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Roost Selection by Formosan Leaf-Nosed Bats (*Hipposideros armiger terasensis*)

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ABSTRACT—Patterns of roost use by Formosan leaf-nosed bats (*Hipposideros armiger terasensis*) were studied from November 1998 to April 2000. Structural characteristics, microclimates, and disturbance levels of 17 roosts used by *H. a. terasensis* and 15 roosts either used by other bat species (2) or not occupied by any bat species were compared. Roosts used by these bats were significantly larger in size and had greater areas covered by water compared to unused roosts. Entrances of active roosts were more likely to be east-west oriented. Hibernacula had lower entrances and ceilings than did roosts used only in summer.

Higher temperatures were recorded in non-breeding roosts than in breeding roosts, but temperature gradients in these two types of roosts did not differ. In winter, hibernacula were warmer, and the temperature fluctuated less than in non-hibernacula. The relative humidities in summer roosts and hibernacula were nearly 100%. Disturbance levels were significantly higher in non-breeding roosts than in breeding roosts, and in non-hibernacula than in hibernacula.

These results suggest that the Formosan leaf-nosed bats are selective of their roosts, but the pattern of their roost selection differs from those reported for bats of temperate regions. The reasons for such differences may be related to differences in body size, behavior, and reproductive strategy of the Formosan leaf-nosed bats living in a subtropical climate in Taiwan.

Key words: roost, temperature, humidity, hibernacula, *Hipposideros armiger terasensis*

INTRODUCTION

Bats spend over half of their lives in roosts, which provide them with protection and sites for resting, mating, hibernation, rearing young, and social interactions (Kunz, 1982). The suitability and availability of roosts may influence the survival, reproduction, and distribution of bats (Humphrey, 1975; Bell *et al*., 1986).

Roosting ecology of bats were well studied in the temperate zone species. Bats may use different roosts according to different requirements for environmental conditions in different seasons. In summer or the breeding season, maternity colonies usually occur in roosts that have higher ambient temperatures (Henshaw, 1960; Betts, 1997; Entwistle *et al*., 1997; Williams and Brittingham, 1997). Reproductive females, which need to maintain a higher body temperature to facilitate fetal growth or who are rearing young, may take advantage of higher ambient temperatures in roosts to reduce metabolic energy expenditure (McNab, 1982). In contrast, males or non-breeding females, which do not have the pressure of maintaining a higher body temperature for fetal growth, choose roosting sites with lower ambient temperatures and frequently use torpor to reduce metabolic energy expenditure (Hamilton and Barclay, 1994). In winter, most temperate zone bats hibernate in cooler roosts so that they can survive through the period of cold and food shortages (Kurta, 1986).

Many factors, such as microclimate, structural characteristics of the roost, surrounding habitat, disturbance by humans, and risk of predation, may influence roost selection by bats (Brigham and Fenton, 1986; Usman, 1988; Churchill, 1991; Vonhof and Barclay, 1996; Entwistle *et al*., 1997; Williams and Brittingham, 1997; Jenkins *et al*., 1998; Sedgeley and O'Donnel, 1999). Microclimates can affect bats' energy budget, development of fetuses or young, and water balance (Humphrey, 1975; Tuttle, 1976; McNab, 1982; Webb *et al*., 1995). Physical characteristics, such as the space, shape, thickness of the wall, and orientation of the roosts alter the microclimates in roosts and in turn affect roost selection by bats (Kurta, 1985; Vonhof and Barclay, 1996; Entwistle *et al*., 1997; Williams and Brittingham, 1997; Sedgeley and O'Donnell, 1999; Sedgeley, 2001). In addition, the shape, size, and coverage of the entrance and the height of the tunnels or entrances can influence the probability of predation (Medway and Marshall, 1970; Vonhof and

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Barclay, 1996; Jenkins *et al*., 1998). Some recent studies also showed that the distance to the nearest water or woods can influence roost selection by affecting food and water supply (Entwistle *et al*., 1997; Williams and Brittingham, 1997).

Formosan leaf-nosed bat (*Hipposideros armiger terasensis*) is the largest microchiropteran bat and a common cave-dwelling insectivorous bat species in Taiwan. Its forearm length ranges about 85 to 100 mm, and it weighs from 50 to 75 g. It maintains an individual space when it roosts, and may enter torpor or hibernate in winter. Ovulation and fertilization occur before September, and embryo development is delayed until March and April (Chen, 1998).

Previous studies of *Hipposideros armiger terasensis* in Taiwan showed that some colonies use the same roosts year round (Chen, 1995), whereas others may use certain roosts only in summer. According to the sex ratio of the colonies, their summer roosts can be categorized into two types: breeding colonies consisting mainly of females and non-breeding colonies consisting mostly of males (Chen, 1995; Chen, 1998; Cheng, 1999a). Similar sexual separation has also been found in *H. armiger* in Kunming, China (Shiung, 1975).

The purposes of this study were to examine differences in environmental conditions of roosts used by *Hipposideros armiger terasensis* in different seasons and by different sexes in various reproductive conditions, and to compare the results with the patterns of roost selection of temperate zone bats. We also discuss the environmental requirements of *H. a. terasensis* in roost selection. Such information is critical for the proper management of this species and its roosts.

MATERIAL AND METHODS

We conducted the study from November 1998 to April 2000. In total, 32 potential roosts in Taipei, Taichung, and Nantou were monitored. Mean monthly temperatures in northern (Taipei) and central (Nantou) Taiwan are similar (15–25°C), however relative humidities and total precipitation are higher in Taipei than in Nantou.

Thirty-two potential roosts were found using previous records and field inquiries. They were either currently being used by certain species of bats, including *Hipposideros armiger terasensis*, or had once been occupied but were no longer used by bats. Roosts with a light intensity of greater than 1.0 lux in the daytime, a length of main tunnels shorter than 5 m, or a ceiling lower than 1 m were excluded from the selection of potential roosts, because these roosts are unlikely to be used by the Formosan leaf-nosed bat. All roosts are located at suburban areas or countryside and are nearby natural forest, secondary forest or agricultural areas. The distance between each roost and the nearest woods was always less than 10 meters.

Thirteen structural variables were recorded for each of the 32 potential roosts. These variables were the elevation of the roost, number of entrances, orientation of entrances, height and width of entrances, total length of all tunnels, average height and width of all tunnels, volume of the roost, composition of the surface rock, distance to the nearest water, the total floor area covered by water inside the roost, and light intensity. For roosts that were occupied by bats, we recorded the species that were present.

The area covered by water was classified into three levels: 1) > 90%, 2) between 10% and 90%, and 3) < 10%. Light intensity was measured with a light meter (TES-1330, TES Electric Electronic Corp., Taipei, Taiwan) at sites where bats were present or at equivalent sites within roosts that were not being used by bats.

Thirteen of the 32 roosts containing large colonies of the Formosan leaf-nosed bat were monitored for colony size using visual emergence counts or direct counts inside roosts. Bats of these roosts were also captured monthly to identify their sex and age composition. Captured bats were weighed, measured, and assessed for their reproductive condition (Chen, 1998; Cheng, 1999b). Roosts used by the Formosan leaf-nosed bat were categorized into two types according to the time when the bats appeared in the roosts, i.e., hibernacula used from December to February and summer roosts used from March to October. Summer roosts were further divided into breeding roosts consisting mainly of reproductive females and non-breeding roosts consisting mainly of males.

We applied Mann-Whitney U-test to compare differences in most of the structural variables between different types of roost, except for the number of entrance and composition of the surface rocks, which were compared by Fisher's exact probability test, and the differences in the orientation of entrances were compared by Watson's test.

We also collected microclimate data, i.e. temperature and humidity, within 14 roosts, including 12 roosts of *H. a. terasensis* and two roosts not used by *H. a. terasensis* but by *Rhinolophus monoceros.* Thermistor probes (TMC6-1T) attached to StowAway XTI data loggers, StowAway RH data loggers, and HOBO Pro RH/Temp data loggers (Onset Computer Corp., Pocasset, MA) were used to gather data of temperature and relative humidity. These data loggers were placed within 0.5 m of where the bats rested, and data were recorded automatically at 60 to 90-min intervals from November 1998 to February 1999 and at 30-min intervals from March 1999 to April 2000. All data loggers were removed at 2-week intervals to download data and be reset in the field or laboratory.

Because of instrument failure from the high relative humidities in the roosts and from earthquakes, some data loggers did not function and record continuously as originally designed. To avoid comparing data collected on different dates or for different lengths of time, only data from roosts where 5 to 7 days of consecutive data were recorded at about the same period in a month were included in the analysis. The SAS GLM procedure and Duncan's new multiple range test were applied to compare microclimate data between roosts.

Finally, we estimated the level of disturbance in roosts in three ways. By putting sand pads at the entrance of 13 potential roosts, we were able to check if there were any human footprints, which reflected the degree of disturbance, monthly from May 1999 to April 2000. We also measured both the distance of each roost to the nearest road and building as an index of disturbance.

RESULTS

Structural variables

Among the 32 potential roosts, 25 were occupied by bats. *Hipposideros armiger terasensis* occupied 17 of them. Nine of the 17 roosts were also occupied by other bat species, including *Myotis taiwanensis, Miniopterus schreibersii, Rhinolophus monoceros, Rhinolophus formosae, Coelops frithi formosanus*, and *Eptesicus serotinus*. Different species of bats generally occupied different portions of the roosting caves. All of the 17 roosts were summer roosts, while six of them were also used by the Formosan leaf-nosed bat in winter.

Table 1. Comparison of the physical structures between 17 summer roosts and 15 roosts not used by *Hipposideros armiger terasensis*, and between six hibernacula and 11 summer roosts not used in winter.

Structural variables	Roost type		Test Statistics	Roost type		Test Statistics
	Summer Roost	Unused Roost		Non-hibernacula	Hibernacula	
Elevation (m)^{a}	428	190	–1.48	340	427.5	–0.41
Number of entrances^{b}	2	1		2	1	
Orientation of entrance (bearings)^{c}	228	180	0.50***	240.00	109.00	0.12
Height of entrance (m)^{a}	2.36	1.48	–3.12**	3.36	1.61	–2.23*
Width of entrance (m)^{a}	2.40	2.02	–1.30	2.40	2.29	–0.55
Total length of tunnels (m)^{a}	113.14	19.00	–1.95	113.14	117.25	0.1
Mean height of tunnels (m)^{a}	3.40	1.93	–3.30***	3.88	2.71	–2.18*
Mean width of tunnels (m)^{a}	3.39	1.55	–2.51*	3.64	3.03	–0.77
Volume of roost (m^{3})^{a}	902	48	–3.40***	1748	764	–0.41
Composition of the surface rock^{b}	1	2		1	2.5	
Distance to the nearest water (m)^{a}	20	165	1.88	80	10	–1.49
Level of floor area covered by water^{a}	2	3	3.21**	3	2	–0.95
Light intensity (lux)^{a}	0.02	0.05	0.88	0.20	0.01	0.09
Sample size	17	15		11	6	

Numbers in the table represent the median, except those in the column of statistics

Different letters indicate different statistics method; a: Mann-Whitney U test, Z value; b: Fisher's exact probability test; c: Watson's test, U^2 value

* $p<0.05$; ** $p<0.01$; *** $p<0.001$.

All of the 32 potential roosts located at an elevation between 30 m to 820 m. Fifteen of them are natural caves (46.9%), seven are abandoned military tunnels or facilities (21.9%), seven are abandoned traffic tunnels (21.9%), one is a railway tunnel (3.1%), one is a water canal (3.1%) and one is in a basement (3.1%). Twenty of the potential roosts had only one entrance, and twelve had two. The composition of rock type in 14 potential roosts was concrete (43.8%), ten sandstone (31.3%) and eight andesite (25.0%). The maximum distance from these roosts to the nearest permanent water was 590 m. The distance from 12 of these potential roosts to the nearest permanent water were within 100 m.

We compared the physical structure between the 17 summer roosts of *H. a. terasensis* and 15 roosts not used by the species, and between the six hibernacula and 11 summer roosts not used in winter. Summer roosts contained higher ceilings both at the entrances and in the tunnels, wider tunnels, larger roost spaces, and more area covered by water than did unused roosts. Entrances of summer roosts were more likely to be oriented east-west (39.1%), whereas those of unused roosts were more likely to be oriented towards the south (54.5%). Hibernacula generally had lower entrances and tunnels than did summer roosts not used in winter (Table 1).

Microclimate

Among the 14 roosts in which microclimates were measured, 12 were occupied by *H. a. terasensis* with or without other species of bats, while the other two were occupied mainly by *Rhinolophus monoceros*. Among the 12 roosts of *H. a. terasensis*, three were non-breeding roosts, four were breeding roosts used only in summer, and five were breeding roosts used both in summer and as hibernacula.

Although average ambient temperatures and temperature gradients recorded in certain months were not significantly different among some types of roosts, overall measurements of these two factors from March to November were significantly different among these four types of roosts (average ambient temperature: F=416.91–3867.35, p<0.001; temperature gradients: F=11.24–95.99, p<0.001). The temperature gradient was defined as the difference between the daily maximum and minimum temperatures in each roost. Non-breeding roosts had significantly higher average ambient temperatures than the two types of breeding roosts and *Rhinolophus monoceros* roosts from May to October in 1999, and lower average ambient temperatures than the two types of breeding roosts in March and November (Fig. 1). Average ambient temperatures did not greatly differ between the two types of breeding roosts (Fig. 1a). Temperature gradients were significantly higher in breeding roosts used only in summer from March to November than in other types of roosts, except in April and May when non-breeding roosts had equally high temperature gradients as breeding roosts used only in summer (Fig. 1b). *Rhinolophus monoceros* roosts and breeding roosts of *H. a. terasensis* used both in summer and as hibernacula had the lowest temperature gradients, which were <0.5°C.

Average relative humidities (RH) in all four types of roost were nearly always >90%. However, monthly average

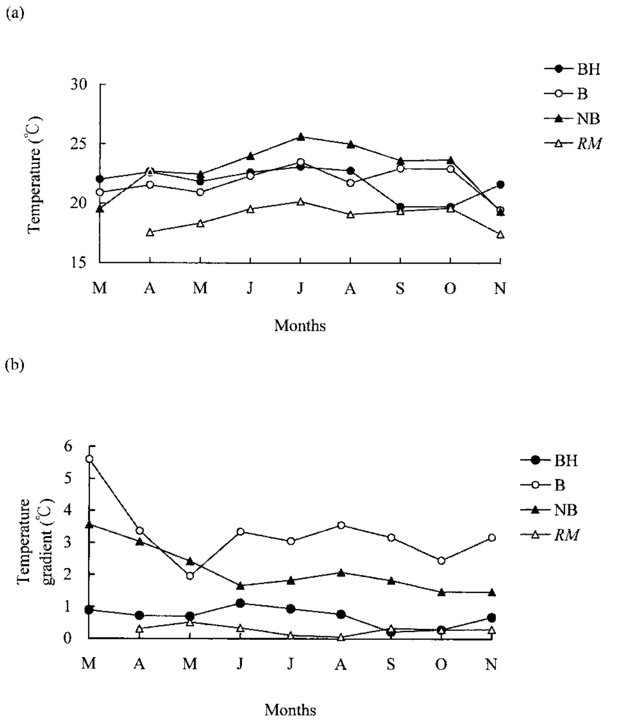

Fig. 1. Average ambient temperatures **(a)** and temperature gradients **(b)** in three types of *Hipposideros armiger terasensis* roosts in active season (BH – breeding roost and hibernacula, B – breeding roost only, NB – non-breeding roost) and roosts of *Rhinolophus monoceros* (*RM*) from March to November 1999.

RH fluctuated differently in different types of roost, and the overall average RH differed significantly between months (F=11.05–599.17, $p<0.001$). From June to October, average RHs in all four types of roost were close to 100% (Fig. 2a). Breeding roosts used only in summer had significantly higher RH gradients (F=7.04–72.64, $p<0.001$) in March, October, and November, as did non-breeding roosts in April, May, and August (F=7.47–16.05, $p<0.001$) (Fig. 2b). However, RHs in these two types of roost did not change much during the months of June, July, and September. RHs in roosts used both in summer and as hibernacula and *Rhinolophus monoceros* roosts were constantly around 100% (Fig. 2a).

Average ambient temperatures and temperature gradients significantly differed among hibernacula of *H. a. terasensis*, non-hibernacula roosts, and one hibernacula of *M. schreibersii*, which was used by *M. schreibersii, H. a. terasensis*, and *R. monoceros* in summer, but not by the latter two species in winter, from November to next February in both 1998 and 1999 (average ambient temperature: F=112.25–4284.78, $p<0.001$; temperature gradients: F= 3.35–255.25, $p<0.05$). Ambient temperatures in the hibernacula of *H. a. terasensis* were higher and more stable than those in other roosts (Fig. 3). Relative humidities in the hibernacula of *H. a. terasensis* and *M. schreibersii* did not significantly differ, but both were higher than those in the non-hibernacula of *H. a. terasensis* (F=67.26–456.10,

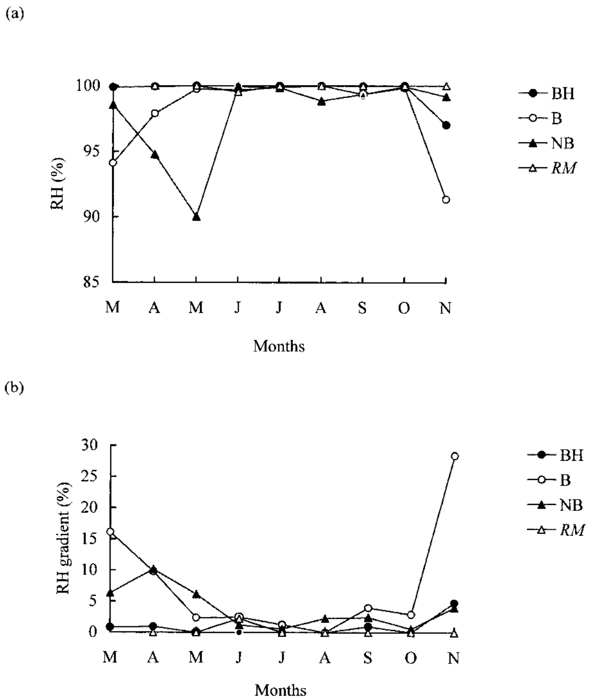

Fig. 2. Average relative humidities **(a)** and gradients of relative humidity **(b)** in three types of *Hipposideros armiger terasensis* roosts in active season (BH – breeding roost and hibernacula, B - breeding roost only, NB – non-breeding roost) and roosts of *Rhinolophus monoceros* (*RM*) from March to November 1999.

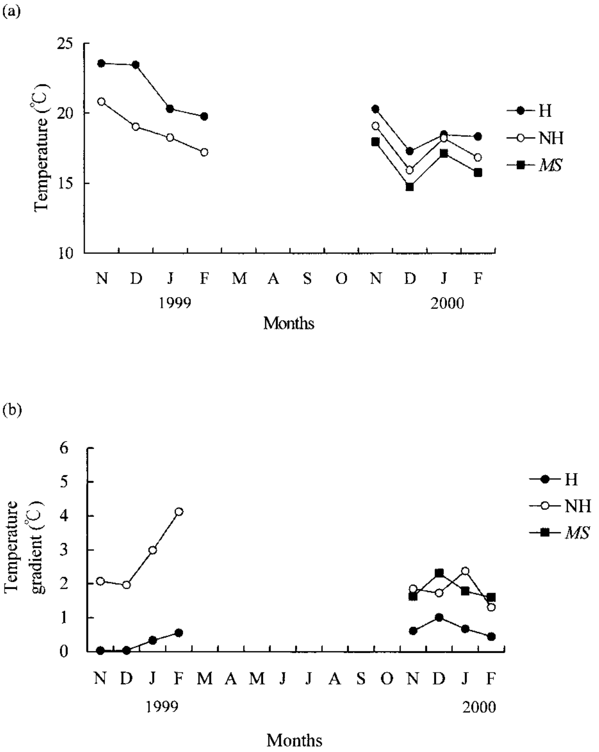

Fig. 3. Average ambient temperatures **(a)** and temperature gradients **(b)** in two types of *Hipposideros armiger terasensis* roosts in inactive season (H - hibernacula and NH - non-hibernacula) and roosts of *Miniopterus schreibersii* (*MS*) from November 1998 to February 1999 and from November 1999 to February 2000.

p<0.001). In addition, RH gradients were significantly higher in non-hibernacula than in six *H. a. terasensis* hibernacula and *M. schreibersii* roost recorded in winter months (*F*= 9.74–21.21, *p*<0.01) (Fig. 4).

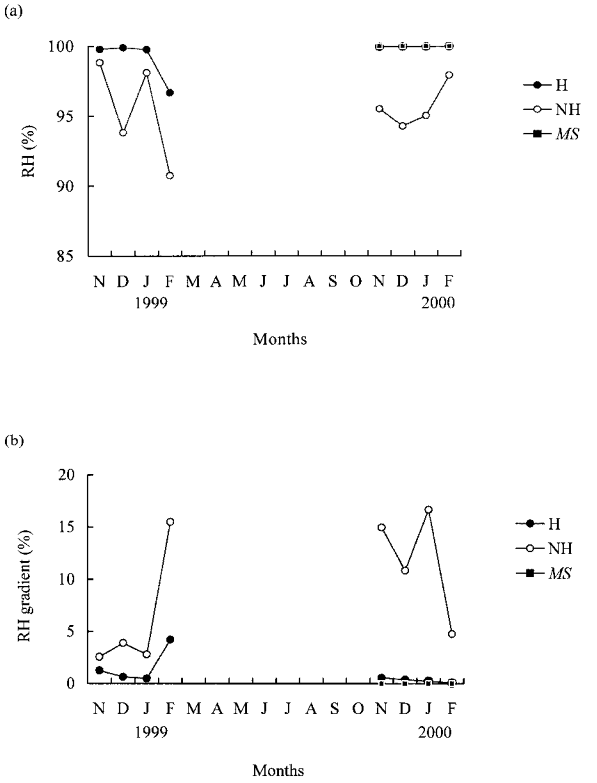

Fig. 4. Average relative humidities **(a)** and gradients of relative humidity **(b)** in two types of *Hipposideros armiger terasensis* roosts in inactive season (H – hibernacula and NH – non-hibernacula) and roosts of *Miniopterus schreibersii* (*MS*) from November 1998 to February 1999 and from November 1999 to February 2000.

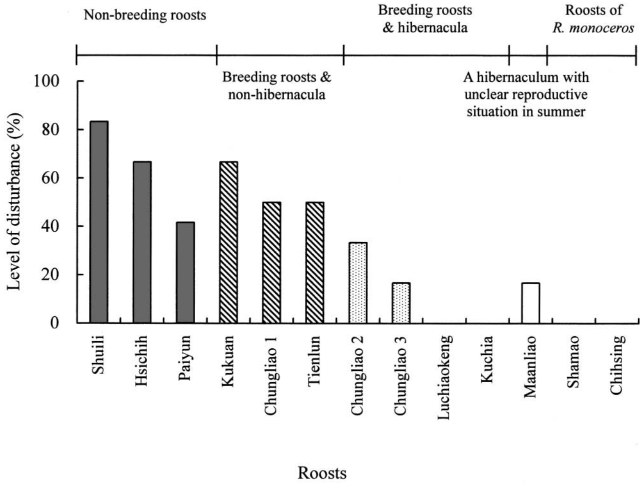

Fig. 5. Frequency of disturbance measured by the percentage of months that footprints appeared on sand pads from May 1999 to April 2000.

Disturbance level

No significant difference was noted in the distance between the roosts to the nearest roads and buildings for any paired comparison between used and unused roosts or between summer roosts (non-hibernacula) and hibernacula (road, Z=–1.69 and –1.95, *p*>0.05; buildings, Z=–1.69 and 0.39, *p*>0.05).

The frequency of disturbance as measured by the percentage of months that footprints appeared on sand pads at the entrances was recorded in two *R. monoceros* roosts, and 11 *H. a. terasensis* roosts, which included five hibernacula, three breeding roosts, and three non-breeding roosts. On average, levels of disturbance were higher in non-breeding roosts than in breeding roosts (χ^2=11.15, *p*<0.001), and higher in non-hibernacula than in hibernacula (χ^2=4.84, *p*< 0.001) (Fig. 5).

DISCUSSION

In this study, we found that summer roosts of *Hipposideros armiger terasensis* had higher ceilings, longer tunnels, larger spaces, and more area covered by water compared to unused roosts. Roosting in a higher place may be beneficial for avoiding terrestrial predators. Vonhof and Barclay (1996) suggested that some forest-dwelling bats prefer to roost on taller trees to avoid potential terrestrial predators, e.g., weasels. In our study, we noticed that *H. a. terasensis* roosting higher responded less to our entry than those that roosted lower (personal observations). Thus, roosting on higher ceiling may also help reduce the energy cost of staying alert or responding to occasional disturbance.

Larger caves may provide more space and various microclimates in which bats can roost, but they may also cause a problem with dissipating heat and providing less total insulation to bats (Kurta, 1985). In the case of *H. a. terasensis*, because of their larger body size, and presumably lower basal metabolic rate, they generally maintain individual distances when roosting, instead of clustering together. The problem of heat loss in large cave may not be so critical for this species. It may benefit more from having various microclimates in large caves.

Bats usually have a higher rate of heat and evaporative water losses due to a relatively higher surface area to volume ratio. *Plecotus auritus* can lose 20% to 30% of its body mass via evaporative water loss (Webb *et al.*, 1995). Replenishing water after daily torpor is thus important for bats. *Eptesicus fuscus* and *P. auritus* select roosts that are closer to water than are unused roosts (Entwistle *et al.*, 1997; Williams and Brittingham, 1997). In our study, however, we found that summer roosts of *H. armiger terasensis* were not significantly closer to water than were unused ones. This is probably due to the fact that all potential roosts in our study were close to water. The maximum distances to water from all potential roosts were less than 600 m. A similar case was also proposed by Jenkins *et al.* (1998) when discussing roost selection by *Pipistrellus pipistrellus*.

Another factor relevant to evaporative water loss is the humidity in roosts. Bats tend to select roosts with high relative humidities (RH) (Twente, 1955; Herreid, 1963; Clawson *et al*., 1980; Van Der Merwe, 1987; Churchill, 1991; Clark *et al*., 1996; Betts, 1997). Webb *et al*. (1995) found that the high ambient temperatures and RHs would tend to slow down the evaporative water loss of active bats. In summer, the RHs in all *H. a. terasensis* roosts were approximately 100%. In winter, the RHs in the hibernacula of *H. a. terasensis* were still approximately 100% in most months, while the RHs often dropped in summer roosts not used in winter (Fig. 2). Furthermore, the area covered by water was significantly larger in roosts used by *H. a. terasensis* than in unused ones. Therefore, *H. a. terasensis* is likely to prefer roosts with high RHs, particularly in winter.

In our study, temperatures in summer roosts of *H. a. terasensis* were stable and seldom exceeded 25°C. Such results are similar to roosting patterns of some bats in tropical or arid areas (Vaugham and O'Shea, 1976; Usman, 1988; Churchill, 1991), but differed from those of temperate zone bats, which usually occupied warmer roosts (Henshaw, 1960; Betts, 1997; Entwistle *et al*., 1997; Williams and Brittingham, 1997). The large body size of *H. a. terasensis* may be a factor contributing to such differences. The average weight of *H. a. terasensis* is about 60 g, which is much larger than most temperate zone bats that seldom exceed 30 g. Therefore, the energy demand for *H. a. terasensis* should be lower than that of temperate zone bats. To select a roost with higher temperatures may thus be less important for *H. a. terasensis*.

The results that daily temperatures did not differ much between breeding and non-breeding roosts of *H. a. terasensis* are in conflict with the prevailing view of temperate zone bats that males and non-reproductive females generally choose cooler roosts while reproductive females choose warmer roosts to enhance the development of fetuses and young (Dwyer and Harris, 1972; Tuttle, 1976; Hamilton and Barclay, 1994). Reasons for such disagreements in the results may be related to the reproductive strategy of *H. a. terasensis*. Delayed ovulation or fertilization is the most common reproductive strategy of bat species in temperate zone, mainly the Vespertilionidae or Rhinolophidae. In this regard, mating usually continue from autumn throughout the winter (Altringham, 1996). In contrast, *H. a. terasensis* has a reproductive pattern of delayed embryonic development. Ovulation and fertilization occur mainly in July and August. Implanted blastula and gastrula were observed in the uterus in September (Chen, 1998). Therefore, the opportunities for male *H. a. terasensis* to mate are limited to 2 or 3 months after females give birth and nurse the young in mid-May to June and before September. Thus the pressure of rapid spermatogenesis in summer for mating might be greater for male *H. a. terasensis* than for male bats in temperate regions. Staying in warmer roosts may help enhance spermatogenesis, and the benefit of reproduction may exceed the energy costs in these roosts. By comparing the reproductive patterns of more than 20 species of bats in Africa, Bernard and Cumming (1997) suggested that spermatogenesis is likely to require more energy than most authors have assumed, and the costs may have played a major role in the evolution of delayed reproduction. Kurta and Kunz (1988) also stated that the use of torpor, which lowers the body temperature and helps save energy, might cost male bats more in terms of delaying spermatogenesis and reproductive success. However, high temperature may affect spermatogenesis in mammals through a "temperature shock". Therefore, further studies are needed to examine the role of temperature and reproduction strategies in roost selection by *H. a. terasensis*.

Most temperate zone bat species lower their body temperature and enter torpor or hibernation to survive frigid winters (Herreid and Schmidt-Nielsen, 1966; McNab, 1974). Therefore, most temperate zone bats select hibernacula with lower ambient temperatures (Clark *et al*., 1996; Webb *et al*., 1996). Contrary to the cases in many temperate zone bats, ambient temperatures of the hibernacula used by *H. a. terasensis* were higher and more stable than those of non-hibernating roosts. Stable microclimates would be helpful for lowering their metabolic rate and energy expenditure (Usman, 1988). The higher ambient temperature in hibernacula might be related to their physical constraints.

Webb *et al*. (1996) compared the ambient temperatures of hibernacula of 34 temperate zone bat species and suggested that higher ambient temperatures of hibernacula may account for the limitation of Rhinolophidae penetrating as far north as members of the Vespertilionidae do. In other words, bats commonly occurring at lower latitudes may not be physically capable of roosting in cooler hibernacula found mostly at higher latitudes. A similar case was found in the distribution of *Tadarida teniotis*. Temperatures in the hibernacula of this species are sometimes 10°C higher than those of other Tadaridae species. Arlettaz *et al*. (2000) suggested that the inability of *T. teniotis* to inhabit higher latitudes might be related to its physical limitations of surviving lower ambient temperatures. Higher temperatures in winter roosts have also been found in *Macrotus californicus*. This species hibernates, and individuals often keep a distance from others when roosting. Temperatures of its winter roosts range from 27 to 30°C. The thermoneutral zone of the species is between 33 and 40°C. Metabolic rates increase dramatically when ambient temperatures drop below the thermoneutral zone. However, evapotranspiration decreases along with a drop in ambient temperatures. Therefore, Bell *et al*. (1986) provided an alternative explanation and suggested that selection of a warm winter roost with a year-round temperature of 29°C may be important in balancing between the costs of energy expenditure and the benefits of saving water for the species.

Human disturbance is a major threat to the survival of many bat species (Speakman *et al*., 1991), and it may influence their roosting behavior and roost site selection. Some hibernating bats may choose a site with lower disturbance rather than those with more-suitable microclimates (Vaugham and O'Shea, 1976; Clawson *et al*., 1980; Clark *et al*., 1996). In our study, little disturbance was noticed in the hibernacula. In fact, the hibernacula of *H. a. terasensis* were usually in protected areas or isolated by water or other types of barriers, and were less accessible to humans. Hibernating *H. a. terasensis* rarely forages in winter, and is supposed to be supported mainly by stored fat. Arousal caused by disturbances would consume extra energy and reduce survival rates in winter (Speakman *et al*., 1991; Thomas, 1995). Selecting roosts with little disturbance may help increase the winter survival rate of bats.

In conclusion, *H. a. terasensis* is selective of its roosts. It prefers roosts with higher ceilings, larger spaces, high relative humidities, and little human disturbance. However, temperatures in breeding roosts and non-breeding roosts of *H. a. terasensis* did not significantly differ, and the hibernacula were not particularly cooler than non-breeding roosts. Such a pattern of roost selection, which differs from patterns reported in temperate regions, may be due to the larger body size and mating strategies of *H. a. terasensis* as well as to the subtropical climate in Taiwan.

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