Perch use by flycatching *Rhinolophus formosae* in relation to vegetation structure

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Flycatching is relatively uncommon in insectivorous bats, yet members of the family Rhinolophidae constitute over one-half of the documented flycatching species. The Formosan woolly horseshoe bat, *Rhinolophus formosae*, is among the largest in size and relies primarily on flycatching for foraging. We assessed perch use of flycatching *R. formosae* in relation to vegetation structure in tropical monsoon forests in southern Taiwan. We located bats using acoustic detectors in forest interior and edge-open forest sites, and measured perch features, dispersion of the nearest trees, and vegetation structure within a 5-m radius of each perch. The same measurements were applied to randomly selected perches in both habitats where bats were not detected. We found no seasonal effects or differences between used and random perches in perch features, dispersion of neighboring trees, or vegetation structure surrounding the perches. Perches used at edge-open forest sites were farther from the perch tree trunk and neighboring trees, and surrounded by larger trees than in forest interiors. In contrast, perches in forest interiors were surrounded by higher shrub and reef layers and greater canopy, shrub, and reef layer cover, than those at edge-open forests. Overall, perches in forest interiors were in more cluttered settings, containing higher vegetation obstacles than edge-open habitats. In both habitats, vegetation obstacles generally increased in a curvilinear manner when moving horizontally and downward from the perch. However, in forest interiors perches used by bats had significantly lower vegetation obstacles horizontally and downwardly and were less cluttered than randomly selected perches. Overall, our results indicate that *R. formosae* in forest interiors selectively used perches associated with more open space that allows for more maneuverable sally flights and a longer detection range suitable for its exceptionally low constant frequency calls to explore less cluttered environments.

Key words: clutter, echolocation, forests, habitats, horseshoe bats, perches, *Rhinolophus formosae*

Flycatching is a form of aerial foraging performed by animal eating bats that involves sallying out from a perch on short flights to intercept and capture prey, often insects, and then returning to the same or a different perch (Schnitzler et al. 1985; Neuweiler et al. 1987). It is also referred to as perch hunting, a sit-and-wait mode (Altringham 2011), or more precisely a hang-and-wait mode (Kalko et al. 1999), although the latter also includes gleaning from the ground or an object (Jones and Rydell 2003). Flycatching is widely reported in some avian groups, notably those sharing the common name of flycatchers, such as Old World flycatchers (muscicapids), monarch flycatchers (monarchids), and tyrant flycatchers (tyrannids), but also some members in non-flycatcher families (e.g., drongos and bee-eaters—del Hoyo et al. 2001–2009). For the predominant

nocturnal aerial predators, bats, flycatching or perch hunting is less common, and its relationship with habitat and vegetation structure is subsequently less known.

Bats that adopt perch hunting are usually medium to large in size (Altringham 2011) and are typified by broad wingtips and low aspect ratios that allow for maneuverable flight in more confined environments with dense vegetation (Norberg and Rayner 1987). While perch hunting has been reported in two dozen or so species of bats from at least five families, some species rely primarily on passive prey detection and gleaning while retaining the flexibility of using echolocation and other foraging modes. These narrow-space gleaning foragers (reviewed in Denzinger and Schnitzler 2013) include members of the families Megadermatidae (e.g., *Cardioderma*

cor—Vaughan 1976; Ryan and Tuttle 1987; *Macroderma gigas*—Kulzer et al. 1984; *Megaderma lyra*—Fiedler 1979; Marimuthu et al. 1995; Schmidt et al. 2011), Nycteridae (e.g., *Nycteris grandis*, *N. thebaica*—Fenton et al. 1983), and Phyllostomidae (e.g., *Trachops cirrhosus*, *Lophostoma silvicolum*—Kalko et al. 1999).

Other perch hunting bats mostly use a true flycatcher style and, apart from African yellow-winged bats (*Lavia frons*—Vaughan and Vaughan 1986) that habitually use vision, constantly emit acoustic signals. These bats comprise some Old World leaf-nosed bats (e.g., *Hipposideros commersoni*, *H. diadema*—Vaughan 1977; Pavey and Burwell 2000) and about a dozen species of horseshoe bats (Rhinolophidae). Hipposiderids and rhinolophids are referred to as narrow-space flutter-detecting bats (Denzinger and Schnitzler 2013). *Rhinolophus*, in particular, are distinguished by their long, high duty cycle constant-frequency (CF) calls (Fenton et al. 2012) accompanied by brief post or initial frequency-modulated (FM) components (specifically defined as FM-CF-FM calls for *Rhinolophus*—Neuweiler et al. 1987). The CF components of these calls are often at higher frequencies and scale negatively more rapidly with body mass than those of bats of other families (Jones 1999). Horseshoe bats are also capable of using acoustic glints from Doppler-shifted frequencies to discriminate fluttering prey from cluttered environments, thereby resolving the problem of masking effects (Neuweiler 1989; Schnitzler and Kalko 1998; Schnitzler and Denzinger 2011; Vanderelst et al. 2013). In comparison, some hipposiderids are capable of less complete Doppler-shifts (Bell and Fenton 1984; Habersetzer et al. 1984).

Nearly all known flycatching horseshoe bats appear to be adapted to cluttered settings but retain the use of continuous aerial hunting in more open settings, and some are capable of gleaning to certain degrees. They differ, however, in size, CF call frequency, and the extent to which they inhabit cluttered habitats (e.g., *R. megaphyllus*—Pavey and Burwell 2004; *R. rouxii*—Schnitzler et al. 1985; *R. hildebrandti*—Fenton and Rautenbach 1986; *R. ferrumenquinum*—Jones and Rayner 1989; *R. blasii*, *R. mehelyi*—Siemers and Ivanova 2004; *R. borneensis, R. clivosus*, *R. fumigatus, R. luctus*, and *R. pearsonii*—Csorba et al. 2003). Among them, *R. formosae* is one of the largest (mean adult body mass ca. 21 g, wingspan ca. 33 cm—Csorba et al. 2003; Lee et al. 2012). Notably, the species prefers edges and open forests to forest interiors, relies almost exclusively on flycatching for foraging, and has a CF-call frequency of 39–42 kHz (Lee et al. 2012; Vanderelst et al. 2013) that is considerably lower than that expected from the frequency-forearm length relationship predicted for rhinolophids (Kingston et al. 2000; Jacobs et al. 2007). In general, larger size hinders a flyer's maneuverability due to increased wing loading (Jones 1999), and, therefore, the space required for efficient sallying flight is greater (Norberg and Rayner 1987). Furthermore, lower frequency calls generally travel farther and thus benefit from signaling in less-cluttered environments for long-range detection (Jakobsen 2013).

We characterized perches used by flycatching *R. formosae* in relation to the surrounding vegetation structure and tested whether they differed between forest settings. We also tested the hypothesis that the perch use of *R. formosae* was affected by clutter condition of the vegetation in that it constrains the maneuverability of the bat in performing sallying flights and limits the detection range of its calls. We predicted that perches used by *R. formosae* in forest interiors and those in edge-open forest sites would be similar in terms of their clutter condition and bats would selectively use perches associated with open space and fewer obstacles in forest interiors.

Materials and Methods

Study area and species.—We conducted field work in the Guijijaou Experimental Forest (GEF) and Hengchun Tropical Botanical Garden (HTBG, 120º48′E, 20º58′N), which are ca. 450 ha in area and 200~300 m in elevation in Kenting, at the southern tip of the Hengchun Peninsula, Taiwan. The area contains the largest and least disturbed tropical lowland monsoon forest on an uplifted coral reef karst terrain of Taiwan, which is among the northernmost of the species-rich Southeast Asian limestone karsts. The area is typified by mean monthly temperatures around 28°C in June–August and generally above 20°C in the coldest months with an annual rainfall of 2,200–2,300 mm occurring from mid-April to October (wet season), particularly during the East Asian plum rain and typhoon seasons (Guijijaou Weather Station data, TFRI). The dominant woody plants in the study area were autumn maple tree (*Bischofia javanica*), bark fig (*Ficus benjamina*), Formosan nato tree (*Palaquium formosanum*), Philippine drypetes (*Drypetes littoralis*), Taiwan aglaia (*Aglaia formosana*), and various species of ebony (*Diospyros* spp.). Vegetation in the forest edge comprised patches of plantations of various types of native or introduced plants, such as Cycadaceae, Lauraceae, Mimosaceae, Moraceae, Palmae, together with various ferns, lianas, and vines (see Lee et al. 2007 for details).

The Formosan woolly horseshoe bat, *R. formosae,* is endemic to Taiwan and generally considered rare, and has one of the most restricted distributions among rhinolophids (Csorba et al. 2003). Even though it is relatively common in the reef-karst areas of Kenting, it is low in abundance and largely solitary (Lee et al. 2007). It resembles *R. beddomei* of South Asia in external morphology but is larger in size (Csorba et al. 2003); both are phylogenetically related and once were classified as subspecies of *R. luctus* (Simmons 2005).

Perching sites and random sites.—We established and mapped numbered grids (200 m × 200 m) that covered a total area of ca. 120 ha and incorporated three types of habitats: forest interiors (13 grids), forest edges (6 grids), and open forests (12 grids). Using the grid, we set up seven transect lines (length: 1,145.7 ± 93.8 m each; 8.02 km in total) based on terrain and accessibility (Lee et al. 2012). We conducted monthly acoustic surveys during 4–6 nights each month over 24 months to search for *R. formosae* along three transect lines in forest interiors and two transects each in forest edges and open forests, respectively. Forest edges and open forests represent background cluttered spaces, whereas forest interiors correspond to highly cluttered spaces (Schnitzler et al. 2003).

We used Pettersson D230 bat detectors (Pettersson Elektronik AB, Uppsala, Sweden) set to the heterodyne mode to search for bats due to its long detecting range. We tuned detectors to the CF frequencies of *R. formosae*'s calls, which can be easily distinguished from those of other bats present in the study sites (Lee et al. 2007, 2012). Upon detecting *R. formosae*'s signals, we slowly and quietly approached the call source while switching down the volume to determine the direction of the calls, and searched for the perching bat aided by available natural light or night vision instruments as necessary. Once we located a bat on a perch, we carried out further acoustical monitoring and visual observations of the bat's behavior. Monitoring and observations lasted until flycatching foraging was confirmed or the bat left the perch, and searching resumed.

As terrain permitted, we measured perch characteristics and surrounding vegetation structure during daytime hours for the bat perches confirmed as foraging perches. *Rhinolophus formosae* may use multiple perches in a foraging bout where adjacent perches are mostly ≤ 30 m apart (Y. F. Lee, pers. obs.). Consequently, for each located perch, we picked an additional perch site of generally similar characteristics (e.g., height and distance from the tree trunk) along a randomly selected aspect at a distance of approximately 25–30 m from the observed perch. If no suitable perching sites were available along the selected aspect, another aspect was chosen at random. In total, we measured 64 perches located at edge-open forest and forest interior sites (32 in each type of habitat) and corresponding randomly chosen perches. Throughout the study these random sites were never observed being used by bats for foraging or perching.

Perches and surrounding vegetation structure.—For each located bat perch and corresponding random perch, we counted the branch order and measured perch diameter (mm), perch height, distance of the perch from the trunk (DFTT), and distance of the perch from the nearest path (DFP) using a measuring tape or a laser distance meter (Leica Disto A5; Geosystems, Tucson, Arizona) as necessary. We also estimated the percent canopy cover above the branch (Jennings et al. 1999); this was done by the same team member throughout the study for consistency. For both the actual perches and the randomly selected perches, we recorded the species and measured diameter at breast height (DBH) of the perch tree, and aspect, distance from the perch tree, canopy height (upper and lower), canopy thickness (the difference between the upper and lower heights), and canopy cover of the four nearest trees. We used the aspects of the four nearest neighboring trees over a two dimensional Cartesian coordinate system centered at the perch to obtain the quadrant occurrence defined as the proportion of quadrants with a nearest tree present. Finally, for each perch, we measured height (m) and cover (%) of the surrounding vegetation over a 5-m radius. The height variables comprised the height of the shrub, herb, reef-rock, or man-made structure layers, while the cover variables included estimated cover of the tree canopy, and the shrub, herb, bare soil, reef-rock, or man-made structure, where the latter five summed to 100% at the ground level.

We also established survey lines along eight aspects oriented at 45°, 90°, 135°, 180°, 225°, 270°, 315°, and 360° to estimate vegetative obstacle cover surrounding each used and random perch. Measurements were taken every 50 cm along each line, giving a total of 81 sampling points for each perch, including 10 points along each of the eight sampling lines and the perch point. At each sampling point, we adopted the point intercept method (Krebs 1999) and used an extensible pole 10 m high to measure the foliage profiles and evaluate the available open space both horizontally and vertically. We counted an obstacle whenever a length of 10 cm on the pole was intercepted by foliage or vegetation.

Data analysis.—Unless otherwise noted, all data reported in this study are presented as the mean ± standard error (*SE*) or relative proportion (%). All of the statistical tests were conducted with an alpha value of 0.05 using Statistica 10 (StatSoft, Tulsa, Oklahoma) for Windows. We used multivariate analysis of variance (MANOVA) tests with Pillai-Bartlett's *trace* values (*V*) to examine whether forest setting, perch type (used or random), and season affected tree dispersion surrounding the perch tree, overall vegetation structure, and characteristics of the perches used by bats. When significant variations were detected, we used Tukey's honest significant difference test (HSD) for unequal sample sizes to determine which means were significantly different (Zar 2010). In addition, we constructed a graphic analysis of the obstacle measurements to compare the extent of the obstacles actually (or potentially) faced by bats perching in different forest settings. In particular, obstacles were summed for each 50 cm from the height of the perch down to the ground. The obstacle measurements taken at the same distance interval of 50 cm from each perch along all eight aspects were then averaged to obtain an estimated overall obstacle index at the corresponding height. Finally, the relationships between the obstacle index, the horizontal distance, and vertical distance in the downward direction were compared by polynomial regression analyses.

RESULTS

Perch features.—Overall, bat perches occurred in edge-open forests more frequently (71.3%) and with a higher density (4.5 ± 0.19 per km transect) than in forest interiors (28.8%, 1.5 ± 0.15 per km transect). Perches in forest interiors did not differ from those in the edges in any of the perch features measured (diameter, branch order, height, and distance from the nearest path; Fig. 1). Moreover, forest setting (edge-open or interior; Pillai-Bartlett trace value $V = 0.064$, $F_{3, 74} = 1.693$, $P > 0.1$), perch type (used or random; $V = 0.062$, $F_{3, 74} = 1.615$, $P > 0.1$), and season (dry or wet; $V = 0.044$, $F_{3, 74} = 1.125$, $P > 0.3$) had no effect on the perch features (all factor × factor interactions, *P*-values > 0.5). The position of the perches in the trees, however, was affected by forest setting ($V = 0.098$, $F_{3, 90} = 3.244$, $P < 0.05$). Perches located in edge-open sites were farther from the trunks of the perch trees (2.75 ± 0.31 m) than those in the forest interiors (1.98 ± 0.29 m, HSD test, $P < 0.05$; Fig. 1). Perch type ($V = 0.076$, $F_{3, 90} = 2.316$, $P > 0.05$) and season ($V = 0.018$, $F_{3, 90} = 0.559$, $P > 0.6$) had no effect on the perch positions.
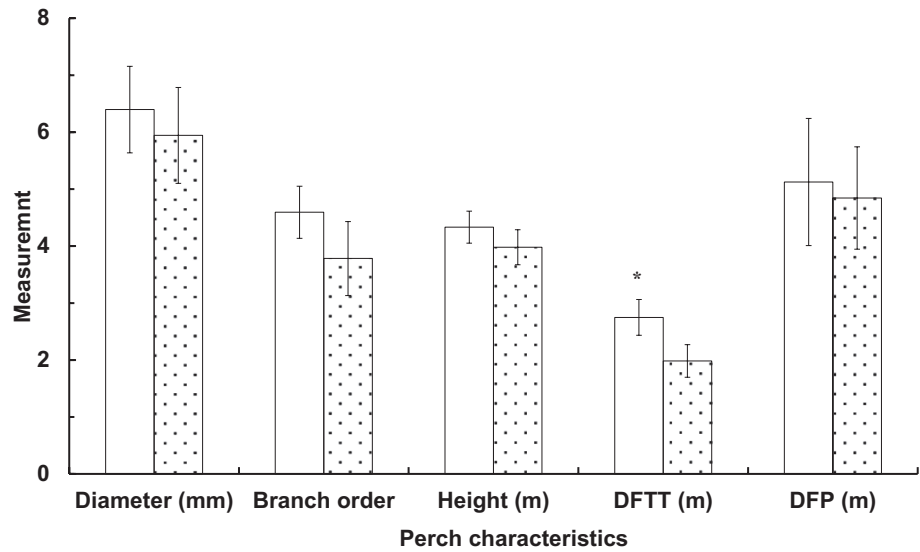
Fig. 1.—Characteristics (mean ± *SE*) of perches used by *Rhinolophus formosae* in edge-open forests (open boxes) and forest interiors (filled boxes) in the Guijijaou Experimental Forest and Hengchun Tropical Botanical Garden (hereafter as the GEF-HTBG forest), Kenting, Taiwan. An asterisk indicates a significant difference between the two habitats on a specific perch characteristic. DFTT, distance of the perch from the trunk; DFP—distance of the perch from the nearest path.

Dispersion and characteristics of nearest trees around perches.—Perch trees and the nearest trees surrounding perches (four for each) comprised 49 different species from 25 families. The most dominant trees were coast persimmon (*D. maritime*), Taiwan ebony (*D. discolor*), autumn maple tree, Japanese mallotus (*Mallotus japonicus*), camphor laurel (*Cinnamomum camphora*), and *Machilus japonica*. The forest setting (edge-open or interior) affected the dispersion patterns of the nearest trees (Pillai-Bartlett trace $V = 0.289$, $F_{6, 91} = 6.155$, $P < 0.001$; all factor × factor interactions, P-values > 0.3). However, perch type (used or random; $V = 0.086$, $F_{6, 91} = 1.434$, $P > 0.2$) and season (dry or wet; $V = 0.063$, $F_{6, 91} = 1.016$, $P > 0.4$) had no effects. For the edge sites, the nearest trees were at a greater distance from the perch, had a greater mean DBH, and contained a slightly thicker canopy than those in the forest interiors (Table 1). The quadrant occurrence proportions of the nearest trees were not significantly different between the forest interior and edge sites ($G = 4.47$, *d.f.* = 2, $P < 0.25$); yet, 84.4% of perches in forest interiors were surrounded by trees that occurred in ≥ 3 quadrants or more, compared to only 62.5% in forest edges. The variability of the aspect angles of the nearest trees relative to the bat perches, expressed by coefficient of variation (%), was also higher in the forest interiors than in the edges (Fig. 2).

Vegetation structure and clutter measurement.—Tree density in forest interiors (0.2 ± 0.01 per m²) was roughly twice that at the edges (0.1 ± 0.01 per m²). The height (Pillai-Bartlett trace $V = 0.193$, $F_{4, 91} = 5.444$, $P < 0.001$; all factor × factor interactions, P-values > 0.2) and cover variables ($V = 0.43$, $F_{6, 91} = 11.429$, $P < 0.001$; all factor × factor interactions, P-values > 0.05) were both affected by forest setting (Table 2). However, they were unaffected by the perch type (used or random; height: $V = 0.018$, $F_{4, 91} = 0.408$, $P > 0.8$; cover: $V = 0.077$, $F_{6, 91} = 1.26$, $P > 0.2$) or season (height: $V = 0.06$,

Table 1.—Mean (± *SE*) characteristics and dispersion pattern of the perch tree and the four nearest trees surrounding each perch used by *R. formosae* in edge-open forest and forest interiors, respectively, in the GEF-HTBG forest, Kenting, Taiwan. *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$; ns = non-significant.

	Edge-open forest ($n = 32$)	Interior ($n = 32$)	P
Distance to perch (cm)	399.73 ± 22.48	313.07 ± 17.23	***
DBH (cm)	24.94 ± 2.0	17.99 ± 1.29	**
Canopy upper height (m)	12.31 ± 0.60	12.88 ± 0.44	ns
Canopy lower height (m)	2.28 ± 0.15	2.67 ± 0.15	ns
Canopy thickness (m)	4.71 ± 0.47	3.74 ± 0.27	*

$F_{4, 91} = 1.453$, $P > 0.2$; cover: $V = 0.041$, $F_{6, 91} = 0.653$, $P > 0.6$). Within the considered 5-m radius, perches used by the bats in the forest interiors were surrounded by a higher shrub layer (HSD test, $P < 0.001$) and reef layer (HSD test, $P < 0.005$) than those in the edge-open sites, and had greater tree cover (HSD test, $P < 0.001$), shrub layer (HSD test, $P < 0.005$), and reef layer (HSD test, $P < 0.001$) cover. However, they had less paved structure (HSD test, $P < 0.001$; Table 2).

For both the observed perches and the random perches, the obstacle index increased with increasing downward distance from the perch, irrespective of the forest setting (edge-open forest or interior; Fig. 3). A similar tendency was noted with increasing horizontal distance from the observed perches (Figs. 3a and 3b). The effect, however, was less evident for the randomly selected sites; particularly those in the forest interior (Fig. 3d). For both the observed perches and the random perches, the obstacle index (OI) was curvilinearly correlated with the horizontal distances from the perch in both the forest interiors (random sites: $R^2 = 0.82$, $F_{2, 8} = 23.46$, $P < 0.001$; used sites: $R^2 = 0.97$, $F_{2, 8} = 163.96$, $P < 0.001$) and the edge-open forests (random sites: $R^2 = 0.84$, $F_{2, 8} = 28.12$, $P < 0.001$; used sites: $R^2 = 0.93$,
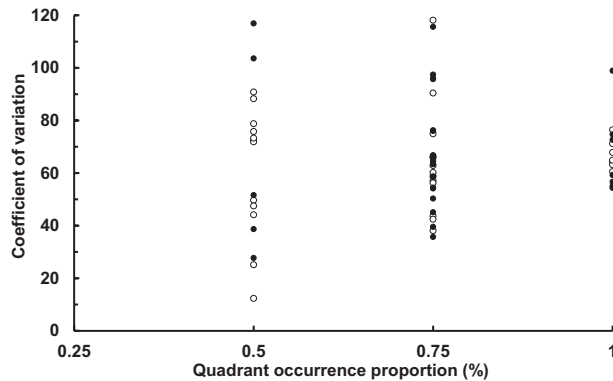
Fig. 2.—Coefficient of variation in the aspect angles of the four closest trees to the perch used by *R. formosae* occurring over four quadrants in edge-open forests (open circles) and forest interiors (filled circles) in the GEF-HTBG forest, Kenting, Taiwan.

Table 2.—Mean values (± *SE*) of four height (m) variables and six cover (%) variables measured for edge-open forest and forest interior habitats (*n* = sample size) in the GEF-HTBG forest, Kenting, Taiwan. *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$; ns = non-significant.

	Edge-open forest (*n* = 32)	Interior (*n* = 32)	*P*
Height			
Shrub	1.02 ± 0.15	1.57 ± 0.37	**
Herb	0.17 ± 0.03	0.86 ± 0.62	ns
Reef	0.01 ± 0.01	0.67 ± 0.29	***
Paved structure	0.01 ± 0.01	0.05 ± 0.05	ns
Cover			
Tree canopy	59.22 ± 3.99	79.06 ± 2.91	***
Shrub	18.28 ± 4.00	20.31 ± 3.32	**
Grass	39.94 ± 4.74	28.75 ± 4.16	ns
Bare soil	37.47 ± 4.21	40.63 ± 4.10	ns
Reef	0.25 ± 0.17	20.47 ± 4.11	***
Paved structure	22.34 ± 4.99	10.16 ± 1.96	***

$F_{2, 8} = 66.83$, $P < 0.001$; Fig. 4a). The OI values in the vertical direction were also curvilinearly correlated to downward distances from the perch in the forest interiors (random sites: $R^2 = 0.96$, $F_{2, 8} = 129.03$, $P < 0.001$; used sites: $R^2 = 0.93$, $F_{2, 8} = 66.48$, $P < 0.001$) and edge-open forests (random sites: $R^2 = 0.98$, $F_{2, 8} = 316.61$, $p < 0.001$; used sites: $R^2 = 0.95$, $F_{2, 8} = 93.01$, $P < 0.001$; Fig. 4b). Horizontally, the obstacles in the vicinity of the randomly chosen interior perches were significantly higher than those in the other three groups ($F_{3, 36} = 4.36$, $P < 0.05$). The differences between the interior random perches and the rest of the groups remained with an increasing distance (Fig. 4a). Vertically, however, the obstacles near the random perches in forest interiors were higher than those near the observed perches, which in turn were higher than those near the two edge-open forest groups (Fig. 4b). The greatest difference in the obstacle heights of the four groups occurred at a distance of around 2 m beneath the perch ($F_{3, 36} = 0.21$, $P > 0.1$; Fig. 4b).

DISCUSSION

This study focused on perch use of flycatching horseshoe bats while foraging and its relationship with the surrounding vegetation structure. Perches used by *R. formosae* in the edge-open forest sites were farther from the perch tree trunk and neighboring trees than perches in forest interiors. In contrast, perches used in forest interiors were surrounded by higher understory shrub and reef terrain, greater canopy, shrub, and reef-rock layer cover, and were surrounded by trees in broader quadrant aspects. These differences largely reflected differences in the two forest settings. That is, forest interiors are more cluttered than edge sites, and contain greater densities of vegetation obstacles. In both habitats, obstacles increased with an increasing downward and horizontal distance from the perch. The perches used in forest interiors, however, were surrounded by fewer obstacles both horizontally and downwardly than random perches. This suggests that bats selectively used perches associated with more open space while perching in forest interiors.

Rhinolophus formosae used forest interior perches that resembled edge-open forest perches in surrounding vegetation. In particular, our results indicate flexible habitat use by *R. formosae*, which deviates from the general conclusion that perch-hunting bats are adapted to more confined environments with dense vegetation (Norberg and Rayner 1987). Flexibility in foraging habitat use has been found in *Hipposideros* (e.g., *H. ruber*—Bell and Fenton 1984; *H. diadema*—Pavey and Burwell 2000; *H. speoris*—Pavey et al. 2001) and was attributed to CF-calls of shorter duration, higher pulse repetition rates, overall lower duty cycle, and less fine-tuned auditory fovea resulting in a less complete Doppler-shift compensation compared to horseshoe bats (Habersetzer et al. 1984; Neuweiler et al. 1987). Flexibility in habitat use, however, also has been observed in horseshoe bats that adopt flycatchting (e.g., *R. megaphyllus*—Pavey 1998; *R. ferrumequinum*—Jones et al. 1995; *R. blasii*—Siemers and Ivanova 2004) as well as species that are typical aerial hunters (e.g., *R. hipposideros*—Bontadina et al. 2002; *R. euryale*—Goiti et al. 2006). In other words, habitat flexibility is more common than previously perceived in these so-called narrow-space flutter-detecting bats, and suggests adaptability associated with wing morphology and call structure while coping with their ecological needs.

Perches in edge habitats or those surrounded by some open space allow for more maneuverable sallies by larger-sized bats, which have higher wing loadings (Norberg and Rayner 1987; Jones 1999), or flycatching birds with elongated wings (Fitzpatrick 1980; 1985). In tyrant flycatchers, for instance, species that adopt this foraging mode generally tend to perch in more open or edge habitats (Fitzpatrick 1980; Robinson and Holmes 1982). Enhanced maneuverability also has been observed in some perch-hunting horseshoe bats (e.g., *R. ferrumequinum*—Jones and Rayner 1989; Funakoshi and Maeda 2003), *L. frons* (Vaughan and Vaughan 1986), and perch-gleaning *T. cirrhosus* (Kalko et al. 1999). This suggests a direct benefit associated with perch selection in addition to other recognized benefits from perch hunting, including more economic energy use compared to continuous flight (Voigt et al. 2010), improved signal-to-noise ratio due to less wind noise, and the possibility of a broadened searching angle (Neuweiler et al. 1987; Surlykke et al. 2013).
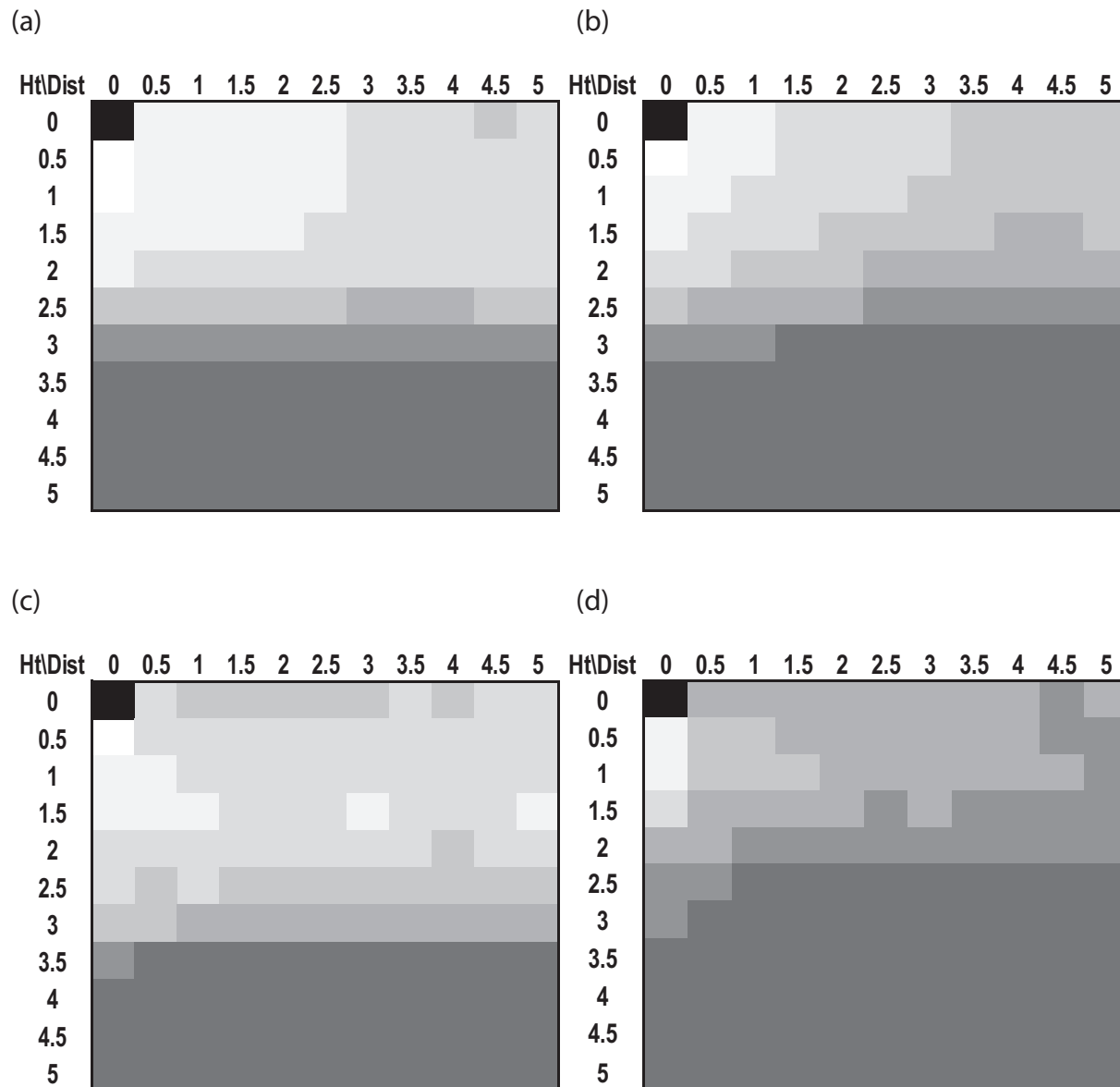
Fig. 3.—Two dimensional depictions of vegetation structure surrounding perches in downward and horizontal directions over a 5-m radius at (a) edge-open forest, (b) forest interior, (c) random edge-open forest, and (d) random forest interior sites in the GEF-HTBG forest, Kenting, Taiwan. Structure was measured by the obstacle index, OI (%; ■: perch location, □: OI = 0, : 0 < OI ≤ 10, : 10 < OI ≤ 20, : 20 < OI ≤ 30, : 30 < OI ≤ 40, : 40 < OI ≤ 50, ■: OI > 50).

More open space surrounding perches offers advantages for perching birds to gain a better field of view for the purpose of vigilance or prey detection (Sonerud 1992; Krams 2001; Leyhe and Ritchison 2004). Bats certainly are not birds and rely mostly on different primary sensory modes than birds (Neuweiler 2000). Nocturnal perching may release bats from most, if not all, aerial predators (e.g., Lee and Kuo 2001; Lima and O'keefe 2013). Perching within open space, particularly away from the tree trunk, main branches, and dense bush may further reduce the risk posed by potential nocturnal predators such as arboreal snakes (e.g., brown tree snakes, *Boiga irregularis*—Mickleburgh et al. 1992), which are common in the tropics (Harrington et al. 2018). The predation risk to *R. formosae* or indeed any flycatching bats has not yet been

fully assessed (Lima and O'keefe 2013). Yet, nocturnal snakes, including at least square-headed cat snakes (*B. kraepelini*), pointed-scaled pit vipers (*Protobothrops mucrosquamatus*), and green bamboo tree vipers (*Trimeresurus stejnegeri*), occur in the area studied in the present work and all are capable of climbing and taking vertebrate prey (Y. F. Lee, pers. obs.).

In general, *R. formosae* showed specific requirements for perch use. Perches used by *R. formosae* in the present study were largely similar to those described previously for *R. rouxi* of Sri Lanka (Neuweiler et al. 1987), which were mostly dry twigs or leafless terminal branches, around 5–7 mm in diameter, protruding below or from the canopy and overhanging forest trails and clearings. The bats also tended to use the same perches repeatedly (Y. F. Lee, pers. obs.), even when similar
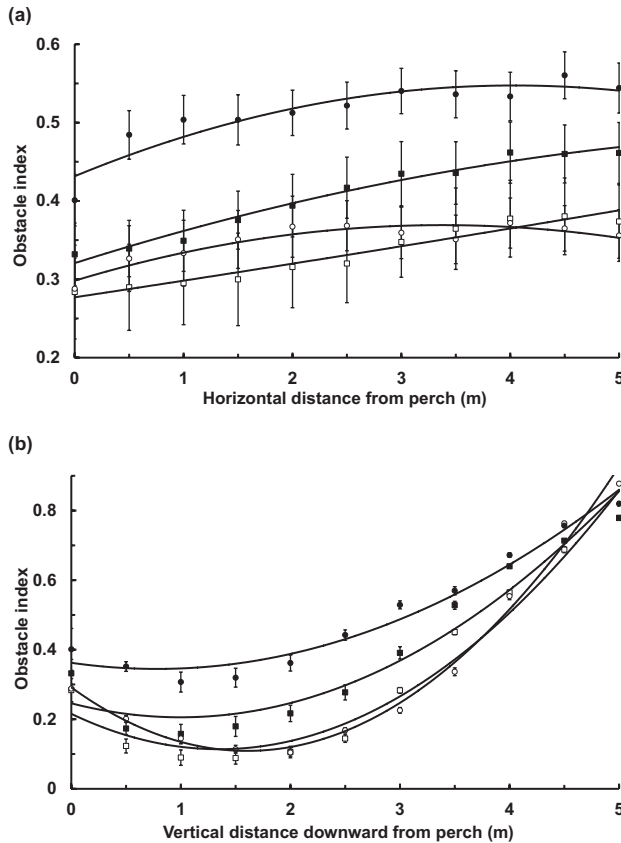
Fig. 4.—Mean (± *SE*) obstacle index (OI, *%*) along (a) horizontal distance within a 5-m radius and (b) vertical downward distance from perches at random sites in edge-open forests (open circles) and forest interiors (filled circles), and observed perches in edge-open forest (open squares) and forest interior sites (filled squares) in the GEF-HTBG forest, Kenting, Taiwan.

twigs or branches were abundant. This seemingly loyal behavior to certain perches is also observed in *R. rouxi* (Neuweiler et al. 1987). Multiple reasons may account for this behavior pattern, including successful feeding experiences over time, territoriality, or both. Both factors may be associated with the quality of the habitats in terms of prey availability. The present findings, however, suggest that the vegetation structure may also play an important role in perch selection. Larger-sized bats may achieve more economic energetic returns by feeding on larger prey and this may be one of the reasons perch-hunting bats are larger in size (Voigt et al. 2010). However, the proportion of large-sized insects tends to decline as moisture level increases in forests (Janzen and Schoener 1968), which suggests that perch-hunting bats should favor forest gaps and forest edges over interiors. The fact that *R. formosae* used edges more frequently than forest interiors supports this inference. Further, their diets consisted mainly of beetles, followed by moths (Lu 2013), which are common edge and open forest insects with more direct flights (Pavey and Burwell 2000).

Rhinolophus formosae used edges and open forests more often than forest interiors (Lee et al. 2012). The two largest horseshoe bats in Europe, *R. ferrumequinum* and *R. mehelyi*, also are capable of flycatching and exploit various habitats (Dietz et al. 2006). Moreover, both bats have higher wing loadings than *R. formosae*, but spend substantial proportions of time in continuous flight (Jones and Rayner 1989; Siemers and Ivanonva 2004). Their long wings, resulting from a longer 3rd finger in relation to the 5th finger, generate a higher aspect ratio, thereby allowing for more economic and faster commuting flights over longer distances (Dietz et al. 2006). In contrast, the aspect ratio of *R. formosae* is smaller (4.46—Lee et al. 2012) than the similar-sized *R. ferrumequinum* (5.8~6.1—Norberg and Rayner 1987; Aldridge 1991) and is further smaller than the smaller-sized *R. mehelyi* (7.75—Voigt et al. 2010). This illustrates the complicated interactions of wing morphological parameters in affecting flight mode and performance (Norberg and Rayner 1987). The smaller aspect ratio at least partially explains why the nocturnal activity of *R. formosae* appears more evenly distributed in time, more restricted in space, and relies almost exclusively on flycatching (Lee et al. 2012).

Perch hunting may be central in the development of high duty-cycle echolocation calls (Fenton et al. 2012), particularly for horseshoe bats with specialized Doppler shifts. In high duty-cycle bats, large-sized species generally emit calls dominated by a lower frequency than smaller species (Bogdanowicz et al. 1999). The call frequency of the CF components of *R. formosae* is lower than that inferred from the CF frequency-forearm length relationship for Malaysian rhinolophids (ca. 55~56 kHz—Kingston et al. 2000) or for 35 *Rhinolophus* species around the world (ca. 63 kHz—Jacobs et al. 2007). In fact, *R. formosae* emits calls at the lowest frequencies of all flycatching rhinolophids, except the larger-sized *R. hildebrandti* and *R. luctus* (Csorba et al. 2003). Larger-sized bats emitting lower-frequency calls tend to have long pulse durations that are adapted for longer detection range in edges and open habitats. This has been reported in some edge space aerial foraging emballonurids, molossids, and vespertilionids, and some high duty-cycle hipposiderids (Jones 1999). The typical pulse duration of *R. formosae* is ca. 50 ms or longer (Vanderelst et al. 2013) and together with their exceptionally low frequency of CF calls, suggests a function for long-range detection. Further studies on *R. formosae* call structure (e.g., the searching volume and directionality—Jakobsen et al. 2013; Surlykke et al. 2013) and foraging behavior (e.g., the foraging success in different forest settings) may better illustrate the adaptability of their low frequency CF-calls in coping with foraging needs in different habitats.

Overall, our findings revealed that flycatching *R. formosae* in forest interiors selectively use perches associated with a certain degree of open space, and suggest a functional integration of the wing morphology of this bat with their exceptionally low CF call frequencies, which collectively allow a more adaptive exploration of less-cluttered environments. This explains *R. formosae*'s predominant use of edge-open habitats over forest interiors and loyalty to particular perches. Their tendency to exploit edges and open forests, however, may expose the bats to higher uncertainty, since forest edges face greater disturbance than forest interiors and potentially high risk of further habitat alteration, particularly fragmentation

(e.g., *R. rouxi*—Pavey et al. 2001). This in turn may negatively impact their populations, suggesting that there may be implications for their conservation.

Acknowledgments

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