



# Greater Horseshoe Bat *Rhinolophus ferrumequinum* (Schreber, 1774)

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## Contents

<b>Common Names</b> .....	2
<b>Taxonomy, Systematics and Paleontology</b> .....	2
<b>Current Distribution</b> .....	4
<b>Description</b> .....	4
Pelage .....	5
Dentition .....	6
Age Determination .....	7
<b>Physiology</b> .....	7
Metabolism .....	7
Body Condition .....	7
<b>Genetics</b> .....	8
Karyotype .....	8
Population Genetics .....	8
<b>Life History</b> .....	9
Reproduction .....	9
Fertility .....	10
Gestation .....	10
Number and Size of Offspring .....	10
Sex Ratio and Growth from Birth by Sex .....	10
Age and Size at Maturity .....	14
Reproductive Lifespan and Ageing .....	14
Sex and Age-Specific Survival Patterns .....	14
<b>Habitat and Diet</b> .....	15
Habitat .....	15
Diet .....	16

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Diet Selection .....	18
Diet Assessments .....	18
Amounts Eaten by Individual Bats .....	19
<b>Behavior</b> .....	19
Foraging Behavior .....	19
Resource Competition .....	21
Personalities .....	21
Life in Groups .....	21
Summer .....	21
Winter .....	22
Mating Behavior .....	22
Movements Between Roosts .....	22
Dispersal .....	23
Social Behavior .....	23
<b>Parasites and Diseases</b> .....	24
Ectoparasites .....	24
Endoparasites .....	24
Infectious Diseases .....	24
Zoonoses .....	24
<b>Population Ecology</b> .....	24
Population Dynamics .....	24
Intraspecific Interactions .....	27
Interspecific Interactions .....	27
Climate Change .....	27
<b>Conservation Status</b> .....	28
<b>Management</b> .....	29
Habitat Management .....	29
Conflicts with Humans .....	30
<b>Future Challenges for Research and Management</b> .....	31
<b>References</b> .....	32

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## Common Names

English	Greater horseshoe bat
German	Große Hufeisennase
French	Grand rhinolophe
Spanish	Murciélago grande de herradura
Italian	Rinolofo maggiore
Russian	Большой подковонос

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## Taxonomy, Systematics and Paleontology

The greater horseshoe bat (Fig. 1) is one of the medium-sized species of the genus (but the largest in Europe with a mass from 13–34 g). It is distributed through Europe to about 52°N in Western

Europe and 48°N in Eastern Europe, south to wetter parts of North Africa to about 32°N (Morocco, Algeria, Tunisia), and east to the Himalayas (Fig. 2). Further to the east it is replaced by subspecies.

It was formerly believed that greater horseshoe bats evolved in the Mediterranean region of North Africa and subsequently spread to many Southern and Western European countries in a northerly direction, and easterly as far as Japan. In Japan it was designated as subspecies *R. ferrumequinum nippon* Temminck, 1835. Transition from the European *Rhinolophus f. ferrumequinum* was thought to occur somewhere east of Afghanistan and before China. A taxonomic review by Thomas (1997) recognized seven subspecies based on morphology. In addition to the two above, Thomas added *R. f. creticum* Iliopoulou-

Georgudaki and Ondria, 1985 in Crete, *R. f. irani* Cheesman, 1921 in Iran, Iraq, and Turkmenistan, *R. f. proximus* K Anderson, 1905 from Afghanistan and Pakistan to India, *R. f. tragatus* Hodgson, 1835 in Northern India and China, and *R. f. korai*

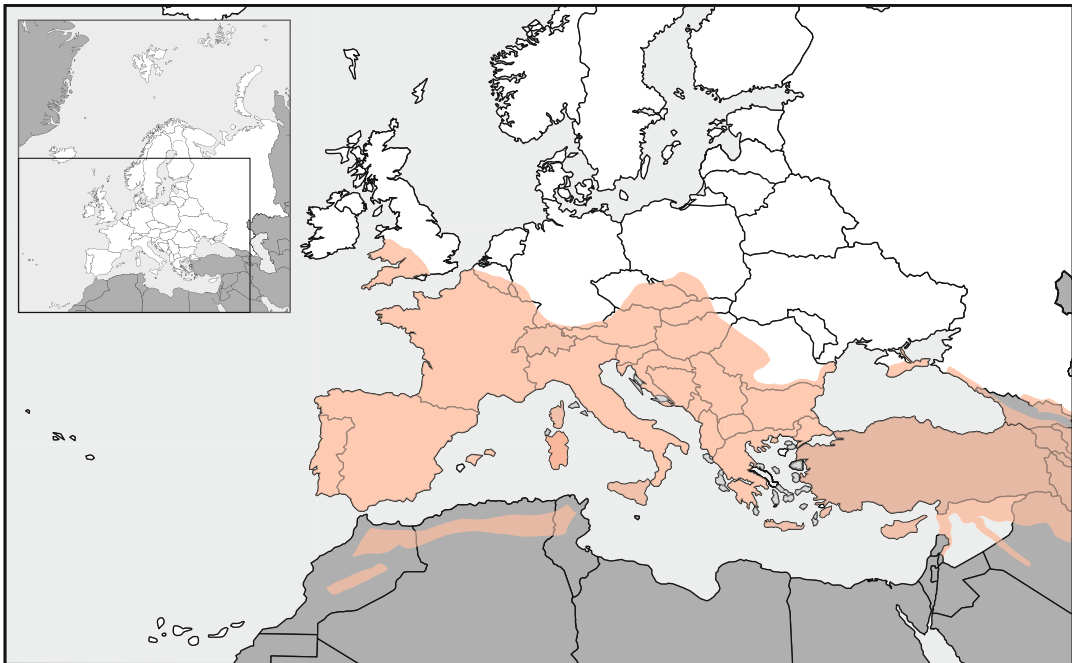
Kuroda, 1938 in Korea. No genetic data were used in these assignments.

Italian greater horseshoe bats were shown to be larger than UK bats (Dinale 1969). However, the suggestion by Barrett-Hamilton (1910–1911) that British greater horseshoe bats should be regarded as a subspecies (*R. ferrumequinum insulanus*) was not adopted. European greater horseshoe bats belong to a single species.

Echolocation call variations among populations show some concordance with genetic discontinuities found by Rossiter et al. (2007) and supports their suggestion that cryptic diversity may occur in oriental populations. G. Jones (unpubl.) found frequencies of their CF call component were 72–74 kHz for bats from Yunnan and Sichuan, and differed from those in East China (74.8–77.1 kHz), confirming Ma et al. (2006). Japanese bats use calls at about 65 kHz. These data contrast with 82–84 kHz in the UK; 80–81 in France and Germany, and 77–81 in Asia Minor.



**Fig. 1** Head showing characteristic nose-leaf and large pinna with antitragus. (Reproduced courtesy of Gareth Jones, 4th July 2019)



Map template: © Getty Images/iStockphoto

**Fig. 2** IUCN (2016) distribution map of *Rhinolophus ferrumequinum* in Europe, Asia Minor, and North Africa. Distribution based on IUCN Red List of Threatened

Species. Version April 2016. <https://doi.org/10.2305/IUCN.UK.2016-2.RLTS.T19517A21973253.en>

## Current Distribution

The greater horseshoe bat, *Rhinolophus ferrumequinum*, is distributed through Europe to about 52°N in Western Europe and 48°N in Eastern Europe, south to parts of North Africa (Morocco, Algeria, and Tunisia), and east to the Himalayas. Further to the east it is replaced by *R.f. nippon*.

Range shown (Fig. 2) covers its European area limits. Within this range it is rarely present above 3000 m a.s.l, restricted northerly to temperate regions by the need to forage significantly during early and late hibernation periods, and even in mid-winter in the UK (Ransome 1968, 2002; Park et al. 1999, 2000). Spring climate at high latitudes, particularly temperature, affects pup growth (Ransome 1989a), birth-timing (Ransome and McOwat 1994), and long-term survival (Ransome 1989b). Short night length in June (6 h at 51°N latitude) makes three foraging bouts/night by lactating females (Duvergé 1996) very stressful. Southerly limits possibly set by arid desert habitats.

## Description

The greater horseshoe bat is a small mammal, but a large species of *Rhinolophus*. Bats are highly specialized for flight (see Hill and Smith 1984; Altringham 2011). Rhinolophids have broad wings and their flight (Norberg and Rayner 1987) and echolocation is designed for foraging in cluttered habitats (Schnitzler 1987; Schnitzler and Ostwald 1983). Nostrils are used for sound emissions via a basin-shaped nose-leaf (Fig. 1) that focuses echolocation and social calls into a torch-like beam. Eyes are small; field of view is partly obscured by nose-leaf. Nostrils open within the parabolic horseshoe (about 14 mm high by 8 mm wide). A few vibrissae occur beneath the horseshoe and on the lower lip. Ears are large, triangular, lacking a tragus but with broad anti-tragus (Fig. 1).

Parous females have a pair of functional pectoral nipples and a pair of pelvic teats which develop slightly anterior to the vulva during late

pregnancy in females breeding for the first time. They lack a milk supply, but are sucked by the young between suckling periods and facilitate close attachment. In summer they are pink and swollen when in use, but turn white and regress during weaning and in the following winter. If breeding is omitted in a summer they shrink further. Subadult females lack pelvic teats.

Mature males carry out spermatogenesis annually in June and July, developing very large testes within a swollen scrotum. Sperm is stored within distended epididymes which show as dual white swellings within the scrotum. Subadult males show no white scrotal areas.

It is the largest *Rhinolophus* in Europe, with the following physical dimensions in the UK (author's data): head and body 56–68 mm, forearm (radius) 50.6–60.4 mm, wingspan 330–395 mm, ear 21–26 mm, and weight 13–34 g. Total length of skull >20 mm. This contrasts with <16 mm for the lesser horseshoe which coexists with it in many parts of Europe.

UK greater horseshoe bats are slightly smaller than in some continental populations. Forearm length (FL) is best judge of skeletal size (Tuttle and Stevenson 1982). Mean FL of 55.7–56.7 mm in Italy (Dinale 1969) is greater than in the UK. The name *R. f. insulanus* (Barrett-Hamilton 1910–1911) was based on this difference in size. It was not accepted.

Jiang et al. (2019) investigated global geographical variation in body size and its possible causes. They assessed body mass and forearm length of male and female bats separately, linked to high-resolution environmental data for their sampled sites. Best model linked populations with longer forearms (for both sexes) with higher mean temperatures in summer, and lower mean temperatures in winter.

Live replete body mass varies considerably annually under the influence of many factors, including forearm length due to growth factors (Ransome 1998); hibernation fat deposition (Ransome 1968); increase in lean body weight with age (Ransome 1995); and gestation period of females (Ransome 1995). Daily mass fluctuations in summer reflect foraging success levels (Ransome 1997b). Mass data must be collected

under consistent protocols to be comparable, especially in summer. Winter data is less problematic (Table 1).

Males are about 2% smaller skeletally than females as measured by forearm, but considerable overlap occurs. Mean forearm length 54.8 mm ( $n = 228$ ) for males and 55.5 mm ( $n = 222$ ) for females, both SD circa 1.0 mm for females occupying unheated roosts in Gloucestershire and Somerset. Following provision of heaters in one maternity roost mean female forearm increased significantly from 55.7 ( $n = 58$ ) to 56.5 mm ( $n = 39$ ) in a study by Ransome (1998).

Changes through the hibernation period largely reflect the level of fat deposits. In October 1964 a parous female weighing 30.1 g had 9.1 g discrete fat reserves compared with a 19.2 g

parous female that had 1.5 g in April 1965. An October first-year male weighing 21.3 g had 3.4 g of fat reserves, and a late winter male weighing 14.6 g had 0.6 g of reserves. Fat use explained most of the hibernation weight loss, but muscle weight also fell as well (Ransome 1990, Table 6.8).

## Pelage

Adult and subadult bat's fur is thick, fluffy; pale buff with darker buff tips becomes progressively darker and reddish with age. Juveniles have grey fur which may develop buff tips ventrally late in their first year (Fig. 3). Both age groups are slightly paler ventrally. Moulting begins once regular

**Table 1** Body mass changes through the winter by age and sex group when no bats are pregnant, and most digested food remains have been egested

Sex and age	Late October	Late January	Early April
<b>Females</b>			
First winter	25.8 ± 0.8	20.4 ± 0.3	16.9 ± 0.2
Second winter	27.9 ± 0.6	22.4 ± 0.5	18.6 ± 0.2
Third winter	28.9 ± 0.8	23.6 ± 0.6	19.5 ± 0.1
Fourth+ winter	30.5.8 ± 0.7	25.0 ± 0.7	19.8 ± 0.1
<b>Males</b>			
First winter	24.4 ± 0.8	19.7 ± 0.4	16.5 ± 0.2
Second winter	26.1 ± 0.8	21.1 ± 0.3	17.5 ± 0.2
Third winter	26.8 ± 1.0	21.7 ± 0.5	17.9 ± 0.1
Fourth+ winter	26.0 ± 1.3	21.9 ± 0.2	18.1 ± 0.4

Somerset winters 1979/1980–1985/1986. Means of annual means, (g ± SD). Source: Ransome 1991

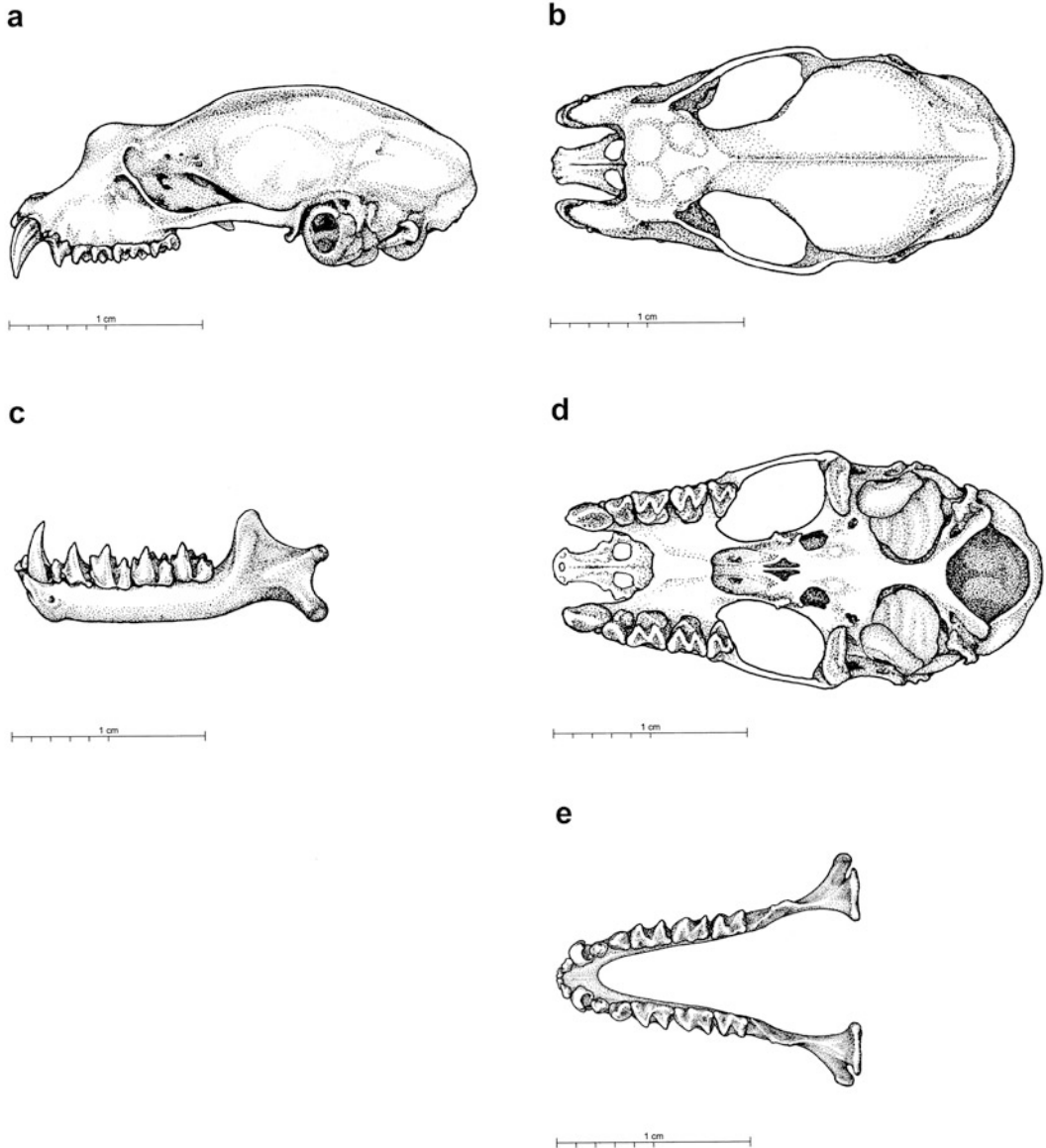
**Fig. 3** Mother with pup showing fur color differences (a); close attachment while resting (b), when pup sucks its mother's posterior nipples. (Photos: Roger Ransome (a) (b) reproduced courtesy of Gareth Jones, 4th July 2019 (b))



dusk and dawn feeding occurs in May or early June, and is usually complete by late June or early July. Cold or wet and windy spring weather may cause moult delay (*pers. obs.*).

### Dentition

Skull is easily recognized from other bats (Fig. 4). All rhinolophids have a bulbous swelling dorsal to the nasal passage, and may lack upper incisors. Large skull length (>20 mm) identifies its



**Fig. 4** Skull of *Rhinolophus ferrumequinum*; (a), (b), and (d) show lateral, dorsal, and ventral view of skull, (c) lateral view of left mandible (view from outside), (e) dorsal view of mandible. (© Franz Müller with kind permission)

occurrence in Europe. Dental formula (permanent dentition only, as deciduous teeth shed into amnion prior to birth (Matthews 1952)) is  $I^1, C^1, P^2, M^3$  for upper jaw, and  $I_2, C_1, P_3, M_3$  for lower jaw. Upper incisors are carried at the tips of slender premaxillae, which often separates from the skull after death and decomposition. Dentition reflects a typical insectivorous diet with large canines and sharp cusps on premolars and molars. Tooth wear provides poor evidence of age, as known 20-plus-year-old bats may show little tooth wear.

### Age Determination

First-year bats are reliably distinguished from older bats by dorsal grey fur color and shape of the metacarpal 5/first phalanx joint. It tapers smoothly at the diaphysis/epiphyseal fusion points. Bats in their second year, or older, have dorsal brown fur and the metacarpal/first phalanx joint is knobbly, with a right-angle ridge across it at the diaphysis/epiphyseal fusion points. Reliable age determination of older age groups depends on marking bats (using rings or pit tags) as pups or first-year bats, and following them throughout their lives.

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### Physiology

#### Metabolism

Although it is a large insectivorous bat, it is a very small mammal that has a very high metabolic rate even when resting. Rate climbs rapidly at low ambient temperature (below about 15 °C), and when flight occurs. Active (thermoregulating) bats normally minimize energy costs by clustering together, and/or by selecting warmer roosts. Above about 25 °C the cost of thermoregulation falls to minimum levels, and above 40 °C they become heat stressed. Few roosts provide continuously ideal thermal conditions for thermoregulation. They may switch off thermoregulation and become torpid at any time of year to avoid

starvation (Ransome 1990). A torpid bat uses less than one hundredth of the energy cost of a resting, thermoregulating bat.

In winter greater horseshoe bats are continuously torpid for periods of up to 12 days (Ransome 1971; Park et al. 2000), gaining further energetic reductions.

To fuel the energetic demands of full activity over 24 h in summer, bats must consume a high proportion of their body mass of food each day, even if merely carrying out body maintenance activities. Reproductive activity, or fat storage, adds considerably to energetic costs, and hence to the levels of food required. Temperate countries have erratic climatic conditions which do not permit regular levels of food consumption to be maintained even in summer (Speakman and Racey 1987; Ransome 1997b).

### Body Condition

Body condition (BC) is often used to indicate the reserves a bat stores for future use. It is obtained by dividing body mass by forearm length. BC changes rapidly in adults after successful foraging, and very slowly (over 2–3 months) during pregnancy, so BC at these times does not indicate body reserve state. BC provides body reserve data only if a bat is replete, and nonpregnant. Ransome (1995) used  $BC \times 56$  (mean female FL) to adjust and make comparisons among age groups. It can be applied to pups during their growth phase.

Table 2 shows the same basic data as in Table 1, but adjusted to body condition. Estimated percentage body reserves for each age and sex group are shown in Table 3.

Table 3 shows a remarkable similarity in percentage body reserve levels in all age and both sex groups, supporting the view of Ransome (1990) that this bat has a fuel gauge that is used for energetic decision-making, such as when to forage, or use torpor. The greatest reserve differences occur between the oldest male and female age groups in October.

**Table 2** Mean adjusted body condition of greater horseshoe bats during hibernation period

Sex and age	Late October	Late January	Early April
<b>Females</b>			
First winter	25.8; 25.85	20.4; 20.44	16.9; 16.93
Second winter	27.9; 27.95	22.4; 22.44	18.6; 18.63
Third winter	28.9; 28.95	23.6; 23.64	19.5; 19.53
Fourth+ winter	30.5; 30.55	25.0; 25.04	19.8; 19.84
<b>Males</b>			
First winter	24.4; 24.89	19.7; 20.10	16.5; 16.83
Second winter	26.1; 26.62	21.1; 21.52	17.5; 17.85
Third winter	26.8; 27.34	21.7; 22.13	17.9; 18.26
Fourth+ winter	26.0; 26.52	21.9; 22.34	18.1; 18.46

Somerset (UK) 1979/1980–1985/1986. Data in (g) Source: Ransome 1991 (adapted). Note first number in each cell is the body mass; second is the calculated  $BC \times 56.0$  in each cell. BC calculation used female mean FL = 55.9 mm and males = 54.9 mm

**Table 3** Mean % body reserves of greater horseshoe bats during hibernation period

Sex and age	Late October	Late January	Early April
<b>Females</b>			
First winter	25.85–13.0 = <b>49.7</b>	20.44 = <b>36.4</b>	16.93 = <b>23.2</b>
Second winter	27.95–14.0 = <b>49.9</b>	22.44 = <b>37.4</b>	18.63 = <b>24.9</b>
Third winter	28.95–15.0 = <b>48.2</b>	23.64 = <b>36.5</b>	19.53 = <b>23.2</b>
Fourth+ winter	30.55–15.5 = <b>49.3</b>	25.04 = <b>38.1</b>	19.84 = <b>21.9</b>
<b>Males</b>			
First winter	24.89–13.0 = <b>47.8</b>	20.10 = <b>35.3</b>	16.83 = <b>22.8</b>
Second winter	26.62–13.5 = <b>49.3</b>	21.52 = <b>37.3</b>	17.85 = <b>24.4</b>
Third winter	27.34–14.0 = <b>48.8</b>	22.13 = <b>36.7</b>	18.26 = <b>23.3</b>
Fourth+ winter	26.52–14.5 = <b>45.3</b>	22.34 = <b>35.1</b>	18.46 = <b>21.5</b>

Somerset 1979/1980–1985/1986. Means of annual means, (g) Source: Ransome 1991 (adapted). Note the October column cells show the adjusted BC data (ABC); then the estimated lean body mass (LBM) is subtracted to give body reserves (BR) (data in g).  $BR/ABC \times 100 = \% \text{ body reserves}$ . January and April columns omit estimated LBM. % body reserves in bold

## Genetics

### Karyotype

Karyotype:  $2n = 58$ ; European data (Zima and Kral 1984).

## Population Genetics

### Genetic Diversity

Genetic subdivision between the UK and continental Europe does not justify subspecies recognition of UK bats. However, Rossiter et al.

(2000a) showed that genetic variation was much lower in the UK compared with continental sites due to isolation. This agrees with Thomas (1997) that continental bats are a single subspecies, and not with Csorba et al. (2003) who claimed that multiple subspecies occur within mainland Europe. No clear differences exist between populations from Asia Minor and Iran either. However, the substantial subdivision within China merits further population investigation of *R. f. tragatus*. Finally, the taxonomic status of *R. f. nippon* is yet to be resolved. Sample data from East China and Japan suggest a recent common ancestor.



## Phylogeography

*Rhinolophus ferrumequinum* is an ancient species, believed to have originated in West Asia Minor (Rossiter et al. 2007), which spread through the Mediterranean region when European climate was tropical. It continued northwards into many European countries. Since late Eocene times (circa 39 mya) it has experienced many climatic changes that repeatedly affected its historical European distribution. Three refuge areas permitted Ice Age survival and recolonization in interglacial periods. They were Iberia, Italy, and the Balkans (Taberlet et al. 1988; Hewitt 1996). This situation was supported by Rossiter et al. (2007) using microsatellite data.

Rossiter et al. (2007) used a microsatellite-based approach to investigate greater horseshoe bat colonization history from the Last Glacial Maximum (Devensian) of the Quaternary (Pleistocene plus Holocene) period. Samples from 56 localities from the UK to Japan were used to assess allelic richness. From derived neighbor-joining trees they were able to depict the overall relationship among all localities. In addition, observed heterozygosity ( $H_{\text{obs}}$ ) and  $F_{\text{IS}}$  were derived from samples with at least five individuals. They argued that European greater horseshoe bat populations originated from West Asia Minor in the ancient past. Allelic richness declined from West Asia to the UK, showing sharp discontinuities in gene frequencies within Europe, and between the Balkans and West Asia (Syria/Russia). The Middle East was the center of allelic diversity, and was identified as the site of greater horseshoe bat origin. Ward et al. (2014) found that heterozygosity ( $H_{\text{obs}}$ ) was higher ( $P = 0.046$ ) in those females that had more pups.

Flanders et al. (2009) examined the contrasting results of using microsatellite and mitochondrial DNA analyses to infer population history. They reanalyzed previous microsatellite datasets and used 1098 base pairs of mitochondrial ND2 genes from 45 locations across its range. They concluded that the double approach prevented a misleading conclusion, by revealing two colonization events in Europe, rather than just one. Overall, these two studies showed the importance of Asia Minor as the ancient refuge for the

species. This conflicts with the earlier view of Csorba et al. (2003) of an African origin. Rossiter et al. (2007) identified a single cluster formed by samples from France, Portugal, Spain, and Italy that suggested a common origin via recolonization from a refuge area as European countries rewarmed after the Last Ice Age.

Echolocation call-pattern variations among populations show some concordance with genetic discontinuities, supporting the suggestion by Rossiter et al. (2007) that cryptic diversity may occur in oriental populations. G. Jones (unpubl.) found their CF component frequencies were 72–74 kHz for bats from Yunnan and Sichuan, and differed from those in East China (74.8–77.1). Taniguchi (1985) and Fukui et al. (2004) showed Japanese bats used calls at about 65 kHz. These data contrast with 82–84 kHz in the UK, 80–81 in France and Germany, and 77–81 in Asia Minor.

Lui et al. (2016) investigated the potential origin and maintenance of acoustic social call divergence over similar geographic ranges. They concluded that distance and geographic barriers were probably the main drivers of dialect differences.

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## Life History

Three stages occur in the lives of both sexes. They are juvenile, subadult, and sexually mature. Juveniles reach full skeletal size within 60 days of birth and dimensions are fixed throughout their lifespan (Ransome 1998), which may last up to 30 years (Caubere et al. 1984). Lean body weight, however, increases during the subadult stage (Ransome 1995). Overall female lifespan and reproductive lifespan are similar, but some females extend their lifespan by having many years off breeding (Ransome 1995).

## Reproduction

At age either 2 or 3+ years both sexes are usually capable of breeding (Ransome 1991), but a delay of up to 8 years may occur, more likely in highly growth-stressed females.

Females start oogenesis in late autumn; suspend egg development during most of the hibernation period (Oh et al. 1985), and complete the final nuclear division to produce a single ovum in late March and early April in the UK. Timing may be earlier in warmer and lower latitudes. Mature males store sperm produced in summer over winter. Mating may occur from September until late March, so sperm storage occurs in both sexes.

After mating, a vaginal plug forms within the female. It forms from secretions by both participants. This is a rigid structure that can be found in a mated female by ventral palpation just anterior to the pelvic ridge. Subadult females starting their first gestation produce short fat posterior nipples late in pregnancy. They grow rapidly just before parturition.

## Fertility

Ransome (1995) followed the life histories of ringed pup cohorts born over 16 years in the UK by repeated captures. Early breeding females bred 96% of their opportunities. Later breeding females bred at 85%. Schaub et al. (2007) used modeling of sparse monitoring data over 15 years to estimate fertility, which was 74%. This lower level is possibly unreliable as they assumed survival rate was independent of age.

## Gestation

Conceptions normally occur from early to late April in the UK, just prior to vaginal plug ejection, when the corpus luteum is already present in the ovary (Matthews 1937). There is no fixed gestation length, due to use of torpor (Ransome 1973) in response to fluctuating insect availability. Birth-timing varied, but was synchronized among years at three colonies near the northwestern edge of its UK range at latitude 52°N (Ransome and McOwat 1994). Mean April/May temperature (mAMT) explained cohort mean birth-timing. Regression of mean birth date (mBD) on mAMT explained 70–93% of timing variation. Cold springs led to late births, via

reduced dry dropping levels. These two studies show that pregnant female greater horseshoe bats are erratically forced to choose between foraging to promote foetal development, and use of torpor to avoid starvation in April and May. Dietz et al. (2006) studied birth-timing and growth of greater horseshoe bats among three *Rhinolophus* species in northern Bulgaria at 43°N (a key glacial refuge area) over four summers. Births of *R. ferrumequinum* mainly occurred in the first 3 weeks of June (compared with early July in the UK). A two-year growth study by Eghbali and Sharifi (2019) in Western Iran at 34°N showed most births occurred in late May. Birth synchrony was marked in both years, but reduced under the impact of high rainfall, which may have reduced foraging success by mothers (Ransome 1997b).

## Number and Size of Offspring

Throughout their whole range, females give birth to a single pup that develops from an ovum within the right ovary. No left ovary is present (Hill and Smith 1984). Mean body mass and forearm length are 6.3 g and 25.5 mm for pups at birth in the UK (Ransome 1998). No sex difference occurs. New-born pups show no sex differences in Western Iran but mean body mass of 5.81 and 5.63 g associated with 27.43 and 26.28 mm forearm length in two consecutive summers (Eghbali and Sharifi 2019).

## Sex Ratio and Growth from Birth by Sex

Ransome and McOwat (1994) found an overall sex ratio of 1:1 at birth in nine cohorts born between 1984 and 1993. A major population crash followed spring 1986, when births were the latest recorded (mBD 29 July). During early population recovery births were male-biased. Later a female-biased phase developed as the population grew, Ransome (1998).

Jones (2000) reviewed the ontogeny of behavior in bats, and Jones et al. (1995) provided an overview of greater horseshoe pup growth and foraging development. Ransome (1998) considered the impact of maternity roost conditions on

**Table 4** Description of growth phases in a greater horseshoe pup's first summer

Growth phase	Age (days)	Pup development notes	Behavior/food
1	0–4	Bald ventrally with dorsal grey fur at start; rapid growth of mass and skeleton; no temperature control (Fig. 5)	Stays still; tends to hang alone in roost; mother's milk
2	5–14	Ventral grey fur grows; eyes open; rapid growth of mass and skeleton; starts to regulate temperature (TR)	Forms creches; more mobile; wing flapping starts; mother's milk
3	15–29	Growth rates of mass and skeleton slow; TR good; helped by creche formation while mothers forage	Wing flap often; flights start – good from 21 days; mother's milk
4	30–45	Radius length (FL) ceases at 40 days; digits continue; Doppler-shift compensate by $\Sigma 45$ days when weaned	Forage outside roost within 1 km. Often perch to feed with other juveniles; milk + <i>Aphodius</i> (small beetles)
5	46–60	Final growth of hand; Digit 5 length (D5) finger bones ends by 60 days; competent flight and echolocation abilities	Foraging range extension to 4+ km; diet range changes to adult levels; self-fed
6	61–105	Bone ossifies before hibernation starts; fat deposition rapid post 75 days in good weather. Poor weather or late birth results in need to forage significantly in winter	Learn and later occupy hibernacula with other colony yearlings and older bats. May form clusters. Can feed on large <i>Geotrupes</i> beetles in winter if available

Source: Derived from Ransome (1998)

growth, survival, and development of pups measured from birth to ~100 days (Table 4). Although juvenile forearm length and body mass change rapidly with age, body condition stays fairly constant through the 60-day growth phase (Ransome 1998). His study continued over many years, including a period with a heater in one roost. In one summer, data from four other maternity roosts were used.

Details of wing development are provided by Hughes et al. (1989) for the UK and Eghbali and Sharifi (2019) for Iran. In both studies, pups were able to fly well from about 24 days post-birth.

Growth phases 1–3 are maintained entirely by a mother's lactation. Her foraging success is crucial to pup FL (forearm length). D5 (digit 5) length continues to grow until age 60 days. Its final length reflects the foraging success of both mother and pup. Lactation level needs to match a pup's growth rate if its genetic potential is to be realized. Rate peaks 4 days after birth and slowly declines. Mothers start lactation with some body reserves, but these are insufficient to sustain lactation for more than one or two missed foraging bouts due to bad weather (Ransome 1997b). In poor weather pups suffer growth retardation and



**Fig. 5** Newly born pup showing attached drying umbilicus soon after birth. (Photo: Roger Ransome)

stunting. Duvergé (1996) found that lactating female bats normally forage for the longest time of any age group each night. Foraging time fell as the pup aged, in line with food consumed (Table 4), and presumably her milk production. A lactating female has to consume over 60% of her lean body mass within a 6-h period of

darkness in June at 52°N in the UK to successfully sustain the early high growth rate of her pup.

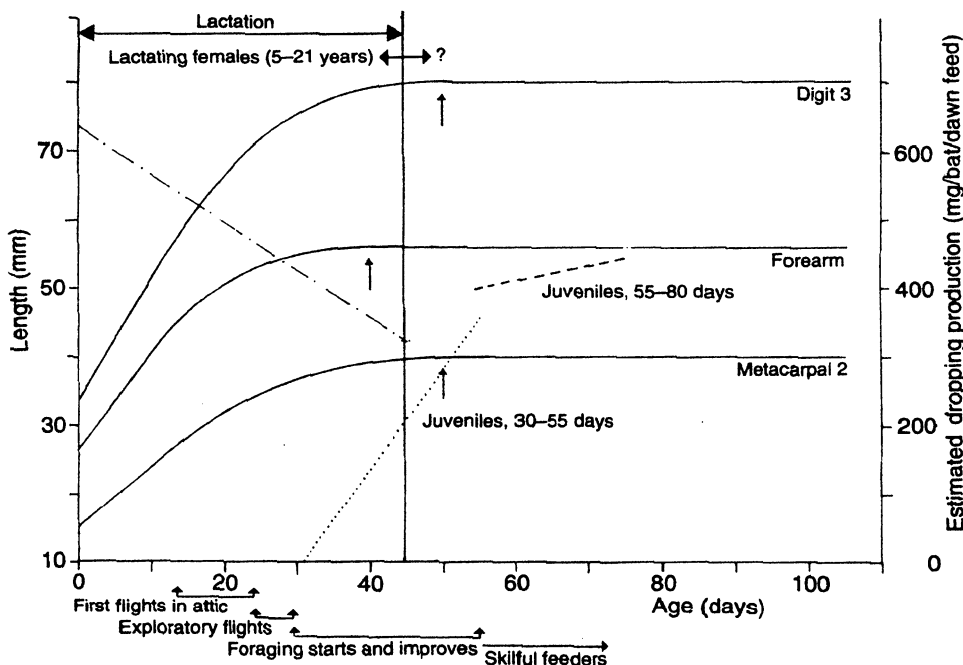
Weaning normally occurs about 45 days after birth. Early weaning may be advantageous to mothers, since it conserves skeletal calcium. Calcium occurs at very low levels in insect prey, and is leached from a mother’s skeleton to boost milk concentration (Kwiecinski et al. 1987). Replacement needs to occur during post-lactation, before hibernation starts, as further losses occur in winter. Late parturition and prolonged lactation increase mortality risks to the mother late in her following spring (Ransome 1995). A summary of these events is shown in Fig. 6.

Growth pattern of forearm length is similar in the two sexes; it accelerates from birth to peak at 4 days and slows in a curvilinear manner to cease by 40 days (vertical arrow). Digit 5 growth may continue to 60 days. Early growth rate (EGR) between day 4 and 14 is significantly greater in females at resulting in larger females (Table 5). EGR is the main single factor influencing final forearm length (FL) of both male and female

pups. However, it only explains 28% of the variation in males, compared with 45% in females. Heaters used to raise roost temperature to Σ26 °C (previously 19–21 °C) produced significant growth improvement (Table 5). It also resulted in a higher female birth ratio.

Heater insertion increased EGR in both sexes and was predicted to result in larger FLs and D5s. However, the opposite was the case for males, but the significance level was much lower. This anomaly was reversed when growth at five different maternity roosts were compared (Table 6). Male FL and D5 slightly increased, but the differences were not significant.

The two significant advantages to growth only applied to female FL and D5 (EGR data unavailable). Male data, although slightly improved in both aspects, were not significant (Table 6). Thermal conditions in the three roosts without a heater in 1997 were not monitored, however. Higher roost temperatures are particularly important for female pup growth and survival in temperate regions at high latitudes.



**Fig. 6** Pup growth and development (solid lines), linked to dawn foraging changes by mothers and pups (broken lines). (Source: Jones et al. (1995). Reproduced courtesy of

Linda DaVolls on behalf of the Zoological Society of London 16th July 2019)

**Table 5** Significant effects of heating the Woodchester maternity roost on pup growth by sex

Sex and parameter	Without heater	With heater	T-test results
Male; FL EGR mm/dy	1.593 <i>n</i> = 54	1.639 <i>n</i> = 38	$t_{83} = 3.96; P = 0.0002$
Male; mother's FFL mm	56.19 <i>n</i> = 39	55.72 <i>n</i> = 36	$t_{72} = 2.24; P = 0.028$
Male; mother's FD5 mm	72.50 <i>n</i> = 28	71.74 <i>n</i> = 33	$t_{48} = 2.26; P = 0.028$
Female; pup's FFL mm	55.74 <i>n</i> = 58	56.54 <i>n</i> = 39	$t_{71} = 3.41; P = 0.0011$
Female: FL EGR mm/dy	1.617 <i>n</i> = 60	1.670 <i>n</i> = 41	$t_{76} = 5.09; P < 0.0001$

Source: Ransome (1998) Tables 7 and 8 combined. EGR is early growth rate; FL is forearm length during growth; FFL is final forearm length; FD5 is final 5th digit length (wing width)

**Table 6** Pup final growth at five UK maternity roosts in 1997 by sex and heating regime

Sex and parameter	Without heater (Three roosts)	With heater (Two roosts)	T-test results
Male; pups FFL mm	54.80 <i>n</i> = 38	55.45 <i>n</i> = 14	$t_{21} = 1.72; P = 0.10$
Female; pups FFL mm	55.82 <i>n</i> = 38	56.43 <i>n</i> = 22	<b><math>t_{47} = 2.28; P = 0.027</math></b>
Male; pup's FD5 mm	70.96 <i>n</i> = 38	71.41 <i>n</i> = 14	$t_{21} = 0.88; P = 0.39$
Female; pup's FD5 mm	71.97 <i>n</i> = 38	72.73 <i>n</i> = 22	<b><math>t_{49} = 2.53; P = 0.015</math></b>

Source: Ransome (1998) Table 19 modified. FFL is final forearm length; FD5 is final 5th digit length (wing width). T-test results in bold are significant. 1997 was an unusually warm summer for the UK, so unheated roosts would have been warmer than usual as well

Eghbali and Sharifi (2019) also show data that supports the impact of thermal roost conditions and EGR on pups born in Western Iran.

Ultrasonic calls are initially pup isolation calls whose function is to attract its mother. They are produced straight after birth and emitted mainly orally. By 11–19 days, precursors of echolocation calls are emitted nasally, and these lose harmonics while increasing in frequency as the bats grow. Echolocation call frequency of weaned juveniles correlate with those of their mothers, and there is evidence that learning plays a role in echolocation development (Jones and Ransome 1993). Pups Doppler-shift compensate after 45 days (Konstantinov 1989; De Fanis 1994). Food consumption rises rapidly from age 30–55 days, then the rate slows as skeletal growth ceases. Foraging range reaches adult levels by this age (Jones et al. 1995).

Dietz et al. (2006) studied the growth of three species of *Rhinolophus*, including greater horseshoe bats, over 4 years in underground maternity roosts in Northern Bulgaria (latitude 43°N). Climate was described as temperate continental. Mean ambient temperatures (MAT) are 10 °C in the Southwestern UK and 12 °C in Northern Bulgaria. Stagnant cave temperature reflects

MAT, so breeding Bulgarian *Rhinolophus* should enjoy slightly warmer conditions than underground UK bats. Ambient mean roost temperature of 22.5–23.2 °C (mean daily range 2.4–3.1 °C) over 3 years of the study could have been achieved by large clusters of bats roosting in a vertical shaft. Mean FL of adult greater horseshoe bats (sexes combined) was 58.3 mm and mean D5 was 71.4 mm. Parturitions normally occurred in the first 3 weeks of June (3 years of study), and skeletal growth ceased by late August. Most births occurred over a 10-day period. FLs were much larger than those in the UK, but D5s were smaller. Conditions in Bulgaria apparently favor lactation of mothers (possibly due to extended foraging bouts under longer night length), but shorter pup D5s suggest that pup early foraging was not optimal. No foraging or diet studies accompanied this study. A similar study was carried out at a cave maternity roost in Western Iran (latitude 34°N) by Eghbali and Sharifi (2019), but only for two summers. Climate was continental, with very cold wet winters and hot dry summers. Birth-timing and pup growth performance were compared between one dry and one very wet summer. Parturition was very synchronized and even earlier in summer (late May). Median birth date was 7 days later in

the cooler, very wet summer and pup growth was reduced. Mean FL of adult females was 58.2 mm, but no D5 data were provided.

### Age and Size at Maturity

Reproductive maturity normally takes place either at age 2 or 3+ years (Ransome 1995, 1998). Delay in age of first breeding is linked to the completion of lean body mass growth and body condition (Tables 2 and 3) in the mid- to late hibernation period prior to parturition. Neither FL nor birth date were significant factors in the UK.

### Reproductive Lifespan and Ageing

Ransome (1995) found mean female longevity was 5.6 years for earlier breeders (EB aged 2 years), and 8.1 for later breeders (LB aged 3+ years), but no difference in LRS. Both groups showed high mortality (EB 38%; LB 27%) after the first parturition, possibly due to late birth-timing. Maximum age of 30 years is a rare event. Longer life in LB was linked to the extra year(s) without breeding, and lower breeding frequency of 85% compared with 96% for EB (see “Fertility”), but no evidence of incapacity to breed in old age (*pers. obs.*). Very old females show normal birth-timing, and give birth to normal-sized pups whose growth and survival are usually inferior.

Ward et al. (2014), in a 19-year cohort study of the same colony as Ransome (1995), used DNA microsatellite genotyping to extend investigation into factors that affect reproductive success. Genotyping allowed LRS of individual male and female bats to be determined. Male success was highly skewed toward a few highly successful males. Only 135 individual males contributed to the 710 paternities assigned (mean 5.3 pups/male). The most successful male fathered 47 pups over 19 years, and six males fathered nearly 20% of all pups. Larger males were more successful than smaller ones ( $P = 0.012$ ). A third of all males achieved no paternities within the colony. Rossiter et al. (2000b, 2006b) investigated

**Table 7** Survival of female bats by age

Year age group	N caught first year	% surviving 1 year later
1	92	53
2	57	72
3	42	79
4	35	66
5	21	71
6	24	87
7	22	91
8–12	56	86
13–17	39	82
18–25	12	58
<b>All</b>	<b>400</b>	<b>73</b>

Source: Ransome (1990) Table 9.6. Data from 1980–1983 inclusive. Note that the same dataset cannot be generated for male bats. The reliability of these data depends on the very high roost fidelity of females, and the repeat capture protocol instituted. Male roost fidelity only lasts into their second summer (Table 8).

other possible reasons for the high level of skew. Ward et al. (2014) also showed female skew was lower than in males; 216 females contributed to the 919 maternities assigned (mean 4.3 pups/female). The most successful female had 18 pups over her lifespan. Heterozygosity was higher ( $P = 0.046$ ) in those that had more pups. In both sexes age-related success showed a similar pattern reflecting survival rate (Table 7). It rose from age 2–12 years, and leveled off before declining after 14 years.

### Sex and Age-Specific Survival Patterns

Pups rarely die at birth, but late embryos sometimes aborted in cold or wet and windy weather (*pers. obs.*). Mortality up to day 28 is very low in favorable weather. Mortality rate increases once the young fly outside the roost and begin foraging. Highest juvenile mortality occurs between the age of 45 and 55 days, after weaning (Ransome 1991), when the young extend their foraging range (Jones et al. 1995). They also spend longer out of the roost each night, visiting more foraging areas, night roosts, and hibernacula. These activities may expose them to predators, or inability to find their way back to the maternity roost.

Alternatively, mortality rise after weaning may be due to poor foraging capabilities by some of the young, car collisions, or capture by cats (*pers. obs.*). The last two events are connected with low flight level of 1–2 m above the ground while commuting or foraging.

Mothers leave the maternity roost soon after pups are 55–65 days old. Poor weather in September contributes to further pup mortality before hibernation starts. The proportion of first-year bats reaching hibernacula varies considerably (10–80%) in a given year. High mortality follows late births and poor September weather and vice versa. About half of those reaching hibernacula survive to age 2 years. Table 7 shows changing survival rates up to 25 years in the UK.

Complete population datasets are known to be superior to limited datasets for annual survival rates. This particularly applies to those that involve repeated captures in the same season and long-term studies over decades.

Schaub et al. (2007) used integrated modeling to enhance estimates of population dynamics in Switzerland from limited maternity roost data, collected inconsistently. They deduced that survival rates did not differ between the sexes, and estimated first-year pup survival at 49% (0.49). Breeding females had low fecundity of 74% (0.74). Maximum likelihood estimates of survival rates are only reliable if certain demanding conditions are satisfied. One of them is that survival rate must be independent of age. This is not the case (Table 7).

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## Habitat and Diet

### Habitat

#### Spatial Movements

No cross-channel movements recorded, despite earlier extensive ringing studies in England and Northern France over four decades. Intrinsic and extrinsic factors linked to major population declines reviewed by Ransome and Hutson (2000). Warmer climate since 1995 has allowed recovery (Froidevaux et al. 2017) and spread into more northerly and easterly UK regions.

Disappearance from former European strongholds likely to be linked with key roost losses, or major habitat changes. These include large arable fields replacing grazed ecosystems and subsequent loss of hedgerows (eg. Baudry et al. 2000), or the loss of traditional grazing practices (Ransome 1990, 1996, 1997a; Ransome and Hutson 2000).

### Habitat Selection

Populations in much of Europe are promoted by foraging habitat which consists primarily of permanently grazed pastures interspersed with blocks or strips of deciduous woodland, or substantial hedgerows (Jones and Morton 1992; Beck et al. 1994; Duvergé 1996; Dietz et al. 2013). In the absence of grazed pastures, riverine habitats are used (Fonderflick et al. 2015). Bats do not usually forage within woodland, but generally use woodland or hedgerow edges. Such pasture/woodland habitats generate large levels of their preferred prey (Ransome 1996). Pastures should be cattle-grazed by preference, as their dung sustains the life cycles of the most important beetles, but sheep and horse-grazing may also be beneficial in a rotation to reduce parasite problems. Sheep-grazing, which results in a short sward, also benefit the life cycles of insect prey. Summaries of habitat preference are in Duvergé (1996), and Jones et al. (1995). Downs and Sanderson (2010) suggest that cattle presence in a field is more important to foraging bats than just fresh dung. Dietz et al. (2013) strongly recommend the conservation of traditional land use practices to preserve both endangered bats and local biodiversity in Belgium. Fonderflick et al. (2015) used modeling to investigate habitat use in arid Southern France. Riparian vegetation and woodland were key habitats used. However, in the extreme aridity of Western Iran, bats foraged over sparse vegetation cover, including oak woodland and deciduous dwarf scrubland (Eghbali and Sharifi 2019). The absence of dietary analysis in most continental habitat studies limits an understanding of detailed habitat needs. The largest reported maternity colonies of 2,000 bats occur in lowland France and UK.

## Roosts

Within suitable habitat, two types of summer roost and three types of winter roost must be present for a population to exist (Ransome 1991, 2008). Some roosts function as both summer and winter roosts. In summer a population usually occupies a single maternity roost, which has many surrounding night roosts nearby within foraging range (4 km; 34 km<sup>2</sup> area, but exceptionally up to 14 km; 420 km<sup>2</sup> area). Night roosts are used for resting between foraging bouts.

In winter a range of three hibernacula types are needed, usually within a 40 km radius of the maternity roost. Type 1 hibernacula are partly dynamic underground systems (caves, disused mine, and tunnels) providing a range of temperatures (Ransome 1968, 1971). They should be as close as possible, but within 12 km of the maternity roost close to good foraging habitat. Type 2 hibernacula are also partly dynamic. Type 3 hibernacula are small underground sites used for mating by a single adult male and up to eight adult females early and late in the hibernation period, which runs from October to May. They may be stagnant systems, lacking variable temperatures, and up to 55 km from the maternity roost, often only used in Autumn and Spring.

Maternity roosts are generally located underground throughout most of their European range where mean ambient temperatures (MAT) exceed 11 °C. At cooler extremes they often use large attics of old country houses, especially if they have substantial cellars. Maternity roost populations can vary from 80–2,000 at similar latitude and climate, hence habitat and roost conditions seem crucial. Population size also linked to genetic diversity by Tournayre et al. (2019) in a major study that ranged from the UK through France and the Spanish Basque Country to Tunisia.

Night roosts can be any building or system providing shelter from wind and rain, such as chimneys of derelict buildings, garages, stables, porches, caves, and even the branches of large trees. As they are only used at night, they can be open structures which are brightly lit in daytime. Studies of their microclimates do not exist, but the most suitable ones are waterproof, with vertical

rifts that retain body heat from small groups of bats while digestion occurs.

Hibernacula can be any underground structure, of almost any size. Short tunnels only 10 m long may be used as territories for mating and early pregnancy. Extensive multientranced cave and/or mine systems, or groups of smaller sites, may be used as type 1 or 2 hibernacula. The more variable the air flow pattern present, and hence the ambient temperature regime provided, the greater the potential use of the site for hibernation by bats of all ages and both sexes (Ransome 1968, 1971). A vertical rift or shaft near the entrance where bats can cluster after foraging is highly beneficial. Close proximity to favorable winter foraging habitat is essential to support large winter (October to May) populations (Ransome 2002). The presence of free-range grazers, such as sheep, horses, deer, and cows, is key to large winter populations. In oceanic temperate climate some greater horseshoe bats reduce their mid-winter body reserve loss rates by foraging (Fig. 7). In continental countries with colder climates mid-winter foraging may be rare. However, such populations are predicted to benefit from foraging in the much warmer October, November, and March to May temperatures that occur at lower latitudes.

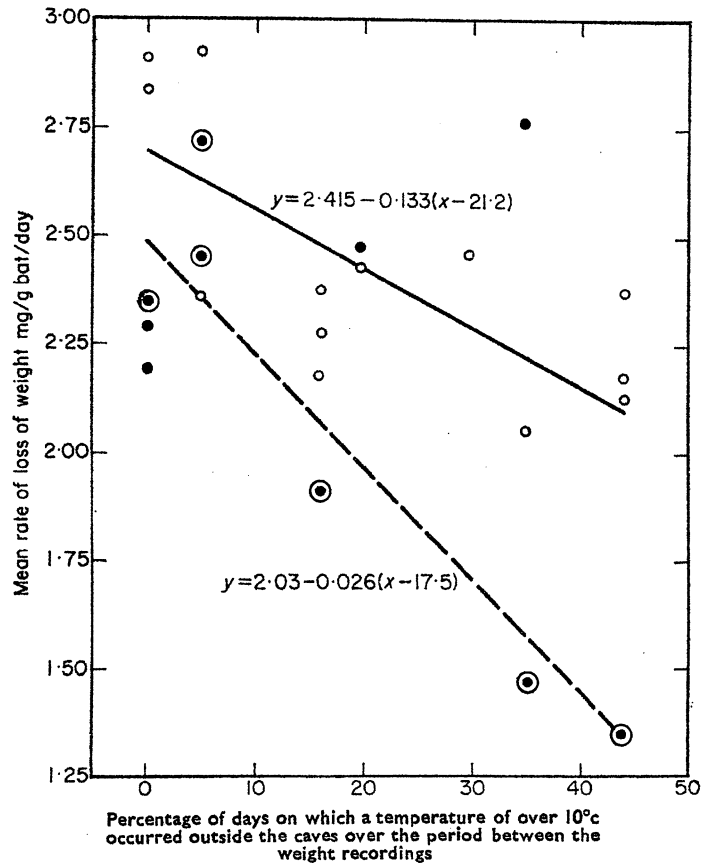
Bats select ambient temperature ( $T_a$ ) for torpor precisely.  $T_a$  affects the length of time it can remain in hibernation torpor (Ransome 1971). Selected  $T_a$  changes in spring in relation to external weather temperatures, so that arousal frequency remains the same (Fig. 8). Ransome postulated that the hibernation period was under the influence of an unidentified hormone, whose function was to suppress arousals in response to a circannual rhythm.

## Diet

Diet has usually been investigated using fecal pellets collected at roosts over a known period of time (usually weeks or months). Feces c. 9–13 × 2.5 mm, vary in size, color, and texture according to diet: larger and black after *Melolontha* and *Geotrupes* beetles; dark brown after *Aphodius*, ichneumonids, and tipulids; and smaller and grey to light brown after moths. Brittle after beetles are



**Fig. 7** Juveniles and mature males lose less body mass during mild winter spells. Open circles are juveniles (born previous summer); solid black circles are mature females; ringed black circles are mature males. Regression lines for juveniles and mature males were significant. Mature female data were too sparse. (Source: Modified from Ransome (1968). Reproduced courtesy of Wiley and Sons 16 July 2019)



eaten; sticky after moths. Prey remains of larger insects are often near entrances of hibernacula, night roosts, or maternity roosts where bats perch in rifts or shafts to dismember them (Jones 1990). These are also found beneath trees used as nocturnal perches (Beck et al. 1994). Insect remains are usually wings, heads, and legs, but even the thoraxes of large beetles may be dropped.

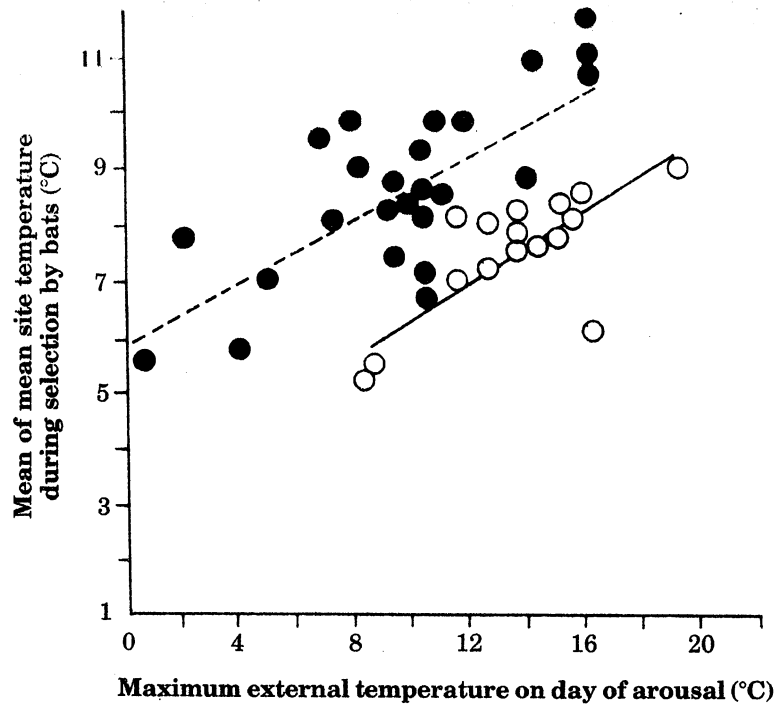
Summer diet (April to September) fecal pellet analysis studies from many maternity roosts (Jones 1990, UK, Pir 1994, Belgium, Beck et al. 1994, Switzerland, Ransome 1996, 1997a, UK) confirm they are selective feeders. Diet is very similar across the countries listed. No data from Eastern Europe or Iran. Larger prey, described as key prey by Ransome (1996), are preferred. Key prey include beetles (Coleoptera, especially Scarabaeidae), and moths (Lepidoptera, especially Noctuidae). Crane flies (Diptera, Tipulidae), caddis flies (Trichoptera), and ichneumonoid parasitic wasps (Hymenoptera,

Ichneumonoidea) are taken in decreasing order of preference as secondary prey if key prey are unavailable. The prey of last resort in the UK is yellow dung fly *Scatophaga stercorarius* (Table 9).

Summer beetle prey are mostly scarabaeids. They include cockchafer, *Melolontha melolontha*, summer chafer *Amphimallon solstitialis*, small dung beetles, *Aphodius sp.*, and large dung beetles, *Geotrupes sp.*

Winter diet (October to March) show similar insect content to summer (Ransome 2002), but smaller prey range. *Aphodius sp.* are eaten in October. *Geotrupes sp.* are key prey in UK winters from December to March. If beetles are unavailable *Ophion sp.* are taken as secondary prey from late October to February. In their absence dung flies are eaten, usually up to December. In March, moths feature in the diet of bats in hibernacula located within deciduous woodland. Insects adapted to cold winter survival

**Fig. 8** Temperature selection compensation in Spring. Black circles show winter data; open circles show spring data. (Source: Ransome (1990); modified from Ransome (1971))



after the Last Ice Age. Overwintering strategies minimizing cold mortality in insects are numerous and often complex (Leather et al. 1993).

## Diet Selection

Jones (1990) first showed that these bats were highly selective in summer. Ransome (1996) concluded cockchafer are the preferred spring prey to other concurrent insects when abundant. They may promote the rapid pregnancy of breeding females in years of abundance through their four-year life cycle. From June to August, adults eat various types of large noctuid moths, e.g., yellow underwing moth, *Noctua pronuba*, and occasionally sphingid (hawk) moths. Moths are eaten by lactating mothers, but their young prey almost exclusively upon *Aphodius* beetles when they begin to feed at age 28–30 days (Ransome 1996). In their absence, they eat tipulids and moths, but only after they reach age 45 days.

In some continental European countries one diet difference occurs. *Aphodius* beetles rarely feature in the diet (Zahner 1984; Pir 1994).

Tipulids may be the key prey of the young in continental colonies. Whether this difference reflects availability of grazing regimes or preferences among metapopulations is not known.

## Diet Assessments

Data from fecal analysis, such as those in Table 8, are influenced by many factors. Insect phenology of key prey varies seasonally by latitude, and abundance affected by climatic conditions in previous years. The number of years depends upon the insect's life cycle. Most have annual cycles, but cockchafer (*Melolontha*) take four years.

Weather conditions, including wind speed, rainfall, and temperature, affect prey availability to foraging bats throughout the year, including the summer (Ransome 1997b). In winter there are no months in the Southwest UK when foraging does not occur (Ransome 1968, 2002). Foraging bout frequency reduces from 3 nightly in lactating females in June and July (Duvergé 1996; Jones et al. 1995) to 1 at dusk erratically within the hibernation period (Ransome 1971). Ambient

**Table 8** Survival to age 1 year of both sexes combined

Years of birth	Total N pups born	Total N known to reach hibernacula (% N born)	% surviving to 1 year later
1984–1988	171	77 (45)	28
1989–1993	126	62 (49)	39
1994–1997	116	70 (60)	52
All	413	229 (55)	38

Source: Ransome (2008). First period included a severe population crash (Ransome 1989b). The last period had an incubator set at 26 °C in the roost to improve growth rates (Ransome 1998). All data suggest the incubator also improves survival rates to age 1 year (Chisquare = 5.47 df = 1;  $P = 0.019$ ; with incubator versus without)

**Table 9** Mean diet from late April to early October at seven UK maternity roosts in 1995

Prey item	% Diet by volume (Standard deviation)
Moths	38.6 (6.45)
<i>Aphodius sp.</i>	21.7 (3.31)
Tipulidae	14.3 (8.92)
Ichneumonoids (Ophion complex)	9.4 (5.18)
<i>Melolontha melolontha</i>	8.0 (2.94)
Trichoptera (Caddis flies)	5.7 (3.74)
<i>Geotrupes sp.</i>	1.5 (1.59)
Small Diptera	0.4 (0.55)
Other insects	0.4 (0.34)

Five roosts were located within a 40 km radius of Bristol; two were in Southwest Wales. In some years moth consumption is much lower, and *Aphodius* much higher. Source: Ransome 1997a

temperature usually peaks later in daytime, falls gradually toward dusk, and rapidly to a low level just before dawn. Above 14 °C peak daytime, all the main UK insect prey (Table 8) can fly. As temperature falls, some insects cannot fly, and so are unavailable to foraging bats (Taylor 1963). Most summer-flying moths require at least 12 °C to fly; whereas *Ophion sp.* can fly above 3 °C. Above about 8–10 °C maximum climatic temperature on a day, foraging is profitable at dusk (Ransome 1973). Above about 8 °C minimum night temperature foraging is profitable at dawn as well. Below 6 °C only dusk foraging is successful. Bat numbers fluctuate with fecal production level in April and May (Fig. 9), as bats repeatedly return to hibernacula for torpor. In June the fall is related to diet changes and consumption falls in late pregnancy.

## Amounts Eaten by Individual Bats

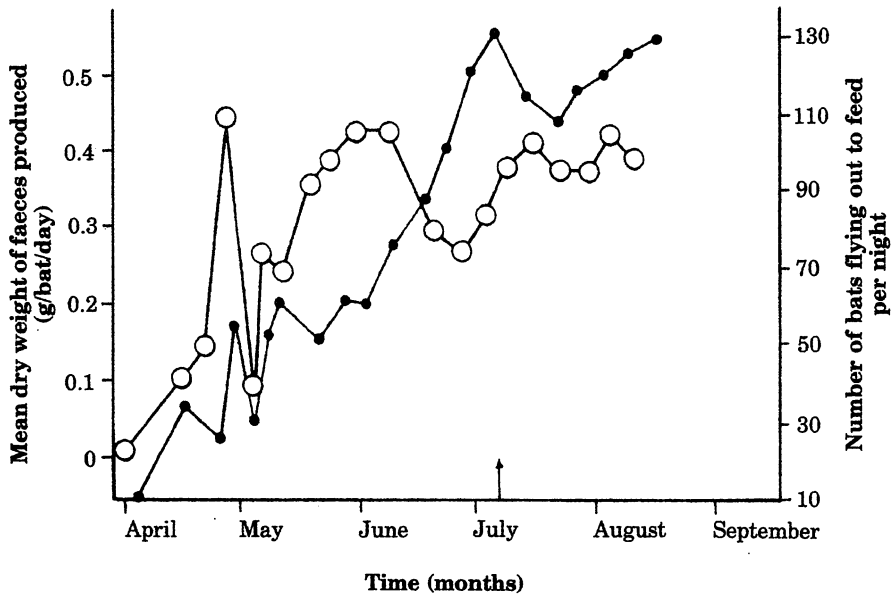
Ransome (1997b) estimated dry dawn dropping production levels (EDP) for individual female bats caught soon after dawn and kept separately in clean bags.

The EDP of individual bats varied from 0–1000 mg according to reproductive state and weather conditions before dawn. In good weather, lactating females had a median of 481 mg compared with 245 mg for late-pregnant females, 324 mg for subadults, and 161 mg for non-breeding mature females. EDP varied considerably among individuals of both lactating and subadult groups even after good weather. After severe weather a significant reduction (Table 10) applied to all subadults, but not to all lactating females. Some lactating females achieved EDPs of 400–500 mg while most produce less than 100 g. These levels may either reflect variable female foraging capabilities or insect availability in their foraging areas. Whatever the reasons, pup growth and survival will be impacted (Tables 4, 5, 6, and 8), with serious implications for specific female LRS (Ransome 1995).

## Behavior

### Foraging Behavior

Greater horseshoe bats only eat live prey caught mainly on the wing. Echolocation calls used during foraging are long (45–55 ms), and dominated by a constant frequency (CF) component at about 83 kHz (UK data), with frequency-modulated sweeps initiating and terminating them (Jones and Rayner 1989). CF changes with season and



**Fig. 9** Foraging success and population changes from Spring to mid-August. Open circles show feces data; closed circles bat numbers. Vertical arrow shows the mean birth date. (Source: Ransome (1990); from Ransome (1973))

**Table 10** The impact of severe weather during dawn foraging on median estimated dry dropping production by female bats in summer

Reproductive group	Good weather (>8 °C; dry; low or no wind)	Cold weather (<6 °C; dry; low or no wind)	Wet/Windy weather (heavy rain; windy)	Severe weather (columns 3 and 4 combined)
Subadult	324.0 (53)	72.0 (7)	48.0 (5)	60 (12)
Lactating	481.0 (125)	87.5 (22)	127.0 (9)	98 (31)
Early post-lactating	273.5 (48)	67.5 (6)	81.0 (13)	81 (19)

Data are dry mass (mg/bat/dawn feed). Parentheses show sample size. Kruskal-Wallis tests showed significant differences between good weather and severe weather medians for all three reproductive groups ( $p < 0.0003$ ). No significant differences occur between the severe weather medians of the three reproductive groups ( $p = 0.413$ ). (Source: Ransome (1997b))

age (Jones and Ransome 1993), and falls with distribution eastwards, reaching 77 kHz in China (Ma et al. (2006) and 65 kHz in Japan.

Radiotelemetry studies of many colonies in four different European countries (Stebbing 1982; Jones and Morton 1992; Beck et al. 1994; Pir 1994; Duvergé 1996; Fonderflick et al. 2015) show that these bats have a consistent specialized hunting technique, and use foraging areas with a similar structure. Bats commute from their daytime roost to a foraging area (FA), flying low above grassland, close to linear features such as tall hedgerows and woodland edge. FAs may be

close to a maternity roost or up to 14 km away (mean 3–5 km).

Whatever the commuting range, individuals normally fly up to 21–25 km total distance in a night, during 1–3 distinct foraging bouts (FBs) (Duvergé 1996). Duvergé's major study of UK summer (May to September) foraging behavior found FBs last from 1–2.5 h. FBs are separated by rest periods when rapid digestion and egestion of feces occur, sometimes in night roosts, allowing further food to be eaten.

Hunting mainly involves either hawking along the edges of linear habitat features, or perching on

a bare twig some 2 m from the ground and scanning for passing prey which they intercept like a flycatcher (Jones and Rayner 1989). Pir (1994) also reports gleaning, when bats hover. Most prey are caught close to the ground as they emerge from the soil beneath short grassland, oviposit in it, or feed on the dung of domestic animals. Occasionally groups of bats hunt together from perches within the same core area. This includes related older females (Rossiter et al. 2002, 2006a).

Emergence timing relative to dusk, and hence to light levels at emergence, seems to reflect a conflict between the need to forage and the avoidance of predators (Jones and Rydell 1994; Duvergé et al. 1999). Sparrowhawks (*Accipiter nisus*) and some owls are known to catch greater horseshoe bats. Rarely owls or cats enter roosts or catch bats as they leave via low-level entrances (Ancillotto et al. 2019). Adult bats usually leave the roost to forage 13–22 mins after sunset, but females emerge later as pregnancy advances, and earlier under lactation stress. Juveniles emerge later than adults when they start foraging at age 28–30 days. Emergence from bright exposed roosts is later than from darker tree-sheltered ones (Jones et al. 1995).

## Resource Competition

Females are strongly philopatric to their natal roost. They occupy it for up to 18 h daily in June at 51°N latitude (Ransome 1990). Clustering behavior is strongly selected on energetic grounds. Roost temperatures below about 23 °C limit female thermoregulation options in spring, and later growth of pups (Table 4). Bat numbers in spring are linked to foraging success via insect availability (Fig. 9), suggesting competition for food supplies may occur. Duvergé (1996) tracked mother/pup pairs when pups first started to forage. Pairs neither emerged together, nor used the same FAs. Rossiter et al. (2002, 2006a) tracked older females from two large matriline to their FAs and night roosts. They shared both within each matriline (females derived from a single mother), but not across them. Duvergé (1996) had previously seen groups perch-hunting together. Bats

usually forage singly, avoiding competition, but sometimes associate in related groups in mid-summer. Prey availability may be an important factor affecting sharing.

## Personalities

Long-term studies at Woodchester Mansion in the UK, where bats are repeatedly caught, revealed rare individuals with different behavioral characteristics to the majority, in addition to the variations in foraging success. Most bats accept handling with benign resignation, having been caught and ringed within a week of being born. One female stood out. She was difficult to handle from the start, and when she had her own pups, she sometimes hid them in other temporary roosts (*pers.obs.*).

## Life in Groups

Ringed bats captured in roosts provide data on social organization by sex and age as well as movements and life histories of individuals. Detailed summer studies refer mainly to UK's Woodchester maternity roost (Ransome 1973, 1978, 1995). Winter studies are widespread from the 1940s, starting in the UK (Hooper and Hooper 1956; Ransome 1968) and France (Saint Girons et al. 1969), before spreading more widely. Rossiter et al. (2005) considered that kin selection, favored by repeat mating over years with the same male at mating sites, underpins social cohesion.

## Summer

Peak colony aggregations occur in maternity roosts for females to give birth from late May to early August depending on country, latitude, and spring climate. Between 100 and 400 adults typically congregate when births start. In the range 20–1,200 pups are born in a maternity roost. Sub-adult bats of both sexes with some pregnant females form active clusters in spring whenever

the weather permits regular feeding. More pregnant females return in late May to early July; some just before giving birth. Some adult males return in May and June for spermatogenesis, and leave by early August, segregating from females (Saint Girons et al. 1969; Ransome 1973; Kuramoto 1979). By mid-August most roosts contain post-lactating females, juveniles, and subadults of both sexes. In early September mothers and most subadults depart, leaving juveniles and a few subadults until early October.

The pattern above seems flexible, especially with regard to adult male occupation. Comparison of the proportions of nonbreeding bats present among roosts (Ransome 1997a), and limited capture data from other roosts suggest that surplus adult males (ones without a mating roost) may remain at some roosts throughout the summer.

## Winter

Greater horseshoe bats partially segregate by age and sex groups throughout the winter according to their sex and age group (Hooper and Hooper 1956; Ransome 1968; Saint Girons et al. 1969). The pattern changes through the hibernation period. Type 1 hibernacula contain mainly first-year bats and older subadults of both sexes. Adult males join them in mid-winter. If favorable roost thermal conditions and external habitat have winter foraging potential (Ransome 1968, 2002) large clusters (400+) may develop. Parous females are few, and generally found isolated in deeper parts of such hibernacula. Type 2 hibernacula contain few first-year bats, but mostly second- and third-year subadults, plus adult males without mating territories (Rossiter et al. 2001). Clusters can also form. As in type 1, adult females if present are usually solitary. Type 3 hibernacula are used by a single adult male bat as a mating territory with up to 8 adult females.

## Mating Behavior

Mating is rarely observed, but DNA paternity evidence (Rossiter et al. 2006b; Ward et al.

2014) suggests it mainly occurs within type 3 mating hibernacula. Such roosts show orange/brown stains along the edges of projections from the ceiling produced by the male, possibly by facial glands. Mating can be prolonged (up to 40 min). During copulation the male hangs dorsally to the female and bites her neck fur. The female may be semi-torpid at the time, since when mating pairs are approached, the dorsal (presumed) male escapes, leaving the female to be caught by net (*pers.obs.*).

Mature males occupy their territories from late August to early winter, and sometimes again in the spring. In September and most of October a male is joined by varying numbers of older females for mating, while they also store fat for hibernation. The same females may return again in the spring. Much of early pregnancy occurs either in these male sites, or in satellite maternity roosts. Dispersal of breeding females in small numbers widely, at a time when insects are erratically available due to severe weather or phenology, may promote early foetal development.

## Movements Between Roosts

Few type 1 and 2 hibernacula normally exist in a region. However, 30 or more male territorial sites may be linked to a single maternity roost. These may be spread over a 40 km radius from the maternity roost, whereas other hibernacula are usually less than 12 km away (examples in Ransome 2000). Where several maternity roosts occur close together, bats from each population share all types of winter roosts. Rarely, first-year bats travel up to 45 km to winter with bats from other colonies. Exceptionally, a single 96 km first winter movement occurs (J. Flanders and R. Ransome unpubl.). Bats rarely return to their natal roost after moving more than 45 km.

The failure to catch a bat in its second winter is therefore not absolute evidence of its death. Mature male and female bats gradually tend to occupy the same hibernacula as they age on a repeated annual cycle (*pers.obs.*). They use them for the remainder of their lives, and their disappearance indicates mortality. Confirmation of

presumed female death comes from subsequent absence from the maternity roost. Male confirmation sometimes supported by cessation of DNA evidence.

## Dispersal

Within a 40 km radius of a maternity roost bats disperse annually to hibernacula (R. Ransome and D. Priddis unpubl.). Bats, particularly males, may leave type 1 or two hibernacula and move up to 65 km to a type 3 hibernaculum (Ransome 2000). Longer movements (142 km over 8 years) seem to either result in a permanent shift or death. Colony members may disperse over an area of some 5,000 km<sup>2</sup> based on a 40 km radius. If this area is shared with other colonies, gene flow occurs among them at mating sites enabling out-breeding to occur (Rossiter et al. 2001). Occasional long-distance movements would be an important behavior allowing recolonization from refuges between ice ages (Rossiter et al. 2007; Flanders et al. 2009).

## Social Behavior

### Parental Care

Ransome (1990) provides birth details, and Matsumura (1979, 1981) describe mother-pup call recognition signal system and its development to 3-weeks-old pups. Mother-pup interactions help ensure, possibly with other cues such as scent, that a mother suckles her own pup after she returns from foraging. Infrared CCTV shows pups born within large matriline are deposited closely together and form creches (Table 4). Birth-timing is often highly synchronized among pups at the same roost in a particular summer (Dietz et al. 2006; Eghbali and Sharifi 2019). This suggests mutual benefits accrue. Mothers remain with their pups for 10–22 days after weaning. In winter they separate, but rejoin again the following spring.

### Aggressive Behavior

Video studies of active bats in clusters around dusk exit periods show little aggression and no evidence of hierarchy. In unheated roosts clusters form and disperse largely in relation to ambient temperature and need to conserve energy for reproduction. Marked individuals occupy the same roost positions over weeks, and sometimes years. Minor disputes occur as individuals enter or leave tight clusters for defecation or urination but no aggression ever seen. No aggressive interactions reported while foraging away from the roost (Duvergé 1996).

### Communication

Ultrasonic calls emitted from birth are isolation calls which attract mother, and are emitted orally. This aspect has already been considered (in Reproduction).

In contrast to echolocation during foraging, our understanding of ultrasonic communication calls (UCCs) between bats during social interactions is at an early stage. Andrews and Andrews (2003) provide the first UCC call data for greater horseshoe bats at a maternity roost in the UK. They recorded similar calls to those obtained by Matsumura (1979, 1981), and described 12 different types of call, some of which were complex. Andrews et al. (2011) describe how infant calls develop into adult social calls. Ma et al. (2006) studied adult greater horseshoe bats in a free-flight captive situation that allowed social calls to be linked to observed behavior. They classified calls into 17 syllable types; 10 were simple and 7 were complex. Syllables were combined into six types of simple phrases, and four combination phrases. Some of the calls were made between non-contacting conspecifics, and appeared to involve true social communications.

Social calls are not only made when bats are present in summer roosts, they also occur in hibernation roosts (Andrews et al. 2006).

## Parasites and Diseases

### Ectoparasites

Most common ectoparasite is the wing mite *Eyndhovenia euryalis* (Acarina: Mesostigmata). Mites are most common on young infants and in larger maternity colonies (C. Paresce, G. Jones and R. Ransome unpubl.). They disperse into the bat's fur in winter (Deuff and Beaucornu 1981). Another wing mite, *Paraperiglischrus rhinolophinus* (Acarina: Mesostigmata), is widely distributed in Europe, and found mainly in the winter. Male mites live on the wing membranes and females plus nymphs on the tail membrane. In the UK the tick *Ixodes vespertilionis* (Acarina: Ixodidae) is regularly found in winter (R Cropper and R Ransome, pers. obs.). Other less typical mites, such as *Alabidicarpus megalonyx*, on bristles in the nose-leaf, *Nycteridocoptes eyndhovenia* in cysts on the forearm. Baker and Craven (2003) list seven mite species from greater horseshoe bats. Lanza (1999) list many more for mainland Europe. The nycteribiid bat fly, *Phthiridium biarticulum* (Diptera: Nycteribiidae), is widespread in Europe, but is extinct in the UK where it occurred mainly on *R. hipposideros*, although also formerly on this species (Hutson 1984). The flea *Rhinolophopsylla unipectinata* (Siphonaptera) has not been recorded in Britain, despite its widespread occurrence in Europe.

### Endoparasites

Lanza (1999) reviewed world endoparasite fauna, and lists a number of Bacteria, Cestoda, Digenea, and Nematoda, some of which are endoparasites of European greater horseshoe bats.

### Infectious Diseases

Infectious diseases are rarely reported in the UK, and only encountered once over six-decade study. In the severe winter of 1962/3, heavy snowfall and severe frost prevented foraging from early January to mid-March. By late February many

bats showed varying levels of an unknown fungal infection, with ulcerated forearms and emerging sporangia from the patagium. No fungal growths from nostrils, mouth, or ears were observed. By late March no surviving bats showed any symptoms of infection. Many of the most severely impacted bats disappeared, and were never caught again. Does this happen in severe continental European winters? The infection seemed not to be white-nose syndrome (WNS), currently the subject of intense research in Europe and the USA following its emergence in 2006 as a highly pathogenic disease in North America. Its causative fungus, *Pseudogymnoascus destructans*, probably originated in Europe, where it occurs widely without causing mass mortality in many *Myotis* species (Puechmaille et al. 2011; Drees et al. 2017)). So far it has not been recorded in greater horseshoe bats.

### Zoonoses

No zoonosis has been associated with *Rhinolophus* species in Europe, but antibodies to European Bat Lyssavirus type 1 (EBLV1), a rabies-related virus, have been identified in *R. ferrumequinum* in Aragon and the Balearic Islands (Spain) (Serra-Cobo et al. 2002). However, it is not considered an important host to the virus and has not been implicated in its transmission.

## Population Ecology

### Population Dynamics

The population of a species is usually defined as the number of individuals in an area at a certain time. Populations fluctuate as time passes due to life history events and factors as follows:

$$N(t + 1) = N(t) + (B - D) + (I - E)$$

$N(t)$  = original number;  $N(t + 1)$  = number present after time interval  $t$ ;  $B$  = birth number;  $D$  = death number;  $I$  = immigrant number;  $E$  = emigrant number



Reliable estimates of a mammal's population depend upon many factors (Caughley 1977). Estimates of large, evenly spread mammals occupying open plains are easily assessed. Small, highly concentrated mammals occupying an unknown number of widely dispersed roosts is extremely challenging. Estimates are also affected by unknown rates of fission and fusion. There is no general agreement on what constitutes a bat population (Ransome 1990). It can refer to the numbers using one or more hibernacula, or those occupying summer roosts. Count data at summer roosts on one date may differ considerably on another a few days later as bats relocate in response to weather and food availability (Ransome 1973). Unknown roosts are a major difficulty in attempting to assess populations in a given area due to extreme philopatry. Studies providing long-term reliable data are sparse.

Ransome and Hutson (2000) reviewed intrinsic and extrinsic factors affecting populations. Population changes of bats mainly reflect the balance between births and deaths over a period. Either long-term ringing or PIT tag studies are necessary to discover them. B is quite easy to determine for a bat colony, provided all maternity roosts are known (Ransome 1997a), but D can only be judged for philopatric females recaptured at their natal maternity roost (Ransome 1990, 1995). Male greater horseshoe bat survival was only reliably followed by capture at natal roosts for their first two summers.

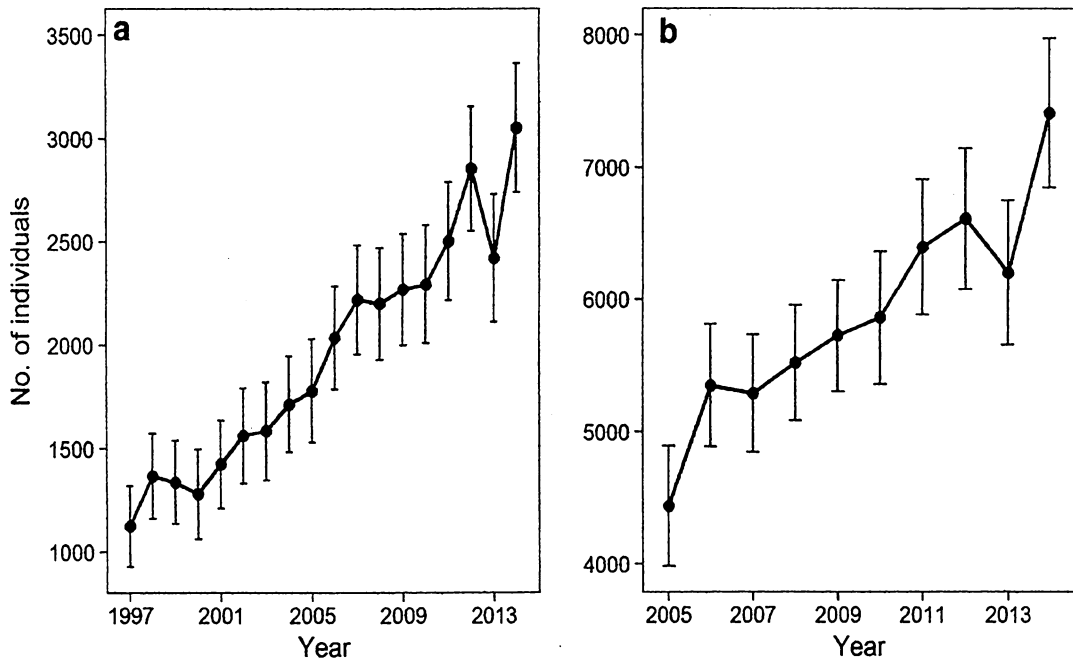
Ransome (1989b) counted bats in three sets of hibernacula around Bristol UK over a 26-year survey period. Bats mainly hibernated in disused limestone mines with white surfaces that allowed reliable counts. Two sets involved four visits per winter, and the third a single one to check on disturbance impacts. The similarity of population changes at all three sites suggested a common major factor, such as climate, acting via birth-timing (Ransome and McOwat 1994).

Estimations of maternity roost populations from single dusk exit counts at maternity roosts are fraught with difficulties. Ransome (1997a) argued that pup counts inside maternity roosts after adults have left are best, but their timing is crucial. Single pup counts are unreliable if older

pups have left to forage, or further pups are born afterwards. These problems mean that reliable counts of total births require repeat visits over an extended period, even when birth-timing is highly synchronized (Eghbali and Sharifi 2019).

Froidevaux et al. (2017) analyzed summer roost count data from the UK National Bat Monitoring Program between 1997 and 2014. They investigated the impact of 3 km range landscape habitat and climate on annual population changes. Eight colonies were followed for 18 years, and 19 colonies for 10 years. The 18-year period covered a time of rapid population growth after the serious crash in the UK in 1986 (Ransome 1989b). The known UK population was estimated at 4,000–5,000 (Harris et al. 1995). A 5% annual increase from 1997 resulted in an estimated population of 7,300 by 2014 (Fig. 10b). However, some sites remained stable. Their conclusions supported the importance of warm spring temperatures, and also suggested that spring precipitation negatively influenced populations in the following year. The reason for the latter was not investigated. The decline shown in 2012 and 2013 (Fig. 10) reflected cold springs and very late birth-timing in those years (Ransome and McOwat 1994). Froidevaux et al. (2017) identified a density-dependent effect within colonies, but no Allee effect.

Torpor use to survive poor spring climate prevents the rapid foetal development needed for early birth-timing. This conflict is key to birth-timing in June or July. Late-born UK cohorts show poor initial survival and longevity (Ransome 1989a); reduced growth (Ransome 1997a); and adverse sex ratios favoring males (Ransome and McOwat 1994). Late birth-timing results in stunted female pups that have low lifetime reproductive success (LRS) as shown by Ransome (1995). The number of females generated by a cohort over its lifespan is affected by mean birth date (determined by mean spring temperature), and mean temperature in April and May of the following spring (when lean body mass increases). Ransome (2016) combined these factors showing that female cohorts exposed to mean spring ambient climatic temperatures (mean  $T_a$ ) of 8 and 10 °C for two successive springs



**Fig. 10** Population trends from Bat Conservation Trust's annual UK count data. Graph **a** shows 18-year period from 1997–2014 at 8 colonies. Graph **b** shows data from 2005–

2014 at 19 colonies over 10 years. Total annual count and 95% confidence intervals are shown. (Source: Froidevaux et al. (2017). Reproduced courtesy of Springer)

generated no female pups, whereas exposure to 10.5 °C during both springs resulted in 45 female pups. Such small differences in mean spring temperatures emphasize the importance of spring climate to bat populations via female LRS changes. Lower temperatures, combined with heavy Spring rainfall, delayed birth-timing at one Iranian maternity roost studied for two consecutive summers, and caused reduced pup growth (Eghbali and Sharifi 2019). Possibly prolonged rainfall prevented, or reduced, pregnant and lactating female foraging success (Ransome 1997b). If low mature female survival ensued, it may explain the negative impact of heavy rainfall upon populations (Froidevaux et al. 2017).

While climate is clearly a major factor affecting population fluctuations over time, it does not seem to control the size of a maternity colony within its range. Comparisons between pairs of close maternity populations in the UK (Ransome 1997a) showed that habitat factors and higher levels of key prey consumption (diet quality) were more important. Adjacent colonies, exposed

to similar climate, can have markedly different populations as shown by Longley (2003) in Devon (UK). One colony had 80 adults, while two others nearby had 150 and 700, at that time. About 80% of the roost sustenance zone (RSZ) of the smallest colony was over the sea, and about a third of its land area was urban. Bats from this colony foraged at distances up to 14 km from the roost (Robinson et al. 2000). This is well above the 3–5 km at most roosts. The largest colony had a RSZ without sea areas; a small urban area, and very favorable close habitat promoted by an agri-environment management agreement. Ransome and Priddis (2005) studied the impact of foot-and-mouth disease slaughter in spring 2001 on two close maternity roosts. One had all grazers removed from its RSZ; the other was just outside the slaughter area. Summer 2002 dung beetle consumption fell at both sites, and briefly reduced the growth and survival of pups at both roosts.

The law of limiting factors seems to apply to bat populations. Within its latitudinal range (affects summer foraging time) and critical

climatic conditions (temperate oceanic or continental with mild winters between glaciation peaks), numbers are primarily regulated by summer and winter roost thermal quality, plus roost access to high-quality habitat. Roost quality affects a bat's daily energy expenditure while resting for long periods, and habitat affects their foraging quality and quantity. These factors interact to influence the survival and LRS of colony members. Mortality is greatest in males during cold and prolonged winters, and in females after late birth-timing. This hypothesis predicts that a bat colony should stabilize its population numbers once the carrying capacity of its accessible habitat is reached.

### Intraspecific Interactions

Significant aggregations of mature males and females occur annually, but at different times of year. Mature males congregate in type 1 or 2 hibernacula after autumn mating. Adult females are mostly solitary in winter, and only form small groups in mating territories. In late pregnancy they gather in largest numbers to give birth and rear their young. Large clusters reduce energetic costs for all individuals after foraging, and may be the driver of this behavior at any time of year. Numbers of bats in a roost depends upon insect availability in the RSZ habitat, and its structure. Insect availability varies erratically according to phenology and ambient temperature at any time of year. Individual bats seem to make decisions about which roost they should return to after each foraging bout.

### Interspecific Interactions

Few studies have investigated this topic. Pir (1994) described interactions between greater horseshoes and *Myotis emarginatus* in Belgium. Although they shared the same maternity roost void, there were few signs of aggression between them. The two species fed on different diets, and showed different emergence timing. Dietz et al. (2013) radio-tracked the two species at the same

time to determine their habitat use and interactions while foraging. Both species commuted along similar linear features such as hedgerows, streams, and forest edges. Maximum flight range, home range size, and habitat diversity did not differ between them. Furthermore, they both made frequent use of cowsheds as night roosts. However, only *Myotis emarginatus* foraged on the many dung flies that were present in them. Hence, they showed low dietary conflict. Fonderflick et al. (2015) conducted a similar dual radio-tracking study at two roosts, but it lacked dietary data.

In the UK, greater and lesser horseshoe bats commonly share hibernacula, and are known to share very large maternity roosts. They have some dietary overlaps, and emerge at similar times around dusk. At one underground summer roost a single greater horseshoe bat regularly chased exiting lesser horseshoe bats at dusk (A. Pinch unpubl.). Lesser horseshoes waited until the greater horseshoe left. Greater horseshoe bats have displaced several lesser horseshoe colonies from their UK maternity roosts.

### Climate Change

Many factors may influence climate both globally and at different latitudes. They include greenhouse gases, volcanic eruptions, solar variations, Milankovitch cycles (Bennett 1990), and increasing human impacts such as carbon dioxide and world human population rise. Since no direct long-term past temperature records are available, proxy information is used to indicate past temperature conditions.

The Lower Pleistocene and Holocene period fossils of the UK were reviewed by Yalden (1999) and Yalden and Kitchener (2008). These periods included three glacial and four interglacial periods. The last glacial period was the Devensian that began 45 k years ago and ended between 25 k and 18 k years ago. UK fossils recorded at that time included lemmings, reindeer, musk ox, arctic fox, wolf, and musk ox. Milder conditions from 15 k to 11 k years ago saw the return of elk and red deer alongside reindeer and horse. Another colder

spell from 11–10.2 k years ago was followed by the final ice retreat from the UK. By 9.6 k years ago warming had allowed colonization by hedgehog, hazel dormouse, red squirrel, Eurasian beaver, roe deer, weasel, stoat, badger, and red fox. The mean July temperature rose by 8 °C in no more than 50 years at one stage. Such changes indicate the complete substitution of one ecosystem (arctic) by another (deciduous woodland) at the same location. No reference was made by Yalden and Kitchener (2008) to any bat species. Presumably no fossil evidence exists, but the presence of greater horseshoe bats in any part of Europe subjected to glaciation in the Last Ice Age is not tenable on ecological grounds. Its presence in current times must have involved recolonization within the last 9.6 k years from refuge areas (Rossiter et al. 2005).

Rebelo et al. (2009) used spatial principal component analysis modeling to investigate the impact of climate change from 1961–1991 predicted to occur during three twenty-first-century periods upon 28 European bat species. Future predicted mean, minimum, and daily temperature range, RH%, and monthly precipitation were used. Five *Rhinolophus* species, including the greater horseshoe, were among the species. The periods were from 2020–2030, 2050–2060, and 2090–2100. Bat species were divided into three biogeographic groups and the impact of four climate change scenarios (IPCC categories A1FI – most severe, to A2, B2, B1 – least severe) upon the predicted distributional range of each group for each time period. The biogeographic groups were boreal, temperate, and Mediterranean. *Rhinolophids* were included in the Mediterranean group. The Mediterranean and European *rhinolophids* seemed to be more tolerant of temperature increases, but projections varied considerably under the different scenarios. A1FI caused most damage, and the greener B ones could even increase their geographical ranges during some periods. They cautioned that available habitat and species interactions could also play important roles as well as climate changes.

The climate change predictions outlined above are supported by fluctuations in UK greater horseshoe populations over many decades. They show

both downward trends after a series of cold winters and springs, due to the impact of delayed birth-timing and higher horseshoe winter mortality rate of adult males and young of the year (Ransome 1989b). Recoveries occurred after a prolonged period of warm years (Froidevaux et al. 2017). Climatic change impacts do not occur in smooth predictable stages.

Human impacts influenced these major cyclical ecosystem changes when arable cultivation started over 6 k years ago. Intensively farmed arable land is one of the least-used habitats for foraging greater horseshoe bats (Duvergé 1996). Removal of extensive rainforest often led to ultimate replacement by desert at an increasing rate in middle latitudes, driven by the need to feed rising global human populations. As a consequence of deforestation, thermal ranges become extreme, and rainfall reduces in these regions. In contrast, in temperate ecosystems, cattle goats, sheep, or horses kept on permanent pastures adjacent to blocks of deciduous woodland have been highly beneficial to biodiversity via dung fauna (Ransome 1996). This benefit applies not only to bats but also to many other fauna and flora.

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## Conservation Status

The species is included in *The 2018 IUCN Red List of Threatened Animals* as Lower Risk: Least concern for its global status, but declining within its geographic range. It is now extinct in Belgium, Gibraltar, the Netherlands, and possibly Malta. In Europe its status is given as Least Concern by Piraccini (2016). Its conservation is discussed in a *Global Action Plan for Microchiropteran Bats* published by IUCN/SSC's Chiroptera Specialist Group, where it is highlighted in a sample summary Species Action Plan (Hutson et al. 2001).

It is included in Appendix II (species requiring special protection) of the Convention on the Conservation of European Wildlife and Natural Habitats (Bern, 1979) and is specified in its recommendation 43 (1995) on the conservation of threatened mammals in Europe and in its Emerald Network for species requiring sites of specific measures for habitat protection. Conservation of

bat species would also be influenced by Recommendation 36 (1993) on the conservation of underground habitats. The Council of Europe commissioned an action plan for the species (Ransome and Hutson 2000).

It is included in Annex II of the Convention on the Conservation of Migratory Species of Wild Animals (Bonn, 1981) and its Agreement on the Conservation of Population of European Bats (EUROBATS). EUROBATS takes account of the agreement's conservation and management plan and other resolutions adopted by parties to the agreement as outlined in a guide to the implementation of the agreement (Hutson et al. 2019).

It is included in Annex II and Annex IV of the EU Directive on the Conservation of Natural Habitats and of Wild Fauna and Flora (92/43/EEC). Special Areas for Conservation are required to be established for Annex II species, and these were developed as Natura 2000 sites. The EU and EUROBATS compiled a joint action plan for the conservation of bats in Europe (Barova and Streit 2018).

The Convention on Biological Diversity was an important product of the Earth Summit held in Rio de Janeiro (1992). Signed in Rio by 153 nation states and with others that have acceded since, it requires each contracting party to “develop national strategies, plans or programmes for the conservation and sustainable use of biological diversity, or adapt for this purpose existing strategies, plans or programmes which shall reflect, inter alia, the measures set out in the convention relevant to the contracting party concerned.” It seeks sustainable development, with one of the key tests of sustainability being the conservation of biodiversity; development cannot be regarded as sustainable unless biodiversity is conserved. A range of actions are identified to meet this aim. Although the greater horseshoe bat is not specified in this convention, much of the conservation effort on species is based on the CBD.

“BatLife Europe & National Agreements” also exist.

## Management

### Habitat Management

Ransome and Hutson (2000) synthesized relevant published worldwide research for the European Action Plan. Data from arid regions were lacking then, and are still sparse. Greater horseshoe bat populations need a foraging habitat which consists primarily of grassland interspersed with blocks or strips of deciduous woodland, or substantial hedgerows. Grassland should include substantial areas of grazed pastures, and also meadows that were not cut until late summer. Such pasture/meadow/woodland habitats generate large levels of their key prey, especially dung beetles and moths, but also tipulids and ichneumonids. Pastures should be cattle-grazed in summer by preference, especially close to maternity roosts to benefit juvenile bats when they first forage, as their dung sustains the life cycles of the most important beetles (*Aphodius sp.*). Sheep and horse-grazed areas are also beneficial for rotation to reduce parasite problems which otherwise lead to avermectin treatments that adversely affect the insect dung fauna (Wall and Strong 1987). Sheep-grazing results in a short sward, and benefits the life cycles of tipulids, cockchafers, and summer chafers (Ransome 1996). Unlike cattle, sheep do not damage pastures during wet winters, so can be used to generate dung beetles (*Geotrupes sp*) for winter foraging in oceanic climates. Amounts eaten can match summer levels in mild spells (Ransome 2002). Summer diet studies in Belgium (Pir 1994) show that continental European bats eat very similar insect prey, and so should forage over similar habitats. This is supported by a Swiss radio-tracking study (Beck et al. 1994). Fonderflick et al. (2015) demonstrated the importance of woodland and riverine habitat to Mediterranean bats in more arid regions. In mountainous regions suitable foraging habitat may be isolated or have restricted access. In such regions, conservation planning can be complex (Le Roux et al. 2017).

Areas of nongrazed meadows should be left uncut until after key prey, such as moths, have completed their life cycles. Meadows should be adjacent to deciduous woodland blocks or strips linked by suitable tall hedgerows as flight lines for access (Le Roux et al. 2017). Substantial broad hedgerows with frequent emergent trees can provide suitable foraging conditions, both in their structure and prey supplies, especially if woodland is scarce (Froidevaux et al. 2019). Hedgerow lines are used as important commuting routes as long as gaps do not exceed 38 m (Pinaud et al. 2018). Mature grazed parkland, orchards, and aquatic habitats are also suitable. Cattle are preferred to smaller grazers in summer, since they create the ideal structural conditions for perch-hunting bats in hedgerows and woodland edge (Duvergé and Jones 1994). They are also less likely to be attacked by dogs than sheep in public areas. In addition to the grazed pasture/woodland ecosystem, lakes and rivers close to the roost are beneficial, especially if they are surrounded by tree lines. Such habitats generate the maximum populations of insect prey types required by bats in oceanic and Mediterranean climates throughout the year. Insecticides should not be used to control pest species, nor avermectin nematode parasite control for grazers (Sands and Wall 2018).

Habitats which are avoided by greater horseshoe bats include urban areas, arable land, amenity areas such as playing fields, and many types of coniferous forest (Duvergé 1996). Lights, such as street lights or security lamps, are strong deterrents to lesser horseshoe bats, both when they emerge from roosts, and when they commute to forage (Stone et al. 2009). Greater horseshoes are even more light averse (Froidevaux et al. 2018), or when in underground roosts (Straka et al. 2019).

Within suitable habitat, a range of three roost types must be present for a colony to exist as already described. A single maternity roost exists with many surrounding night roosts nearby (usually up to 5 km, but exceptionally up to 14 km) for resting between foraging bouts and three types of suitable hibernacula within a 60 km radius. A type 1 hibernaculum should be as close as possible, but within 12 km of the maternity roost. In the

absence of roosts, they can be provided by building new ones, or changes to existing ones. However, it can take many years before a roost is used.

## Conflicts with Humans

Public attitudes to all bat species in the past were negative in many European countries (Ransome and Hutson 2000). Bats were classed as pests, and treated as such by many house owners. Following publicity and education, this attitude has changed in many countries. Only a minority of people are now averse to them. Genuinely bat-phobic owners have had their fears allayed by visits from bat workers who show them how small they are, and explain about the many fascinating aspects of their long lives.

Serious direct conflicts with humans rarely occur. Interactions may involve problems caused by excrements (feces and urine) in occupied buildings which may stain or cover property. These problems can usually be overcome by the use of plastic sheeting or trays. Maternity roosts may occur in parts of occupied buildings, and bats may hibernate in cellars which are beneath them. In many cases the bats and owners happily coexist for many years. When ownership changes, the new owners may be less tolerant to bats, or wish to utilize the roost spaces for other purposes. Legislation provides protection, and mitigation can solve problems, if properly designed and implemented. In some caves the interests of hibernating bats conflict with the desire of cavers (speleologists) to carry out their sport without restrictions. Alternatively, an owner may wish to open up the cave for commercial visits which involve disturbance due either to lighting regimes or noise.

Indirect conflicts occur when local habitats or large areas of favorable ecosystems are lost to alternative uses, such as for urban development, amenity sports use, or management changes such as from grazing to arable food production. Changes may happen slowly over many decades, and escape recognition.

## Future Challenges for Research and Management

Significant progress is needed in several areas. One aspect is social interaction among individuals and matriline within roosts, mating sites, and at foraging grounds. Behavioral observations linked to their varied complex social calls are key areas. These studies are likely to be challenging for wild populations (Wilkinson 1995).

Diet assessments using either microscopical examination or PCR analysis rarely accompany investigations into other aspects, yet are likely to have significant impacts affecting conclusions made. Microscopical analysis is much easier to complete. The comparative study of climate and diet by Zahn et al. (2007) of *Myotis myotis* in Germany and Portugal is a rare example of what is needed for rhinolophid bats to help fully understand their distribution limits.

DNA studies have had significant impacts on many ecological bat studies. However, the populations studied have usually lacked key information about individual bats, such as year of birth and hence age determination. Few long-term studies exist to support them. Short-term research contracts are not appropriate.

Telomere studies of bats in relation to their extreme longevity (e.g., Foley et al. 2018) is a promising recent topic, as is DNA methylation. Both should significantly add to our understanding of the biochemistry underpinning hibernation, growth, survival, and LRS of individual bats.

Much has been achieved, through education, legislation, and agri-environmental schemes, to protect the species in many parts of Europe. However, agriculture and forestry changes continue apace. As a Habitats Regulations schedule II species, its foraging areas are protected if a population is threatened by development. No protection exists if farmers close to roosts switch from hay-making to silage, or green silage. This switch prevents many insects, such as moths, from completing their life cycles. Some mitigation can be achieved by agri-environment schemes that encourage farmers to allow substantial hedgerows to develop by reducing annual trimming (Froidevaux et al. 2019).

Reduced insect biomass, however caused, is clearly a major cause for concern. Hallmann et al. (2017) recorded a 75+% reduction of insect biomass over 27 years within protected areas. This decline occurred regardless of habitat type. However, declines for moths are more complex (Macgregor et al. 2019). They collected moth biomass data for 50 years at multiple British-fixed monitoring sites. Biomass increased from 1967–1982, then gradually declined from 1982–2017. High between-year variability and multi-year periodicity in biomass emphasizes the need for long-term data to detect trends and identify their causes robustly. They thought that changes in weather, land use, and habitat characteristics were likely factors.

Ridding et al. (2015) studied the fate of semi-natural grassland in England from 1960–2013 in an investigation of the effectiveness of national conservation policy. They used GIS to show that 47% of this habitat was lost through conversion to agriculturally improved grassland (45%) or arable cultivation (43%). While land improvement and use for livestock rearing does not necessarily harm greater horseshoe populations, arable conversion is clearly detrimental. Sites that were statutorily protected retained 91% of their semi-natural grassland, showing that protection was both effective and needed. Froidevaux et al. (2019) supports this view regarding the management of hedgerows by targeted agri-environment schemes. As long as livestock are kept out on pastures as free-ranging animals, they are a huge benefit to their populations if adjacent to deciduous woodland and/or substantial hedgerows. Conversion to arable use from semi-natural grassland has slowed due to higher productivity gains on existing land (Ridding et al. 2015). However, there are likely to be limits to productivity gains at some stage in the future.

Any factor that reduces the availability of grazed/woodland habitat using traditional land management practices will adversely impact the populations of many bat species, including horseshoes, and a wide range of other flora and fauna. This habitat is a major contributor to biodiversity. It will only be maintained if grazing animals are eaten by humans, or used to provide milk or dairy

products. Intensive arable ecosystems are least used by European bats, and most other mammal and bird insectivores. The case for maintaining large domestic free-range ruminant populations in Europe, despite their methane emissions, should be made. A balanced assessment of reliable ecological studies coordinated across all flora and fauna NGOs will be necessary.

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