



## Resource distribution and social structure in harem-forming Old World fruit bats: variations on a polygynous theme

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The prediction that the spatial dispersion of resources that are important to females should dictate female dispersion and male mating tactics has not been previously tested in harem-forming bats. We investigated the relation between the estimated spatial distribution of available roosts, female group size, male roost fidelity and the strength of social associations in two species of harem-forming fruit bats in the genus *Cynopterus*. We evaluated the daily movements of individuals and groups among roosts using radiotelemetry and roost censuses at two sites in northern peninsular Malaysia. We found a high correspondence between the distribution of roost sites, female group size and male behaviour, supporting the prediction that clumped resources would promote female aggregation and high roost fidelity in males. However, there were significant interspecific differences in the strength of male–female associations, which suggested that, where roosts are abundant and similar in quality, regardless of their spatial distribution, the potential for males to monopolize mates depends on whether females move among roosts with, or independently of, males. We propose that interspecific differences in female behaviour may be related to the costs of moving between clumped versus randomly dispersed males.

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In the classic theory of mating systems, the spatial and temporal clustering of receptive females around resources mediates the potential for sexual selection, measured as the variance in male reproductive success (Orrians 1969; Emlen & Oring 1977; Borgia 1979; Clutton-Brock 1989). In this paradigm, the potential for individual males to monopolize multiple females depends primarily on the spatial distribution of resources necessary to females and the degree of synchrony in female receptivity. However, paternity data from a wide range of vertebrate taxa indicate that previous assumptions of a static distribution of females among males frequently underestimates the environmental potential for extrapair or extraharem copulations (Pemberton et al. 1992; Heckel et al. 1999; Griffith et al. 2002). Thus, even where females are spatially clumped and reproductively asynchronous, generating a high environmental potential for polygyny, the degree of variance in male reproductive success depends on the

ability of males to restrict the reproductive access of other males and/or to restrict female movements between males (Bradbury & Vehrencamp 1977; McCracken & Wilkinson 2000). Assuming that females benefit from active mate choice (Drickamer et al. 2000) and, in some cases, from mating with multiple males (Jennions & Petrie 2000; Zeh & Zeh 2001; Foerster et al. 2003), the costs associated with female movements among males may provide a reasonable measure of the environmental potential for female promiscuity.

The mating systems of bats follow the general mammalian pattern: the majority of species whose social structure has been studied are polygynous (Bradbury 1977; McCracken & Wilkinson 2000). A harem-based social structure, in which males defend female groups and/or resources important to females, is particularly common in tropical species, whose breeding seasons are not constrained by the climatic extremes experienced by temperate bats. Paternity data for a number of harem-forming species in both the Old and New World tropics support the prediction that, when males defend roost sites, harem males will have higher within-breeding season reproductive output than will solitary or satellite males (McCracken & Bradbury 1977; Storz et al. 2001; Ortega et al. 2003; but see Heckel et al. 1999).

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Long-term data sets for tropical harem-forming species suggest a general pattern of high roost fidelity in harem males within and, in some cases, across breeding seasons (Williams 1986; Fleming 1988; McWilliam 1988; Ortega & Arita 1999; Storz et al. 2000a, b). However, considerable variation exists in the stability of female groups, ranging from female–female associations that persist across multiple breeding seasons (e.g. *Pyllostomus hastatus*: McCracken & Bradbury 1981; *Saccopteryx bilineata*: Bradbury & Emmons 1974) to highly labile female groups (e.g. *Pipistrellus nanus*: O’Shea 1980; Happold & Happold 1996).

The ecological and social correlates of roost fidelity, group size and social cohesion in female bats have been studied primarily in the context of maternity colonies in temperate species, in which female movements and social associations are not directly related to female mating tactics (Lewis 1996; Kerth & König 1999; Rossiter et al. 2002; Willis & Brigham 2004). Neither the relative strength of female–female versus male–female associations, nor the relative daily rates of movements by males and females, have been quantified in any harem-forming species. Likewise, to our knowledge, the relationship between the spatial distribution of roost resources and social mating system has not been formally tested in any species of bat.

Here, we investigate the relationship between the spatial distribution of available roosts, female group size, and male and female associations in two nominal species of Old World fruit bats in the genus *Cynopterus*. Recent phylogenetic analysis indicates that there are two divergent mitochondrial lineages within *C. brachyotis* in peninsular Malaysia (Campbell et al. 2004). The two lineages are almost completely allopatric and strongly associated with distinct habitat types: *C. brachyotis* Sunda (32–42 g) is abundant in highly disturbed habitats and *C. brachyotis* Forest (24–37 g) is mainly restricted to forest habitats (Campbell 2006). Ecological separation and concordance between morphological differentiation and nuclear and mitochondrial markers support our treatment of *C. brachyotis* Sunda and *C. brachyotis* Forest as ecologically and evolutionarily distinct species (Campbell et al. 2006, in press).

All *Cynopterus* species studied to date have a polygynous, harem-based mating system in which varying numbers of females roost with single males, a social structure that is maintained year-round (Bhat & Kunz 1995; Tan et al. 1997; Storz et al. 2000a; Campbell et al., in press). *Cynopterus* roosts are mainly found beneath large leaves, or in other semienclosed plant structures such as creepers and fruit clusters, which the bats may modify by chewing or severing plant material, increasing protection from the elements and potential predators (Boon & Corlett 1989; Balasingh et al. 1995; Tan et al. 1997; Storz & Kunz 1999). Roost modification in bats is presumed to be a male activity, which may influence female mate choice (Balasingh et al. 1995; Kunz & McCracken 1996).

Unlike larger Old World fruit bats such as members of the genus *Pteropus*, which typically forage in flocks and have been observed defending portions of fruiting or flowering trees while feeding (Gould 1977; Elmquist et al. 1992), *Cynopterus* fruit bats forage singly and remove fruit

to nearby night roosts (Boon & Corlett 1989; Tan et al. 2000; Fletcher 2001). Direct observations of the solitary foraging and night-roosting behaviour of *C. brachyotis* in both forest (Funakoshi & Zubaid 1997) and disturbed habitats (Bumrungsri 2002) strongly suggest that the day roost is the main venue for social interactions, including mating.

At our study sites, pregnant and lactating *C. brachyotis* Forest and *C. brachyotis* Sunda females were captured throughout the year. While births were not highly synchronized, peak numbers of lactating females were captured in April–June and December–January (P. Campbell, unpublished data; C. Wong, personal communication), suggesting a pattern of weakly seasonal bimodal polyoestry, with postpartum oestrus and delayed embryonic development following the first parturition period (Kofron 1997; Racey & Entwistle 2000).

We estimated the spatial distribution of available roosts at two sites in northern peninsular Malaysia for *C. brachyotis* Forest and *C. brachyotis* Sunda. We used radiotelemetry and daily roost censuses to assess the movements of individuals and groups, and to estimate the strength of associations between and within genders. These data were used to describe the social mating system of each species from both male and female perspectives, and to test two predictions. (1) Based on the expectation that females form larger, more defensible, aggregations when resources are clustered and that female defensibility dictates male mating tactics (Emlen & Oring 1977), we expected to observe larger harem sizes and stronger male roost fidelity in habitats where potential roost sites were spatially clumped. (2) Female reproductive asynchrony should favour a sedentary, mate-guarding strategy in males that are successful in attracting or locating groups of females (Shuster & Wade 2003). Thus, we predicted that harem males of both species would show higher roost fidelity than solitary males.

## METHODS

### Study Sites

Field work was conducted at two sites in northern peninsular Malaysia: Perlis State Park (Perlis State, 06°42′–39′N, 100°11′E) and Taiping (Perak State, 04°50′–51′N, 100°45′–46′E). Both sites feature tracts of selectively logged primary forest, bordered by secondary growth, small fruit orchards and human settlements.

Perlis State Park (50 km<sup>2</sup>) features steep limestone hills; the vegetation is characterized as semideciduous limestone hill forest (Latiff et al. 2001; Wong 2002). At this site, *C. brachyotis* Forest used a variety of plant species as roosts, but favoured pinnate-leaved palms and large-leaved *Macaranga* species. The only modified roosts were found in an understory fan palm that was uncommon within the study area (Campbell et al., in press). *Cynopterus brachyotis* Sunda were radiotracked at Bukit Jernih, a small agricultural village (06°33′N, 100°15′E), 15 km southeast of Perlis State Park. Village houses are dispersed around the bases of a series of limestone tower karsts that rise out of

flat cultivated fields dominated by rice, mango orchards and banana plantations. Roosts of *C. brachyotis* Sunda at this site were unmodified and were found predominantly beneath the fronds of coconut palms, which grow abundantly in the yards of village houses (Campbell et al., in press).

At the Taiping site, Larut Hills Forest Reserve comprises 72 km<sup>2</sup> of mixed lowland dipterocarp forest (Putz 1978). The forest is bordered by small durian orchards and banana plantations, giving way to a series of landscaped parks surrounding the town of Taiping. We worked near the edge of the reserve in forest that had been heavily logged and, in some areas, clear-cut within the last two decades. Here, *C. brachyotis* Forest roosted mainly in the pinnate-leaved palm, *Arenga obtusifolia* and in *Macaranga gigantea*. A few modified roosts were observed in the latter species (Campbell et al., in press). All *C. brachyotis* Sunda roosts were unmodified and were concentrated in coconut palms in suburban gardens, and in the shrub *Dillenia suffruticosa* growing around the edge of an ornamental lake. The latter roosts were natural bowl-shaped cavities formed by intertwined branches of *D. suffruticosa*, overlain with an unidentified creeper (Campbell et al., in press).

### Bat Capture and Species Identification

Bats were captured in mist nets set at ground level. The two species were discriminated based on length of forearm ( $\bar{X} \pm \text{SD}$ : *C. brachyotis* Forest:  $59.5 \pm 1.7$  mm,  $N = 52$ ; *C. brachyotis* Sunda:  $63.8 \pm 1.6$  mm,  $N = 57$ ), coloration of nuchal collar (Forest = dark orange-red; Sunda = pale orange-yellow) and habitat associations (Campbell 2006, unpublished data). Approximately 640 base pairs of the mitochondrial control region were sequenced for all radiotracked individuals to confirm field identifications (methods in Campbell et al. 2004). Adults were distinguished from juveniles by relative closure of the phalangeal epiphyses (Anthony 1988) and parity of adult females was assessed by examination of the nipples (Racey 1988) and by palpating the lower abdomen for a detectable fetus. All adults were marked with a uniquely numbered 2.9-mm monel-lipped forearm band (Lambournes Ltd., Birmingham, U.K.) and with one to three coloured plastic split-ring bands (size 2X, A. C. Hughes, Ltd., Hampton Hill, U.K.). The latter marking system facilitated the identification of individuals in roosts without the need to recapture the animals (Kunz 1996).

### Radiotelemetry and Roost Censuses

Bats were radiotracked at Perlis June–August 2002, April–May 2003 and November 2003–January 2004. At Taiping, radiotracking periods were September–November 2002 and June–August 2003. Radiotransmitters (1.1 g, model MD-2C, Holohil, Carp, Ontario, Canada) were attached to adult males and females; all transmitters weighed less than 5% of the bat's body mass. The transmitters were secured with neck collars and labelled with reflective tape to improve their visibility in roosts (Kunz 1996).

Radiotagged bats were held for a maximum of one hour and released before midnight. Roost searches were initiated the following day using portable receivers (model TRX 1000S, Wildlife Materials, Carbondale, Illinois, U.S.A.) and five-element Yagi antennae. The location of a roost was determined as closely as possible using telemetry, after which a thorough visual search was made of all surrounding foliage until the bat or bats were seen. Confirmed roosts were marked with flagging tape, numbered and mapped using a hand-held GPS unit (Magellan 315). Radiotagged individuals were tracked to roosts daily for the life of the transmitter (28–46 days), or longer if the bat remained in the same roost (maximum, 77 consecutive tracking days). Additional roosts that were found opportunistically while searching for transmitter-carrying bats were marked and monitored in the same manner. To maximize the number of individually marked bats in the local population, mist nets were set several times a week throughout the census periods at the sites where the radiotagged individuals had been captured while foraging. Initial attempts to capture and mark the roostmates of transmitter-carrying bats at the roost were abandoned because the disturbance invariably disrupted the composition of groups, causing some or all of the bats to move to different roosts.

Group size, composition and individual positioning within the roost were observed with binoculars. Because both species roosted mainly in open foliage, in the majority of cases we were able to observe and count the number of individuals in a roost on a daily basis. It was not possible to distinguish all banded roostmates at every census, however, because females of both species typically roosted in close physical contact. Uncertain identifications were treated as follows: the identity of group members was assumed to remain the same as long as (1) the number of individuals in the group remained constant and (2) every individual presumed to be in the group was positively identified at least every 3 days. If these criteria were not met, individuals were included in group counts but excluded from association analyses until they were positively identified again. Because we were unable to band all bats in the study populations, censused groups often contained one or more unbanded individuals. These were excluded from association analyses unless they were lactating females with pups whose size was different from that of pups associated with other females in the roost, or they were adult males. The second assumption was justified by the observation that no radiotracked adult male of either species was ever observed in a roost previously occupied by another male. Adult males were readily distinguished from females by having brighter orange pelage around the neck and shoulders.

### Estimated Roost Distributions

The spatial distribution of available roosts was estimated for each species in their respective habitats using the distance method of Byth & Ripley (1980). Data were collected after the end of census periods at both field sites; a potential roost was defined as a plant species used as

a day roost by the focal bat species at either site (Campbell et al., in press). Individual plants below the minimum roosting height used by the focal species were excluded. The following sampling protocol was used at both sites in both forest and disturbed habitats. A grid of 24 points, approximately 150 m apart, was established in an approximately 35-ha quadrat. At 12 points, selected at random without replacement, we measured the distance ( $x_i$ ) from the point to the nearest potential roost. At the 12 remaining points we measured the distances between four pairs of potential roosts. These were selected by walking in each compass direction from the original sampling point until a potential roost was located, and then measuring the distance ( $r_i$ ) to the next nearest potential roost. One roost-to-roost distance per point was selected at random, resulting in 12 measures of point-to-nearest roost distances and 12 measures of roost-to-nearest roost distances. We used the test statistic  $h$  to test for significant departures from a random spatial distribution, and the index of spatial patterning  $I_H$ , to distinguish between clumped and uniform distribution types. As defined by Hopkins (1954),  $h = \sum(x_i^2) / \sum(r_i^2)$  and is distributed as  $F$  with  $2N$  degrees of freedom in both the numerator and the denominator, and  $I_H = h/1 + h$ . Values of  $I_H$  approach 1 when clumping is maximal, 0 when spatial dispersion is uniform and 0.5 when dispersion is random (Krebs 1999).

### Population-level Associations

Estimates of associations within and between sex classes in both populations of both species were obtained using the program SocProg2 (v. 2.2, Whitehead & Dufault 1999). We chose to use the simple ratio association index because it is more appropriate for describing associations between pairs of individuals in groups than other commonly used indexes such as the half-weight or twice-weight indexes (reviewed in Cairns & Schwager 1987; Ginsberg & Young 1992; see also Vonhof et al. 2004). The simple ratio index is calculated as  $X/(X + Y_{AB} + Y_A + Y_B)$ , where  $X$  is the number of observation periods when individuals A and B were observed in the same group,  $Y_{AB}$  is the number of periods in which A and B were both observed in different groups,  $Y_A$  is the number of periods when only A was observed and  $Y_B$  is the number of periods when only B was observed. To avoid overestimating associations by the inclusion of transient individuals, only individuals that were observed seven or more times during the census period were included; bats that were solitary for the entire census period were excluded from the association analyses.

A Mantel test was used to test for significant differences in the strength of individual associations within sex classes (female–female, male–male) and between sex classes (male–female). The association matrixes for each population were visualized using hierarchical cluster analysis, implemented in SocProg2.

### Fidelity Indexes

Roost fidelity (FID) was quantified using the index proposed by Chaverri & Kunz (2006):  $FID = (2(STAY) +$

$1(RETURN) - 1(MOVE))/(STAY + RETURN + MOVE)$ , where STAY is the number of times a bat was observed in the same roost on consecutive days, RETURN is the number of times a bat moved to a previously identified roost, and MOVE is the number of times an individual moved to a previously unidentified roost. Possible values for FID range from  $-1$  (no fidelity) to  $2$  (complete fidelity). For *C. brachyotis* Forest, roost switches within the same plant or tree were treated as nonindependent roosting decisions and were scored as STAY. For *C. brachyotis* Sunda, however, the frequent observation of two or more harem groups in different fronds of the same coconut palm indicated that movements within the same plant could involve social decisions, and therefore were scored as roost switches. One-way ANOVAs were used to test for effects of species, and sex within species, on roost fidelity.

We compared the daily rate of roost switching for solitary versus harem males. The 'solitary' group comprised males that roosted alone throughout the census period. 'Harem' males were defined as males that spent no more than three consecutive days roosting alone during the census period.

The degree of coordination in the movements of pairs of individuals between roosts was used as a measure of social fidelity (SOCFID). Focusing on movement patterns between roosts, rather than on periods of time spent in the same roost, allowed us to discriminate between social attraction and passive attraction to a familiar roost (sensu Wilkinson 1985). Social fidelity was calculated as the ratio of the number of times that a pair of individuals were observed together in two different roosts on consecutive days to the total number of times that the focal individual in the pair changed roosts. Possible values of SOCFID ranged from 0 (no coordinated movements) to 1 (all movements together). Whichever bat in the pair had been observed on more census days was selected as the focal individual; the analysis was restricted to pairs of individuals that were each observed for a minimum of 14 consecutive days during the census period.

To examine the relation between the use of modified roosts by *C. brachyotis* Forest males and harem size and stability, we tested for a correlation between the sum of within-harem male–female associations (calculated in SocProg2) for each male, and the proportion of modified roosts that he occupied. The sum of within-harem associations provided a combined measure of harem size and female fidelity to harem males, which avoided nonindependent comparisons between one male and multiple females.

### Variance in Mate Number

The ratio of the variance in harem size ( $V_{\text{harem}}$ ) to mean harem size ( $H$ ) can provide a first approximation of the degree of short-term variance in male reproductive success, where  $V_{\text{harem}} > H$  indicates an aggregated distribution of females across males (Wade & Shuster 2004). We estimated  $V_{\text{harem}}$  and  $H$  for the two species from the mean number of adult females roosting with focal males during the first 30 consecutive days of observations for each male. To assess harem stability from the male

perspective, we calculated the ratio of the variance in female group size experienced by each focal male ( $V_{\text{harem-within}}$ ) to the mean harem size experienced by that male ( $H_{\text{within}}$ ), where  $V_{\text{harem-within}} > H_{\text{within}}$  indicates lower harem stability and  $V_{\text{harem-within}} < H_{\text{within}}$  indicates higher harem stability. To assess the female perspective, we calculated the mean number of males that females of each species associated with over a 30-day period and used these values as indirect estimates of female mating strategy.

## RESULTS

We collected 997 bat-days of census data for *C. brachyotis* Forest and 1500 for *C. brachyotis* Sunda, where bat-days = ( $N$  days of observations per individual)  $\times$  ( $N$  individuals observed for  $\geq 7$  consecutive days). The mean  $\pm$  SD number of consecutive census days per bat was  $27.7 \pm 10.1$  (Perlis,  $N = 7$  males and 13 females; Taiping,  $N = 7$  males and 10 females) for *C. brachyotis* Forest and  $34.1 \pm 19.4$  for *C. brachyotis* Sunda (Perlis  $N = 15$  males and 23 females; Taiping  $N = 9$  males and 15 females). The original number of radiotagged bats was the same for both species ( $N = 8$  at each site); the larger census sample sizes for *C. brachyotis* Sunda reflect the fact that radiotracked individuals of this species typically interacted with more individuals than did radiotracked *C. brachyotis* Forest.

For *C. brachyotis* Sunda, the estimated spatial distribution of potential roost sites was significantly different from random at both sites (Taiping,  $h_{24,24} = 43.99$ ; Perlis,  $h_{24,24} = 33.20$ ,  $P < 0.0001$  for both sites) and was highly clumped (Taiping,  $I_H = 0.98$ ; Perlis,  $I_H = 0.97$ ). For *C. brachyotis* Forest, the distributions of potential roosts were not significantly different from random (Taiping,  $h_{24,24} = 2.16$ ; Perlis,  $h_{24,24} = 2.26$ ) but tended towards clumped, rather than uniform (Taiping,  $I_H = 0.68$ ; Perlis,  $I_H = 0.69$ ).

### Population-level Associations

The most salient feature of the social structure of *C. brachyotis* Forest was the absence of interchange between harem groups. We identified five distinct harem groups at each site (Fig. 1a, b). Female group size ranged from one to four. Three females (Fig. 1b, subgroup b) roosted with male 84 for the first 13 days of the census period, then moved as a group to roost with male 33 for the duration of the census period (29 days) while male 84 roosted alone. All other females were associated with one male only. When males or females that were associated with a particular group were found in separate roosts they were invariably alone.

The structure of *C. brachyotis* Sunda harem groups was labile in contrast. With the exception of two highly stable male–female pairs (subgroup a in Fig. 1c, d), subsets of harem groups and single males were weakly interconnected by the movements of females among males (Fig. 1c, d). Two such subsets were identified at each site (Fig. 1c, d, subgroups b and c). At Taiping, five females

roosted primarily with male 349 for 28 days, and then transferred to the harem of male 241 for the remaining 47 days of the census period (Fig. 1d, subgroup c). This was the only record of coordinated female movements in *C. brachyotis* Sunda.

In *C. brachyotis* Forest at both sites, male–female associations were higher than female–female associations (Table 1). In contrast, for *C. brachyotis* Sunda at Perlis, female–female associations were higher than male–female associations, while the indexes for the two comparisons were equal at Taiping. All male–male associations for both species were zero. However, differences between the strength of within-sex (female–female and male–male) versus between-sex (male–female) associations were not statistically significant for either species at either site (Mantel tests: *C. brachyotis* Forest: Perlis:  $t = -1.16$ ,  $N = 18$ ,  $P = 0.12$ ; Taiping:  $t = -1.07$ ,  $N = 16$ ,  $P = 0.14$ ; *C. brachyotis* Sunda: Perlis:  $t = 0.56$ ,  $N = 35$ ,  $P = 0.71$ ; Taiping:  $t = -0.53$ ,  $N = 23$ ,  $P = 0.30$ ). The uniformly higher mean association values for females than males reflects the fact that females associated with both other females and males, while males associated only with females, resulting in a larger number of nonzero pairwise comparisons for females (Table 1).

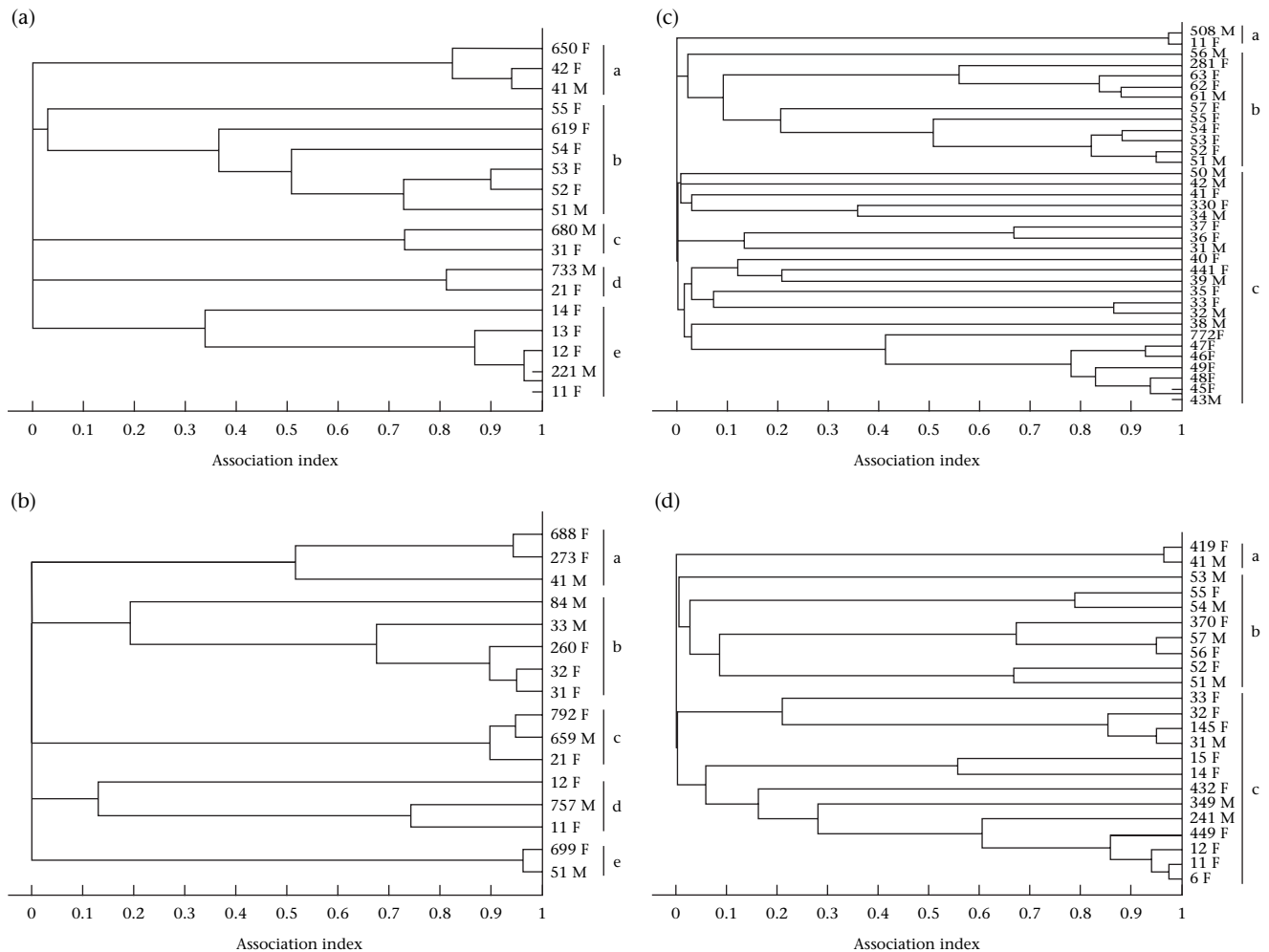
### Roost Fidelity

With the sexes combined, mean  $\pm$  SD roost fidelity was significantly higher in *C. brachyotis* Sunda ( $FID = 1.70 \pm 0.08$ ,  $N = 26$ ) than in *Cynopterus brachyotis* Forest ( $FID = 1.27 \pm 0.07$ ,  $N = 27$ ; one-way ANOVA:  $F_{1,51} = 16.16$ ,  $P < 0.0001$ ; Table 2). Sex had a significant effect on roost fidelity in *C. brachyotis* Sunda, with males showing significantly higher fidelity than females ( $FID_{\text{male}} = 1.80 \pm 0.10$ ,  $N = 14$ ;  $FID_{\text{female}} = 1.59 \pm 0.11$ ,  $N = 12$ ;  $F_{1,24} = 4.6$ ,  $P = 0.04$ ), but not in *C. brachyotis* Forest ( $FID_{\text{male}} = 1.26 \pm 0.14$ ,  $N = 12$ ;  $FID_{\text{female}} = 1.28 \pm 0.13$ ,  $N = 15$ ;  $F_{1,25} = 0.02$ ,  $P = 0.9$ ).

The mean  $\pm$  SD frequency of roost switching (switches/day) in males that were solitary throughout the census period versus males that were consistently associated with one or more females was slightly higher in *C. brachyotis* Forest (solitary:  $0.40 \pm 0.31$ ,  $N = 2$ ; harem:  $0.33 \pm 0.21$ ,  $N = 9$ ) and approximately three times higher in *C. brachyotis* Sunda (solitary:  $0.23 \pm 0.19$ ,  $N = 3$ ; harem:  $0.07 \pm 0.02$ ,  $N = 5$ ). However, these differences were not significant in either species (two-sample  $t$  test, two tailed: Forest:  $t_9 = -0.40$ ,  $P = 0.70$ ; Sunda:  $t_6 = -1.84$ ,  $P = 0.12$ ).

### Social Fidelity

Interspecific differences in the estimated strength of male–female associations at the population level were amplified at the level of individual pairs. Coordinated movements by male–female pairs between roosts were significantly higher in *C. brachyotis* Forest ( $\bar{X} \pm SD$  SOCFID =  $0.55 \pm 0.33$ ,  $N = 10$ ) than in *C. brachyotis* Sunda (SOCFID =  $0.23 \pm 0.23$ ,  $N = 10$ ; one-way ANOVA:  $F_{1,18} = 7.50$ ,  $P = 0.01$ ; Table 2). Coordinated movements of female–female pairs that were noncoincident with



**Figure 1.** Dendrograms constructed in SocProg2 (Whitehead & Dufault 1999) from association matrixes using the simple ratio index for *C. brachyotis* Forest at (a) Perlis and (b) Taiping, and for *C. brachyotis* Sunda at (c) Perlis and (d) Taiping. Letters indicate associated subgroups within each population; M = male, F = female; numbers are individual IDs.

movements of harem males were equally rare in both species (*C. brachyotis* Forest:  $0.28 \pm 0.28$ ,  $N = 3$ ; *C. brachyotis* Sunda:  $0.35 \pm 0.21$ ,  $N = 2$ ; two-sample  $t$  test, two tailed:  $t_3 = -0.34$ ,  $P = 0.8$ ), albeit based on small sample sizes. In *C. brachyotis* Forest, there was a positive but nonsignificant correlation between use of modified roosts by males and the combined measure of harem size and female

fidelity (Pearson correlation:  $r_8 = 0.60$ ,  $t = 2.11$ ,  $N = 10$ ,  $P = 0.07$ ).

**Harem Size and Stability**

Observed harem sizes ranged from one to four adult females in *C. brachyotis* Forest, and from one to 17 adult

**Table 1.** Mean association values within and between sex classes for *C. brachyotis* Forest and *C. brachyotis* Sunda at two sites in peninsular Malaysia

Species	Site	Mean association (SD)				
		f	m	m-f	f-f	m-m
<i>C. b. Sunda</i>	Perlis	0.07 (0.05)	0.04 (0.05)	0.05 (0.07)	0.08 (0.06)	0
	Taiping	0.09 (0.06)	0.06 (0.04)	0.09 (0.08)	0.09 (0.05)	0
<i>C. b. Forest</i>	Perlis	0.11 (0.06)	0.10 (0.06)	0.14 (0.08)	0.10 (0.07)	0
	Taiping	0.11 (0.06)	0.09 (0.04)	0.13 (0.05)	0.10 (0.08)	0

f = female; m = male.

**Table 2.** Mean values ( $\pm$ SD) for the roost fidelity index (FID), by species and by sex within species, and for the social fidelity index (SOCFID), measured among male–female pairs

	Species			Species/sex					
	C. b. Forest	C. b. Sunda	P	C. b. Forest ♀	C. b. Forest ♂	P	C. b. Sunda ♀	C. b. Sunda ♂	P
FID	1.27 (0.07)	1.70 (0.08)	<0.0001	1.28 (0.13)	1.26 (0.14)	0.9	1.59 (0.11)	1.80 (0.10)	0.04
SOCFID	0.55 (0.31)	0.23 (0.23)	0.01						

C. b.: *Cynopterus brachyotis*.  
P values obtained using one-way ANOVAs.

females in *C. brachyotis* Sunda. Mean  $\pm$  SD harem sizes ( $H$ ), based on 30 consecutive census days, were  $1.64 \pm 0.84$  for *C. brachyotis* Forest ( $N = 11$  harem males) and  $2.37 \pm 1.23$  for *C. brachyotis* Sunda ( $N = 11$  harem males). The two species' means were not significantly different (two-sample  $t$  test, two tailed:  $t_{20} = -1.64$ ,  $P = 0.12$ ). Variance among males ( $V_{\text{harem}}$ ) was low in *C. brachyotis* Forest (0.71) and moderate in *C. brachyotis* Sunda (1.51). However, among-male variance in harem size was less than mean harem size in both *C. brachyotis* Forest ( $V_{\text{harem}}/H = 0.43$ ) and *C. brachyotis* Sunda ( $V_{\text{harem}}/H = 0.64$ ), suggesting that the opportunity for short-term variance in male reproductive success is low in both species. The measure of harem stability, within-male variance in harem size ( $V_{\text{harem-within}}$ ), was consistently low in *C. brachyotis* Forest ( $V_{\text{harem-within}} < H_{\text{within}}$  for 10/11 harem males) and variable in *C. brachyotis* Sunda ( $V_{\text{harem-within}} > H_{\text{within}}$  for 5/11 harem males; Fig. 2).

The differences in harem stability experienced by males of the two species were clearly reflected in the behaviour of females. Of 15 *C. brachyotis* Forest females censused on 30 consecutive days, two were associated with two males and the remaining 13 were associated with single males (mean  $\pm$  SD number of males =  $1.13 \pm 0.34$ ). In contrast, 15 *C. brachyotis* Sunda females were associated with a mean of  $2.27 \pm 1.28$  males (range 1–5 males) during

a 30-day census period. This difference was highly significant (one-way ANOVA:  $F_{1, 36} = 16.52$ ,  $P < 0.0001$ ).

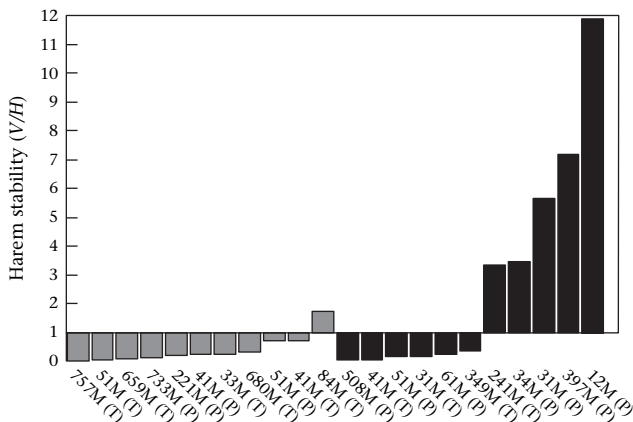
A few radiotracked females roosted alone for periods of several weeks. There was no evident relationship between solitary behaviour and reproductive state. *Cynopterus brachyotis* Forest female 619 (Perlis, Fig. 1a, subgroup b) was solitary for 15 days while lactating and two other females were solitary for the duration of the census period: a late pregnant female (12 consecutive census days) and a female whose pup was weaned and left the roost during the 41-day census period. Two female *C. brachyotis* Sunda, female 330 (early pregnant) and female 441 (postlactating) (Fig. 1c, subgroup c), were solitary for 18 and 13 days, respectively.

**DISCUSSION**

In this study we estimated the spatial distribution of available roosts for two Malaysian populations of two congeneric species of harem-forming bats, and asked whether differences in this ecological variable could be used to predict differences in female group size, male roost fidelity and the strength of male–female associations. We found a high correspondence between the distribution of roost sites, female group size and male behaviour. Where roosts were clumped, female group sizes were generally larger and males showed higher fidelity to single roosts. However, because males do not control female movements in either species, our results suggest that when roosts are abundant and similar in quality, regardless of their spatial distribution, the potential for males to monopolize mates depends on whether females move between roosts with, or independently of, males.

**Male Perspective: the Environmental Potential for Polygyny**

Estimates of the spatial dispersion of available roosts for *C. brachyotis* Sunda and *C. brachyotis* Forest indicate a clear difference in the environmental potential for polygyny experienced by males of the two species. *Cynopterus brachyotis* Forest uses a fairly broad range of roost plants, most of which are common in the primary and secondary forest habitats to which this species is restricted (Campbell et al., in press). At both field sites, we found that the distribution of potential roosts in the forest was not significantly different from random, but tended towards



**Figure 2.** Harem stability, measured as the ratio of the variance in harem size ( $V$ ) to mean harem size ( $H$ ) experienced by individual *C. brachyotis* Forest males (■) and *C. brachyotis* Sunda males (■), at Taiping (T) and Perlis (P). Males IDs are the same as in Fig. 1.

clumped rather than uniform. While this pattern of resource distribution promotes polygyny, it is not expected to facilitate the monopolization of a large number of mates (Emlen & Oring 1977). The general pattern of female dispersion among males supported this expectation: female group sizes in *C. brachyotis* Forest were small, with a maximum of two females per male in 70% of observed harems and a maximum of four females in the remaining 30%.

In contrast, the distribution of potential roosts for *C. brachyotis* Sunda was significantly clumped at both sites, providing high environmental potential for polygyny. Without taking individual female movements into account, the uneven distribution of females among *C. brachyotis* Sunda males, as indicated by moderately high among-male variance in harem size and large maximal harem sizes, supported the prediction that females should aggregate where resources are clumped, generating the potential for high among-male variance in mate number.

We found no evidence that males of either species adopt alternative mating tactics such as those reported for *Artibeus jamaicensis* (Ortega & Arita 1999), in which larger female groups are often attended by a dominant harem male and a peripheral subordinate male. Likewise, sub-adult males did not form bachelor groups, as have been observed in several Neotropical harem-forming species (*A. jamaicensis*: Kunz et al. 1983; *Phyllostomus hastatus*: McCracken & Bradbury 1981; *Carollia perspicillata*: Williams 1986; *Lophostoma silvicolium*: Dechmann et al. 2005). Roosts invariably contained a maximum of one adult male regardless of female occupancy. This pattern of segregation among males is consistent with observations of *C. sphinx* in India (Storz et al. 2000a).

The results of our study suggest that male occupancy of roosts in both *C. brachyotis* Forest and Sunda does not postdate female occupancy: solitarily roosting females were never joined by males, and within-roost harem male tenure was stable. Thus, in the sense that roosts are a resource necessary to females and that males do not attach themselves to single females or pre-existing female groups, a male mating system based on resource defence rather than female defence may be ascribed to both species (e.g. Ostfeld 1987). However, we found no direct evidence that males of either species actively defended roosts from other males. This, coupled with the significant differences between *C. brachyotis* Sunda and *C. brachyotis* Forest in male versus female roost fidelity and in the coordinated movements of males and females among roosts, suggests that, within the broad framework of polygyny, males of the two species use distinctly different reproductive tactics.

We predicted that female reproductive asynchrony combined with spatially clumped resources and consequent aggregation of females would promote a sedentary strategy in males. This was observed in terms of significant interspecific differences in roost fidelity: *C. brachyotis* Sunda males moved infrequently among roosts relative to *C. brachyotis* Forest males. Within *C. brachyotis* Sunda, the contrastingly low frequency of male relative to female movements suggested that, rather than tracking female movements, males of this species adopt a sit-and-wait

strategy in relation to potential mates. High roost fidelity in harem males is typical of most harem-forming species of bats for which behavioural data are available (*P. hastatus*: McCracken & Bradbury 1981; *Carollia perspicillata*: Williams 1986; *Tadarida pumila*: McWilliam 1988; *A. jamaicensis*: Ortega & Arita 1999; *C. sphinx*: Balasingh et al. 1995; Storz et al. 2000a, b; *Balionycteris maculata*: Hodgkison et al. 2003; *L. silvicolium*: Dechmann et al. 2005).

*Cynopterus brachyotis* Sunda males that were solitary for an entire census period showed considerably lower roost fidelity than males that were consistently associated with females. Although based on small sample sizes, this result suggests that the presence of female roostmates enforces roost fidelity in males, and that this constraint is relaxed during protracted periods of solitary roosting. Morrison (1978) observed a similar pattern in *A. jamaicensis*, in which solitary males switched roosts more frequently than did harem males, apparently moving in response to the changing distributions of ripe fruit.

In highly mobile taxa such as bats, when males monopolize resources rather than mates, the degree to which the environmental potential for polygyny is realized probably depends on the local abundance of resources and the extent of variation in resource value to females. For *C. brachyotis* Sunda, highly clumped roosting resources and large aggregations of reproductively asynchronous females translated to only moderate among-male variance in number of potential mates, countered in some cases by high within-male variance in harem size. A possible explanation for this result is that the high local abundance of coconut palms used by *C. brachyotis* Sunda at both field sites, and the homogeneous structure of palm fronds, provide females with a large number of similarly attractive roosts to choose among, effectively leveling the competitive field for resource-defending males and decreasing the potential for sexual selection introduced by high among-male variance in harem group size within a given day (e.g. Wade & Shuster 2004). While our small sample size precluded statistical analysis, it was notable that males defending naturally enclosed roosts in *Dillenia suffruticosa* at the Taiping site experienced higher harem fidelity than did most coconut palm-roosting males. The combination of interwoven branches and overhanging creeper that characterized the *D. suffruticosa* roosts was unique, suggesting that these well-protected sites might be preferred by females over other potential roosts.

The frequent movements of male and female *C. brachyotis* Forest among roosts indicate that individuals of both sexes are more strongly associated with a small roosting home range than with particular roost sites within that range. The minimal differences in roost fidelity between solitary and harem males suggests that the rate of male movements among roosts is not directly related to the presence of females. This labile pattern of roost occupancy is common in forest-associated bats, particularly in species that form small single-sex maternity colonies or mixed-sex groups (Bradbury & Vehrencamp 1976; Lewis 1996; Vonhof & Barclay 1996; Kerth & König 1999; Vonhof et al. 2004; Willis & Brigham 2004). However, low male



roost fidelity is rare in harem-forming species (reviewed in Lewis 1995), presumably because male–female associations are typically maintained in the context of a single male-defended resource, to which females are attracted.

The most striking feature of the social structure of *C. brachyotis* Forest was the coordinated movement of males and associated females, exemplified by the high social fidelity and male–female association values and low within-male variance in harem size in both study populations. This pattern of low roost fidelity and strong male–female association could be explained in the context of resource defence polygyny if males defend territories rather than roosts (Clutton-Brock 1989). However, overlap in the roosting home ranges of males is not consistent with territorial behaviour (Funakoshi & Zubaid 1997; P. Campbell, unpublished data). Alternatively, the use of spatially dispersed and relatively ephemeral roosts results in a sufficiently low encounter rate among individuals that both sexes benefit from social fidelity. We consider this possibility from the female perspective in the following section.

From the perspective of *C. brachyotis* Forest males, the environmental potential for polygyny provided by asynchronous female receptivity is limited by the spatial overdispersion of females. If, when harem membership is stable, mean harem size can be treated as a first approximation of within-season variance in male reproductive success (e.g. Wade & Shuster 2004), then our results suggest that, in our study populations, less than 50% of *C. brachyotis* Forest males fail to reproduce each season. However, the high associations between males and females and the lack of observed interchange between identified harem groups suggest that extraharem paternity is likely to be rare.

Clearly, the proposed differences between the two species in the reproductive success of harem males can only be evaluated directly with paternity analysis. However, paternity data would probably be meaningful only if collected from a substantial proportion of the adult male population over two or more breeding seasons. The frequency of female movements, particularly in *C. brachyotis* Sunda, suggest that, even in compositionally stable harems, females are unlikely to remain associated with the same male across breeding periods. Thus, harem male reproductive success may best be measured by the proportion of pups sired in the next cohort of offspring produced by harem females, rather than by paternity estimates for pups currently in the roost.

### Female Perspective: the Environmental Potential for Promiscuity

The tendency of females to aggregate where critical resources are concentrated is sufficiently common that resource distribution has been used to predict male mating strategy in a wide range of taxa (e.g. antelope: Jarman 1974; bats: Bradbury & Vehrencamp 1977; pinnipeds: Casini 2000; frogs: Pröhl & Berke 2001). In contrast, consideration of males as resources for females has been mainly limited to lek-mating species, where female aggregations

are a direct consequence of spatially and temporally clumped male distributions (Bradbury 1981; Clutton-Brock et al. 1993; Höglund & Alatalo 1995). However, when males do not restrict female movements, increasingly clumped male distributions generally increase the opportunity for females to sample multiple potential mates, regardless of whether male aggregation is a consequence or cause of female aggregation (Pröhl & Berke 2001; Hutchinson & Halupka 2004).

In *C. brachyotis* Sunda, the clumped distribution of roost sites and the occurrence of large harem groups suggest that females aggregate in response to locally concentrated resources. However, low fidelity to both roosts and males in coconut palm-roosting populations suggests that, where resources are abundant and similar in quality, females may take advantage of the opportunity to sample and potentially mate with multiple males. It is notable that the mean number of males that *C. brachyotis* Sunda females were associated with was only slightly less than the mean number of females that males of this species were associated with during a time period of equal length. This intersexual similarity in potential mate number suggests that female movements among males may minimize the variance in male reproductive success.

In *C. brachyotis* Forest, small observed harem sizes suggest that a random spatial dispersion of available roosts promotes correspondingly dispersed female populations. The combination of low roost fidelity and high female–male social fidelity observed in both study populations indicate that the strong intersexual associations observed in this species were not an artefact of female attraction to particular roosts. Why should females of the two species show such striking differences in fidelity to single males? One reasonable explanation is that a trade-off exists between the potential benefits of sampling multiple males and the probability of encountering one during the relatively brief postpartum period of receptivity. Thus, in an environment where roosts and males are randomly and therefore unpredictably distributed, female *C. brachyotis* Forest may increase their reproductive fitness by maintaining a strong association with one male per breeding period.

The correlates of female choice in bats are not well defined (Heckel et al. 1999; McCracken & Wilkinson 2000). In *Artibeus jamaicensis*, both dominant and subordinate harem males are significantly larger and heavier than nonharem (satellite) males (Kunz et al. 1983; Ortega & Arita 1999) and sire a significantly larger proportion of pups (Ortega et al. 2003). However, it is not known whether male size in *A. jamaicensis* influences male reproductive success via male–male competition, or is directly selected by female preference for larger males. A study of the social structure of *C. sphinx* in India found no relationship between male social status and either size or body mass (Storz et al. 2000a). The fact that neither of the *Cynopterus* species we studied show significant sexual size dimorphism (Campbell 2006) indicates that male size is probably not an important factor in roost defence, or in female mate choice. Whether females of these species use other aspects of male phenotype to assess male quality remains to be tested.

It has been suggested that, when males occupy modified roosts, females may either use properties of the roost to infer male quality, or chose males based on roost quality (Kunz et al. 1994; Balasingh et al. 1995; Kunz & McCracken 1996). If either factor is a determinant of female mate choice, then males in modified roosts might be expected to have larger, more stable harems. While there was a weak positive relationship between male use of modified roosts and harem size/female–male fidelity in *C. brachyotis* Forest, the generally low fidelity of both sexes to any roost, modified or unmodified, suggests that male investment in modification is relatively low and that females do not consistently prefer modified to unmodified roosts.

### Female–Female Associations

The gregarious roosting behaviour of female bats is a defining feature of the social structure of most species for which behavioural data are available (Kunz 1982; McCracken & Wilkinson 2000; Kunz & Lumsden 2003). Studies of maternity colonies in temperate species have reported nonrandom female–female associations, suggesting that social attraction promotes group cohesion (Lewis 1996; O'Donnell 2000). However, distinguishing between passive attraction to resources (e.g. roosts, food, males) and social attraction to familiar roostmates has been attempted in relatively few species (Wilkinson 1985; Vonhof et al. 2004; Willis & Brigham 2004), and would be particularly challenging in species in which males defend resources.

Our results suggest that, in *C. brachyotis* Forest, female–female associations may be a secondary consequence of male–female associations. In both study populations, male–female associations were stronger than female–female associations and coordinated female movements were rarely observed independently of male movements. The relatively high frequency of male–female pairs and the solitary roosting patterns of three radiotracked females suggest that social attraction among females is not a primary cause of harem group formation in this species.

In *C. brachyotis* Sunda, female–female associations were either slightly higher than (Perlis) or equal to (Taiping) male–female associations. However, the Perlis result may have been biased by the large sample of females relative to males, resulting in substantially more female–female than male–female comparisons. No coordinated female–female movements were observed at Perlis, and female group stability was low because of the frequent movements of single females among roosts. While it is possible that nonrandom associations between females exist at the population level, the duration and scope of our study was not sufficient to demonstrate this. At Taiping, associations between males and females and among females were elevated by the high stability of female groups occupying *Dillenia suffruticosa* cavity roosts, suggesting that, like female fidelity to males, female group cohesion may covary with perceived variation in roost quality.

### Conclusions

It has long been recognized that animal mating systems are the outcome of interplay between male and female reproductive tactics under a given set of environmental conditions (Emlen & Oring 1977; Clutton-Brock 1989). However, the singular classification of mating systems by male mating strategy may sometimes obscure the underlying congruence or conflict between male and female reproductive behaviour (Alonzo & Warner 2000; Shuster & Wade 2003; Smith & Sandell 2005). Our analysis of daily patterns of movement and social associations in two closely related, sympatric species of harem-forming fruit bats revealed striking differences in the social mating systems of males and females. *Cynopterus brachyotis* Sunda males showed a classic pattern of resource defence polygyny, maintaining high fidelity to single roosts. However, females of this species were generally highly labile and associated with multiple males over short time periods, factors that are likely to reduce the variance in male reproductive success expected for polygynous species. In contrast, *C. brachyotis* Forest males were only moderately polygynous, switched roosts frequently and did not appear to defend territories. *Cynopterus brachyotis* Forest females were correspondingly labile and showed high fidelity to single males, suggesting a female strategy of short-term social monogamy that is likely to enhance the within-breeding season reproductive success of harem-holding males. Determining whether these distinct differences in social mating system reflect fixed interspecific differences in behaviour, or population-level responses to different environments, will require comparative data from sites where both species experience strong variation in the quality of available roosts and optimal roost sites are limited.

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