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Conservation biology of an endangered species: field studies of greater horseshoe bats

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Synopsis

We overview an autecological study of the endangered greater horseshoe bat *Rhinolophus ferrumequinum* in south-west England. Bats from a woodland site generally emerged earlier than did bats from an exposed roost, except in early spring when tree leaf cover was minimal. Foliage around the roost may benefit bats by extending foraging time and reducing predation. Bats older than one year foraged between 2 and 4 km from their day roosts. Hence conservation of foraging habitats within this range is important. Ancient semi-natural deciduous woodland was used intensively by foraging bats during spring, while during late summer the bats fed mainly over pasture. Woodland was usually warmer than pasture, and the relative temperature difference between the two habitats was greatest at low temperatures. Insect abundance increased rapidly above 6–10 °C. Hence, in spring, it may be more profitable for bats to forage in woodland. The shift to feeding over pasture was associated with the dominance of *Aphodius* dung beetles in the diet during summer. Juveniles foraged independently of their mothers before weaning. Prime foraging habitat close to the maternity roost is probably important to initial and long-term juvenile survival. The hibernation requirements of *R. ferrumequinum* are briefly reviewed. Insights into the foraging needs (e.g. commuting distances) of other species may be gained from predictions based on flight morphology.

Introduction

The protection of foraging habitats is arguably the aspect of bat conservation that most urgently requires implementation. In the United Kingdom all bat species and bat roosts are protected by the Wildlife and Countryside Act (1981), but the need to protect feeding habitats has, until recently, received little attention, although legislation is being prepared to protect important feeding areas used by bats (see Hutson 1993). However, basic biological

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information on where the bats feed, what they feed on and how far they travel is lacking for most species.

The aim of this study is to provide recommendations for the conservation of feeding grounds used by the endangered greater horseshoe bat *Rhinolophus ferrumequinum*. We give an overview of an autecological study of this species, which we hope will be of use in assessing the habitat requirements of other bats. We also aim to show how foraging ranges may be estimated for other species by using predictions based on flight morphology.

The greater horseshoe bat is considered to be endangered in Britain and Europe, with the current British population estimated at *c.* 4000 individuals in about 14 major maternity colonies (Hutson 1993). The British population of *R. ferrumequinum* has declined substantially during the past century (Stebbings & Arnold 1987), though detailed population studies show that numbers remained relatively stable from the mid 1960s in some areas until a serious decline after 1986 (Ransome 1989). A recent review of the biology of this species is given by Ransome (1991). The aim of the present paper is to answer the following questions:

1. How important are the conditions around the roost for conservation?
2. How far do the bats travel to forage, and what sort of area around a maternity roost should be conserved if feeding habitats are to be protected?
3. How is habitat use influenced by habitat microclimate and insect abundance?
4. How does diet reflect habitat use?
5. Do the habitat needs of juveniles differ from those of adults?
6. Can foraging distances of other bat species be predicted from flight morphology?

In addition we briefly review studies on the hibernation requirements of *R. ferrumequinum*.

The study populations

The work described here was performed in three areas within 50 km of Bristol, Avon. The sites are described in Ransome (1968, 1990). Most of the radio-tracking work was performed at a site on the edge of the Mendip Hills. The bats here (Site A, up to 110 adults, 30–50 young born per year) roosted in a disused mine in woodland. Breeding also occurred in a nearby (2 km distant) stable block. At least 35 bats winter in underground sites within 2 km of Site A, though many individuals fly to sites 10 km distant in the Mendips to hibernate. Site B (up to 210 adults, 70–90 young born per year) is in a coach-house in south-west Avon. Site C (currently up to 90 adults, 25–30 young born per year) is Woodchester Mansion near Stroud, Gloucestershire (see Ransome 1989, 1990 for details). Most of the work described here was performed at Site A, though smaller-scale studies were conducted at Sites B and C to investigate the generality of our findings. Sixty-six bats were radio-tracked between 1990 and 1993, giving 192 complete nights (contact maintained with bats from dusk to dawn with no gaps of longer than 1 h) of telemetric data. Bats up to three months of age are referred to as juveniles; bats which have not yet reached breeding age (usually three years) are termed subadults. Day 0 is the day of birth, and 'first-year bats' are animals in their first year of life.

The importance for conservation of conditions around the roost

Many bat species, including *R. ferrumequinum*, sometimes linger close to the roost before leaving for more distant foraging areas. Conditions around the roost may have important implications for the conservation of bats, especially in terms of protection from predators and extending potential foraging time. To illustrate the effects of cover on the emergence behaviour of the greater horseshoe bats, we documented emergence times at Site A, which is surrounded by woodland, and at the associated stable site (which has an open aspect) on the same nights (Fig. 1). Median emergence time (MET) was always earlier at Site A than at the stable block, except on the first visit of the year (6 May 1992, 21 April 1993), when bats emerged from the stable site with the same or earlier MET than at Site A. From May onwards, the woodland leaf cover caused the area around Site A to be darker than that at the stable block. Under these conditions bats emerged with a MET 5–37 min earlier at Site A. For six nights when light level data were available, bats emerged at slightly higher light intensities at Site A than at the stable block (Site A mean light level at MET = 0.83 ± 0.41 W/m^2, stable block = 0.00 W/m^2 on all six nights; paired *t*-test $t_6 = 5.00$, $P<0.01$). Thus bats at Site A emerged not only earlier, but also at higher light intensities. This may be because the perceived risk of predation was lower in the roost surrounded by trees.

Daylight flying appears to increase the risk of being captured by diurnal avian predators (Speakman 1990, 1991). Presumably such predation risks will also affect emergence time, with bats emerging only once the risks of being seen by visual predators are minimized. Predation from diurnal predators is probably important in shaping the emergence patterns of *R. ferrumequinum*. Sparrowhawk, *Accipiter nisus*, predation occurs at Site B, with at least two different hawks capturing bats in 1992–1993, and one bird capturing about 10 bats over a two-week period. The presence of tree cover around roosts may screen the bats from predatory birds. Furthermore, many aerial insects show a peak in abundance soon after dusk (Racey & Swift 1985), so the extension of feeding time into this peak may be important, especially when energy demands are high, as in lactation. Therefore, all roosts used by *R. ferrumequinum* should be at least partly surrounded by tree cover.

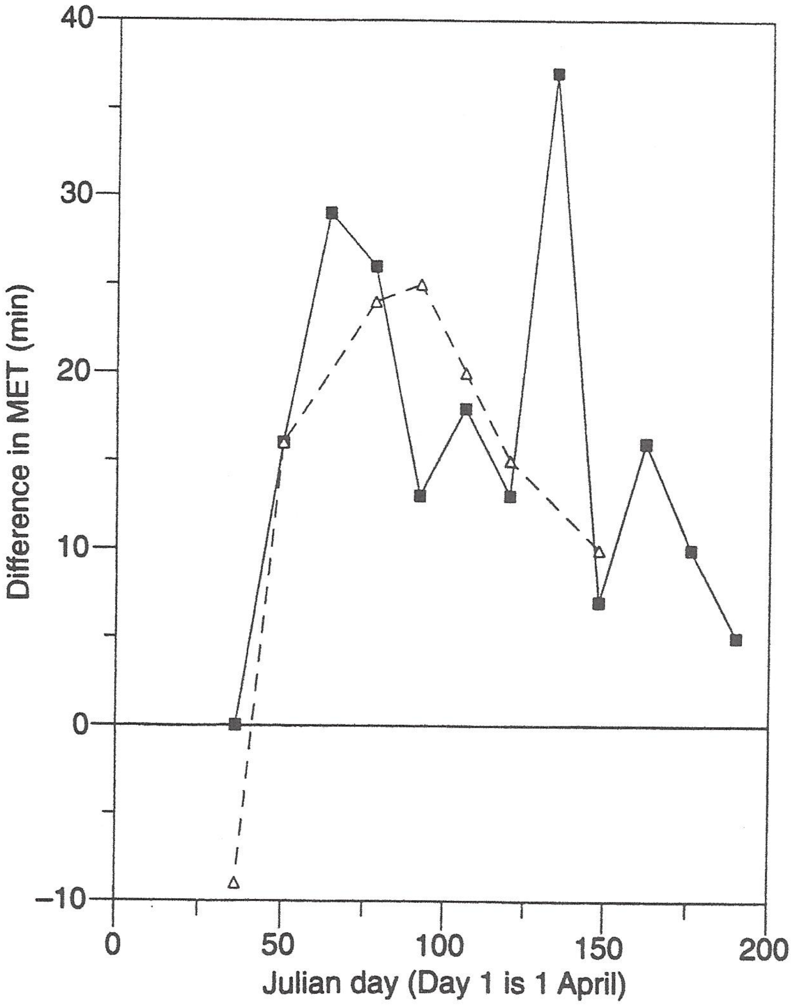

Fig. 1. The difference between median emergence time (MET) at two roost sites (Roost A and a neighbouring roost 2 km distant). Roost A is in woodland, while the neighbouring roost is exposed. The difference in MET is expressed as (Roost B minus neighbouring roost), so that positive values reflect earlier emergence at roost A. Data for 1992 are shown by squares and a solid line, 1993 by triangles and a pecked line.

Foraging distances, habitat use and diet

Foraging distances

Our data on habitat use have been obtained by radio-tracking, and the methodology is summarized by Jones & Morton (1992). All data presented here are for bats which were tracked for a complete night (defined above).

After their first year of life, *R. ferrumequinum* travel, on average, between 2 and 3 km from their day roosts to feeding areas (Table 1). These distances are representative of bats at all three study sites, so foraging range seems to be independent of colony size. Most of the data are from nursery colonies, though most bats spent at least one day in satellite roosts close to their nursery colony. Excluding the data for post-lactating females (taken from one individual only), the greatest foraging distances were found in lactating females (Table 1). Thus, lactating *R. ferrumequinum* differ from female *P.*

Table 1. The effect of sex and age on foraging distances in adult greater horseshoe bats. Data were collected in 1991 and 1992. Total distance represents the distance covered in the whole night, range is the straight line distance to the furthest point travelled.

Bat class	Bats (*n*)	Nights (*n*)	Total distance (km)	Range (km)
Females:				
Subadult	7	18	7.94±3.16	2.50±1.16
Pregnant	4	8	7.47±1.55	2.05±0.34
Lactating	3	8	12.90±2.85	2.84±0.91
Post-lactating	1	3	8.11±1.82	4.03±0.49
Males:				
Subadult	4	14	8.70±2.62	2.31±0.82

pipistrellus, whose foraging ranges remained the same or contracted between pregnancy and lactation (Racey & Swift 1985). However, the Ozark big-eared bat *Plecotus townsendii ingens* also achieves maximum foraging range during lactation (Clark, Leslie & Carter 1993). The total distance covered in a night was also greatest for lactating females. The increased flight time involved must add to the already high energetic costs of lactation (Racey & Speakman 1987) and presumably contributes to an increase in food consumption. Indeed, dawn feeds of *R. ferrumequinum* result in the production of approximately 380 ± 153 mg ($n=10$) dry droppings per bat in non-breeding females compared with 544 ± 118 mg ($n=24$) from lactating females captured on the same date in July 1993 ($t_{32} = 3.38$, $P<0.01$: see below for methodology). From our studies, it seems that to conserve foraging areas up to 3–4 km from the nursery sites is crucial for conservation of *R. ferrumequinum* habitat.

Habitat use and diet

Greater horseshoe bats at Site A forage mainly in ancient woodland during the spring, and over pasture habitats during late summer (Jones & Morton 1992; P. L. Duvergé unpubl.). A similar shift in habitat use was alluded to by Stebbings (1989), who performed preliminary radio-tracking work on this species (Stebbings 1982). This shift in habitat use was evident also from dietary studies (Jones 1990). In a study close to Site A during 1988, *R. ferrumequinum* ate mainly moths (41% of diet by volume) and beetles (33% of diet). Beetles were especially important from July to August, when scarabaeid beetles of the genus *Aphodius* dominated the diet (64% of all beetles by volume in 1988). Other beetles of the cowpat community, especially *Geotrupes* spp., were important prey in spring and autumn, as were tipulid flies. The latter, and large noctuid moths, e.g. *Noctua pronuba*, which were important from June, are often found over pasture. The shift in habitat use from woodland to pasture may be associated with *Aphodius* beetles becoming abundant during

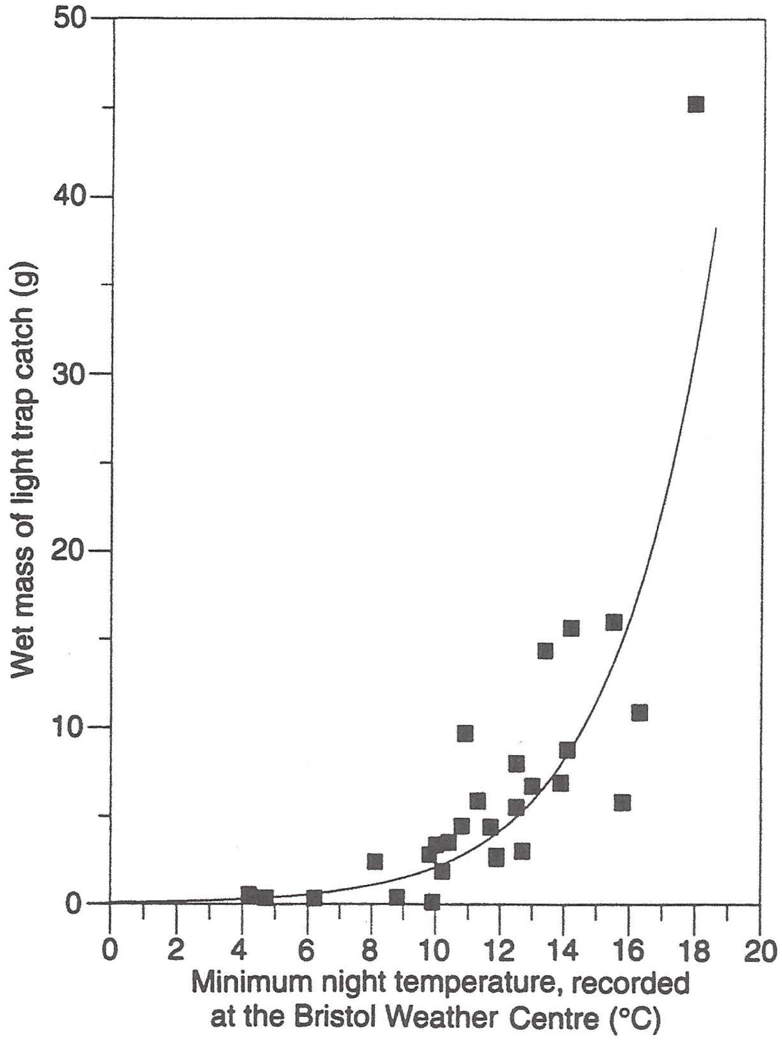

Fig. 2. The relation between light trap catch (wet mass) and minimum night temperature recorded at the Bristol Weather Centre (10 km from the study area) in 1991. The relationship is described as light trap catch (g) = $0.07 \times 10^{0.15\,(\text{temperature})}$, $r = 0.82$, $P < 0.001$.

midsummer, but microclimatic factors might also favour woodland foraging during cooler nights.

How habitat microclimate may influence insect abundance

Rydell (1989a) found a threshold for insect flight at 6–10 °C, and the temperature threshold for moth flight (as documented by light-trap catches) is similar (Fig. 2). Light trap catch biomass increases exponentially as temperature increases, and a small increase in temperature above the 6–10 °C threshold could potentially result in a large increase in the abundance of moths, which constitute most of the diet by volume in *R. ferrumequinum* (Jones 1990). It is therefore likely that habitat microclimate plays a key role in determining insect abundance and that this effect will consequently influence habitat use by bats.

We investigated the temperature differences between woodland and pasture habitats in order to determine whether woodland was consistently warmer than pasture, and whether any temperature difference between the two habitats was relatively constant. We used temperature probes accurate to

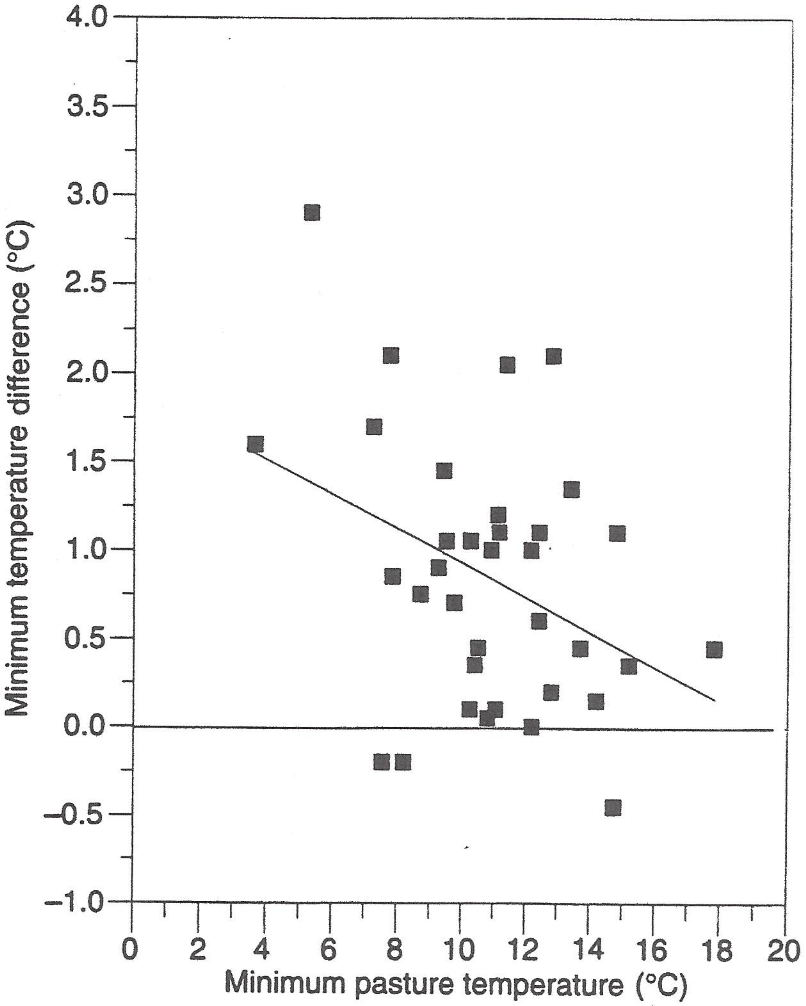

Fig. 3. Differences in minimum night-time temperatures between woodland and pasture compared with minimum temperature in pasture. See text for methods. The relationship is $y = 1.91 - 0.10x$, $r = -0.38$, $P < 0.05$.

0.2 °C on two eight-bit Squirrel Meter/Loggers. We chose three pasture and three woodland habitats in the foraging radius of bats at Site A, and measured night-time temperature in one pair of habitats chosen at random per night. Woodland was always warmer than pasture in terms of minimum overnight temperature (Fig. 3), except on three of 36 nights. Moreover, on colder nights the temperature difference between woodland and pasture was greater. Between 6 and 10 °C, woodland averaged about 1.3–0.8 °C higher minimum temperatures than did pasture. On cool nights, therefore, the temperature threshold for insect flight might be achieved in woodland, but not in pasture. The increased abundance of insects in woodland expected on these cold nights (such as occur during spring) might therefore make it profitable for bats to feed in woodland rather than over pasture.

The development of foraging in juveniles—implications for conservation

We conducted simultaneous radio-tracking of mother–young pairs to determine whether the habitat requirements of juveniles differed from those of their mothers. The transmitters used on mothers weighed 1.0–1.3 g and were made by Biotrack (UK) and Holohill (Canada). We used only 0.6 g Holohill transmitters on the juveniles.

Development in juveniles—an overview

The development of early flight ontogeny is summarized by Hughes, Ransome & Jones (1989) and further relevant data are given in Fig. 4. Evidence from the state of the nipples and rapid hair regrowth on the mammary glands suggests that lactation ends at about 45 days (R. D. Ransome unpubl.). Juveniles make their first flights in the attic from 15 days and begin exploratory flights around the building by about 24 days. At this stage juveniles become volant during the night, but restrict flights to within the building (P. L. Duvergé unpubl.). The first flights are made from the

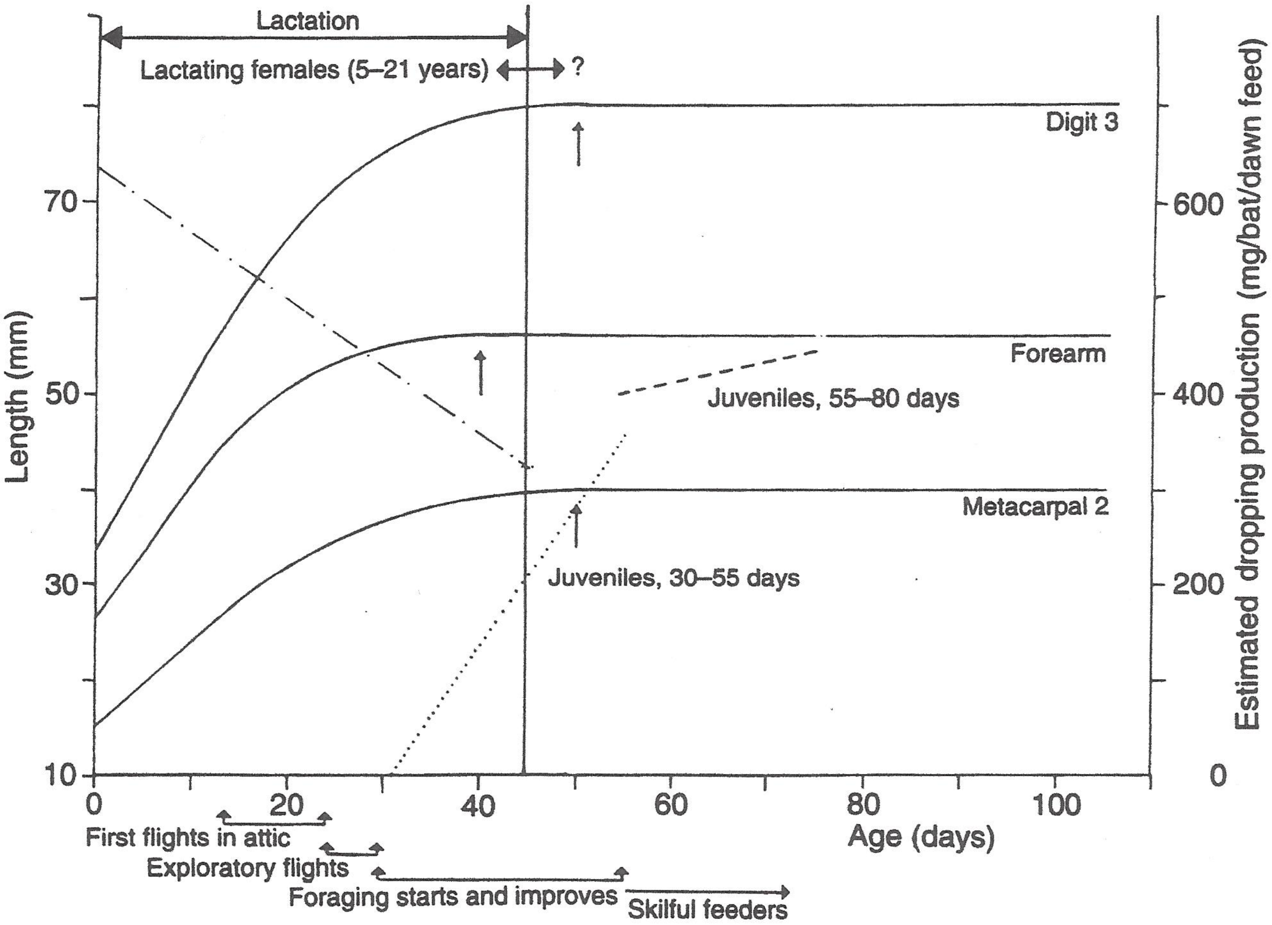

Fig. 4. Schematic representation of the development of greater horseshoe bats. Lactation ends at the vertical line, 45 days, with some individual variation. The uppermost curve is growth of digit 3, the lowest curve shows metacarpal 2. The middle curve shows forearm length. The dropping rate of juveniles is shown between days 30 and 55 on 1 September 1991, and between days 55 and 80 on 22 September 1991. The relationship for bats aged 30–55 days was described from 24 juveniles ($P < 0.001$), while that for the juveniles aged 55–80 days was not significant (range given in text). A regression line for females is drawn, based on data for females aged 5–21 years (R. D. Ransome unpubl.; $P < 0.001$).

roost at about 28–30 days (see below), and insects appear in the droppings of juveniles of these ages, suggesting that feeding begins immediately. Doppler shift compensation in echolocation first appears in a rudimentary form at about 30 days, though juveniles may still overcompensate when aged 35 days. Juveniles aged 40–45 days appear to be able to compensate for Doppler-shifts in echolocation as efficiently as can adults (Konstantinov 1989). If the bats in this study developed at the same rate as did those studied by Konstantinov, they would be flying and foraging with incomplete Doppler-shift compensation for the first 12 nights of activity outside the roost.

Dropping production as an index of food consumption

Dropping production, as an estimate of food consumption, was measured by catching bats soon after dawn and keeping them for measured periods in individual bags. Droppings were dried to constant mass and the dropping-production rate was calculated for that period of containment. Complete data were obtained from 14 individuals bagged for a total of 10 h immediately after dawn in September and moved into clean bags every 2 h. From these two-hourly data sets, mean production rates for each period were calculated. An exponential decay curve of the dry dropping rates against time since dawn was used to estimate total production for individuals on other dates when periods of containment were much shorter (R. D. Ransome unpubl.). All dropping-production estimates quoted refer to bats feeding on dung beetles, to ensure comparability. Data should be regarded as minima, since 10 h is insufficient time to permit all food eaten at dawn to be egested as faeces. Robinson & Stebbings (1993) showed that *Eptesicus serotinus* retained food items for up to 32 h after ingestion. However, since production rates fall below 5 mg/h after 10 h, and estimates for most bats lie in the range 300 to 600 mg, errors are likely to be low.

Faecal production of lactating females aged 5–21 years showed a marked decline from 640 mg/bat/dawn feed at the start of lactation to 323 mg/bat/dawn feed at the end (45 days) (Fig. 4). Younger females were much more erratic, with some showing an increase in consumption during the early part of lactation.

The dropping production of juveniles increased progressively between days 30 and 55, with an increase of about 15 mg/day up to about 350 mg/bat/dawn feed (Fig. 4). The increase in dropping production of juveniles coincides with an increase in the amount of time spent foraging (P. L. Duvergé unpubl.), distance travelled from the roost and, perhaps, with an increase in the efficiency of prey capture. Between days 55 and 100, the young may travel 2 km or more from the roost to forage (Fig. 5). At this time there is no significant relationship between dropping production and age (range = 195–744 mg/bat/dawn feed) and production falls within the range of those recorded from post-lactating females.

Range expansion by juveniles

Foraging range (straight line distance from nursery roost to furthest point visited) of juvenile *R. ferrumequinum* (Fig. 5) increases gradually with age. For two bats telemetered before first foraging flights began, one left the roost at 28 days and the other at 30 days. For the first five days of nocturnal activity outside the nursery roost juveniles remain within 1 km of the roost. Figure 5 shows how the foraging range reaches that typical of adults. Before weaning occurs at about 45 days, the juveniles return to the roost during the middle of the night, together with their mothers, presumably to suckle. By remaining close to the roost, juveniles may facilitate rapid returns for suckling, but it is also possible that flight is still handicapped by incomplete growth and a lack of ossification of the wing bones. Furthermore, they may risk disorientation and become unable to find the roost from greater distances until they have thoroughly learned the local topography. Whatever explanation, or combination of explanations, is correct, Ransome (1990) showed that the mortality rate of juveniles rises significantly between 45 and 55 days, when the foraging distance rises rapidly (Fig. 5).

After 55 to 60 days juveniles forage up to distances of 2–3 km, similar to the distances covered by adults. The range expansion described here is similar to that observed in *M. myotis* by Audet (1990). Investigations into the types of prey consumed by mothers and offspring are currently in progress, but *Aphodius* dung beetles are clearly important to juveniles for the first 2–3 weeks of foraging at Woodchester (R. D. Ransome unpubl.).

Growth of the forearm is largely complete by 40 days, but the fingers do not reach their final length until after 50 days and ossification may continue beyond 60 days (R. D. Ransome unpubl.—see Fig. 4). Hence the final skeletal size achieved by a juvenile bat depends not only on maternal quality, but also on the efficiency of its own foraging during at least the first 20 days of self-feeding. The survival of female *R. ferrumequinum* is influenced by forearm length, with large females surviving better than small females (Ransome 1989, 1990). Since the initial foraging success of this bat influences its subsequent survival potential, the provision of favourable feeding habitat (cattle-grazed permanent pasture alongside deciduous woodland) close to the maternity roost should significantly increase population levels.

Mother–young associations

In total 25 nights of data were obtained from eight mother–young pairs of bats where the location of both animals was known on the same night. Juveniles were tracked before they left the roost until 96 days of age. On only one occasion did mother and young leave the roost together, and only once were a mother and young seen foraging together. While mothers travelled rapidly to

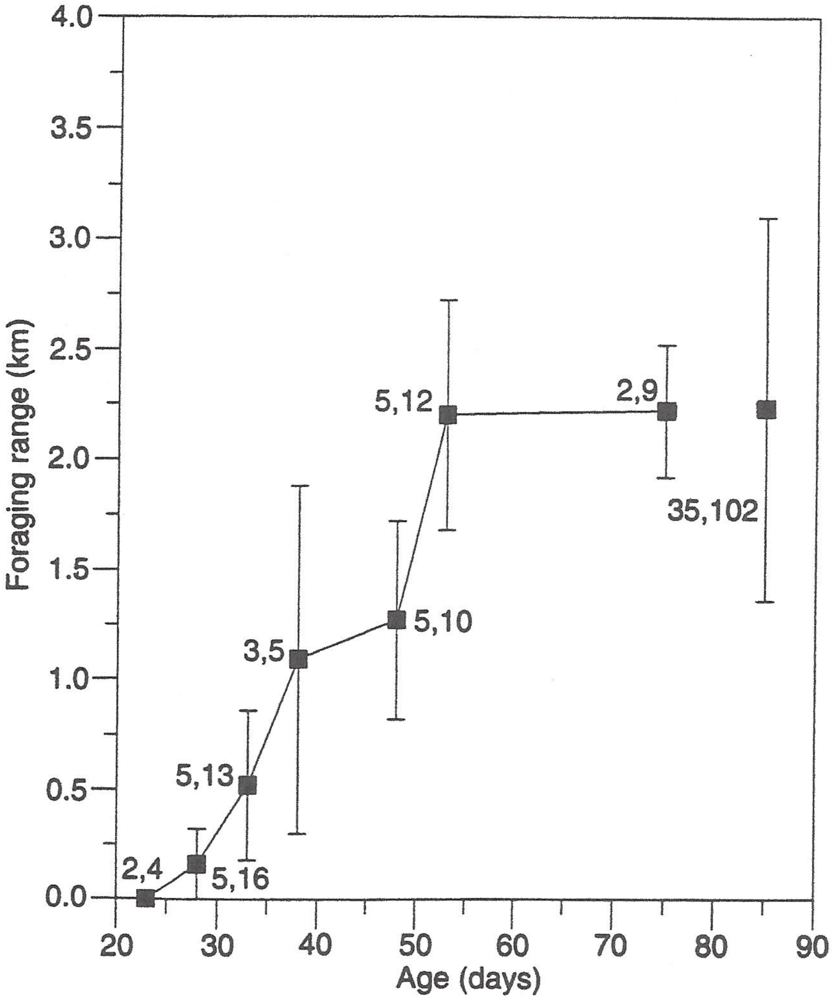

Fig. 5. The expansion of foraging range (straight line distance from maternity roost to furthest point reached) in juvenile greater horseshoe bats. Data are means for bats in five-day age classes ± SDs. The number of bats and the number of bat-nights for each data point are given, together with data for bats older than one year (point on right of graph).

foraging areas, usually 2–3 km from the roost, juveniles remained close to the roost at first. We conclude that the development of foraging behaviour in *R. ferrumequinum* involves no tuition from the mother, and is almost certainly self-taught. Some studies have suggested that maternal tuition may be important in the development of foraging in some species (*Noctilio albiventris*: Brown, Brown & Grinnel 1983; *Eptesicus fuscus*: Brigham & Brigham 1989), though *R. ferrumequinum* resembles *Myotis myotis*, in which young forage independently of their mothers (Audet 1990). Our data are valuable in that the ages of the young were known precisely, and because two bats were tagged before they started self-feeding.

Hibernation requirements relevant to conservation

Hibernation in this species has been investigated by Ransome (1968, 1971) and a more extensive coverage of hibernation, including a range of other species, is given in Ransome (1990). Suitable sites permitting greater horseshoe bats to remain throughout their hibernation period (October to May) need the following attributes:

1. Parts with complete darkness and a relative humidity exceeding 96%.
2. A range of ambient temperatures between 5 °C and 12 °C.
3. Regions of slow air-flow achieved either by having two or more entrances, or by having a downward sloping entrance.
4. Close access to suitable winter foraging areas which are preferably sheltered and facing southwards, so that insect availability in winter is maximized.
5. Freedom from repeated disturbance by human activities.

Sites which do not have all attributes may contain bats at certain times of the hibernation period, e.g. autumn and spring, but not continuously. Many male territorial sites are like this. Those which do not have access to good feeding sites, but which possess a good internal climate for bats, may only be used for short stops *en route* to other hibernacula. This is because a large proportion of the population feeds during the hibernation period (Ransome 1968). Arousal from hibernation torpor in this species is normally highly synchronized with dusk (R. D. Ransome pers. obs.).

Implications for the conservation of other species of insectivorous bats

We have identified several factors which should improve the conservation of foraging habitats for greater horseshoe bats. An important question for bat conservation is, how far do different species travel from their roosts to forage? Once this is known, effective protection or creation of suitable foraging habitats crucial to the bats at a particular colony may be attempted.

Although foraging range may be influenced by factors such as colony size, reproductive status of bats and, as shown here, by age, it should be possible to make some predictions about foraging ranges for other species. Flight performance in bats is influenced by wing morphology (Norberg & Rayner 1987). Two features of flight morphology which may be important in determining foraging range are wing loading and aspect ratio. Bats with higher wing loadings fly faster. If time constraints are important during foraging, then bats with high loadings are predicted to travel further from the roost, since they can travel further in a given time. Species with high aspect ratios (narrow, pointed wings) are predicted to range further, since unit energy costs are lower. It may therefore be possible to predict foraging ranges from wing loading and aspect ratio for species which cannot be studied directly (e.g. those too small to carry transmitters), or when rapid decisions about conservation must be made before autecological studies are possible.

A review of 18 species of microchiropteran bats showed no correlations between body mass ($r_{17} = 0.178$) or wing loading ($r_{16} = 0.313$) and foraging range. However, aspect ratio and foraging range were correlated positively ($r_{16} = 0.694$, $P < 0.01$, Fig. 6). Many species have foraging ranges between 1 and 3 km, irrespective of diet or body size. High aspect ratio species commute further to forage, in line with the above predictions. One important factor which may also influence foraging range is colony size. Bats in very large

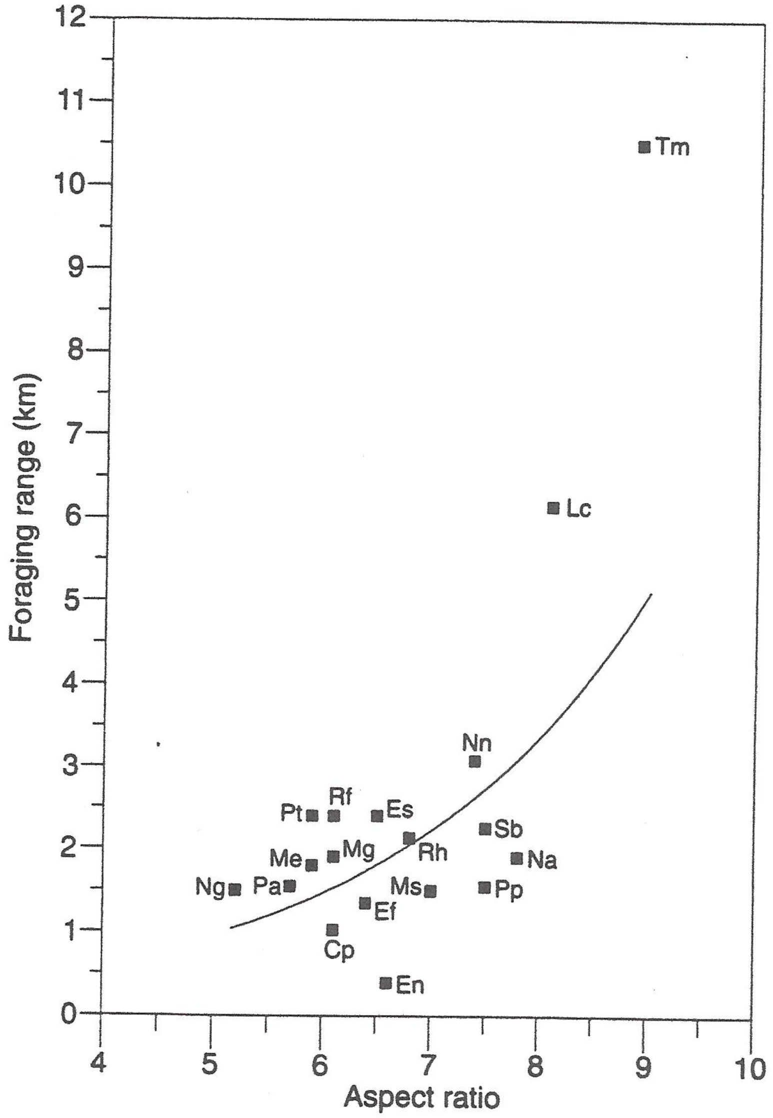

Fig. 6. The relationship between foraging range and aspect ratio in microchiropteran bats. The fitted line is described by an exponential equation: foraging radius (km) $=0.12 \times 10^{0.18(\text{aspect ratio})}$ $r = 0.58$, $P < 0.01$. The line may not fit data for high aspect ratio species ideally, but fits data for low aspect ratio species better than does a linear equation. Acronyms are: Cp—*Carollia perspicillata* (Fleming & Heithaus 1986); Ef—*Eptesicus fuscus* (Brigham 1991); En—*Eptesicus nilssonii* (Rydell 1989b); Es—*Eptesicus serotinus* (Catto 1993); Lc—*Lasiurus cinereus* (Barclay 1989); Me—*Myotis emarginatus* (Krull *et al.* 1991); Mg—*Macroderma gigas* (Tidemann *et al.* 1985); Ms —*Miniopterus schreibersii* (McDonald, Rautenbach & Nel 1990); Na—*Noctilio albiventris* (Fenton, Audet *et al.* 1993); Ng—*Nycteris grandis* (Fenton, Swanepoel *et al.* 1990); Nn—*Nyctalus noctula* (Kronwitter 1988); Pa—*Plecotus auritus* (Swift & Racey 1983; Fuhrmann & Seitz (1992); Pp—*Pipistrellus pipistrellus* (Racey & Swift 1985); Pt—*Plecotus townsendii ingens* (Clark, Leslie & Carter 1993); Rf—*Rhinolophus ferrumequinum*—this study; Rh—*Rhinolophus hildebrandtii* (Fenton & Rautenbach 1986); Sb—*Scotophilus borbonicus* (Barclay 1985); Tm—*Tadarida midas* (Fenton & Rautenbach 1986). All species were radiotracked with the exception of En, Ms, Pp and Swift & Racey's study on Pa—these studies used light-tagging. Aspect ratios were taken from Norberg & Rayner (1987).

colonies, such as *Tadarida* spp., may need to travel far to reduce competition with conspecifics. The relationship between colony size and foraging range deserves more attention in both intra- and interspecific analyses.

This study has summarized some of the information necessary to formulate a conservation strategy for the endangered greater horseshoe bat. Although some data obtained are obviously species-specific, it seems that most microchiropteran bats forage within 4 km of their day roosts, and habitats within this sort of radius should be critical for conservation. High aspect ratio species should require the protection of habitats at greater distances.

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