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Roost-site selection among flat-headed bats (*Tylonycteris* spp.)

LORD MEDWAY

School of Biological Sciences, University of Malaya, Kuala Lumpur, Malaysia

AND

ADRIAN G. MARSHALL

Department of Natural History, Marischal College, University of Aberdeen, Scotland

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(With 2 plates and 1 figure in the text)

During six years, 1962–68, the biology of the bats *Tylonycteris pachypus* and *T. robustula* has been studied at the University of Malaya Field Studies Centre, Ulu Gombak, Selangor, Malaysia. Both species were often found roosting within internodes of the bamboo *Gigantochloa scortechinii*, entering and leaving through narrow vertical slits caused by the beetle *Lasiochila goryi*. In this paper the roost sites are described and evidence is presented that each species of bat actively selected roosts of a different range of dimensions. The ecological implications of the separation of the species by this factor are discussed.

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Introduction

The genus *Tylonycteris* Peters (Chiroptera: Vespertilionidae) comprises two species, *T. pachypus* (Temminck) and *T. robustula* Thomas (Medway, in press) both of which have extensive overlapping ranges in South and South-east Asia (Walker, 1964). In the States of Malaya, Western Malaysia, recent collections have shown that both are sympatric, widespread and locally common in forest at elevations ranging from the lowlands to over 4000 feet (1220 m). Although distinguishable in the hand by a number of characters including texture and colour of the pelage, body measurements and weight, both species are small (Table I) and similar in general appearance. Both exhibit the principal characters of the genus, viz. a dorsoventrally flattened skull (from which the colloquial English name is derived) and expanded fleshy pads at the base of the pollex and covering the sole of the foot. These characters seem to be adaptations to roosting in protected cavities which can

be entered only through narrow, slit-shaped apertures. In Malaya the internodal spaces of bamboo provide just such roost sites when the culm wall has been pierced by an opening of appropriate shape (see also Harrison, 1966; Lim, 1967).

The University of Malaya Field Studies Centre reserve at Ulu Gombak forms a small part of an extensive State Forest Reserve covering the western slopes of the Main Range of Malaya from 600 feet (183 m) elevation upwards, in the headwaters of the river Gombak and its tributaries, at 3° 20′ N, 101° 45′ E. A major sector of the Field Studies Centre reserve was logged commercially in 1956–58, and among the regenerating vegetation the large bamboo *Gigantochloa scortechinii* Gamble is abundant. In some localized areas this bamboo is aggregated to form nearly pure stands; more commonly, isolated clumps are separated by broad-leafed forest. During the course of this investigation, between 1962

TABLE I

Selected measurements and weights of adult ***Tylonycteris pachypus*** *and* ***T. robustula;*** *taken from Medway* (1969)

	T. pachypus	*T. robustula*
Head and body length (mm)	35–40	45–50
Forearm length (mm)	25–28	27–32
Condylocanine length (mm)	10·4–10·6	12·3–12·7
Live weight (g)	3·5–5·0	7·0–10·0

and 1968, a total of 448 roosting parties (i.e. one or more bats at roost on one occasion in a single internode) of both species of *Tylonycteris* were taken from internodes of *G. scortechinii*. In the present paper the roost sites are described and evidence is presented that each species of bat actively selected roosts of a different range of dimensions. The ecological implications of the separation of the species by this factor are discussed.

Methods

Flat-headed bats at roost in bamboo were taken by two methods. Firstly, within a small area of regenerating forest at the Field Studies Centre, 78 active roost sites were individually marked by serial number. At intervals varying irregularly from one day to several months, these roosts (referred to in the text below as "marked roosts") were inspected and any bats present were caught on emerging by means of a simple wire mesh funnel-trap tied over the entrance hole. secondly, an additional 83 roosting groups were collected in 1966–68 by felling the bamboo culm, and cutting out the occupied internode which was then brought back to the Field Studies Centre. These, referred to below as "collected roosts", were taken from different sectors of the Ulu Gombak State Forest Reserve within a radius of 2 miles from the area of marked roosts.

Selected measurements were taken of the bamboo internodes of collected roosts after felling, and of the marked roosts *in situ*. The dimensions of the entrance holes were measured to the nearest 0·1 mm by engineers' sliding calipers with a vernier scale, the length and width recorded being the greatest dimensions measured at any point of the hole. Culm diameter was measured by calipers to the nearest 1 mm, and other dimensions by ruler or flexible tape to the nearest cm.

Results

The stem wall of the standing, unbroken bamboo culm may be pierced by holes of many shapes and sizes at different heights from the ground as a result of the activity of a variety of different agents. Accidental damage to the young shoot in an early stage of growth can produce longitudinal rows of large, more or less coalesced holes in the wall of the mature culm at any height. An undetermined number of boring insect larvae make holes and tunnels of varying diameters characteristic for each species. And finally the activity of vertebrates, including woodpeckers, the Pencil-tailed tree mouse *Chiropodomys gliroides* and man, will produce new openings in the bamboo stem wall or modify existing holes.

Despite the variety of holes available, we found that in the Ulu Gombak reserve both species of flat-headed bat roosted only in internodes entered by holes of a limited and characteristic size range (Fig. 1). These holes in every case were narrow vertical slits in the walls of standing green culms of the one bamboo species, *Gigantochloa scortechinii*. All collected roosts were broken open and examined internally. In most cases only one sizeable

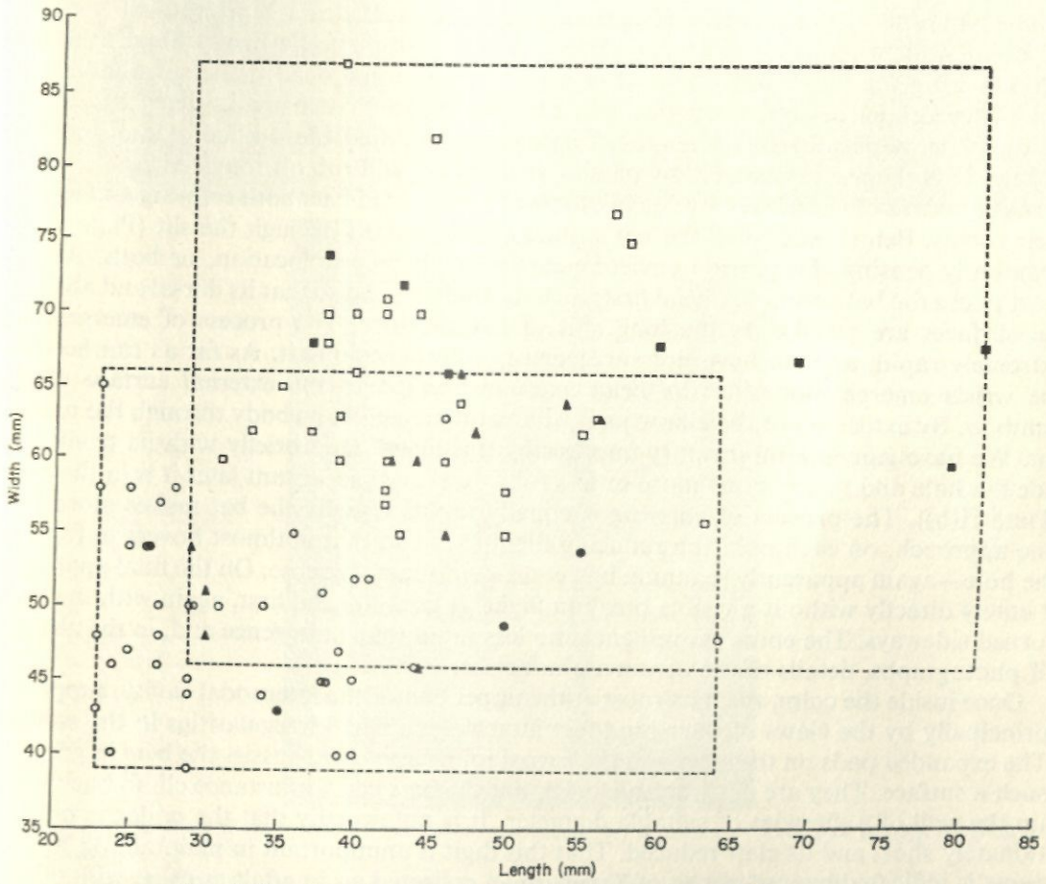


FIG. 1. Size of roost entrance hole in relation to species of *Tylonycteris*.

T. pachypus: ○, single collection; ●, three or more trappings. *T. robustula:* □, single collection; ■, three or more trappings. *T. pachypus* and *T. robustula:* ▲, three or more trappings.

hole gave access to the internodal space in which the bats were found, and the nodal septum at each end was intact. In one instance among collected roosts and in at least three instances among marked roosts there were two or more holes in the culm wall large enough to allow the bats to enter but invariably one could be distinguished as the functional entrance by a definite smoothing of its edges, presumably the result of friction of the bats passing through it.

In all cases it appeared that utilized entrance holes were originally made by the beetle *Lasiochila goryi* (Guérin) (Coleoptera, Chrysomelidae) on emergence from the internode (see Plate I). Salient aspects of the biology of this beetle in the Ulu Gombak Forest Reserve have been discussed by Macdonald (1960) under the name *Anisodera goryi*, and our investigations confirm his observations. At least five other species of bamboo occur in the Ulu Gombak Forest Reserve but no instances of attack by *L. goryi* has been observed among these, and no flat-headed bats have been collected from them. The adult beetle apparently lays on the growing tips of young bamboo shoots. On hatching the larva bores through the culm wall into the internodal space, where it feeds on the internal lining of parenchymatous tissue. When fully grown the larva excavates a short vertical tunnel in the culm wall, where it pupates. On emergence, the adult beetle finally breaks the thin skin covering the pupal chamber. After a time the residual dead tissue surrounding the emergence tunnel decays, becoming soft and friable so that it breaks away easily. The action of woodpeckers in some cases has clearly modified the outline of the aperture, and the bats themselves, merely by passing in and out, will rub off rough edges.

In the course of the survey, we have observed flat-headed bats both entering and leaving their roosts. Before emerging, the bat's muzzle can be seen through the slit (Plate II(a)), apparently sensing the outside environment by smell or echolocation, or both. After a short pause the bat comes out head first, with the body turned so that its dorsal and abdominal surfaces are parallel to the long axis of the aperture. The process of emergence is extremely rapid, and we have not succeeded in photographing it. As far as can be seen, the wrists emerge alongside the head and are applied to the external surface of the bamboo. By extension of the elbow joint, the bat then heaves its body through the narrow slit. We have gained a momentary impression of the bat static briefly with its trunk outside the hole and its forearms more or less fully extended; an instant later it is in the flight (Plate II(b)). The process of entering is equally rapid. Usually the bat makes more than one approach, on each occasion reducing flight speed so that it almost hovers in front of the hole—again apparently scanning by acoustic or olfactory sense. On the final approach, it enters directly without a visible break in flight. It goes in head first, again with the body turned sideways. The entire movement is no less rapid than emergence and, in the absence of photographs, details of the action are not clear.

Once inside the culm, the bats roost at the upper end of the internodal cavity, supported principally by the claws of their hind feet attaching to small irregularities in the surface. The expanded pads on the soles and the carpal joints apparently assist the bats in gripping such a surface. They are not truly suctorial, but the bats can for instance climb backwards up the wall of a glass jar of suitable diameter. It is noteworthy that the pollex is proportionately short and its claw reduced. That this digit is unimportant in maintaining hold at roost is indicated by a specimen of *T. robustula*, collected as an adult at roost with others, which lacked a claw on both pollices by congenital deformity, apparently without suffering ill effect.

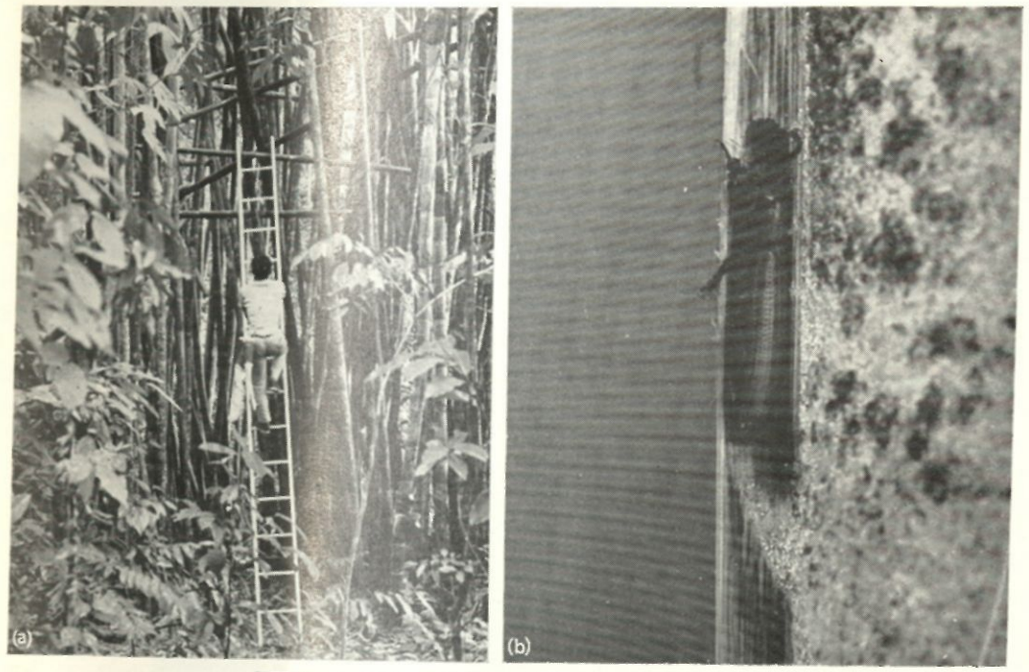
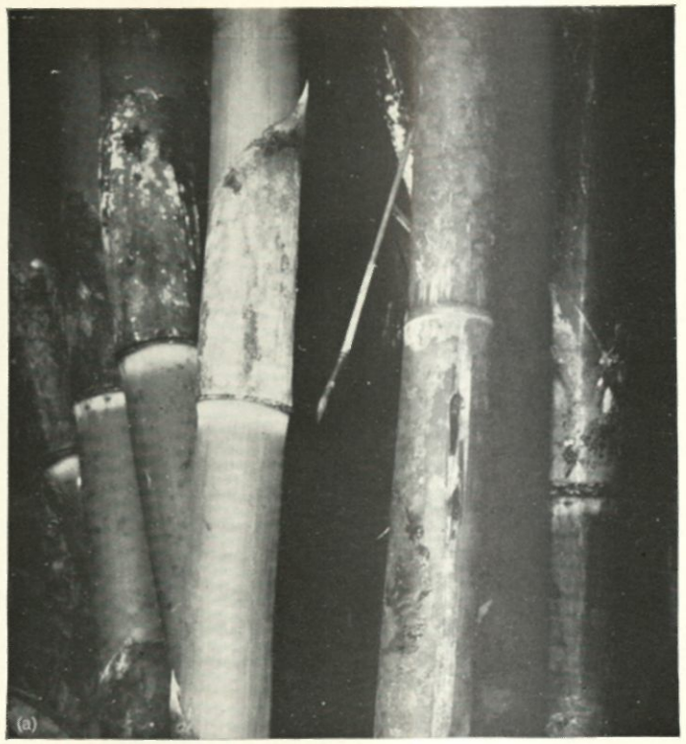


PLATE I. (a) A stand of the bamboo *Gigantochloa scortechinii* (cross poles used to move from one roosting site to another).

(b) Adult *Lasiochila goryi* burrowing in bamboo. It will emerge from the bamboo to the left at the top of the burrow; the walls dorsal and ventral to the beetle will then collapse forming the roost entrance hole.

(c) *Tylonycteris pachypus* by a typical roost entrance hole.

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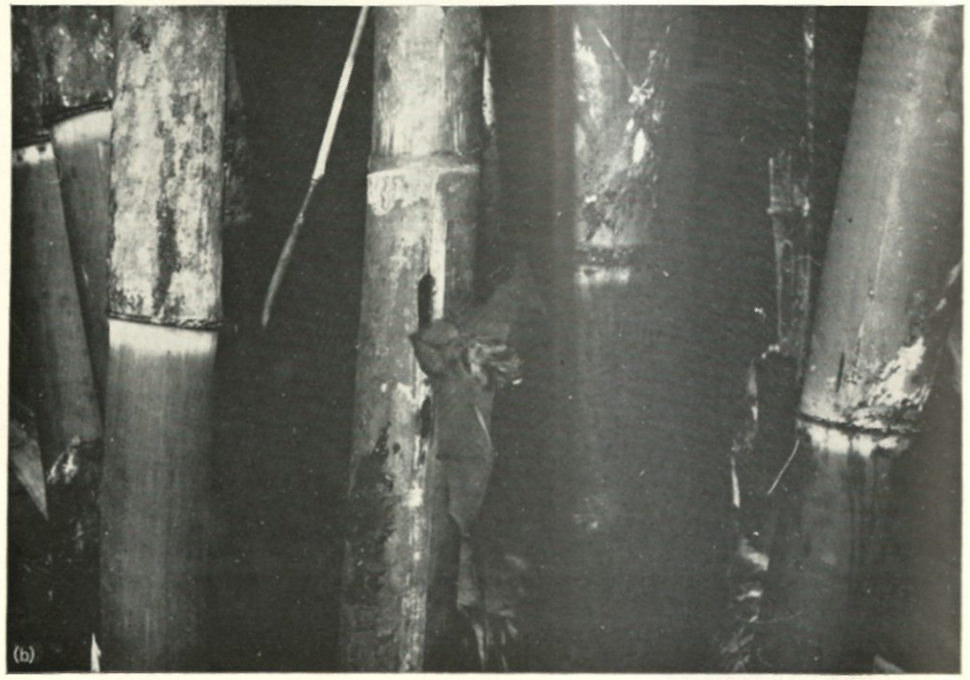


PLATE II. *Tylonycteris robustula* emerging from its roost in the bamboo *Gigantochloa scortechinii*. (a) A moment before emerging, the muzzle of the bat is seen in the upper part of the roost entrance; (b) the bat shortly after emerging. (J. D. Broomhall.)

During the course of this survey, the two species of *Tylonycteris* were only once found at roost together. The composition of 402 roosting parties was accurately determined (Medway & Marshall, in prep.). Of these, 193 comprised only *T. robustula*, 208 only *T. pachypus*, and one both species. Forty-six roosts were classed as incompletely collected, either because one or more bats escaped before being examined, or because one or more failed to emerge and be trapped; mixed species were not found among the remaining bats in these 46 roosting parties. Yet repeated trapping at the marked roosts showed that a proportion were occupied by both species on different occasions. Of the 78 marked roosts, *T. pachypus* only was taken from 34 (44%), *T. robustula* only from 22 (28%) and both species from 22 (28%). In an attempt to determine the factors governing the selection of roost sites by the two species of bat, the following measurements have been analysed: (i) height above ground of roost entrance, (ii) length of occupied internode, (iii) external diameter of culm (iv) the width of the entrance hole, (v) vertical length of the entrance hole, (vi) position of the entrance hole in relation to the nodal septa.

Height above ground of roost entrance

The height above ground of the occupied internodes of collected roosts was not measured exactly but apparently varied from about 1 m to at least 10 m. Among the marked roosts, the height of the base of the entrance hole above ground varied from 250–830 cm. The upper limit in this case was determined by the greatest height to which we or our assistants were able to climb, and is accordingly biased for we saw apparently suitable holes beyond our reach. If there is an upper limit, it is likely to be imposed by the progressive reduction of the diameter of the bamboo culm towards its tip (below). Both the highest and the lowest marked roost yielded only *T. robustula* on trapping, and there is no evidence of different preferences by the two species.

Length of internode

The external internodal length and external diameter of the culm were measured for all collected roosts and many marked roosts. The internodal length of 36 collected roosts occupied by *T. robustula* varied from 32–63 cm, mean 48 cm, and of 45 collected roosts occupied by *T. pachypus* varied from 38–66 cm, mean also 48 cm. In this species of bamboo, the range of natural variation in internodal length probably does not fall far outside the limits of this dimension recorded among occupied roosts. There is therefore no evidence of active selection for this character by the bats.

External diameter of culm

The external diameters of 88 roost sites with a variety of different histories are given in Table II. The difference between the mean culm diameter of (*a*) collected roosts of *T. pachypus* (70 mm) and of (*g*) collected roosts of *T. robustula* (78 mm) is significant ($P<0{\cdot}001$). The mean external diameters of all categories of marked roosts occupied at least once by *T. robustula* are close to the figure for collected roosts of this species, although the samples are too small for the difference between means, e.g. (*b*)/(*f*), or (*a*)/(*f*), to be significant. It is noteworthy that for marked roosts in categories (*c*), (*d*) and (*e*), i.e. those from which both species were trapped, the minimum diameter is within the limits for

roosts from which only *T. robustula* was trapped, and the maximum diameter is within the limits for roosts from which only *T. pachypus* was trapped.

The lower parts of the culm of *Gigantochloa scortechinii* within the range of heights of our marked roosts are more or less parallel-sided, so that there is little variation in diameter between successive internodes. The range of variation between different culms, however, is relatively great corresponding closely to the range of variation of occupied roost sites. At Gombak few culms have been observed thicker than the greatest measured diameter of any occupied roost, i.e. 102 mm for *T. robustula*, although Holttum (1958) recorded 12 cm as the maximum for the species. But in each clump there are usually one or two abnormally slender culms. The least diameter measured at Gombak is 38 mm, well below the lower limits recorded for roosts of *T. pachypus*. The indications are that both bats occupy roost sites above a certain minimum culm diameter which is species specific.

TABLE II

Roost sites of **Tylonycteris** *in Ulu Gombak: external diameter of bamboo culms at roost site, and dimensions of entrance aperture (mm)*

Record type	Frequency of occurrence *pachypus*	*robustula*	No. of roosts measured	External diameter Range	Mean	S.D.	Entrance aperture: Vertical length Range	Mean	S.D.	Horizontal width Range	Mean	S.D.
a Collected	1	0	36	48–90	70	10·8	23–64	33	9	3·9–6·5	4·9	0·6
b Marked	>3	0	5	52–97	68	17·5	26–55	42	13	4·3–5·4	5·0	0·5
c Marked	>1	1	6	68–87	78	7·2	29–46	37	8	4·6–6·0	5·2	0·5
d Marked	>1	>1	4	66–96	81	12·4	44–56	49	5	6·0–6·6	6·3	0·3
e Marked	1	>1	1	94	—	—	54	—	—	6·4	—	—
f Marked	0	>3	8	62–96	79	12·5	37–81	57	18	6·0–7·4	6·8	0·4
g Collected	0	1	28	56–102	78	11·9	31–63	44	8	5·5–8·7	6·5	0·8

This same factor presumably also imposes an upper limit to the height of the roost above ground, even though this was not observed. Although successive internodes vary little in diameter within the height range of our marked roosts there is a distinct taper at the upper end of the bamboo culm, which may attain a length of 20 m (Holttum, 1958). In the terminal region progressive reduction in diameter will presumably exclude first *T. robustula*, then *T. pachypus*, and will finally impose an upper limit to the height above ground of acceptable roost sites for both species.

Horizontal width of entrance hole

Table II also gives the dimensions of the entrance aperture of the 88 roost sites examined, and from Fig. 1 it is clear that both species select holes falling in a limited range of size. The most critical dimension is horizontal width. There is no overlap between the width of entrance holes of marked roosts used three or more times by *T. pachypus* only (category *b*) and those with a similar history of occupation by *T. robustula* (*f*). Among collected roosts, the previous history of occupation of which is unknown, the range of variation is greater

for both species, with an overlap of 1 mm. However, the difference between the mean width of collected roosts occupied at the time of collection by *T. pachypus* (category *a*) and those occupied by *T. robustula* (*g*) is significant ($P = <0{\cdot}001$).

The width of the aperture is presumably determined by the girth of the beetle larva as it bores into the culm wall shortly before pupation. Measurements of the external diameter of the culm and width of the entrance hole show no significant correlation ($P > 0{\cdot}1$), and the two characters are evidently independent.

Vertical length of entrance hole

In the vertical length of the entrance hole a proportionally greater range of variation is observed (Table II), and there is broad overlap among all categories of roost. The difference between the means of collected roosts of *T. pachypus* (*a*) and those of *T. robustula* (*g*) approaches significance ($P = 0{\cdot}1-0{\cdot}05$).

The variation in vertical length of all holes apparently made by the beetle *Lasiochila goryi* is evidently greater than the variation of utilized roost entrances for both species of bats, particularly at the lower limit. The vertical length of the hole in the bamboo culm wall depends on the angle and length of the pupal chamber which the beetle excavates. We have frequently observed holes less than 20 mm long, down to a minimum (14 mm) which is apparently little greater than the length of the pupa itself. It is therefore clear that both species of *Tylonycteris* utilize roost entrances of a limited range of vertical length.

Position of entrance hole in internode

The position of the roost entrance in the internode was assessed by measuring the distance from the base of the hole to the node below. Among all collected roosts of both species, the entrance hole was located in the lower half of the internode, with a single exception (*T. robustula*). In this case, the internodal length was 38·5 cm, the entrance hole 5·0 cm long, and its base 30 cm above the node below. There was also a second small hole lower in the stem, only 5 cm above the node. In three other collected roosts of *T. robustula*, and in one of *T. pachypus*, a subsidiary hole, not used by the bats, was noted lower on the stem than the functional roost entrance. If these five roosts are excluded, the percentage of the length of the internode below the base of the entrance hole varied from 2–39% among *T. robustula*, and 2–44% among *T. pachypus*. Inspection of other bamboos has shown an apparently random distribution of holes of appropriate size throughout the length of the internode. The restriction of utilized holes to the lower half of the internode thus once more indicates active selection by the bats.

As a likely explanation we note that except in periods of prolonged drought, *Tylonycteris* roosts invariably contain a certain amount of liquid. This fluid may originate partly as conducted sap (Macdonald, 1960), and partly from the urine and faeces of the bats. Most of it, however, is probably derived from rain water which trickles down the culm and enters through any aperture, filling the internodal cavity to the level of the bottom of the lowest hole. The available roosting space above water level in an internode is therefore determined by the height of the lowest hole above the nodal septum. This is usually the entrance itself, and unless the entrance is low, the roost space is limited. The instance of a collected roost of *T. robustula* mentioned above demonstrates that an internode with an entrance in the upper half will be selected if drainage is provided by a lower hole.

Discussion

It should be stressed that bamboo culms pierced by the emergence holes of *Lasiochila goryi* do not provide the only acceptable roosting sites of flat-headed bats. Even in the Ulu Gombak forest reserve, a single *T. pachypus* has been found roosting in a narrow cavity between boulders (R. L. Rudd, pers. comm.). Near Kuching, Sarawak, Medway has collected roosting groups of *T. pachypus* in the internodal spaces of unidentified bamboos entered by larger, more irregular holes than those produced by *L. goryi* (Table III). Yet in the Ulu Gombak forest the large number of suitable roost sites resulting from attacks of the beetle on the common bamboo is undoubtedly the major factor contributing to the local abundance of flat-headed bats.

TABLE III

Roost sites of ***Tylonycteris pachypus*** *in bamboo at Kampong Segu, near Kuching* (1963)

No. ♂♂	No. ♀♀	Culm diameter (cm)	Entrance hole dimensions (mm) Vertical length	Horizontal breadth	Nature of entrance
1	1	13·0	90	10	Irregular tear
1	12	15·5	60	13	Irregular gash
1	6	12·5	38	8	Irregular tear

Both species of *Tylonycteris* appear equally able to take advantage of this situation. As shown above, both occupy the same roost site on different occasions. Apart from slight differences in the size and composition of roosting groups, we have been unable to detect any important differences in their ecology (Medway & Marshall, in prep.). Both species have been observed feeding together on termite swarms at dusk, although we have little knowledge of their precise food preferences. The entire populations of both at Gombak apparently give birth during the same restricted period each year (details in preparation). Such extensive overlap of ecological niche among closely related sympatric species is not unique in the tropical environment (cf. Klopfer, 1961, for birds), and it is of interest to examine the isolating mechanisms which restrict interspecific competition and prevent the local extinction of one species ("Gause's hypothesis").

Among the sample of 78 sites represented by the marked roosts, 28% were occupied by both species. Yet of 448 roosting parties only one (0·023%) was definitely known to have included both. This difference indicates that the two species are normally exclusive and do not voluntarily associate at roost. If the supply of mutually acceptable roosts was limited, the two species would be competing for a common resource. At Gombak, however, there is apparently a great excess of suitable roosting sites available; on any one day only a very small percentage or sometimes none of the marked roosting sites examined would be found to contain bats. This may to some extent be an "unnatural" situation (cf. Lack, 1968; 6–7), in which the common resource is not limited and Gause's hypothesis is not applicable. None the less, our results clearly indicate that both flat-headed bats actively select roost sites which differ with respect to certain metrical characters. The

characters for which statistically significant differences in mean dimensions have been demonstrated between roosts of the two species are culm diameter, and the length and the width of the entrance hole. Of these, the last is apparently the most critical, although in all there is a broad zone of overlap recorded.

For both species there is apparently a preferred upper limit to the size of the entrance, which restricts the type of hole chosen to those made by *L. goryi*. The equally critical lower limit is presumably dictated by body size, being effectively the smallest slit through which the skull and trunk of the bat can pass. The smaller species *T. pachypus* thus has available to it a range of roosts with narrower entrances, from which *T. robustula* is excluded by its physical size. Ecological separation of the two species may be based only on this small difference.

Summary

Tylonycteris pachypus and *T. robustula* are locally abundant in Ulu Gombak, Selangor, Malaysia where apparently suitable roosting sites, associated with the bamboo *Gigantochloa scortechinii* and the beetle *Lasiochila goryi*, are available in great excess. Although the two species appear to occupy very similar ecological niches, they do not voluntarily associate at roost; although 28% of marked roosting sites were seen to be occupied by both species on different occasions, only 0·023% of roosting parties examined were known to have included both species of bat together. Measurement of various dimensions of the roosts indicated that statistically significant differences between roosts of the two species existed between the culm diameter, and the length and the width of the entrance hole; the last was apparently the most critical. The lower limit of hole width is dictated by the body size of the bat, and the small *T. pachypus* has available to it a range of roosts with narrower entrances from which the larger *T. robustula* is excluded. Ecological separation of these two sympatric species may be based only on this small difference.

We are both much indebted to all those more agile than ourselves who assisted in the field collection of flat-headed bats, notably Inche Bah Tera and Inche Bah Chong of the University of Malaya Field Studies Centre, Ulu Gombak. Dr J. A. Bullock kindly suggested appropriate statistical tests. Metal bands for use in this project were provided by the Australian bat-banding scheme, C.S.I.R.O., Wildlife Division. Marshall is most grateful to the Carnegie Trust for the Universities of Scotland for a grant which made possible his two year secondment from the University of Aberdeen to the University of Malaya.

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