calculation suggests it is probably a minimum estimate. Despite the apparent low representation of bats in the diets of predatory birds, the effects of this predation on bat behaviour and population dynamics cannot be ignored.

INTRODUCTION

Throughout the world bats are known to fall prey to a large diversity of predators (Gillette & Kimbourgh, 1970). Bats have been reported as components in the diets of invertebrates (Rice, 1957), fish (Ingles, 1947), amphibia (Kinsey, 1961), reptiles (Hamilton, 1943; Rice, 1957), birds (Taylor, 1964; Fenton & Fleming, 1976) and mammals (Ryberg, 1947), including other bats (Allen, 1939). However, much of this reported predation represents occasional opportunistic events. Very few species make bats a major component of their diet, the most notable exceptions being the tropical bat hawks (*Macheiramphus alcinus* and *Falco rufigularis*) (Eccles, Jensen & Jensen, 1969; Black, Howard & Stjernstedt, 1979). Although bats are of relatively minor importance as prey for most predators, the impact of such predation is not necessarily trivial from the perspective of the prey. Indeed it has been suggested that many aspects of bat behaviour, for example, coloniality and roost selection (Barclay, Thomson & Phelan, 1982; Kunz, 1982), emergence behaviour at roosts (Swift, 1980; Bullock, Combes &

Eales, 1987) and even nocturnality itself (Moore, 1975; Speakman, 1991), may have an anti-predator component to their function.

In the present review I have drawn together several strands of information in an attempt to assess the contribution that predation by birds might make to the annual mortality of bats in the British Isles. Clearly there is substantial variation from area to area in the impact that avian predation has on bat mortality. Individuals of some predatory species, for example Barn Owls *Tyto alba*, obviously specialize on bats (e.g. Bauer, 1956) which may lead to very high local mortalities and even loss of entire colonies. Although such events are noteworthy, they may lead to an erroneous impression of the impact of avian predation in bat population dynamics. The approach taken in the present study is essentially the same as that adopted by Ticehurst (1935), Tinbergen (1946), Lockie (1955), Newton (1986) and Korpimaki (1977 in Mikkola, 1983) for assessing the role played by predatory birds in the mortality and population dynamics of small terrestrial mammals, but it has not been used previously to examine the role of predation in bat populations. The current estimates of the impact of predation, although relatively crude, do overcome the problems of local bias.

METHODS

The literature was searched for information on four topics: the diets and rates of prey capture of potential predatory birds, the populations of these birds and populations of their bat prey. The search concentrated on studies from within the British Isles.

Many bird species have been reported preying on bats in Britain and the adjacent European mainland, including several species that would not be immediately recognized as potential predators, e.g. tits *Parus* sp. (Ryberg, 1947). The major avian predators, however, are undoubtedly the owls, hawks and falcons. In the United States the seven genera that comprise these three groups account for more than 50% of predation records from all sources, including non-avian predation (Gillette & Kimbourgh, 1970). The only other potential predators of any significance are corvids which are known to take bats in the U.S.A. and Africa (Rosevear, 1965; Elwell, 1962), and the gulls (Laridae) and possibly skuas (Stercorariidae), which have been reported previously to take bats in the U.K. (Cleeves, 1969; Paterson, 1927). Together these birds probably account for almost all the avian predation on bats in the British Isles and therefore the analysis was restricted to species in these groups. I excluded from the analysis the Golden Eagle *Aquila chrysaetos* and White-tailed Eagle *Haliaetus albicilla* which are probably too large and cumbersome to prey on bats, the Arctic Skua *Stercorarius parasiticus* which is a specialist kleptoparasite and the following species which, although they are potential predators of bats, are not well enough represented in Britain to have any important impact on bat populations (Spencer *et al.*, 1988): Marsh Harrier *Circus aeruginosus*, Montagu's Harrier *Circus pygargus*, Goshawk *Accipiter gentilis*, Osprey *Pandion haliaetus*, Honey Buzzard *Pernis apivorus* and Snowy Owl *Nyctea scandiaca*. Table 1 details the species of predator included in this review.

The impact of predation on separate bat species was not investigated for two reasons. Firstly, studies of diet choice by predators often do not identify the species of bat involved. Secondly, there are no complete data concerning all the four aspects which are necessary to assess the impact for any single species. Interspecific comparisons at present would consequently be premature.

Table 1

Potential avian predators of bats resident in the British Isles, included in this review, with an indication of their body sizes (From Bruun & Singer, 1970)

Common name	Scientific name	Body size (length, cm)
Diurnal predators		
Hawks and falcons		
Peregrine	*Falco peregrinus*	40–50
Hobby	*Falco subbuteo*	27·5–30
Merlin	*Falco columbarius*	27·5–30
Kestrel	*Falco tinnunculus*	30–32·5
Sparrowhawk	*Accipiter nisus*	30–37·5
Hen Harrier	*Circus cyaneus*	50–55
Red Kite	*Milvus milvus*	60–65
Buzzard	*Buteo buteo*	65–70
Corvids		
Jay	*Garrulus glandarius*	33–35
Magpie	*Pica pica*	45–47
Rook	*Corvus frugilegus*	45–47
Hooded/Carrion Crow	*Corvus corone*	44–46
Raven	*Corvus corax*	61–64
Gulls and skuas		
Black-headed Gull	*Larus ridibundus*	38–43
Common Gull	*Larus canus*	44–47
Herring Gull	*Larus argentatus*	56–61
Lesser Black-backed gull	*Larus fuscus*	51–61
Great Black-backed gull	*Larus marinus*	69–76
Great Skua	*Catharacta skua*	53–58
Nocturnal predators		
Barn Owl	*Tyto alba*	34–37
Tawny Owl	*Strix aluco*	37–39
Short-eared Owl	*Asio flammeus*	37–39
Long-eared Owl	*Asio otus*	34–37
Little Owl	*Athene noctua*	24–26

Diet choice

Several different methods have been used to study dietary habits of predatory birds. These include direct observation of prey taken in the field (e.g. Village, 1982), observations of prey delivered to a nest site (e.g. Parr, 1985), collections of prey remains beneath a nest site or plucking post (e.g. Newton, 1986), reconstruction of the diet from remains in regurgitated pellets (Glue, 1970a), and analysis of gizzard and stomach contents of freshly dead birds (e.g. Holyoak, 1968). No single method is completely unbiased. Direct observation would appear the most unbiased method, but in practice predation events are seldom observed in large numbers. The resultant small samples are prone to bias by idiosyncratic diet selection by individual predators (e.g. Bauer, 1956) and the fact that noteworthy events are more likely to be published than potentially ecologically more important records of routine predation. For example, a report of 'Kestrel preys on bat' is more likely to be published (e.g. Shimmings, 1985) than a report of 'Kestrel preys on vole' although more extensive studies reveal that voles *Microtus* sp. are frequently the largest component of the Kestrel's diet (e.g. Yalden &

Warburton, 1979). Direct observations of single (or small numbers of) predatory events were recorded but excluded from the analysis.

Observations made at nests may over-represent items that are brought specifically to the young. Mikkola (1983) suggested that prey brought to the nests of owls were larger than those consumed by the adults. Southern (1969) also noted differences between the diets observed directly at the nest and those reconstructed from pellets. Sparrowhawks (Newton, 1986) and Kestrels (Masman, 1986) brought smaller items to the nest than those plucked at a distance, possibly for the Sparrowhawk because of the cost or difficulty of carrying larger items. The direction of any bias in nest observations therefore appears to be dependent on the species involved.

Observations made at plucking sites may under-represent small prey which are eaten whole on the wing, for example insects (Parr, 1985), but also possibly larger items (e.g. Tucker, 1989) and bats (Black *et al.*, 1979). Furthermore, prey that are eaten on the ground but do not need plucking—including bats—will be under-represented by samples collected at these stations. Potentially the most biased method is that of reconstructing the diet from prey remains in regurgitated pellets, because this is affected by problems of differential digestability, and of identifying prey correctly from crushed remains. It has been suggested that this bias is greater for falcons and hawks than for owls (Dare, 1961; Yalden & Yalden, 1985; Mikkola, 1983). Moreover, Lowe (1980) found that some prey that were fed to captive Tawny Owls did not appear in the pellets at all, and the probability of complete digestion was greater for those mammals with lighter skeletons. This could be a serious source of bias when considering the role of bats in the diet, as bats have very light skeletons for their size. Contradicting these data, however, Clark (1975) found that when small birds, which also have light skeletons, were fed to captive Tawny Owls, the original diet could be reconstructed from analysis of pellets. One advantage of pellet analysis is that large numbers of pellets can be collected and analysed, overcoming the problems of bias in small samples (but not of differential digestability) for relatively little investment of observer effort. Although gizzard analysis is not beset with the problems of differential digestion, only a small prey sample is obtained for each predator killed, and whilst this may be an acceptable approach for the study of the diets of 'pest' species, e.g. gulls, the currently low populations of predatory birds makes it an unacceptable alternative. Historically this technique was used to assess the diet of Little Owls (Hibbert-Ware, 1938). Taking all these factors into account, Southern (1969) considered analysis of pellets the most valuable approach for analysis of diets, and it is the most widely employed approach in the studies reviewed here.

Prey intake rates

The rates at which predators capture prey were evaluated in five ways: (a) observations of food intake rates of birds kept in cages in captivity were collected; (b) observations of food intake of birds kept in captivity, but exercised regularly, were compiled; (c) I predicted the intake rate in captivity from the body mass, using the empirical relationship derived by Mikkola (1983) for captive owls; (d) direct estimates of prey capture rates, either measured directly as prey observed eaten per day, or reconstructed from the numbers of items per pellet produced, assuming production of two pellets per day (Wijnandts, 1983), were collected; and (e) I predicted intake rates on the basis of energy requirements. To make this prediction it was assumed that the daily energy requirement was a fixed multiple of 3·1 times the basal metabolic rate [mean of five studies of daily energy requirements in relation to BMR of falcons and owls, reviewed in Wijnandts

(1983)]. The basal metabolic rates of falcons and owls were predicted using the non-passerine equation of Lasiewiski & Dawson (1967), which is an appropriate estimator for temperate species of owls and falcons (Wijnandts, 1983). The mass of food required to meet the daily energy requirements was estimated by assuming an assimilation efficiency of 70% and a prey energy content of 8·4 kJ/g wet weight of meat eaten (Ratcliffe, 1980).

Populations of birds

Breeding populations of birds in Britain were assessed throughout the years 1968–72 (Sharrock, 1976). Wintering populations were assessed throughout the years 1981–84 with some updated information on breeding populations (Lack, 1986). The most up to date estimates of population for breeding birds were presented by Marchant *et al.* (1990). Furthermore there have been several estimates of the breeding populations of individual falcons and owls (e.g. Shawyer, 1987). The breeding populations were evaluated using primarily Sharrock (1976), Lack (1986) and Marchant *et al.* (1990).

Populations of bats

There have been relatively few attempts to assess the populations of bats in Britain. Where direct estimates of populations of a given species were available these were used [e.g. Greater Horseshoe Bat *Rhinolophus ferrumequinum* populations estimated by Stebbings (1988)]. The populations of Pipistrelle Bats *Pipistrellus pipistrellus* and Brown Long-eared Bats *Plecotus auritus* were evaluated by multiplying independent evaluations of the population densities of these bats in the U.K. by the areas occupied by the species (Stebbings, 1977). For the remaining species, for which there were no direct estimates or population density estimates, I evaluated the populations from the frequency of reports of roosts of these species to the Nature Conservancy Council (NCC) relative to those for Pipistrelle Bats (Mitchell Jones *et al.*, 1986). This approach was not possible for two species which do not routinely use houses for their nursery roosts—Daubenton's Bat *Myotis daubentoni* and the Noctule Bat *Nyctalus noctula*, and are hence only infrequently reported to the NCC. For these species national populations were estimated from general reports of abundance relative to other species in surveys organized by local bat groups throughout the U.K. These latter estimates are the least accurate and may have wide confidence limits.

RESULTS

Diet choice

Some of the potential predators of bats (Table 1) are omnivorous scavengers. In this group are the corvids and gulls. The diets of these species in Britain are summarized in Table 2. The most extensive surveys of diets in these animals revealed that small mammals and birds may occasionally play a large role in the diet. It is unclear from the diets reconstructed from pellets whether these prey are taken as carrion, or whether they are hunted as live quarry. There are several records of these species hunting live prey (e.g. Carrion Crow: Pipes, 1976) which suggests that at least some of the prey were taken alive. In none of the extensive studies were there any records of bats being eaten. There are, however, anecdotal records of predation, or attempted predation, on bats by four of the species: Herring Gull (Cleeves, 1969), Black-headed Gull (Paterson, 1927; in Gillette & Kimbourgh, 1970; Speakman, 1991), Carrion Crow (Arnold, 1955) and Rook (Radford, 1984).

The remaining predators (Table 1) feed almost exclusively on live prey. The diets of these species are summarized in Table 3. Across all the species, a total of 135 547

Table 2
Representation of mammals in the diets of British corvids and gulls

Species	Details	Reference
Carrion Crow/ Hooded Crow	6–31% of gizzards contained mammal remains ($n = 234$)	Holyoak (1968)
	5 mammals recovered from 56 gizzards. No bats	Yom-Tov (1975)
Rook	0% of gizzards contained mammal remains ($n = 264$)	Holyoak (1968)
Magpie	5–30% of gizzards contained mammal remains ($n = 77$)	Holyoak (1968)
	8/4092 items recovered from pellets were mammal bones	Tatner (1983)
Jay	0–4% of gizzards contained animal remains ($n = 74$)	Holyoak (1968)
Raven	151 small mammals recovered from 433 pellets; no bats	Bolam (1913)
Herring Gull	Very diverse diet includes prey from 12 different families. Mostly food obtained at rubbish tips in U.K. Rodents rarely taken, but recorded taking bat	Cramp (1983)
Black-headed Gull	Earthworms and insects major prey. Mammals very rare	Vernon (1972a)
	Earthworms and insects major prey, 80–90% of biomass	Cramp (1983)
Common Gull	Earthworms and insects major prey. Occasional fish but mammals very rare	Cramp (1983)
Lesser Black-backed Gull	Mostly fish and scavenged/stolen items	Verbeek (1977)
	Occasional small mammals but no bats	Cramp (1983)
Great Black-backed Gull	Mostly marine birds, but also mammals scavenged, or predated, and human refuse important. No records of bats	Cramp (1983)

vertebrate prey items were identified. The representation of bats in this sample was very low. Only 37 (0·0273%) bats were positively identified. The occurrence of bats in the diets of owls (0·03619%) was about ten times greater than the representation in the diets of small falcons and hawks, which averaged 0·00339% but for all except one of the species was zero in the available diet sample. There were also some differences between the owls. For Little Owls bats were an extremely rare prey item, with only a single reference to 'some hairs' in a single pellet examined by Hibbert-Ware (1938), with no indication as to how these hairs were identified as of bat origin. Short-eared Owls also took relatively few bats (0·0176%) compared with Barn (0·0332%), Tawny (0·0514%), and Long-eared Owls (0·0466% of the diet).

On the basis of these dietary data, the predators were divided into three groups: Group 3—those predators for which there was no evidence from the extensive dietary studies reviewed here, nor from any anecdotal evidence, that these species ever feed on bats. In this group were: Buzzard *Buteo buteo*, Hen Harrier *Circus cyaneus*, Red Kite *Milvus milvus*, Jay *Garrulus glandarius*, Magpie *Pica pica*, Raven *Corvus corax*, Lesser Black-backed Gull *Larus fuscus* and Great Skua *Catharacta skua*. Group 2—those species for which there was no, or only very minor, evidence from the extensive studies of diet reviewed that they feed on bats, but there was anecdotal evidence either from Britain or elsewhere that bats are occasionally taken. This group included (anecdotal data referenced in parentheses): Herring Gull (Cleeves, 1969), Black-headed Gull (Paterson, 1927 in Gillette & Kimbourgh, 1970), Carrion Crow (Arnold, 1955), Rook (Radford, 1984), Peregrine Falcon (Stager, 1949; Ratcliffe, 1980), Hobby (Aymerich & Garcia, 1983), Kestrel (Shimmings, 1985; Speakman, 1990), Sparrowhawk (Rowarth & Wright, 1989; Speakman, 1991), Merlin (Newton, Meek & Little, 1984; Speakman, 1991), Little Owl (Hibbert-Ware, 1938; Mikkola, 1983) and Short-eared Owl (Glue, 1977). Finally, Group 1—those species for which there was evidence from the extensive dietary studies that bats turn up more regularly in the diet. In this group were the Barn Owl, Tawny Owl and Long-eared Owl.

Prey intake rates

Prey intake rates for some of the predators in Groups 1 and 2 are shown in Table 4. Estimates of prey intake rates for caged birds were lower than the other estimates, presumably reflecting the lack of exercise. There was a close correspondence between the estimates based on food intakes of exercised captive birds and the predictions from energy requirements. Furthermore these latter estimates of prey requirements were consistent with the direct observations of daily prey capture rates for those species in which both measures were available. For example, the daily food requirements of the Kestrel (*c*. 50 g) combined with the observed prey capture rates (*c*. 3–4 per day) implies a mean prey mass of about 15–20 g. This is consistent with observations that the majority of the prey taken in the field are voles (*c*. 20 g), mice (Muridae) (*c*. 20 g) and shrews (Soricidae) (*c*. 10 g). The mean mass of 212 prey captured between October and March by Kestrels in the Netherlands was 15·5 g (Masman, 1986). For Sparrowhawks, the intake of about 60 g/day and 2 captures implies a mean prey mass of about 30 g, which is consistent with the fact the major prey of this species are House Sparrows *Passer domesticus* (*c*. 25 g) and Blackbirds *Turdus merula* (*c*. 90 g) (Newton, 1986). I evaluated the prey intake rates in items per day for those species where direct data were lacking from direct observations, by dividing the predicted daily food requirements by the mean mass of prey taken in the field. This gave average intake rates of two and three items per day for the Merlin and Hobby, respectively. The daily intake rates of small mammals/birds for the Little Owl, Herring Gull, Black-headed Gull, Carrion Crow and Rook could not be estimated because intakes of live avian and mammalian prey were such small and unquantified components of their diets (Tables 2 and 3).

Predator populations

The estimated populations of all the predators which occasionally or regularly feed on bats in the British Isles are summarized in Table 5.

Table 3

The representation of bats in the diets of predatory birds

	Total prey	Bats	%bats	Method
Diurnal predators				
Falcon-sized predators				
Peregrine				
Mearns (1983)	3579	0	0	P
Ratcliffe (1980)	4130	0	0	N
Total	7709	0	0	P/N
Hobby				
Parr (1985)	422	0	0	N/D
Merlin				
Newton *et al.* (1984)	1950	1	0·051	P
Bibby (1987)	6366	0	0	P
Watson (1979)	161	0	0	P
Total	7477	1	0·0134	P
Kestrel				
Village (1982)	890	0	0	P
Yalden & Warburton (1979)	1772	0	0	P
Roberts (1980)	161	0	0	P
Shrubb (1980)	290	0	0	P
Yalden (1980)	90	0	0	P
Davis (1975)	130	0	0	P
Glue (1967)	180	0	0	P
Simms (1961)	596	0	0	P
Total	4109	0	0	P
Sparrowhawk				
Newton (1986)	9802	0	0	N
Total	**29 519**	**1**	**0·003387**	
Buzzard-sized predators				
Red Kite				
Davis & Davies (1981)	1665	0	0	P
Hen Harrier				
Balfour & MacDonald (1970)	49	0	0	N
Watson (1977)	650	0	0	N
Total	699	0	0	N
Buzzard				
Dare (1961)	1063	0	0	P
	493	0	0	N
McNally (1962)	73	0	0	N
Total	1629	0	0	P/N
Great Skua				
Furness & Hislop (1981)	2172	0	0	P
	145	0	0	N
Total	2317	0	0	P/N

P = pellet analysis; N = items brought to nest/plucking sites; D = direct observation; G = Gizzard analysis.

*Total for Barn owl assumes the data in Glue 1970a are included in the total for Glue 1974.

†Total for Short-eared Owl assumes the total for Glue (1970a and b) are included in the total for Glue (1977).

Table 3
Continued

	Total prey	Bats	% bats	Method
Nocturnal predators				
Owls				
Barn Owl				
Glue (1970a)	31 491	11	0·035	P
Smal (1987)	?	+	+	P
Dickson (1974)	635	0	0	P
Brown (1981)	4752	2	0·042	P
Glue (1974)	47 865	14	0·029	P
Webster (1973)	2055	0	0	P
Glue & Nuttall (1971)	259	0	0	P
Glue (1967)	3663	3	0·081	P
Bunn *et al.* (1983)	769	2	0·26	P
	2650	1	0·038	P
Mikkola (1983)	1033	0	0	P
Ticehurst (1935)	646	0	0	P
Yalden (1985)	1949	0	0	P
Total*	66 276	22	0·03319	P
Tawny Owl				
Glue (1970a)	61	0	0	P
Glue (1967)	164	0	0	P
Harrison (1960)	102	0	0	P
Southern (1969)	1416	0	0	P
	278	0	0	N
	413	0	0	N
Southern (1954)	9494	4	0·042	P
Yalden (1985)	946	2	0·211	P
Beven (1966)	743	1	0·134	P
Total	13 617	7	0·0514	P/N
Long-eared Owl				
Glue (1970a)	99	0	0	P
Village (1981)	514	0	0	P
Flegg & Cox (1968)	124	0	0	P
Wooller & Triggs (1968)	251	0	0	P
Glue & Hammond (1974)	7761	4	0·052	P
Fairley (1967)	1157	0	0	P
South (1966)	710	0	0	P
Ticehurst (1939)	1026	2	0·194	P
Yalden (1985)	1228	0	0	P
Total	12 870	6	0·0466	P
Short-eared Owl				
Glue (1970a)	56	0	0	P
Roberts & Bowman (1986)	696	0	0	P
Glue (1977)	4120	1	0·024	P
Vernon (1972b)	200	0	0	P
Glue (1970b)	1483	1	0·067	P
Jeal (1976)	76	0	0	P
Lockie (1955)	541	0	0	P
Yalden (1985)	139	0	0	P
Total†	5772	1	0·0173	P
Little Owl				
Glue (1970a)	33	0	0	P
Hibbert-Ware (1938)	911	0	0	G/N
Total	944	0	0	P/G/N
Total	**99 479**	**36**	**0·03619**	

Table 4

Prey intake rates for birds which feed regularly (Group 1) or occasionally (Group 2) on bats. Method A—food intake of caged captive birds with no activity (g/day); Method (B)—food intake of exercised captive birds (g/day); Method C—predicted intake of captive from Mikkola (1983); Method D—directly observed intake rate or inferred from pellets (items/day); Method E—inferred from daily energy requirements (g/day)

		Method				
Species	Body mass (g)	A	B	C	D	E
Group 1						
Barn Owl	300–350	48	95	111	3–6 8·2 4·5–10 5	72
Tawny Owl	450–550	50	180	155	7 6	99
Long-eared Owl	280–330	41	60–90	105	4 1–15	69
Group 2						
Peregrine	600–900	73	80–120 140	205	2–3	135
Sparrowhawk	240–280	29·5	40–70	83	1–3	59
Kestrel	190–210	31	48	59	3–10 3 2–4 4–8	50
Merlin	150–190	36	?	45	?	44
Hobby	150–180	?	?	52	?	44
Little Owl	170–175	31·4	65	66	?	45
Short-eared Owl	350–410	47	78	126	2·7–3·9	81

Bat populations and survival

Estimated populations of British bats are presented in Table 6. Direct estimates were available for Greater Horseshoe and Lesser Horseshoe Bats *Rhinolophus hipposideros* (Stebbings, 1988). In addition populations of three rare species—Bechstein's Bat *Myotis bechsteini*, Grey Long-eared Bat *Plecotus austriacus* and Barbastelle *Barbastella barbastellus* were evaluated from known records throughout the U.K. (Stebbings & Griffiths, 1986).

There are three published estimates for the densities of Pipistrelle Bats in Britain. These are all based on surveys of nursery roosts during early summer, which consist almost entirely of females (Speakman *et al.*, 1991). The estimated densities from these studies are all similar; Walsh, Stebbings & Thomson (1987) found 0·05 females/ha around York, whilst Pritchard & Murphy (1988) found densities of about 0·2 bats/ha occupying two glens in the centre of Scotland, which gave an overall estimated density of about 0·05 females/ha, when the adjacent unsuitable moorland was included. Similarly, Speakman *et al.* (1991) found 0·18 bats/ha in the valleys of the Dee and Don in North East Scotland, which again is equivalent to about 0·05 bats/ha when the surrounding land, where no bats were found, is included in the estimate. Three independent estimates of the densities of breeding female pipistrelles from across the country therefore indicate 0·05 bats/ha (equivalent to 5 bats/km^2).

Table 5

Estimated populations of birds in the British Isles which regularly (Group 1) or occasionally (Group 2) feed on bats. A—after Sharrock (1976) and Lack (1986) unless referenced; B—after Marchant et al. *(1990), breeding pairs (×2); C—composite estimate used in this study*

Species	A	B	C
Group 1			
Barn Owl	14 000[1]	8800	10 000
Tawny Owl	150 000	150 000	150 000
Long-eared Owl	22 000	8000	15 000
Group 2			
Herring Gull	800 000	400 000	600 000
Black-headed Gull	2 000 000	350 000	1 000 000
Rook	3 500 000	1 710 000	2 000 000
Carrion Crow	750 000	1 800 000	1 000 000
Little Owl	30 000	21 000	25 000
Short-eared Owl	22 000	11 000	15 000
Peregrine	1650[2]	1900	1650
Hobby	700[3]	1000	1000
Merlin	2500[4]	1200	2000
Kestrel	200 000	140 000	170 000
Sparrowhawk	100 000	50 000	75 000

[1] Shawyer (1987); [2] Ratcliffe (1984); [3] Spencer *et al.* (1986); [4] Newton *et al.* (1986).

Pipistrelles are found throughout the British Isles (Stebbings, 1977). The area of the British Isles is 308 700 km^2 (*Oxford Universal Atlas*, 1958). The population of female Pipistrelles is thus about 1 543 500. Walsh *et al.* (1987) assumed that there was also an equal population of males. The validity of this assumption remains in doubt. Males are not captured as frequently as females in mist nets set at foraging sites in north-east Scotland (Swift, 1982; Speakman *et al.*, 1991) and a lower population of males might be anticipated from their lower survival (Lundberg, 1989). In other species the composition in hibernacula suggest an approximately equal sex ratio (e.g. Daubenton's Bat: Speakman, 1990a). If it is assumed there are equal numbers of males and females, the total population of Pipistrelles in the British Isles is around 3 087 000 bats. Two estimates of population density of the Brown Long-eared Bat (Boyd & Stebbings, 1989; Speakman *et al.*, 1991) indicate a density about one-tenth that of Pipistrelles (0·005 bats/ha). Because Brown Long-eared bats occupy about 80% of the area of Britain occupied by Pipistrelles (Stebbings, 1977) this suggests the population of Brown Long-eared Bats is around 8% of the population of Pipistrelles. Roost reports to the NCC suggest Brown Long-eared Bat roosts are about half as common as roosts of Pipistrelles (30·4% of reports for Long-eared Bats compared with 58·5% of reports for Pipistrelles; Mitchell Jones *et al.*, 1986). Because roosts of Brown Long-eared Bats are about 14% the size of Pipistrelle roosts (Speakman *et al.*, 1991) this also points to a population of Brown Long-eared Bats about 8% of the population of Pipistrelles, i.e. 246 960. I estimated the populations of Whiskered/Brandt's Bats (*Myotis mystacinus*/*Myotis brandti*, Natterer's Bats *Myotis nattereri*, Serotines *Eptesicus serotinus* and Leisler's Bats *Nyctalus leisleri* from the reports of roosts of these species to the

Table 6

Population and annual mortality estimates for British bats assuming all females produce one young per year

Species	Adult population	Total population	Annual mortality rate*	Total deaths
Greater Horseshoe Bat	3000[1]	4500	0·27[2]	1215
Lesser Horseshoe Bat	8000[1]	12 000	0·27	3240
Whiskered/Brandt's Bat	169 150	253 725	0·248[3]	62 924
Daubenton's Bat	200 000	300 000	0·206	60 000
Natterer's Bat	74 003[4]	111 004	0·33	36 631
Bechstein's Bat	*c*.100	150	0·33	50
Barbastelle	*c*.100	150	0·33	50
Pipistrelle	3 087 000	4 630 500	0·33	1 528 065
Serotine	19 029	28 543	0·33	9419
Noctule	50 000	75 000	0·33	24 750
Leisler's Bat	5286	7929	0·33	2616
Brown Long-eared Bat	246 960	370 440	0·242[4]	89 646
Grey Long-eared Bat	*c*.1000	1500	0·33	495
Total (all species)		5 795 442		1 819 101

*The mortality rate of Lesser Horseshoe Bats is assumed to be equal to that of Greater Horseshoe Bats, and that of Pipistrelles is assumed for those other species given a value of 0·33.

[1]Stebbings (1988); [2]Ransome (1990); [3]Bezem, Sluiter & van Heerdt (1960); [4]Stebbings (1977) for females.

NCC relative to reports of Pipistrelle Bats (Mitchell Jones *et al.*, 1986), assuming that on average roosts of Whiskered/Brandt's and Natterer's Bats were the same size as Pipistrelle roosts, Serotine roosts were on average a tenth the size of Pipistrelle roosts (C.M.C. Catto, pers. comm.) and roosts of Leisler's Bat were on average half the size of Pipistrelle roosts. The population of Daubenton's Bat was estimated at 200 000, i.e. between the populations of Brown Long-eared Bats and Whiskered/Brandt's Bats, and the population of Noctules was estimated as 50 000, i.e. between the populations of Natterer's and Serotine bats.

Female Pipistrelle Bats breed in their first summer and probably every year thereafter (Racey, 1982). In contrast, female Greater Horseshoe Bats do not mature until they are 3 years old and do not breed in every summer (Ransome, 1990). Most other bats probably lie between these extremes; e.g. Brown Long-eared Bats breed after 1 or 2 years but not always annually thereafter (Stebbings, 1976). In the present study I have made the conservative assumption that females of all species produce a young in every year. The total populations for each species thus include adults and juveniles (Table 6). Using these estimates, the total bat population of Britain is about 5·8 million.

Estimates of the annual probability of mortality for each species are presented in Table 6. In the absence of information for any species, I made the conservative estimate that mortality was equal to the highest estimate for a species where estimates were available (Pipistrelle Bats, 0·33; Thompson, 1987). Applying these mortality estimates to the estimated national populations of each species suggests that each year, throughout the British Isles, 1·82 million bats die.

Table 7

The impact of predation on the mortality of British bats. The national populations of regular (Group 1) and occasional (Group 2) predators of bats were multiplied by their intake of prey per day to give daily and annual numbers of prey items taken. The total prey taken were then used to estimate the number of bats predated annually

Species	Daily intake of all prey (*n*/day)	Annual intake of all prey (*n*/year)	Bat intake (*n*/year)
Group 1			
Barn Owl	72 500	26 462 500	8783
Tawny Owl	900 000	328 500 000	168 849
Long-eared Owl	60 000	21 900 000	10 205
Group 2			
Rook	?	?	?
Carrion Crow	?	?	?
Herring Gull	?	?	?
Black-headed Gull	?	?	?
Little Owl	?	?	?
Kestrel	680 000	248 200 000	8406
Hobby	3000	1 095 000	37
Merlin	4000	1 460 000	49
Sparrowhawk	150 000	54 750 000	1854
Peregrine	4125	1 505 625	52
Short-eared Owl	49 500	18 067 500	3180
Total predation on bats (*n*/year)			201 415

Synthesis—the impact of predatory birds on bat mortality

Given the estimated numbers of bats that die in the British Isles each year, what proportion of this mortality can be accounted for by predation? The impact of the various predators on bats was estimated by multiplying their estimated national populations (Table 4) by their estimated daily food intake rates (items/day; Table 5 and text), and by the contribution made to the diets by bats (Table 3). This calculation was not possible for the Herring Gull, Black-headed Gull, Carrion Crow, Rook and Little Owl for which the intake rates of live mammalian/avian prey and the contributions made by bats to their diets were unknown. It was assumed that the estimated contribution of bats to the diets of small falcons and hawks was the same for them all (0·00034% of prey taken). The calculations are summarized in Table 7. In total, occasional predators (excluding those species for which no calculation could be made) take approximately 13 578 bats annually, whilst the regular predators between them account for about 187 837 bats, leading to a total annual mortality attributable to predation of around 201 415 individuals. This is about 11·1% of the independently estimated total annual mortality.

DISCUSSION

The occurrence of bats in the diets of British predatory birds was low when compared with the diets of the same species elsewhere in Europe. For example, the review of

British studies (Table 3) indicated that bats comprise 0·0332% of prey taken by Barn Owls. This is about a fifth the contribution calculated by Uttendorfer (1943) for studies across Germany (0·15%), an eighth the contribution calculated by Ruprecht (1979) for studies across Poland, and 70% of the estimated representation of bats in the diet of Barn Owls from Morocco (0·0469%; Aulagnier, 1989). Similar lower representations of bats in the diets of British predators are evident for the Little Owl (Mikkola, 1983), Long-eared Owl (Uttendorfer, 1952), Kestrel (Tout, 1986), Peregrine (Stager, 1949), Short-eared Owl (Huey, 1926; Aulagnier, 1989) and Hobby (Aymerich & Garcia, 1983), although the representation of bats in the diet of Long-eared Owls was greater than that reported by Wijnandts (1983), who found only one bat in 47 764 prey captured on the polders of The Netherlands, where bats are perhaps extremely scarce. The reasons why bats are generally under-represented in the diets of birds in Britain are unclear. One factor may be the lack of relatively large bats in the British bat fauna, as most of the bats taken elsewhere in Europe and in the U.S.A. by predatory birds are of larger species than those common in Britain; e.g. Mouse-eared Bats *Myotis myotis* and Serotines, both of which are heavier than 20 g and have wing spans in excess of 30 cm, comprised over 50% of the prey taken by Barn Owls in Poland (Ruprecht, 1979), whilst Pipistrelles contributed only 2% of the bat prey. Similar biases towards large bats were also evident for Tawny Owls (Ruprecht, 1979), which the current study indicates is probably the most important predator in Britain.

The low representation of bats in the diets of falcons and hawks reflects the fact that these birds are predominantly diurnal (Masman, 1986) and hence will not encounter many bats because daylight flying by bats is relatively rare (Speakman, 1986; 1990b). However, diurnal predators may occasionally extend their feeding activity well into twilight when bats are active (e.g. Tout, 1986) and it may be at these times that most of the prey accounted for by these predators are taken. The low representation of bats in the diets of the Short-eared and Little Owls may also reflect the fact these two species are the most diurnally active of the owls.

The calculated impact of predatory birds on bat mortality (at 11·1%) was surprising in view of the very low contributions that bats make to the diets of the predators (Table 3). The calculated numbers of prey taken by diurnal predators each year are also surprisingly high. The figure of 8406 bats taken each year by Kestrels implies that on average every day in Britain 23 daylight (or twilight) flying bats are attacked and killed by this species. This apparently large number of events begs the question of why such an event is not more frequently reported as an aspect of the behaviour of Kestrels, which are a commonly encountered and observed species; it also calls to question the assumption that the mean capture rate across all small falcons and hawks is the same. To understand this anomally it is instructive to recalculate the predation rates in terms of what they mean for the average predator (Table 8). This indicates that although across the country 23 bats may be killed every day by Kestrels, for the individual Kestrel this implies only a capture of a bat once every 20 years. Even in a prolonged study of Kestrel behaviour which involved teams of observers watching Kestrels around the clock (Masman, 1986), the total accumulated observation time was only 8800 h, which is approximately 2 years of a Kestrel's life, assuming a 12-h active day. This may explain why the apparently high rate of capture is so infrequently reported, and why it does not necessarily follow that the estimated capture rate for bats was too large.

The impact of predatory birds on bat mortality is in the same range but slightly lower than that calculated for the impact of Short-eared Owls on vole populations (Lockie, 1955), of Sparrowhawks on populations of small birds (Newton, 1986), and raptors on

Table 8

Calculated rates of predation on bats by individual predators. Total number of items of all types and numbers of bats per year are shown with the average number of years of hunting before capturing a single bat (reciprocal of number of bats per year) for individuals of each predatory species

Species	Prey items eaten per year	Bats eaten per year	Years between bats
Kestrel	1460	0·0494	20·2
Hobby	1095	0·0371	26·9
Merlin	730	0·0247	40·4
Sparrowhawk	730	0·0247	40·4
Peregrine	912	0·0308	32·5
Short-eared Owl	1204	0·206	4·34
Barn Owl	2646	0·878	1·13
Tawny Owl	2190	1·125	0·889
Long-eared Owl	1460	0·680	1·46

small-mammal populations (Korpimaki, 1977 in Mikkola, 1983). The population consequences of this figure remain uncertain because it is not clear whether the mortality acts in a density-dependent or -independent fashion. Nevertheless, in terms of individual survival strategies, it is clear that predation is a significant factor amongst the risks influencing annual survival. As such, the low contribution of bats to the diets of predatory birds cannot be used as an argument against hypotheses that the selective advantages of behaviours like roost selection and roost emergence patterns are that they reduce the risks of predation (e.g. Swift, 1982; Kunz, 1982; Barclay *et al.*, 1982; Bullock *et al.*, 1987).

In view of the importance of the calculated impact of predatory birds on bat survival, it is instructive to consider the assumptions that are involved in its calculation and the sensitivity of the estimate to those assumptions. First, most of the observations depend on pellet analyses. The limitations of this technique have already been discussed (see methods). With respect to bats, differential digestibility will lead to the calculated contribution of predation to mortality being underestimated. It is not possible to assess accurately the contribution of this effect; however, it could potentially be of extreme importance. For example, if the bias in the diets of Polish Barn Owls towards larger prey (Ruprecht, 1979) was an artefact of the bones of the small bats being more fully digested, and if Pipistrelles were actually selected as frequently as Mouse-eared Bats, the effect would be to increase the representation of small bats in the diet by about nine-fold. Predation might then account for 90% of the mortality of British bats! The low representation of bats in direct observations of prey taken by, for example, Tawny Owls (Southern, 1969) suggests the extent of differential digestion is not this great; however, studies quantifying the bias involved in assessing the numbers of bats ingested by predators from regurgitated pellets are urgently required.

Secondly, in assessing the contribution to annual mortality, it was not possible to make estimates for four species which only occasionally attack or feed on bats. Because the national populations of these birds are very large, the rates of predation need only be extremely small to produce a still noticeable effect. For example, if it is assumed that 90% of these birds never feed on bats, and that the remaining 10% each take only one bat every 10 years, the total annual mortality from this source would still equal 70 800 bats (35% of the total excluding predation by these species). However, it is unlikely that this source of mortality will ever be adequately quantified. The error in ignoring this factor will lead to the calculation being an underestimate.

Thirdly, it was also assumed in the calculation that the rate of predation by small falcons and hawks was the same across all the species. This may not be a true reflection of the actual prey capture rates, but insufficient analyses of prey captured by these species were available to assess individual rates for each species. In some cases the method by which the diet was assessed may have contributed to the poor representation of bats in the diet. For example, Sparrowhawks have been reported as predators on bats but the most intensive dietary study relied on prey taken to plucking sites where bats, lacking feathers, will be underrepresented. Because Kestrels are the most abundant predator in this class, the effect on the calculated impact of predation will depend on how realistic the assumption of a constant representation of bats in the diet is for the Kestrel. Paradoxically the number of identified prey taken by this abundant falcon are amongst the lowest of all the British species and further work on diet selected by this species would help clarify their impact on bat populations. If this assumption is abandoned and it is assumed the measured predation rates are appropriate (i.e. zero for all diurnal predators except Merlins), the calculated impact would fall from 11·1% to 10·5%.

Fourthly, the estimates of the national populations of predatory birds are the central points of wide ranges which define the likely population limits. The nature of bird recording may mean that only confirmed instances of breeding have been accepted, consequently the lower population limit would reflect confirmed breeding, whilst the upper limit would reflect probable or possible breeding but not confirmed. Because birds must be present for even a possible breeding record, the true population estimates are probably nearer the upper ends of the ranges from which the central points were taken. Furthermore, there is often also a non-breeding population for most species and an annual population of juveniles recruited into each population which was not always assessed. In view of these factors the populations are more likely to be under- than over-estimates, and this will lead to the calculated contribution of predation to mortality being conservative.

Fifthly, data on bat populations in Britain are sparse. Because Pipistrelles comprise 80% of the estimated British bat fauna and estimates for other species were derived from this, the calculation will be most sensitive to errors in the population estimates for this species. As pointed out by Speakman *et al.* (1991), population estimates based on counts at nursery roosts are probably minima because they assume all roosts are known. The extent of this bias is uncertain but was probably important in north-east Scotland where the numbers of potential roosts was large and only a very small proportion were visited, but of less importance in other studies, notably that by Pritchard & Murphy (1988) in which the total numbers of potential roosts was relatively small and more than 50% were visited. Underestimates of the total bat population will inflate the calculated impact of the contribution of predation to mortality. On the other hand, it was assumed the population densities of Pipistrelles assessed in three habitats where bats are present are applicable across the entire range of the species. This is unlikely to be the case for the barren treeless uplands of Scotland, which account for about 15% of the total land surface, and are included in the range occupied by Pipistrelles by Stebbings (1977), but probably contain few if any bats.

Sixthly, it was assumed in calculating the prey intake rates for the predators that all the prey were vertebrates and that the entire daily energy demand was supplied by predation of vertebrates. This assumption is unrealistic for several of the small hawks and falcons which include significant quantities of invertebrates in their diets (e.g. Parr, 1985). This error will lead to the total number of prey taken being overestimated and hence the total number of bats taken also being overestimated. However, this error will be offset to some extent by the fact predatory birds dramatically increase the number of prey they capture whilst feeding nestlings and this increased rate of predation was not included in the calculations.

Finally, in this review I have only considered the impact of predation by avian predators. However, bats fall prey to several other predatory groups (Gillette & Kimbourgh, 1970; Bekker & Mostert, 1990). Probably the most significant of these other predators, in the British Isles, is the Domestic Cat *Felis catus*. In The Netherlands records of predation of bats by Domestic Cats are almost four times more frequent than records of predation by owls (Bekker & Mostert, 1990). The true impact of predation as a whole on bat populations may therefore be considerably greater than is indicated here.

In conclusion, analysis of these biases suggest the estimate of 11·1% is probably a minimum assessment of the impact of avian predation on bat populations. Although bats comprise only a minor proportion of the prey taken by avian predators, the effects of this predation as a factor influencing bat behaviour and population dynamics cannot be ignored.

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REFERENCES

Allen, G. M. (1939) *Bats*. Harvard University Press, Cambridge.

Arnold, M. A. (1955) Bats as the prey of a carrion crow. *British Birds*, **48,** 91.

Aulagnier, S. (1989) Les Chauves-souris (Chiroptera) dans de régime alimentaire des rapaces nocturnes (Strigiformes) au Maroc. In: *European Bat Research 1987* (ed. by V. Hanak, I. Horacek & J. Gaisler), pp. 457–463. Charles University Press, Prague.

Aymerich, M. & Garcia, R. F. (1983) Predation of peregrine falcon and hobby on bats. *Donana Acta Vertebrata*, **9,** 396–397.

Balfour, E. & MacDonald, M. A. (1970) Food and feeding behaviour of the hen harrier in Orkney. *Scottish Birds*, **6,** 157–165.

Barclay, R., Thomson, C. & Phelan, S. (1982) Screech owl *Otus asio*, attempting to catch little brown bats (*M. lucifugus*) at a colony. *Canadian Field Naturalist*, **96,** 205–206.

Bauer, K. (1956) Schleiereule (*Tyto alba* Scop.) als Fledermausjager. *Journal of Ornithology*, **97,** 335–340.

Bekker, J. P. & Mostert, K. (1990) Predation on bats in the Netherlands: facts and assumptions. Abstract of presentation at the 5th European bat research Symposium, Nyborg, Denmark, August 1990.

Beven, G. (1966) The food of Tawny Owls in Surrey. *Surrey Bird Report*, **1966,** 32–38.

Bezem, J. J., Sluiter, J. W. & van Heerdt, P. F. (1960) Population statistics of five species of the bat genus *Myotis* and one of the genus *Rhinolophus* hibernating in the caves of South Limburg. *Archives Néelandaises de Zoologie*, **13,** 511–539.

Bibby, C. J. (1987) Foods of breeding merlins (*Falco columbarius*) in Wales. *Bird Study*, **34,** 64–71.

Black, H. L., Howard, G. & Stjernstedt, R. (1979) Observations of the feeding behaviour of the bat hawk (*Machierampus alcinus*). *Biotropica*, **11,** 18–21.

Bolam, G. (1913) *Wildlife in Wales*. London, Batsford.

Boyd, I. L. & Stebbings, R. E. (1989) Population changes of Brown Long-eared bats (*Plecotus auritus*) in bat boxes at Thetford forest. *Journal of Applied Ecology*, **26,** 101–112.

Brown, D. J. (1981) Seasonal variations in the prey of some Barn owls in Gwynedd. *Bird Study*, **28,** 139–147.

Bruun, B. & Singer, A. (1970) *The Hamlyn Guide to the Birds of Britain and Europe*. Hamlyn, London.

Bullock, D. J., Combes, B. A. & Eales, L. A. (1987) Analysis of the timing and pattern of emergence of the pipistrelle bat (*Pipistrellus pipistrellus*). *Journal of Zoology (London)*, **211,** 267–274.

Bunn, D. S., Warburton, A. B. & Wilson, R. D. S. (1982) *The Barn Owl*. T & AD Poyser, Calton.

Clark, R. (1975) A field study of the Short-eared owl *Asio flammeus* in North America. *Wildlife Monographs*, 47, 1–67.

Cleeves, T. R. (1969) Herring gull catching and eating bat. *British Birds*, **62,** 333.

Cramp, S. (ed.) (1983) *Handbook of the Birds of the Western Palaearctic*, Vol. III. *Waders to Gulls*. Oxford University Press, Oxford.

Dare, P. J. (1961) *Ecological observations on a breeding population of common buzzards* (Buteo buteo) *with particular reference to diet and feeding habits*. Ph.D. thesis, University of Exeter.

Davis, P. E. & Davies, J. E. (1981) The food of the Red Kite *Milvus milvus* in Wales. *Bird Study*, **28**, 33–41.
Davis, T. A. W. (1975) Food of the kestrel in winter and early spring. *Bird Study*, **22**, 85–91.
Dickson, R. C. (1974) Barn owl pellets from Wigtownshire. *Scottish Birds*, **8**, 78–80.
Eccles, D. H., Jensen, R. A. C. & Jensen, M. K. (1969) Feeding behaviour of the bat hawk. *Ostrich*, **40**, 26–27.
Elwell, A. S. (1962) Blue jay preys on young bats. *Journal of Mammalogy*, **43**, 434.
Fairley, J. S. (1967) Food of long-eared owls in N.E. Ireland. *British Birds*, **60**, 130–135.
Fenton, M. B. & Fleming, T. H. (1976) Ecological interactions between bats and nocturnal birds. *Biotropica*, **8**, 104–110.
Flegg, J. J. M. & Cox, C. J. (1968) Winter food of long-eared owls in Kent. *Bird Study*, **15**, 163–164.
Furness, R. W. & Hislop, J. R. G. (1981) Diet and feeding ecology of great skuas *Catharacta skua* during the breeding season in Shetland. *Journal of Zoology (London)*, **195**, 1–23.
Gillette, D. D. & Kimbourgh, J. D. (1970) Chiropteran mortality. In: *About Bats* (ed. by B. H. Slaughter & D. W. Walton), pp. 262–281. Dallas Southern Methodist University Press, Dallas.
Glue, D. E. (1967) Prey taken by the barn owl in England and Wales. *Bird Study*, **14**, 169–184.
Glue, D. E. (1970a) Avian predator pellet analysis and the mammalogist. *Mammal Review*, **1**, 53–62.
Glue, D. E. (1970b) Prey taken by Short-eared owls at British breeding and winter quarters. *Bird Study*, **17**, 39–42.
Glue, D. E. (1974) Food of the Barn owl in Britain and Ireland. *Bird Study*, **21**, 200–211.
Glue, D. E. (1977) Feeding ecology of the short-eared owl in Britain and Ireland. *Bird Study*, **24**, 70–78.
Glue, D. E. & Hammond, G. J. (1974) Feeding ecology of the long-eared owl in Britain and Ireland. *British Birds*, **67**, 361–369.
Glue, D. E. & Nuttall, J. (1971) Adverse climatic conditions affecting the diet of a barn owl in Lancashire. *Bird Study*, **18**, 33–35.
Hamilton, W. J. Jr (1943) *The Mammals of Eastern United States*. Comstock, Ithaca, NY.
Harrison, C. J. O. (1960) The food of some urban Tawny owls. *Bird Study*, **7**, 236–241.
Hibbert-Ware, B. (1938) Report on the little owl enquiry. *British Birds*, **31**, 162–187; 205–229.
Holyoak, D. (1968) A comparative study of the food of some British Corvidae. *Bird Study*, **15**, 147–153.
Huey, L. M. (1926) Bats eaten by short-eared owl. *Auk*, **43**, 96–97.
Ingles, L. G. (1947) *The Mammals of California*. Stanford University Press, Stanford.
Jeal, P. E. C. (1976) Prey of the short-eared owl in breeding quarters in Outer Hebrides. *Bird Study*, **23**, 56–57.
Kinsey, C. (1961) Leopard frog attacks bat. *Journal of Mammalogy*, **42**, 408.
Kunz, T. H. (1982) Roosting ecology. In: *The Ecology of Bats* (ed. by T. H. Kunz), pp. 1–46. Plenum, New York.
Lack, P. (1986) *The Winter Atlas of Birds in Britain*. T. & AD Poyser, Calton.
Lasiewiski, R. C. & Dawson, W. R. (1967) A re-examination of the relation between standard metabolic rate and body weight in birds. *Condor*, **69**, 13–23.
Lockie, J. D. (1955) The breeding habits and food of Short eared owls after a vole plague. *Bird Study*, **2(2)**, 54–67.
Lowe, V. P. W. (1980) Variation in digestion of prey by the tawny owl (*Strix aluco*). *Journal of Zoology (London)*, **192**, 283–293.
Lundberg, K. (1989) *Social organisation and survival of the pipistrelle bat (*Pipistrellus pipistrellus*) and a comparison of advertisement behaviour in three polygynous bat species*. Ph.D. thesis, University of Lund, Sweden.
Marchant, J. H., Hudson, R., Carter, S. P. & Whittington, P. (1990) *Population Trends in British Breeding Birds*. British Trust for Ornithology, Tring, Herts.
Masman, D. (1986) *The annual cycle of the Kestrel* Falco tinnunculus: *a study in behavioural energetics*. Ph.D. thesis, University of Groningen, Netherlands.
McNally, L. (1962) Food at a buzzard's nest. *Scottish Birds*, **2**, 196–198.
Mearns, R. (1983) The diet of the peregrine falcon *Falco peregrinus* in South Scotland during the breeding season. *Bird study*, **30**, 81–91.
Mikkola, H. (1983). *Owls of Europe*. T & AD Poyser, Calton.
Mitchell-Jones, A. J., Jefferies, D. J., Stebbings, R. E. & Arnold, H. R. (1986) Public concern about bats (Chiroptera) in Britain: an analysis of enquiries in 1982–83. *Biological Conservation*, **36**, 315–328.
Moore, N. H. (1975) The diurnal flight of the Azorean bat (*Nyctalus azoreum*) and the avifauna of the Azores. *Journal of Zoology (London)*, **177**, 483–506.
Newton, I. (1986) *The Sparrowhawk*. T & AD Poyser, Calton.
Newton, I., Meek, E. R. & Little, B. (1984) Breeding season foods of merlins *Falco columbarius* in Northumbria. *Bird study*, **31**, 49–57.
Parr, S. J. (1985) The breeding ecology and diet of the hobby *Falco subbuteo* in Southern England. *Ibis*, **127**, 60–73.
Pipes, K. T. (1976) Carrion crow preying on small birds. *Bird study*, **23**, 213.
Pritchard, J. S. & Murphy, F. M. (1988) A highland bat survey 1986–1987. Glen Lyon and Rannoch, Perthshire. Unpublished report, Fife Bat Group.
Racey, P. A. (1982) The ecology of bat reproduction. In: *Ecology of Bats* (ed. by T. H. Kunz), pp 57–93. Plenum Press, New York.
Radford, A. P. (1984) Rook chasing small bats. *British Birds*, **77**, 119–120.
Ransome, R. (1990) *The Natural History of Hibernating Bats*. Christopher Helm, London.
Ratcliffe, D. (1980) *The Peregrine Falcon*. T & AD Poyser, Calton.
Ratcliffe, D. (1984) The peregrine breeding population of the UK in 1981. *Bird Study*, **31**, 9–28.
Rice, D. W. (1957) Life history and ecology of *Myotis austroriparius*. *Journal of Mammalogy*, **38**, 15–32.
Roberts, P. J. (1980) Diet of the kestrel on Bardsey island. *Bird Study*, **27**, 116–117.

Roberts, J. L. & Bowman, N. (1986) The diet and ecology of short-eared owls *Asio flammeus* breeding on a heather moor. *Bird Study,* **33,** 12–18.

Rosevear, D. R. (1965) *The Bats of West Africa.* British Museum (Natural History), London.

Rowarth, P. & Wright, E. (1989) Sparrowhawk attacking noctule bats. *British Birds,* **82,** 564.

Ruprecht, A. L. (1979) Bats (Chiroptera) as constituents of the food of barn owls *Tyto alba* in Poland. *Ibis,* **121,** 489–494.

Ryberg, O. (1947) *Studies on Bats and Bat Parasites.* Svensk. Natur., Stockholm.

Sharrock, J. T. R. (1976) *The Atlas of Breeding Birds in Great Britain and Northern Ireland.* T & AD Poyser, Calton.

Shawyer, C. R. (1987) *The Barn Owl in the British Isles, its Past, Present and Future.* The Hawk Trust, London.

Shimmings, P. (1985) Kestrel attempting to catch bat. *British Birds,* **78,** 109.

Shrubb, M. (1980) Farming influences on the food and hunting of kestrels. *Bird Study,* **27,** 109–115.

Simms, C. (1961) Indications of the food of the kestrel in upland districts of Yorkshire. *Bird Study,* **8,** 148–152.

Smal, C. M. (1987) The diet of the Barn owl in southern Ireland, with reference to a recently introduced prey species—the bank vole *Clethrionomys glareolus. Bird Study,* **34,** 113–125.

South, G. R. (1966) Food of long-eared owls in South Lancashire. *British Birds,* **59,** 493–497.

Southern, H. N. (1954) Tawny owls and their prey. *Ibis,* **96,** 384–410.

Southern, H. N. (1969) Prey taken by Tawny owls during the breeding season. *Ibis,* **111,** 293–299.

Speakman, J. R. (1986) Diurnal activity in bats. *Batchat,* **2,** 14–16.

Speakman, J. R. (1990a) Daubentons bat. In: *The Handbook of British Mammals* (ed. by G. B. Corbet & S. Harris), 3rd edn, pp. 108–111. Blackwell Scientific Publications, Oxford.

Speakman, J. R. (1990b) The function of daylight flying in british bats. *Journal of Zoology (London),* **220,** 101–113.

Speakman, J. R. (1991) Why do insectivorous bats in Britain not fly in daylight more frequently? *Functional Ecology,* **5,** (in press).

Speakman, J. R., Racey, P. A., Catto, C. M. C., Swift, S. M., Webb, P. I. & Burnett, A. (1991) Minimum population estimates and densities of bats in N.E. Scotland, near to the northern borders of their distributions, in summer. *Journal of Zoology (London),* in press.

Spencer, R. and the Rare Breeding Birds Panel (1988) Rare breeding birds in the UK in 1986. *British Birds,* **81,** 417–444.

Stager, K. E. (1949) Falcons prey on Ney cave bats. The caves of Texas. *Bulletin of the National Speleological Society,* **10,** 97–99.

Stebbings, R. E. (1976) *The Population Ecology of British Bats.* Ph.D. thesis, University of East Anglia.

Stebbings, R. E. (1977) Order Chiroptera. In: *The Handbook of British Mammals* (ed. by G. B. Corbet & H. N. Southern), 2nd edn. Blackwell Scientific Publications, Oxford.

Stebbings, R. E. (1988) *Conservation of European Bats.* Christopher Helm, London.

Stebbings, R. E. & Arnold, H. R. (1982) Bats—an insecticide under threat. *Naturalist in Devon,* **3,** 7–26.

Stebbings, R. E. & Griffith, F. (1986) *Distribution and Status of Bats in Europe.* Institute of Terrestrial Ecology, Peterborough.

Swift, S. M. (1982) *Foraging, colonial and maternal behaviour of bats in North-east Scotland.* Ph.D. thesis, University of Aberdeen.

Tatner, P. (1983) The diet of urban mapgies *Pica pica. Ibis,* **125,** 90–108.

Taylor, W. P. (1964) Noteworthy predation on the guano bat. *Journal of Mammalogy,* **45,** 300–301.

Thompson, M. J. A. (1987) Longevity and survival of female pipistrelle bats (*Pipistrellus pipistrellus*) in the Vale of York, England. *Journal of Zoology (London),* **211,** 209–214.

Ticehurst, C. B. (1935) On the food of the barn owl and its bearing on Barn Owl population. *Ibis,* **13,** 329–335.

Ticehurst, C. B. (1939) Food and feeding habits of the long-eared owl *Asio otus otus. Ibis,* **14,** 512–520.

Tinbergen, N. (1946) Sperver als roofvij and van zangvogels. *Ardea,* **34,** 1–123.

Tout, P. (1986) Kestrel regularly catching bats. *British Birds,* **79,** 431–432.

Tucker, V. (1989) Peregrine eating prey on the wing. *British Birds,* **82,** 620.

Uttendorfer, O. (1943) Fledermause als Raubvogel—und Eulenbeute. *Zeitschrift für Saugetierkunde,* **15,** 315–319.

Uttendorfer, O. (1952) *Neue ergebnisse uber die ernahrung der greifvogel und eulen.* Eugen Ulmer, Stuttgart.

Verbeek, N. A. M. (1977) *Ardea,* **65,** 25–42.

Vernon, J. D. R. (1972a) Feeding habits and food of the Black-headed and Common gulls. Part two. Food. *Bird Study,* **19,** 173–184.

Vernon, J. D. R. (1972b) Prey taken by Short-eared owls in winter quarters in Britain. *Bird Study,* **19,** 114–115.

Village, A. (1981) The diet and breeding of long-eared owls in relation to vole numbers. *Bird Study,* **28,** 215–224.

Village, A. (1982) The diet of the kestrel in relation to vole abundance. *Bird Study,* **29,** 129–139.

Walsh, S. T., Stebbings, R. E. & Thompson, M. J. A. (1987) Distribution and abundance of the pipistrelle bat *Pipistrellus pipistrellus. The Vincent Wildlife Trust Report 1987,* pp. 43–46. The Vincent Wildlife Trust, London.

Watson, D. (1977) *The Hen Harrier.* T & AD Poyser, Berkhamsted, Surrey.

Watson, J. (1979) Food of merlins nesting in young conifer forest. *Bird Study,* **26,** 253–259.

Webster, J. A. (1973) Seasonal variation in mammal contents of barn owl castings. *Bird Study,* **20,** 185–196.

Wijnandts, H. (1983) *Ecological Energetics of the Long-Eared Owl.* Ph.D. thesis, University of Groningen, Netherlands.

Wooler, R. D. & Triggs, G. S. (1968) Food of Long-eared owl in Invernesshire. *Bird Study,* **15,** 164–166.

Yalden, D. W. (1980) Notes on the diet of urban kestrels. *Bird Study*, **27**, 235–239.

Yalden, D. W. (1985) Dietary separation of owls in the Peak District. *Bird Study*, **32**, 122–31.

Yalden, D. W. & Warburton, A. B. (1979) The diet of the kestrel in the Lake District. *Bird Study*, **26**, 163–171.

Yalden, D. W. & Yalden, P. E. (1985) An experimental investigation of examining kestrel diet by pellet analysis. *Bird Study*, **32**, 50–55.

Yom-Tov, Y. (1975) Food of nestling crows in Northern Scotland. *Bird Study*, **22**, 47–52.