

SEXUAL SEGREGATION IN IBERIAN NOCTULE BATS

CARLOS IBÁÑEZ, ANTONIO GUILLÉN, PABLO T. AGIRRE-MENDI, JAVIER JUSTE, GODFRIED SCHREUR,
ANA I. CORDERO, AND ANA G. POPA-LISSEANU*

Estación Biológica de Doñana (CSIC), Apartado 1056, 41080 Sevilla, Spain (CI, JJ, AGP-L)

Departamento de Diversidad y Ecología Animal, Instituto de Ecología, A. C. Km 2.5 Antigua

Carretera a Coatepec #351, Congregación El Haya, Xalapa 91070, Veracruz, México (AG)

Paseo del Río Grande, 7, 3 I, 01320 Oyón, Álava, Spain (PTA-M)

CI/La Lamparona 3, 06518 La Codosera, Badajoz, Spain (GS, AIC)

Present address of AGP-L: Leibniz Institute for Zoo and Wildlife Research (IZW),

Evolutionary Ecology Research Group, PF 601103, 10252 Berlin, Germany

Sexual segregation during the breeding season is common in many temperate bat species, and may be related to sex-specific thermoregulatory, microclimatic, or energetic requirements. We compiled capture data for 3 species of *Nyctalus* (noctule bats) obtained over >20 years to study reproductive and migratory strategies of these species in southwestern Europe. Within the Iberian Peninsula, several different strategies regarding sex distribution and migratory behavior were observed within each of the 3 *Nyctalus* species. In the northern part of Iberia there are populations of the 3 species composed of males all year-round with females appearing only during the mating season. Reproduction by females in this area has not been confirmed. In central and southern Iberia there are breeding populations in which sexual segregation occurs only at the roosts or at a regional scale, possibly with females located at lower elevations during the breeding season. Female-biased, long-distance migration is likely to be the cause of sexual segregation in populations of *N. noctula* and *N. leisleri* in northern and central Iberia, but not of *N. lasiopterus*, absent in central Europe. For this latter species, segregation by elevation also could occur in northern Iberia. The Iberian Peninsula is a good example of how breeding strategies and migratory behavior in bats can be very flexible and vary across relatively small geographical scales.

Key words: migration, *Nyctalus lasiopterus*, *Nyctalus leisleri*, *Nyctalus noctula*, segregation by elevation, sex ratio, sexual segregation

Many vertebrate groups, including fish, birds, and mammals, live in all-female or all-male societies during part of their life cycle (Croft et al. 2006; Loe et al. 2006; Phillips et al. 2004). Good examples are temperate bat societies, which usually exhibit sexual segregation during the breeding season (Bradbury 1977; McCracken and Wilkinson 2000). Although intersexual competition for resources, differential resource use, and differences in activity budgets between sexes have been proposed as forces driving sexual segregation in animals (Main et al. 1996; Phillips et al. 2004; Yearsley and Pérez-Barbería 2005), sex-specific thermoregulatory and energetic requirements appear to be the primary cause in bats (Altringham and Senior 2005). Females aggregate in warm roosts to facilitate homeothermic conditions optimal for fetal

development and milk production, whereas males, with lower energetic demands, seek cooler places where torpor allows them to reduce energy expenditures during the day (Willis 2006).

This common mechanism can act at several different geographical scales in temperate bats. On a fine scale, sexual segregation can be local, with females and males using separate but nearby roosts with different microclimatic conditions (Dietz and Kalko 2006). On a coarser scale, sexual segregation can be in elevation, with females occupying lower and warmer areas with higher insect availability. Males, with lower energetic requirements during the breeding season, instead occupy higher, colder areas that constitute potentially poorer foraging habitats. This type of segregation can occur over several tens of kilometers and occurs in mountainous areas (Barclay 1991; Cryan et al. 2000; Russo 2002). Sometimes females move uphill after the breeding season (i.e., period during which females give birth to and rear their young—Carter 1970) for mating with males (Neubauer et al. 2006), although in other cases a few males that share maternity roosts with the females

* Correspondent: anapopa@ebd.csic.es

monopolize the best mating opportunities toward the end of the breeding season (Senior et al. 2005).

The most extreme case of sexual segregation in bats is represented by those species performing long-distance, sex-biased migrations. These are typically tree-dwelling species in which both sexes mate and roost together in hibernating areas, where mild temperatures make it possible to survive the winter in poorly insulated tree roosts. Females commonly travel >1,000 km in spring toward their breeding grounds, which are located at higher latitudes. Males travel shorter distances from the hibernacula or even stay in the wintering areas all year-round (Cryan 2003; Fleming and Eby 2003; Roer 1995; Strelkov 1969, 1997, 2000). Sex-biased migration in bats still remains to be explained in terms of an energetic cost–benefit balance. Migration in animals has evolved as a strategy to track seasonal peaks of resource abundance (Alerstam et al. 2003). Female bats, with higher energetic demands than males during the breeding season due to pregnancy and lactation, would benefit from moving toward higher latitudes where insect density peaks in this season. This could in turn reduce intraspecific competition for food (Fleming and Eby 2003), constituting an example of intersexual resource partitioning. Clustering at the maternity roosts would still allow females to keep conditions optimal for pregnancy and lactation. Males could accept a lower seasonal peak in food density at the lower latitudes to avoid the many risks associated with migration, or to reduce costs from intermale competition to defend mating roosts year-round (Fleming and Eby 2003). Apart from sex-biased migration, the existence of partial (not sex-related) migration, with a gradient between migratory and sedentary populations of the same species that can even overlap in certain regions, is seen in both birds and bats (Fleming and Eby 2003; Pérez-Tris and Tellería 2002). Despite its complexity, migratory behavior in animals seems to be very flexible (Alerstam et al. 2003) and, at least in birds, it can be generated or suppressed within only a few generations (Berthold 1999). Indeed, selective pressures to migrate seem to be greatly influenced by environmental or demographic factors (Taylor and Norris 2007).

Nyctalus is a genus of Palearctic, tree-dwelling bats in which sexual segregation during the breeding season is the rule, and for which a range of migratory behaviors, from sedentarism to partial and complete sex-biased migration, have been described (Fleming and Eby 2003). Three species of these fast-flying, aerial-hawking bats occur in continental Europe. The species whose movement habits are the most well known is the common noctule (*Nyctalus noctula*). A great deal of information about its central European populations is available (Gebhard and Bogdanowicz 2004). Much less is known of the lesser noctule (*Nyctalus leisleri*—Bogdanowicz and Ruprecht 2004). Lastly, the giant noctule (*Nyctalus lasiopterus*) is one of the rarest and most enigmatic European bats (Ibáñez et al. 2004). A recent review on bat migration in Europe based on banding studies unequivocally included *N. noctula* and *N. leisleri* in the category of long-distance migrants, whereas there are insufficient data to evaluate the migratory status of *N. lasiopterus* (Hutterer et al. 2005). These species of *Nyctalus*

occurring in Europe seem to use variable migration strategies in different parts of their ranges.

In eastern Europe, the little data available point toward complete migratory behavior for the 3 *Nyctalus* species, with no known sedentary breeding populations (i.e., those in which both males and females are present all year-round) in southeastern Europe in areas such as the Balkans and Turkey (Benda and Horáček 1998; Hanák et al. 2001; Miric and Paunovic 1997; Strelkov 1969). Western Europe typically seems to hold migratory populations of *N. noctula* and *N. leisleri* in its north-central area, but also sedentary breeding populations in some regions such as the British Isles (Racey 1991). In this context, the Iberian Peninsula is a particularly interesting region for a number of reasons including the simultaneous occurrence of the 3 species of *Nyctalus* including the rare giant noctule; the existence of breeding populations (i.e., those in which females are present at least part of the year while giving birth and rearing the young) of the 3 species; and the proposed use of the area (at least for its northernmost half) as the wintering grounds of some of the European bats that migrate long distances (Hutterer et al. 2005). However, the latter suggestion is based on anecdotal data because information on sex composition, seasonal distribution, and reproductive status of Iberian populations is virtually nonexistent. We compiled published and new data on the seasonal distribution of sex ratios for the 3 species of *Nyctalus* at several sites throughout Iberia comprising different elevations, with the aim of revealing the breeding status of *Nyctalus* in the region, establishing whether sexual segregation exists, and, if so, determining the geographical scale at which such segregation takes place.

MATERIALS AND METHODS

Study area.—Capture data of *Nyctalus* species used in this study were collected from 1984 to 2007 at different regions across the Iberian Peninsula, representing the north, center, and south of the territory. Capture sites were located at Sistema Ibérico Septentrional (hereafter SIS) in northern Spain, Extremadura (EX) in central-western Spain, and Sierra de Cádiz (SC), Sevilla (Sevilla), Jerez de la Frontera (Jerez), and Doñana National Park (Doñana) in southern Spain (Fig. 1). SIS is a forested mountain range where the most abundant tree species included *Quercus pyrenaica* and *Pinus sylvestris* with *Fagus sylvatica* on shaded slopes and *Quercus ilex* on south-facing slopes. Sampling sites in EX were located within a Mediterranean forest, where the main tree species included *Quercus suber*, *Q. ilex*, *Q. pyrenaica*, and *Castanea sativa*. SC is a mountain area composed of well-preserved, relatively humid Mediterranean forest, with *Abies pinsapo*, *Q. ilex*, and *Q. faginea* dominating in the north, and *Quercus canariensis* and *Q. suber* in the south. In Andalusia, sampled maternity colonies of *N. lasiopterus* were located in 2 urban parks (in Sevilla and Jerez, respectively), where the bats occupied cavities of large and old trees, and in a bat box situated at the border of the Doñana marshlands (Doñana; Fig. 1).

Capture.—Only published data were available for *N. noctula*. Capture data were obtained for the other 2 species at

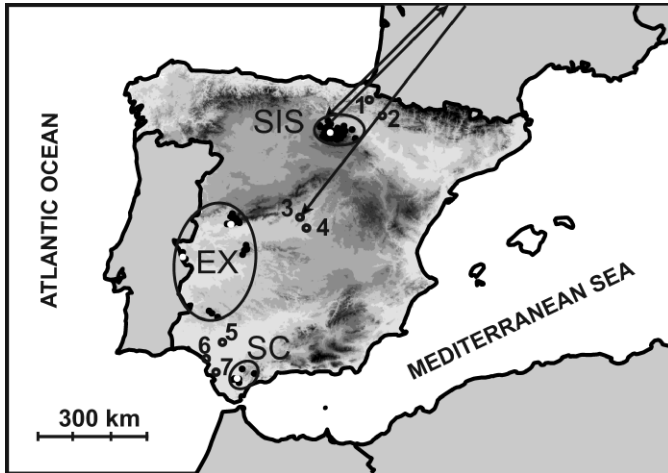


FIG. 1.—Localities throughout Iberia mentioned in this study. These include 3 major study areas (Sistema Ibérico Septentrional [SIS], Extremadura [EX], and Sierra de Cádiz [SC]) with their enclosed capture sites (black circles), localities mentioned in the literature (empty circles; 1 = Pamplona; 2 = Sangüesa; 3 = Fuenlabrada; 4 = Aranjuez), and localities with sampled maternity colonies of *Nyctalus lasiopterus* (empty circles; 5 = Sevilla; 6 = Doñana National Park; 7 = Jerez de la Frontera). Arrows indicate movements of banded individuals of *N. leisleri* between Germany and Spain (Ohlendorf et al. 2000, 2001; Wohlgenuth et al. 2004). White circles within the study areas represent localities for which temperature data are presented in Table 1.

the foraging areas, by mistnetting over ponds or streams (490 *N. lasiopterus* and 775 *N. leisleri*) in SIS, EX, and SC; and at the roosting areas, by capturing bats within or mistnetting them as they emerged from their daytime roosts (479 *N. lasiopterus*) in Sevilla, Jerez, and Doñana.

Bats were weighed and classified by sex and age as adults or young. Young were identified by the cartilaginous plates in the metacarpal–phalangeal joints (Anthony 1988). We recorded reproductive status as nonreproductive, gestating (recognized by palpation), or lactating (enlarged nipples surrounded by hairless skin) for females, and scrotal or nonscrotal testes in males (Racey 1988). All bats captured at the roosts and 25% of bats captured at the foraging areas were banded with aluminum alloy rings (Porzana, Ltd., Icklesham, United Kingdom). Recaptures were not included in the study to avoid pseudo-replication. Less than 3% of the bats banded at the foraging areas were recaptured. Therefore, the influence of pseudo-replication due to inclusion of recaptured bats among non-banded individuals is likely negligible.

Captures were classified according to season either as “breeding period,” during which females gave birth and reared their young (Carter 1970), from 1 May to 14 August, or “mating period,” when males were sexually active and pairings took place (Carter 1970), from 15 August onward. This was based on the phenology of *N. lasiopterus* in Spain (Ibáñez et al. 2004) and observations for *N. noctula* (Alcalde 1999) and *N. leisleri* in Spain (C. Ibáñez and A. Guillén, pers. obs.).

Statistical analysis.—We estimated sex composition in the sampled populations by analyzing deviations from a 1:1 ratio

TABLE 1.—Elevation and monthly mean temperatures (Ninyerola et al. 2005) at selected localities where *Nyctalus* were sampled throughout Iberia, in 3 representative periods: April, prebreeding; June, breeding; and August, postbreeding. Label = refers to study sites identified in Fig. 1.

Locality	Label	Elevation (m above sea level)	Mean temperature (°C)		
			April	June	August
Pamplona	1	450	10.2	17.4	20.8
Valvanera	SIS	1,000	6.8	14.4	17.9
Aranjuez	4	490	12	21.5	24.6
San Vicente de Alcántara	EX	331	12.9	21.3	25.1
Piornal	EX	1,200	9.1	18.1	22.2
Sevilla	5	10	16.3	23.5	26.8
Doñana National Park	6	4	15.1	21.6	24.8
Jerez de la Frontera	7	20	15.9	22.3	25.8
La Saucedá	SC	670	13.0	20.0	24.0

through Fisher exact tests. We performed *t*-tests to test whether males and females showed segregation by elevation within each study area. For all tests, we considered $P < 0.05$ as significant.

The handling of all bats was approved by the Environmental Councils in Andalusia, Extremadura, and La Rioja, and conformed to guidelines for animal care and use established by the American Society of Mammalogists (Gannon et al. 2007).

RESULTS

For SIS, we mistnetted bats during 111 nights (netting elevation $\bar{X} = 1,015 \text{ m} \pm 210 \text{ SD}$) at 37 sampling sites (elevation $\bar{X} = 947 \pm 225 \text{ m}$; range 481–1,343 m); for EX, 40 nights (netting elevation $\bar{X} = 740 \pm 307 \text{ m}$) and 26 sampling sites (elevation $\bar{X} = 820 \pm 309 \text{ m}$; range 331–1,378 m); and for SC, 34 nights (netting elevation $\bar{X} = 449 \pm 254 \text{ m}$) and 11 sampling sites (elevation $\bar{X} = 506 \pm 311 \text{ m}$; range 90–1,260 m). Data on temperature for several sampled localities are shown in Table 1.

Nyctalus noctula is an uncommon species in Iberia, as shown by the few records of solitary individuals that have been reported (Ibáñez et al. 1992). However, colonies of this species have recently been discovered in 2 regions in Spain: Aranjuez in Madrid (Ruedi et al. 1998) and Pamplona and Sangüesa in Navarra (Alcalde 1999). Both areas are located at <500 m above sea level (Fig. 1). In Aranjuez, both sexes were present although they occupied separate but nearby roosts, with females lactating in June (Ruedi et al. 1998). Colonies in Navarra consisted almost exclusively of males during the breeding season (May–August) and of both sexes during the mating season, with females outnumbering males due to the formation of harems (Alcalde 1999).

Nyctalus leisleri was a common species in the sampled areas: 387 individuals were captured in SIS ($\bar{X} = 3.5$ bats per night), 191 in EX ($\bar{X} = 4.7$ bats per night), and 197 in SC ($\bar{X} = 5.1$ bats per night). In SIS, males were present year-round, whereas females occurred there almost exclusively from the end of August until October (Fig. 2). The sex ratio was extremely

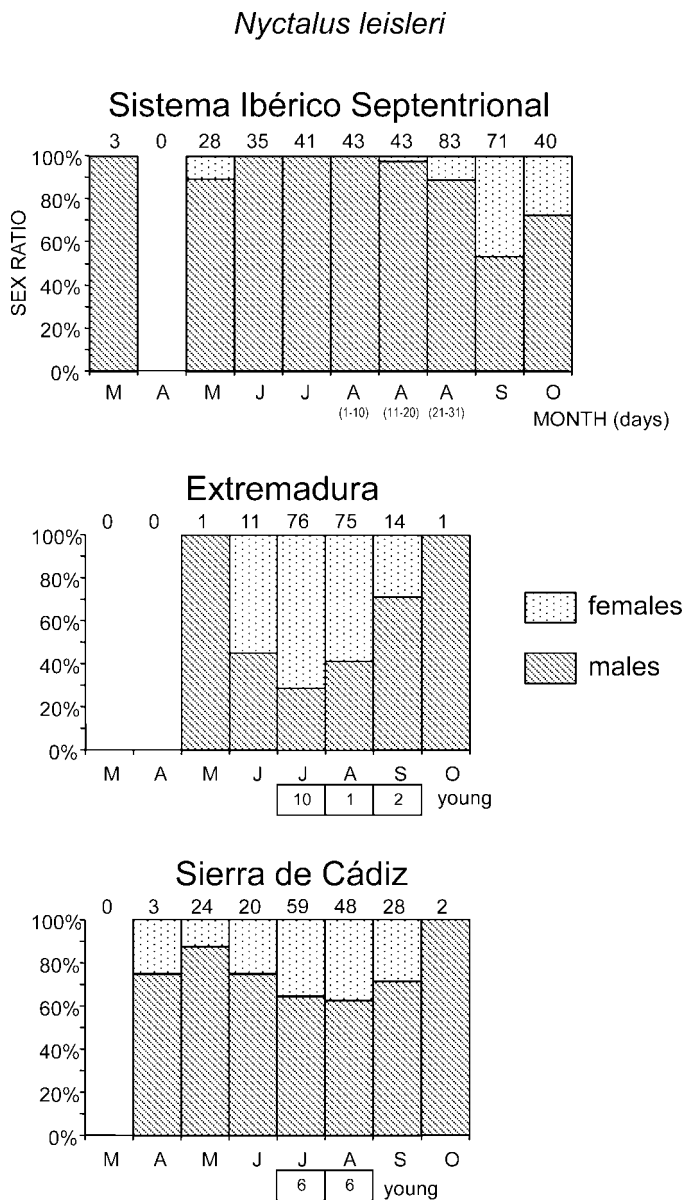


FIG. 2.—Variation in sex ratios of *Nyctalus leisleri* in Sistema Ibérico Septentrional (SIS), Extremadura (EX), and Sierra de Cádiz (SC) through the year. Numbers at the top of the figure represent the total number of captures of both sexes for each considered period. For SIS, August is divided into three 10- to 11-day periods. Numbers of young (at the bottom of figures) were not included in the calculation of percentages.

male-biased during the breeding season, and slightly less so during the mating season (Fisher exact test $P < 0.001$ in both seasons). Numbers of females increased significantly in the mating season (Fisher exact test $P < 0.001$). The proportion of females started to increase toward the end of summer, reaching 50% in September, then decreased again in October (Fig. 2). All 3 females captured during the breeding season showed no signs of pregnancy or lactation, and no young were found. In all 3 regions no significant differences in mean elevations of captures of both sexes were detected, although captures of females always showed lower values (Table 2).

Both sexes of *N. leisleri* could be captured year-round in EX and SC in the same mist nets (Fig. 2). Males were captured more frequently than females during the breeding season in SC, whereas the opposite was observed in EX (Fisher exact tests $P < 0.001$ and $P = 0.009$, respectively). Females in both areas were pregnant in May–June and lactating from June to August. Young were captured through July–August. The sex ratios tended to equilibrate after the breeding period, and during the mating season they were not significantly different from 1:1 (Fisher exact tests $P = 0.055$ and $P = 1$, respectively). A significant change in sex ratio from breeding to mating season occurred in EX ($P = 0.029$) but not in SC ($P = 0.402$). In EX, young could be captured at elevations of up to 923 m and breeding females up to 1,200 m (males up to 1,378 m). In SC, breeding females were mistnetted up to 800 m elevation with only a few capture sites located above this elevation. Again, there were no significant differences in mean elevations for captures of males and females in any season, but a tendency toward occupancy of lower elevations by females was observed (Table 2).

Nyctalus lasiopterus also was regularly captured in the study areas: 374 individuals were captured in SIS (3.4 bats per night), 79 in SC (2.3 bats per night), and 37 in EX (0.9 bats per night). In SIS, the situation was similar to that observed for *N. leisleri*, with males present year-round and females from mid-August until October (Fig. 3). Sex ratio was significantly male-biased in both breeding and mating seasons (Fisher exact test $P < 0.001$ in both cases), although differences were smaller during mating ($P < 0.001$). Females, which were practically absent during the breeding season, reached their greatest proportion of 30% in September and decreased again in October (Fig. 3). The only 3 lactating females were captured in early August at 1 of the lower-elevation sampling sites (750 m above sea level). No young were captured.

Presence of *N. lasiopterus* in EX and SC also follows a pattern similar to that of *N. leisleri* (Fig. 3). Both sexes were captured in all seasons and, overall, males outnumbered females in SC but the opposite trend was observed in EX. However, differences in proportions of each sex were only significant in EX (Fisher exact tests $P = 0.055$ for SC and $P = 0.021$ for EX). Breeding populations were confirmed at both sampling sites through the capture of pregnant and lactating females and of flying young (Fig. 3). During the mating season, the sex ratio was not significantly different from 1:1 ($P = 0.500$ in SC and $P = 0.211$ in EX). A significant change in the sex ratio from breeding to mating season occurred at EX ($P < 0.001$) but not at SC ($P = 0.2877$). The only sampling site where we could confirm breeding in EX was located at 750 m above sea level. (Hervás). In SC, the species was found up to 700 m, which was also the uppermost elevation at which reproductive females were captured. Although the difference in mean elevation of captures between sexes was not significant, mean capture elevation for females tended to be lower (Table 3).

Many *N. lasiopterus* were captured from 3 breeding populations in Andalusia (337 in Sevilla, 80 in Jerez, and 62 in Doñana), with colony sizes ranging between 31 and 150. Almost all adult individuals were females (Fig. 4). Gestation

TABLE 2.—Comparisons between mean elevations (meters above sea level) of capture sites for females and males of *Nyctalus leisleri*, in both seasons (breeding and mating) and 3 study regions in Iberia. Localities are Sistema Ibérico Septentrional (SIS), Extremadura (EX), and Sierra de Cádiz (SC).

Locality	Sex	Breeding $\bar{X} \pm SD$ (n)	Student's <i>t</i> (<i>P</i>)	Mating $\bar{X} \pm SD$ (n)	Student's <i>t</i> (<i>P</i>)
SIS	Males	1,046 ± 153 (151)	1.452	979 ± 180 (176)	1.062
	Females	918 ± 0 (3)	(0.149)	949 ± 203 (54)	(0.290)
EX	Males	744 ± 300 (41)	1.658	721 ± 122 (29)	−0.429
	Females	665 ± 217 (79)	(0.100)	738 ± 180 (29)	(0.670)
SC	Males	492 ± 220 (104)	1.656	517 ± 215 (22)	1.534
	Females	427 ± 226 (47)	(0.099)	376 ± 243 (8)	(0.136)

took place from May to June and lactation from June to early August (Popa-Lisseanu et al. 2008). The colonies reached their maximum size during lactation and after this period the number of bats was greatly reduced (Sevilla, where bats could be captured year-round—Ibáñez et al. 2001), or bats disappeared completely from the breeding roosts (Doñana and Jerez).

DISCUSSION

All 3 European representatives of *Nyctalus* occur and breed in the Iberian Peninsula. The most common of the 3 in Central Europe, *N. noctula*, is very rare in Iberia, which is the southwestern limit of its distributional range. Only 3 localities with stable populations (as opposed to solitary individuals appearing occasionally) have been discovered so far (Fig. 1), in Aranjuez, Pamplona, and Sangüesa (Alcalde 1999; Ruedi et al. 1998). *N. leisleri* and *N. lasiopterus* reach slightly lower latitudes, including North Africa (Bogdanowicz and Ruprecht 2004; Ibáñez et al. 2004). *N. leisleri* ranges widely across much of Europe but is considered rare almost everywhere except in Ireland (Shiel et al. 1999). Examination of our data for *N. leisleri* shows that this species is not rare in Iberia, but is found across large areas in the northern, western, and southern Iberian Peninsula. *N. lasiopterus* is a circum-Mediterranean species and no stable populations have been reported outside of Spain, except for a few sites in Hungary (Estók and Gombkötő 2007) and in Slovakia (Uhrin et al. 2006) and perhaps sedentary all-male populations in Greece (Hanák et al. 2001). Spanish populations of this species are the largest known and probably the most important in Europe (Ibáñez et al. 2004; Popa-Lisseanu et al. 2008). Considering the relative abundance of *N. leisleri* and *N. lasiopterus* in southeastern Europe, it has been hypothesized that these 2 species might occupy empty niches south of the range limit of *N. noctula*, which is thought to be dominant elsewhere (Hanák et al. 2001; Helversen and Weid 1990). Examination of our data supports this hypothesis by showing a similar pattern in southwestern Europe.

Several different life and reproductive strategies can be observed among species of *Nyctalus* on the Iberian Peninsula, and sexual segregation occurs at different spatial scales. We considered the following scales of sexual segregation: local segregation, in which males and females are near each other but in separate roosts; regional segregation, in which males and females are separated by several tens up to a few hundred kilometers; segregation by elevation within a region, in which males and females roost at different elevations; and sexual

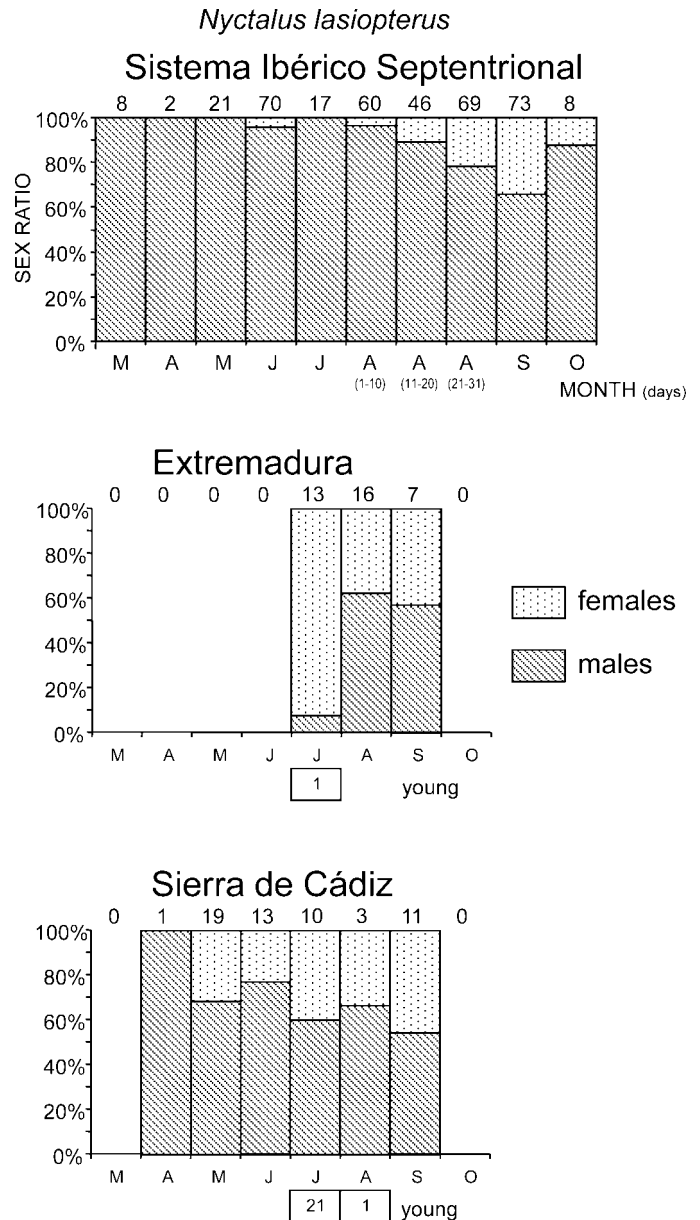


FIG. 3.—Variation in sex ratios of *Nyctalus lasiopterus* in Sistema Ibérico Septentrional (SIS), Extremadura (EX), and Sierra de Cádiz (SC) throughout the year. Numbers at the top of the figure represent total number of captures of both sexes for each considered period. For SIS, August is divided into three 10- to 11-day periods. Numbers of young (at the bottom of figures) were not included in the calculation of percentages.

TABLE 3.—Comparisons between mean elevations (meters above sea level) of capture sites for females and males of *Nyctalus lasiopterus*, in both seasons (breeding and mating) and 2 study regions in Iberia: Sistema Ibérico Septentrional (SIS) and Sierra de Cádiz (SC).

Locality	Sex	Breeding $\bar{X} \pm SD$ (n)	Student's <i>t</i> (<i>P</i>)	Mating $\bar{X} \pm SD$ (n)	Student's <i>t</i> (<i>P</i>)
SIS	Males	1,030 ± 171 (165)	1.336	1,105 ± 140 (148)	0.172
	Females	926 ± 190 (5)	(0.183)	1,101 ± 145 (46)	(0.863)
SC	Males	516 ± 217 (3,130)	1.243	401 ± 251 (7)	0.778
	Females	428 ± 230 (14)	(0.221)	294 ± 210 (5)	(0.454)

segregation due to long-distance migration, that is, one sex migrates several hundred up to a few thousand kilometers, whereas the other travels shorter distances or stays at the same place year-round.

Local sexual segregation (males and breeding females occupying different but nearby roosts) can be observed for *N. noctula* in Aranjuez (central Spain). The existence of a breeding population at this latitude is atypical for the species, because the nearest known breeding population is located 900 km northeast in France, and is considered to be a peripheral population (Petit et al. 1999). The roosting habitat of *N. noctula* in Aranjuez (an urban park located at the margins of the Tajo River in the semiarid Central Plateau) resembled a stepparian landscape such as the one described by Strelkov (2000) for some marginal and isolated breeding localities of this species in central Asia. The populations of *N. leisleri* and *N. lasiopterus* in EX and SC (where both males and females were netted at the foraging areas in all seasons and reproduction was confirmed) can also be included in the category of no or only local sexual

segregation. Nevertheless, sex ratios during the breeding season differ to some extent from 1:1, being female-biased in EX and the opposite in SC. This suggests that a mixed strategy could be taking place, with unequal proportions of sedentary and migratory individuals between the 2 sexes (presumably fewer sedentary individuals among the females). These sedentary breeding populations of the 3 species of *Nyctalus* that show little evidence of sexual segregation at the landscape scale are all located in relatively warm areas (mean temperatures in June and August above 18°C and 22°C, respectively; Table 1), and up to now have only been found in the southern half of Iberia. Outside Iberia, sedentary breeding populations of both sexes have been previously reported for *N. noctula* and *N. leisleri* in the British Isles (Racey 1991).

At a regional scale of sexual segregation, males and females spend the breeding season separated by several tens of kilometers, most likely in regions with different climatic conditions. *N. lasiopterus* in western Andalusia (Sevilla, Jerez, and Doñana) probably follows this pattern of segregation. These breeding colonies are almost exclusively made up of females and their young with most individuals disappearing at the end of the breeding season. During this same period, the number of females captured increased significantly in SC (50 km east of Jerez; Fig. 1), where males dominated during the summer. Short migrations in elevation of females from colonies in southwestern Andalusia to the mountains of SC for mating and hibernating would not be surprising, because examination of banding and radiotracking data revealed movements of bats between Sevilla, Doñana, Jerez, and SC (A. G. Popalisseanu, F. Bontadina, and C. Ibáñez, pers. obs.). For these populations, we suggest a model of partial sexual segregation by elevation, involving only a proportion of the females. As was reported by Neubaum et al. (2006) for *Eptesicus fuscus* in North America, this pattern would imply short migrations of females to lower, warmer elevations before the breeding period, and return migrations to higher elevations for hibernation and possibly mating. This mechanism has been proposed as a means of avoiding the high costs of long-distance latitudinal migrations (Barclay 1991; Cryan et al. 2000), by covering steeper temperature gradients over shorter distances (Neubaum et al. 2006). However, more evidence is needed to confirm this strategy in Andalusian populations of *N. lasiopterus*.

Nyctalus lasiopterus and *N. leisleri* of SIS (northern Spain) also may show sexual segregation by elevation, with reproductive females situated close to males, but at lower elevations (Tables 2 and 3). This hypothesis is supported by the

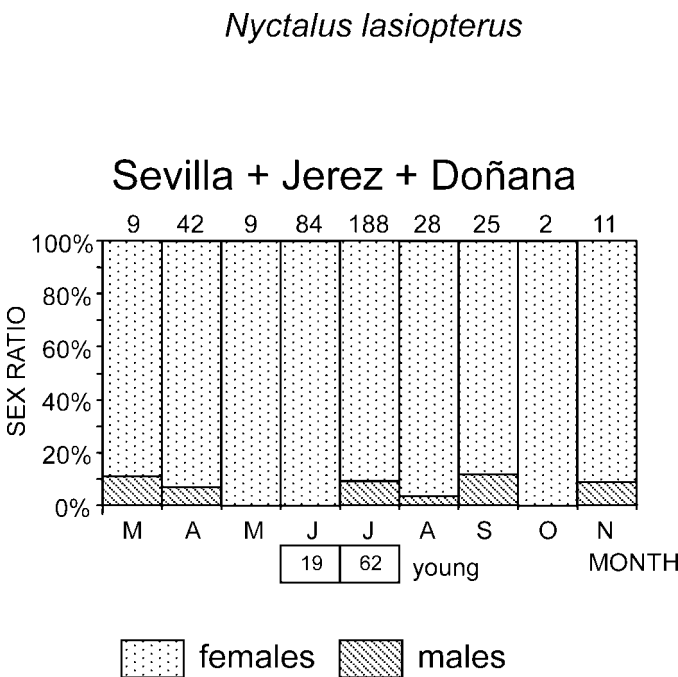


FIG. 4.—Variation in sex ratios in maternity colonies of Andalusia throughout the year. Numbers at the top of the figure represent total number of captures of both sexes for each considered period. Numbers of young (at the bottom of figures) were not included in the calculation of percentages.

observation that during the breeding season the only females captured (3 reproductive *N. lasiopterus* and 3 *N. leisleri* with no evident signs of reproduction) were found among the lowest elevations sampled. Sampling in SIS should be extended to lower elevations to verify the trends found in this study.

Sex-biased migration is the 3rd driver that may produce sexual segregation in Iberian populations of *Nyctalus*. Nursery roosts of *N. noctula* and *N. leisleri* are concentrated in northern and central Europe, whereas winter roosts are located in southern Europe (Hutterer et al. 2005). The absence of females of these species during the breeding season in the southern half of Europe and their arrival in autumn has been reported with sex-biased migrations accepted as the cause (Roer 1995; Strelkov 1969). This pattern is seen in Turkey (Benda and Horáček 1998), Greece (Hanák et al. 2001; Helversen and Weid 1990), Bulgaria (Benda et al. 2003), the Balkans (Miric and Paunovic 1997), and Switzerland (Stutz and Haffner 1986). The all-male sedentary populations of *N. noctula* in Navarra (Pamplona and Sangüesa; Fig. 1) most likely result from sex-biased migration. Females only arrive here during the mating season. Such patterns occur in Switzerland and France, with long-distance migrations to these wintering areas from the northeast documented through recaptures of banded individuals (Gebhard and Bogdanowicz 2004). However, the origin of migrating females wintering in Navarra remains unknown. Long-distance migrations of banded *N. leisleri* from as far as Germany to Spain have been reported on several occasions (Ohlendorf et al. 2000; Wohlgemuth et al. 2004), with 1 of them involving a 2-way migration (Ohlendorf et al. 2001). It is likely that sexual segregation of *N. leisleri* in some areas of Spain is a result of long-distance, latitudinal, sex-biased migration. Because bats banded in Germany have been found in SIS and in Fuenlabrada near Madrid (Ohlendorf et al. 2000; Wohlgemuth et al. 2004; Fig. 1), migratory populations are known to reach at least central Iberia, and potentially could reach further south. If this is true, migratory *N. leisleri* in central and, perhaps, southern Iberia could be sharing mating or hibernating areas with sedentary populations (such as those of EX). *N. lasiopterus* is the only 1 of the 3 species for which sexual segregation cannot be explained by migration in any region of Iberia, because no breeding populations have been identified in central-western Europe. Maternity colonies of *N. lasiopterus* that disappear at the end of summer have been reported from Hungary (Estók 2007) and might also exist in Slovakia (Uhrin et al. 2006) and Russia (Strelkov 1969). It is unlikely that these colonies are related to the distant Spanish populations. Instead, they are probably related to the ones in Greece where females are absent in summer (Hanák et al. 2001; Helversen and Weid 1990). This would support the hypothesis that *N. lasiopterus* is a migratory bat in eastern Europe (Strelkov 1969), but not in southwestern Europe, or that migration in the former region is across latitude, but across elevation in the latter region.

In summary, the Iberian Peninsula provides an excellent example of the flexibility of migratory behavior in European bats, a flexibility that has already been demonstrated in migratory birds (Alerstam et al. 2003; Berthold 1999).

Differences in breeding strategies of *Nyctalus* can take place at relatively small geographical scales. The boundary between populations exhibiting different migratory and reproductive strategies in Iberia, and in southern Europe in general, is unclear and an overlap could exist. Until new techniques help refine our knowledge of bat migration in Europe, the factors determining landscape movements in European bat populations will remain an open question.

ACKNOWLEDGMENTS

We thank L. Gamallo, S. García, J. A. Garrido, M. Iglesias, R. Janssen, E. Migens, J. Noguera, J. L. Pérez-Jordá, J. Quetglas, C. Ruiz, J. Sáenz, and R. Sanabria for their help in capturing bats; the governments of La Rioja, Extremadura, and Andalusia, the Servicio de Parques y Jardines de Sevilla and the Zoo of Jerez de la Frontera for providing permits for collecting samples and handling the bats; J. Noguera for improving the figures of the manuscript; and 2 anonymous reviewers for their valuable comments on the manuscript. This research was partially funded via several bat research projects from the Ministerio de Educación y Ciencia (MEC) (REN2000-1639/GLO, REN2002-01372/GLO, and SAF2006-12784-C02-02), the Organismo Autónomo de Parques Nacionales (MMA) of Spain, project 021/2002, and the government of Extremadura and the European Union from 2001 to 2005 in Extremadura. The Spanish MEC supported AGP-L with a predoctoral grant of the program Formación de Personal Universitario (AP-2002-3721).

LITERATURE CITED

- ALCALDE, J. T. 1999. New ecological data on the noctule bat (*Nyctalus noctula* Schreber, 1774) (Chiroptera, Vespertilionidae) in two towns of Spain. *Mammalia* 63:273–280.
- ALERSTAM, T., A. HEDENSTRÖM, AND S. ÅKESSON. 2003. Long-distance migration: evolution and determinants. *Oikos* 103:247–260.
- ALTRINGHAM, J. D., AND P. SENIOR. 2005. Social systems and ecology of bats. Pp. 280–302 in *Sexual segregation in vertebrates* (K. E. Ruckstuhl and P. Neuhaus, eds.). Cambridge University Press, Cambridge, United Kingdom.
- ANTHONY, E. L. P. 1988. Age determination in bats. Pp. 47–58 in *Ecological and behavioral methods for the study of bats* (T. H. Kunz, ed.). Smithsonian Institution Press, Washington, D.C.
- BARCLAY, R. M. R. 1991. Population structure of temperate zone insectivorous bats in relation to foraging behaviour and energy demand. *Journal of Animal Ecology* 60:165–178.
- BENDA, P., AND I. HORÁČEK. 1998. Bats (Mammalia: Chiroptera) of the eastern Mediterranean. Part 1. Review of distribution and taxonomy of bats in Turkey. *Acta Societas Zoologicae Bohemicae* 62:255–313.
- BENDA, P., ET AL. 2003. Bats (Mammalia: Chiroptera) of the eastern Mediterranean. Part 3. Review of bat distribution in Bulgaria. *Acta Societas Zoologicae Bohemicae* 67:245–357.
- BERTHOLD, P. 1999. A comprehensive theory for the evolution, control and adaptability of avian migration. *Ostrich* 70:1–11.
- BOGDANOWICZ, W., AND A. L. RUPRECHT. 2004. *Nyctalus leisleri* (Kuhl, 1817)—Kleinabendsegler. Pp. 717–756 in *Handbuch der Säugetiere Europas* (J. Niethammer and F. Krapp, eds.). Vol. 4 (II). Aula Verlag, Wiesbaden, Germany.
- BRADBURY, J. W. 1977. Social organization and communication. Pp. 2–72 in *Biology of bats* (W. A. Wimsatt, ed.). Vol. III. Academic Press, New York.

- CARTER, D. C. 1970. Chiropteran reproduction. Pp. 233–246 in *About bats* (B. H. Slaughter and D. W. Walton, eds.). Southern Methodist University Press, Dallas, Texas.
- CROFT, D. P., ET AL. 2006. Predation risk as a driving force for sexual segregation: a cross-population comparison. *American Naturalist* 167:867–878.
- CRYAN, P. M. 2003. Seasonal distribution of migratory tree bats (*Lasiurus* and *Lasionycteris*) in North America. *Journal of Mammalogy* 84:579–593.
- CRYAN, P. M., M. A. BOGAN, AND J. S. ALTENBACH. 2000. Effect of elevation on distribution of female bats in the Black Hills, South Dakota. *Journal of Mammalogy* 81:719–725.
- DIETZ, M., AND E. K. V. KALKO. 2006. Seasonal changes in daily torpor patterns of free-ranging female and male Daubenton's bats (*Myotis daubentonii*). *Journal of Comparative Physiology B. Biochemical, Systemic, and Environmental Physiology* 176:223–231.
- ESTÓK, P. 2007. Seasonal changes in the sex ratio of *Nyctalus* species in north-east Hungary. *Acta Zoologica Academiae Scientiarum Hungaricae* 53:89–95.
- ESTÓK, P., AND P. GOMKÓTÓ. 2007. Review of the Hungarian data of *Nyctalus lasiopterus* (Schreber, 1780). *Folia Historico Naturalia Musei Matraensis* 31:167–172.
- FLEMING, T. H., AND P. EBY. 2003. Ecology of bat migration. Pp. 156–208 in *Bat ecology* (T. H. Kunz and M. B. Fenton, eds.). University of Chicago Press, Chicago, Illinois.
- GANNON, W. L., R. S. SIKES, AND THE ANIMAL CARE AND USE COMMITTEE OF THE AMERICAN SOCIETY OF MAMMALOGISTS. 2007. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. *Journal of Mammalogy* 88:809–823.
- GEBHARD, J., AND W. BOGDANOWICZ. 2004. *Nyctalus noctula* (Schreber, 1774)—Grosser Abendsegler. Pp. 607–694 in *Handbuch der Säugetiere Europas* (J. Niethammer and F. Krapp, eds.). Vol. 4. (II). Aula-Verlag, Wiesbaden, Germany.
- HANÁK, V., P. BENDA, M. RUEDI, I. HORÁČEK, AND T. SOFIANIDOU. 2001. Bats (Mammalia: Chiroptera) of the eastern Mediterranean. Part 2. New records and review of distribution of bats in Greece. *Acta Societas Zoologicae Bohemicae* 65:279–346.
- HELVERSEN, VON O., AND R. WEID. 1990. Die Verbreitung einiger Fledermausarten in Griechenland. *Bonner Zoologische Beiträge* 41:9–22.
- HUTTERER, R., T. IVANOVA, C. MEYER-CORDS, AND L. RODRIGUES. 2005. Bat migrations in Europe: a review of banding data and literature. German Agency for Nature Conservation, Bonn, Germany.
- IBÁÑEZ, C., A. GUILLÉN, R. FERNÁNDEZ, J. L. PÉREZ, AND S. I. GUERRERO. 1992. Iberian distribution of some little known bat species. *Mammalia* 56:433–444.
- IBÁÑEZ, C., A. GUILLÉN, AND W. BOGDANOWICZ. 2004. *Nyctalus lasiopterus* (Schreber, 1780)—Riesenabendsegler. Pp. 695–716 in *Handbuch der Säugetiere Europas* (J. Niethammer and F. Krapp, eds.). Vol. 4 (II). Aula-Verlag, Wiesbaden, Germany.
- IBÁÑEZ, C., J. JUSTE, J. L. GARCÍA-MUDARRA, AND P. T. AGIRRE-MENDI. 2001. Bat predation on nocturnally migrating birds. *Proceedings of the National Academy of Sciences* 98:9700–9702.
- LOE, L. E., ET AL. 2006. Testing five hypotheses of sexual segregation in an arctic ungulate. *Journal of Animal Ecology* 75:485–496.
- MAIN, M. B., F. W. WECKERLY, AND V. C. BLEICH. 1996. Sexual segregation in ungulates: new directions for research. *Journal of Mammalogy* 77:449–461.
- MCCRACKEN, G. F., AND G. S. WILKINSON. 2000. Bat mating systems. Pp. 321–362 in *Reproductive biology of bats* (E. G. Crichton and P. H. Kruttsch, eds.). Academic Press, New York.
- MIRIC, D., AND M. PAUNOVIC. 1997. New data on the Leisler's bat *Nyctalus leisleri* (Kuhl, 1817) (Vespertilionidae, Chiroptera) from the Balkan Peninsula, with a review of the Balkan range. *Myotis* 35:67–75.
- NEUBAUM, D. J., T. J. O'SHEA, AND K. R. WILSON. 2006. Autumn migration and selection of rock crevices as hibernacula by big brown bats in Colorado. *Journal of Mammalogy* 87:470–479.
- NINYEROLA, M., X. PONS, AND J. M. ROURE. 2005. Atlas climático digital de la Península Ibérica. Metodología y aplicaciones en bioclimatología y geobotánica. Universidad Autónoma de Barcelona, Bellaterra, Spain.
- OHLENDORF, B., B. HECHT, D. STRASSBURG, AND P. T. AGIRRE-MENDI. 2000. Fernfund eines Kleinabendseglers (*Nyctalus leisleri*) in Spanien. *Nyctalus* (Neue Folge) 7:239–242.
- OHLENDORF, B., B. HECHT, D. STRASSBURG, AND P. T. AGIRRE-MENDI. 2001. Bedeutende Migrationsleistung eines markierten Kleinabendseglers (*Nyctalus leisleri*): Deutschland–Spanien–Deutschland. *Nyctalus* (Neue Folge) 8:60–64.
- PÉREZ-TRIS, J., AND J. L. TELLERÍA. 2002. Migratory and sedentary blackcaps in sympatric non-breeding grounds: implications for the evolution of avian migration. *Journal of Animal Ecology* 71:211–224.
- PETIT, E., L. EXCOFFIER, AND F. MAYER. 1999. No evidence of bottleneck in the postglacial recolonization of Europe by the noctule bat (*Nyctalus noctula*). *Evolution* 53:1247–1258.
- PHILLIPS, R. A., J. R. D. SILK, B. PHALAN, P. CATRY, AND J. P. CROXALL. 2004. Seasonal sexual segregation in two *Thalassarche* albatrosses: competitive exclusion, reproductive role specialization or foraging niche divergence? *Proceedings of the Royal Society of London, B. Biological Sciences* 271:1283–1291.
- POPA-LISSEANU, A. G., F. BONTADINA, O. MORA, AND C. IBÁÑEZ. 2008. Highly structured fission–fusion societies in an aerial-hawking, carnivorous bat. *Animal Behaviour* 75:471–482.
- RACEY, P. A. 1988. Reproductive assessment in bats. Pp. 31–45 in *Ecological and behavioral methods for the study of bats* (T. H. Kunz, ed.). Smithsonian Institution Press, Washington, D.C.
- RACEY, P. A. 1991. Noctule *Nyctalus noctula*. Pp. 117–121 in *The handbook of British mammals* (G. B. Corbet and S. Harris, eds.). Blackwell Science Publications, Oxford, United Kingdom.
- ROER, H. 1995. 60 years of bat-banding in Europe—results and tasks for future research. *Myotis* 32–33:251–261.
- RUEDI, M., Y. TUPINIER, AND O. DE PAZ. 1998. First breeding record for the noctule bat (*Nyctalus noctula*) in the Iberian Peninsula. *Mammalia* 62:301–304.
- RUSSO, D. 2002. Elevation affects the distribution of the sexes in Daubenton's bats *Myotis daubentonii* (Chiroptera: Vespertilionidae) from Italy. *Mammalia* 66:543–551.
- SENIOR, P., R. K. BUTLIN, AND J. D. ALTRINGHAM. 2005. Sex and segregation in temperate bats. *Proceedings of the Royal Society of London, B. Biological Sciences* 272:2467–2473.
- SHIEL, C. B., R. E. SHIEL, AND J. S. FAIRLEY. 1999. Seasonal changes in the foraging behaviour of Leisler's bats (*Nyctalus leisleri*) in Ireland as revealed by radio-telemetry. *Journal of Zoology* (London) 249:347–358.
- STRELKOV, P. P. 1969. Migratory and stationary bats (Chiroptera) of the European parts of the Soviet Union. *Acta Zoologica Cracoviensia* 14:393–439.
- STRELKOV, P. P. 1997. Breeding area and its position in range of migratory bats species (Chiroptera, Vespertilionidae) in East Europe and adjacent territories. *Zoologicheskoy Zhurnal* 76:1073–1082.

- STRELKOV, P. P. 2000. Seasonal distribution of migratory bat species (Chiroptera, Vespertilionidae) in eastern Europe and adjacent territories: nursing area. *Myotis* 37:7–25.
- STUTZ, H. P., AND M. HAFNER. 1986. The reproductive status of *Nyctalus noctula* (Schreber, 1774) in Switzerland. *Myotis* 23–24:131–136.
- TAYLOR, C. M., AND D. R. NORRIS. 2007. Predicting conditions for migration: effects of density dependence and habitat quality. *Biology Letters* 3:280–283.
- UHRIN, M., ET AL. 2006. On the greater noctule (*Nyctalus lasiopterus*) in central Slovakia. *Vespertilio* 9–10:183–192.
- WILLIS, C. K. R. 2006. Daily heterothermy in temperate bats using natural roosts. Pp. 38–55 in *Functional and evolutionary ecology of bats* (T. H. Kunz, A. Zubaid, and G. F. McCracken, eds.). Oxford University Press, New York.
- WOHLGEMUTH, R., I. DEVRIENT, A. GARCÍA, AND R. HUTTERER. 2004. Long-distance flight of a lesser noctule (*Nyctalus leisleri*) after rehabilitation. *Myotis* 41–42:69–73.
- YEARSLEY, I. M., AND F. J. PÉREZ-BARBERÍA. 2005. Does the activity budget hypothesis explain sexual segregation in ungulates? *Animal Behaviour* 69:257–267.

Submitted 28 January 2008. Accepted 12 May 2008.

Associate Editor was David S. Jacobs.