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Temporal Variations in the Size and Composition of Formosan Leaf-nosed Bat (*Hipposideros terasensis*) Colonies in Central Taiwan

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Hsi-Chi Cheng and Ling-Ling Lee (2004) Temporal variations in the size and composition of Formosan leaf-nosed bat (*Hipposideros terasensis*) colonies in central Taiwan. *Zoological Studies* **43**(4): 787-794. Three colonies of Formosan leaf-nosed bat (*Hipposideros terasensis*), at Shuili, Chungliao I, and Chungliao II in Nantou County, central Taiwan, were monitored by both direct observations and mark-recapture for different periods between 1996 and 2000. The Shuili colony was mostly comprised of adult males and only 2~4 breeding females with pups were observed once during the study period. The size of this bachelor colony peaked in both Mar. and July~Aug., with about 400~700 individuals. The proportion of male bats at the Chungliao I colony was over 50% in most months except in Mar. At Chungliao II, however, the proportion of male bats was less than 30% almost year-round. Other members of the 2 colonies were mostly breeding females and their young. One or 2 peaks in numbers were found in these 2 breeding colonies in different years, with a maximum of 400~500 individuals at Chungliao I between July and Oct., and more than 2300 individuals at Chungliao II in Aug.~Sept. In winter, large numbers of hibernating bats were found only at Chungliao II. Birth and natal dispersal of the young and seasonal migration of adults contributed to temporal changes in size and composition of these colonies. Juvenile female bats showed higher fidelity to their natal roost than did males and bats of other ages. http://www.sinica.edu.tw/zool/zoolstud/43.4/787.pdf

Key words: Bat annual cycle, Fidelity, Hipposideridae, Mark-recapture, Sex ratio.

The size and composition of many vespertilionid bat colonies in the temperate zone exhibit an annual cycle, e.g., those of *Myotis lucifugus* (Humphrey and Cope 1976) and *Pipistrellus pipistrellus* (Speakman et al. 1991). Adult females of these species generally spend the warm months in nursery colonies in order to give birth and rear their young, during which time, adult males and non-pregnant females stay in separate cooler roosts. Such a pattern of sexual segregation in roost selection, particularly in summer, is often explained by constraints of behavioral thermoregulation (Audet 1990, Hamilton and Barclay 1994). Pregnant and lactating females, which need to maintain a higher body temperature in order to facilitate fetal growth or devote extra energy to rearing young, tend to aggregate in roosts with higher ambient temperatures to reduce metabolic energy expenditures (McNab 1982, Racey 1982, Kunz 1987, Zahn 1999, but see Sedgeley 2001). Males and non-breeding females, which are free of the pressure of maintaining a higher body temperature for fetal growth, choose roosts with lower ambient temperatures and use torpor to reduce metabolic energy expenditures (Hamilton and Barclay 1994).

However, a study of *Plecotus auritus* in northeastern Scotland revealed different patterns of colony composition. Male bats were found to be present in all kinds of colonies, including warmer breeding colonies, throughout the period of occupancy (Entwistle et al. 2000). The absence of sex-

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ual segregation was also observed in *Myotis nattereri* (Park et al. 1998) and *Mystacina tuberculata* (Sedgeley 2003). Kurta and Kunz (1988) proposed that higher temperatures in breeding colonies might facilitate spermatogenesis of males during the mating season, and the advantages of associating with females may outweigh the energy costs of thermoregulation in some bat species. Park et al. (1998), on the other hand, suggested that food supply, which determines female dispersion, plays an important role in determining the mating system and group structure of bats.

Fidelity to roosts may also affect the composition of bat colonies. Fidelity of individual bats to a roost may be affected by the relative availability and permanency of roosts, the proximity and stability of food resources, the extent of predator or parasite pressure, and human disturbance (Kunz 1982, Brigham 1991, Lewis 1996). Lewis (1995) reviewed the roosting behavior of 43 species in 12 of 19 chiropteran families and found that roost fidelity is also likely affected by factors such as sex and reproductive condition. However, few data have addressed intraspecific variability in roost fidelity for most species (but see O'Donnell and Sedgeley 1999). In addition, most studies of bat colonies have focused on either the breeding (nursery) or hibernation seasons (Humphrey and Cope 1976, Roer 1986, Ransome 1989, Whitaker and Gummer 1992). Studies on temporal variations in size and composition of bat colonies over an annual cycle are scanty, especially in subtropical regions.

Bats of the family Hipposideridae, the Old World leaf-nosed bats, inhabit tropical and subtropical regions of Africa and southern Asia, east to Taiwan, the Philippine Is., Indonesia, and Australia (Nowak 1999). Some members of the family are among the largest bats in the suborder Microchiroptera. However, studies on the annual cycle of colony sizes and composition of hipposiderid bats are limited. Commerson's leaf-nosed bat, *Hipposideros commersoni*, was reported to exhibit different roosting patterns between sexes of reproducing adults. Reproducing females dispersed twice in an annual cycle, i.e., in mid-pregnancy and after the offspring had weaned, while adult males remained in the same roosting cave (Cotterill and Fergusson 1999). Xiong (1975) found that male and female *H. armiger* roost in separate caves during parturition and the nursing period. However, according to our previous observations, some males of the Formosan leaf-nosed bat (*Hipposideros terasensis*) might stay within maternity colonies in the breeding season, which indicates that potential variations may exist in population structure and life cycles among different colonies.

Hipposideros terasensis is the largest insectivorous bat and one of the common species in Taiwan. The average body weight and body length of an adult *H. terasensis* are about 60~70 g and 9~10 cm, respectively. They generally roost in natural caves, abandoned tunnels, and buildings at an elevation of ≤ 1000 m. The colony size of *H. terasensis* usually ranges from several hundreds to thousands, and bats assemble with individual distances of around 5~10 cm from each other. Pregnant females give birth to a single young each year between May and early June (Chen 1995). *Hipposideros terasensis* was once regarded as a subspecies of *H. armiger* (Kishida 1924). Yoshiyuki (1991) concluded that *H. terasensis* is a distinct species endemic to Taiwan. However, *H. terasensis* was included in *H. armiger* by Corbet and Hill (1991), Koopman (in Wilson and Reeder 1993), and Nowak (1999).

The purpose of this study was to monitor and compare annual patterns in changes of sizes and composition of 3 *H. terasensis* colonies. Roost fidelity of different sex and age groups and interactions of bats among colonies were also examined. The results were compared with smaller microchiropteran bats that exhibit variation in composition of their colonies in temperate zones.

MATERIALS AND METHODS

Study sites

This study was conducted at 3 *H. terasensis* colonies inside abandoned tunnels, one of which is located in Shuili Township (120°52'E, 23°47'N, elevation 320 m), while the other 2 are in Chungliao Township (Chungliao I, 120°44'E, 23°54'N, elevation 150 m and Chungliao II, 120°43'E, 23°54'N, elevation 120 m) of Nantou County, central Taiwan (Fig. 1). The tunnel at Shuili is about 116 m long, 4.2 m wide, and 5.4 m high, has 2 entrances facing northeast and southwest, and is surrounded by broadleaf forest. Bats usually arrive in late Feb. or early Mar. and depart in late Nov. or early Dec. each year. The tunnel of Chungliao I is 300 m long, 3.7 m wide, and 4 m high, and has 2 entrances facing southeast and northwest. Bats usually arrive in late Feb. or early Mar. and depart in late Nov. or early Dec. each year. The tunnel of Chungliao II is 165 m long, 3.7 m wide, and 4 m high, and has only 1 entrance facing east. Despite the floor of this tunnel being constantly covered in water, bats use it year-round. The distance between Chungliao I and II tunnels is 1.5 km, and they are 18~19 km from the Shuili tunnel.

Methods

We studied the Shuili colony from May 1996 to Apr. 1998, Chungliao I from July 1996 to Nov. 2000, and Chungliao II from Aug. 1997 to Nov. 2000. Different methods were used to estimate the sizes of these colonies each month, depending on the accessibility of the roost sites and the sensitivity of bats to researchers. Direct counts inside the tunnel were used to count bats at the Shuili colony (Thomas and LaVal 1988), while emergence counts were used for the Chungliao I and II colonies when bats flew out to forage at dusk. Emergence counts began when the 1st bat flew out of the roost at dusk and ended 10 min after the last bat had emerged. We then checked for individuals remaining inside the tunnel and added this number to the total number of bats roosting in the tunnels. The monthly estimation of colony sizes at Shuili was conducted between May 1996 and Apr. 1998, and those of Chungliao I and II were conducted from May and July 1998 to Nov. 2000, respectively.

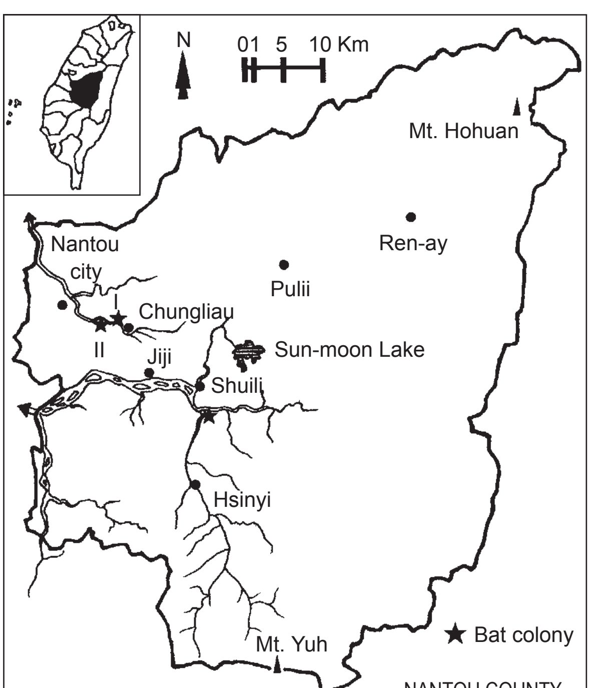

Fig. 1. Map of 3 *Hipposideros terasensis* colonies in Nantou County, central Taiwan.

The composition of the 3 colonies was examined by mark-recapture. Bats were caught when they emerged at dusk in mist nets set at the entrance of the tunnels, and the catching usually lasted 30~60 min until almost no bats were emerging. Mist netting was conducted monthly at each roost except in winter between Dec. and Feb. to avoid disturbing hibernating bats. In those months when both size and composition of colonies were examined, mark-recapture was conducted the day after the bats of the colonies had been counted. Captured individuals were gently removed from the mist net and individually placed in cloth holding bags before being examined for sex, age, and reproductive condition, and their morphological characters measured, after which they were released. Females were considered mature if they were pregnant or showed signs of parturition or nursing, i.e., swollen and elongated nipples and/or pubic nipples. Pubic nipples are a special tissue in *Hipposideros* spp. situated in the pubic region, which can easily be observed on pregnant or nursing females (Racey 1988). Males were considered mature if they had enlarged testes and/or swollen epididymides, indicating active spermatogenesis. During the period of active spermatogenesis, which generally begins in Apr., peaks in June, and ceases in Sept. (Chen 1998), the sizes of the testes may increase from 12.1~24.2 mm^3 in the non-spermatogenesis stage to 38.4~96.1 mm^3, and can easily be diagnosed externally. We weighed individuals to the nearest 0.05 g using a portable electronic balance (PESOLA, Baar, Switzerland) and measured the forearm length to the nearest 0.05 mm using dial calipers (Mitutoyo, Shinazawa, Japan). We marked each bat by fitting a uniquely numbered aluminum band (< 0.05 g, 5.2 x 5.5 mm, Lambournes, Birmingham, UK) to the right arm of females and the left arm of males. Ages of *H. terasensis* were distinguished into 3 classes: juvenile, sub-adult, and adult. Juveniles were those young with an epiphyseal gap, black fur, and very sharp canine cusps. Sub-adults were sexually immature individuals with black fur, sharp canine cusps, and a sealed epiphyseal gap. The forearm lengths of many sub-adult individuals were similar to those of adults, but those bats could easily be distinguished by their fur color, shape of the canines, and sexual characters (Cheng and Lee 2002).

Differences between different sexes in the number of recapture per individual were analyzed by chi-square test at a significance level of 5%.

RESULTS

Colony size

Sizes of bat colonies at Shuili, Chungliao I, and Chungliao II fluctuated throughout the year, and the annual patterns of fluctuation differed among these colonies (Fig. 2). There were 2 peaks in the number of bats using Shuili. Bats left the hibernacula and arrived at Shuili during Mar., and colony size increased to reach the 1st peak in Apr. when about 400 individuals congregated. After that, colony size decreased in May and June, and peaked again in July when about 400 individuals roosted in the tunnel. In Aug. 1996, the colony size at Shuili reached 700 individuals, which was the largest number of bats counted at the Shuili colony during the study period. Then, colony size fell to 0 during the winter.

Colony size at Chungliao I also increased in Mar. By June to July, 400 individuals were congregating in the roost. The maximum colony size of 521 bats was recorded at this colony in Oct. 1999. After that, the colony size decreased and few bats stayed at Chungliao I in winter, except on Dec. 10, 1998, when 14 young *H. terasensis* were found at Chungliao I. However, these bats left the tunnel 1 week later. The colony size at Chungliao II decreased during Mar. to Apr. and peaked during Aug.~Sept. (> 2300 bats). In winter, about 2000 individuals continued to roost at Chungliao II, using it as a hibernaculum.

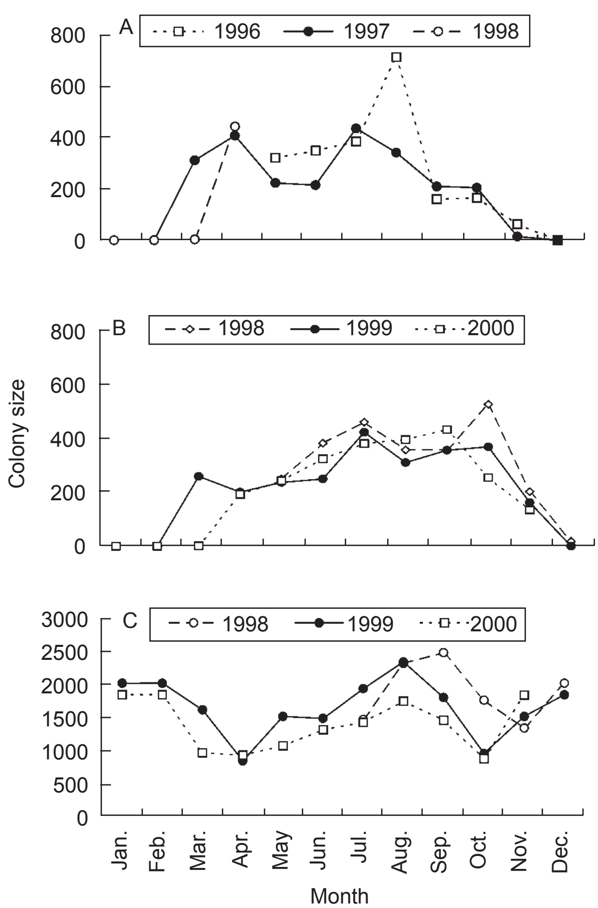

Fig. 2. Seasonal changes in the size of the *Hipposideros terasensis* colony at (A) Shuili, based on monthly direct counts inside the roost between May 1996 and Apr. 1998, and at (B) Chungliao I and (C) Chungliao II, based on monthly emergence counts at dusk between May 1998 and Nov. 2000.

Colony composition

In total, 2606 bats were caught during 90 net-nights from the 3 *H. terasensis* colonies. Among them, 318 individuals (7 adult females, 291 adult males, and 20 juveniles and subadults) were caught at Shuili during 18 net-nights between May 1996 and Apr. 1998; 1604 individuals (336 adult females, 618 adult males, and 650 juveniles and subadults) were caught at Chungliao I during 41 net-nights between July 1996 and Nov. 2000; and 684 individuals (302 adult female, 80 adult male, and 302 juveniles and subadults) were caught at Chungliao II during 31 net-nights between July 1998 and Nov. 2000. We discontinued capturing bats at Shuili after Apr. 1998 because we had observed almost no change in the sex ratio of the bats at this colony. According to marked individuals, some *H. terasensis* were found to use more than one of these roosts over the duration of the study period. In total, 42 bats (22 males and 20 females) banded at Chungliao I were recaptured at Chungliao II, whereas 120 bats (63 males and 57 females) banded at Chungliao II were recaptured at Chungliao I. Only 2 males banded at Shuili were recaptured at Chungliao II, and 2 females banded at Chungliao II were found at Shuili.

The sex ratios, calculated as adult females/all adults captured, differed at the Shuili, Chungliao I, and Chungliao II colonies throughout the year (Fig. 3). The Shuili colony was strongly male biased with a sex ratio always under 0.1, except in Mar. when the colony size was small. The Chungliao I colony was also male biased, and the proportions of adult males was over 50% in most months except in Mar. (38%). However, the proportion of male to female bats was approximately even in the early breeding season (May and June). In contrast, the Chungliao II colony was female biased with a sex ratio > 0.7 almost year-round, except in Sept (32%). The colony maintained about 90% of adult females during the breeding season (May~Aug.).

In addition, breeding females or pups were rarely found at the Shuili colony. Only 2~4 breeding females with pups were observed once in June 1998. Breeding occurred commonly at both the Chungliao I and II colonies, with many adult females giving birth from May to early June.

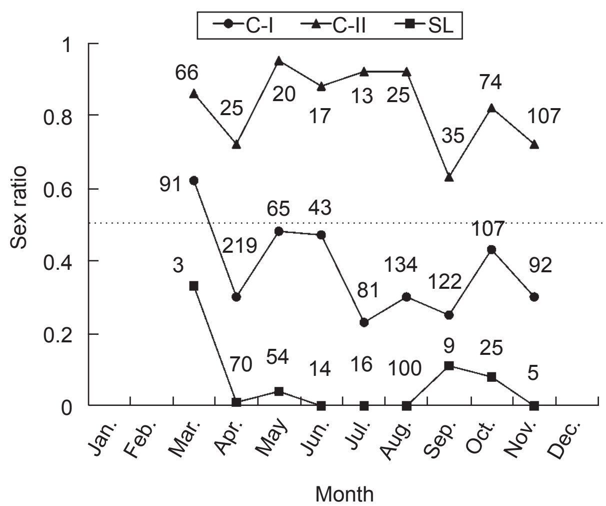

Fig. 3. Seasonal changes in the sex ratio of *Hipposideros terasensis* at the Shuili (SL), Chungliao I (C-I), and Chungliao II (C-II) colonies, based on monthly capture data of adult bats between June 1996 and Oct. 1997, July 1996 and Nov. 2000, and Aug. 1997 and Nov. 2000, respectively. Numbers above the curve indicate the total number of bats caught each month. The sex ratio is the number of adult females/all adults captured. The dotted line indicates a sex ratio of 0.5.

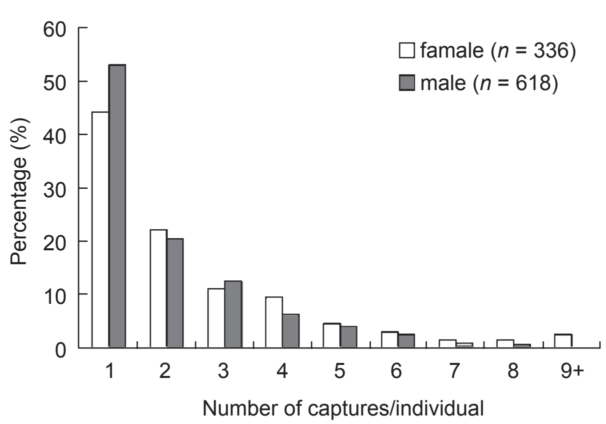

Fig. 4. Frequency distribution of the number of captures of banded *Hipposideros terasensis* at the Chungliao I colony in 1996 through 1998 and those recaptured through Nov. 2000.

Roost fidelity

In total, 717 *H. terasensis* individuals, including 463 males (213 juveniles, 131 sub-adults, and 119 adults) and 254 females (134 juveniles, 60 sub-adults, and 60 adults) were banded at Chungliao I from July 1996 to Nov. 1998, and some were recaptured through Nov. 2000 (Table 1). Among the 717 banded bats, 46% were recaptured at least once, and 32% were recaptured after more than 1 yr throughout the study period.

The rate of recapture of at least 1 time for male and females bats was 45% (208 individuals) and 51% (130 individuals), respectively. The maximum numbers of times bats were recaptured in our study were 8 times (n = 2) for males and 16 times (n = 1) for females, and 9 females were recaptured more than 8 times (Fig. 4). Those 2 males stayed in the colony for 3 and 4 yr, respectively, whereas those 9 females stayed for 3~5 yr. Six of the 9 females (66%) were juveniles when they were first captured. The difference between males and females in the numbers of captures per individual, with the numbers of males and females being recaptured 7 or more times grouped together, was significant (χ^2 = 20.77, p < 0.01, d.f. = 6). The rate of recapture after more than 1 yr was 30% for males and 35% for females (Table 1).

The proportions of recaptures at least once and recaptures after more than 1 yr for female juveniles were 58% and 47%, respectively, which were higher than those of other age-sex groups (Table 1). Adult females showed the lowest rate (33%) of recapture of at least 1 time, while male

Table 1. Recapture rates of different sexes and ages of *Hipposideros terasensis* banded in 1996~1998 at the Chungliao I colony and subsequently recaptured through Nov. 2000

Sex	Age of at first capture	n	Proportion of bats (%) recaptured ≥once	>one year
Male	Juvenile	213	42	23
	Sub-adult	131	49	37
	Adult	119	45	34
	Sum/Average	463	45	30
Female	Juvenile	134	58	47
	Sub-adult	60	55	27
	Adult	60	33	25
	Sum/Average	254	51	35
Total		717	46	32

juveniles showed the lowest rate (23%) of recapture after more than 1 yr.

DISCUSSION

According to monthly changes in the size, composition, and reproduction conditions of bats at the Shuili, and Chungliao I and II colonies, we concluded that *H. terasensis* uses these tunnels for different purposes. The Shuili colony can be regarded as a bachelor colony, as well as a non-breeding colony, whereas Chungliao I and II are breeding colonies. Chungliao II is also used as a hibernaculum. Furthermore, because the peak number of bats generally occurred after the breeding season until autumn (from July to Oct.) at all 3 colonies, and another peak occurred in early spring (from Mar. to Apr.) at non-hibernaculum colonies, such as Shuili and Chungliao I, we interpreted the annual cycle of *H. terasensis* in Nantou as follows. Bats usually begin to arrive at summer roosts, e.g., the Shuili and Chungliao I colonies, in late Feb. and early Mar. from hibernacula. From Mar. to May, pregnant females aggregate to form maternity colonies, e.g., the Chungliao II colony, with some adult males also staying in the same roosts. Some other adult males aggregate to form bachelor colonies at different roosts. Parturition occurs from mid-May to early June (Chen 1998). Young begin to emerge and forage mainly during late June and early July. Starting in late Sept., bats gradually leave their summer roosts for hibernacula.

Colony composition

Unlike the pattern found in *H. armiger* where male and female bats roost in separate caves during the parturition and nursing periods (Xiong 1975), or in several vespertilionid bats of the temperate zone, e.g., *Myotis lucifugus* and *Pipistrellus pipistrellus* (Speakman et al. 1991) where males select cooler roosts to save energy and reproducing females choose warmer roosts to facilitate fetal development or postnatal growth of young, some male *H. terasensis* roosted with females even during the parturition and nursing period, although other male *H. terasensis* may have formed bachelor colonies in separate roosts.

Microclimate, particularly temperature and humidity, inside the roost has been suggested to be important in affecting roost selection by bat species with sexual segregation of roost living (Dwyer and Harris 1972, Hamilton and Barclay 1994). However, a previous study indicated that temperature gradients in breeding versus non-breeding roosts of *H. terasensis* did not differ. Therefore, temperature might not be a decisive factor in roost selection by *H. terasensis*, probably due to (1) the large body size of the species, thus they are more tolerant to changes in ambient temperature, and (2) the warmer subtropical climate in Taiwan (Ho and Lee 2003). Those *H. terasensis* males that roosted with females in breeding colonies might not be at a disadvantage in energy saving. Instead, they may potentially gain some reproductive benefits by staying with reproductive females. *Hipposideros terasensis* females usually give birth between May and early June (Cheng and Lee 2002), and ovulation and fertilization of females occur mainly during July and Aug. after the young wean (Chen 1998); the opportunities for *H. terasensis* males to mate are limited to the 2 to 3 mo between late July and Sept. before bats depart for hibernacula. Therefore, the advantage of rapid spermatogenesis of males in a warm roost in summer and getting ready for mating before hibernation might be greater than the energy savings of a cooler roost. In addition, roosting with females increases the opportunities of finding mates.

Roost fidelity

Several factors may play a role in the evolution of philopatric behavior (Palmeirim and Rodrigues 1995). Some bats exhibit higher fidelity to sites where food sources are stable and nearby (Kunz 1982). Both *Rhinopoma hardwickei* and *Plecotus auritus* demonstrate higher fidelity than other species to their roost sites, probably because these bats seldom make local migrations even during the breeding season (Usman 1984, Entwistle et al. 2000). However, there are different degrees of roost fidelity by sex and age in different bat species. Palmeirim and Rodrigues (1995) found that *Miniopterus schreibersii* females have a strictly philopatric behavior during the nursing season, since they all returned to give birth in the colony where they had been born. Males also showed a high level of attachment to their birth site. Adult females and males of *Plecotus auritus*, however, only showed 39% and 48% return rates to roost sites in the following year at which they had first been captured (Entwistle et al. 2000).

Compared to those of *M. schreibersii* and *P. auritus*, *H. terasensis* adults showed lower across-year recapture rates of 25% for females and 34% for males, although some females and males were recaptured over 4 yr from the time they were first caught. The lower across-year recapture rate might reflect *H. terasensis*' greater foraging distance and range. We found that *H. terasensis* does undergo some local migration to nearby roosts, such as between the Chungliao I and II roosts, which are 1.5 km apart. Another cause of the lower across-year recapture rates might be that because not all bats in the 3 study colonies were marked (mostly only 10%~20% of bats in each colony were captured and marked monthly), the fidelity of these bats might have been underestimated. Meanwhile, females first caught as juveniles showed a higher across-year recapture rate (47%) from their nursery roost than did males first caught as juveniles (23%) and adults of both sexes, although the sex ratio at birth was close to unity (Cheng and Lee 2002). It is unclear whether the lower recapture rate in juvenile male *H. terasensis* was due to a higher mortality rate or a higher dispersal rate, because males of *M. schreibersii* showed a strong attachment to their natal roost (Palmeirim and Rodrigues 1995). However, Greenwood (1980) suggested that male natal dispersal is greater than that of female mammals in order to avoid inbreeding. More-thorough mark-recapture studies are needed to reveal the degree of roost fidelity by sex and age in *Hipposideros terasensis*.

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