8

Bat Mating Systems

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8.1 INTRODUCTION

Although bats are the most gregarious of mammals, most research documenting the complexity of their social interactions dates from only the last 30 years. Twenty years have passed since the last comprehensive review of this literature (Bradbury, 1977a). Bradbury documented the rich diversity of bat social systems by (1) describing the structural diversity that exists in the seasonal and long-term associations of bats, and (2) reviewing the information then available on social interactions and communication in several species. Bradbury's review and earlier papers by Dwyer (1970, 1971), refuted the then common presumptions that bats are forced to aggregate because of thermoregulatory demands or limited roost sites, and that these constraints result in interactions among individuals that are largely passive and random.

Bradbury (1977a) categorized 120 bat species (about 12% of the order) by social structure, but mating systems were described for only a fraction of these species.

Table 8.1 Families of bats, species diversity, and information on bat mating systems

Family	Total species	Information on mating systems	
		# species	% total
Vespertilionidae	330	17	5.2
Pteropodidae	175	16	9.2
Phyllostomidae	147	11	7.5
Emballonuridae	51	7	13.7
Rhinolophidae	129	5	3.9
Molossidae	89	4	4.5
Nycteridae	12	3	25
Megadermatidae	5	2	40
Noctilionidae	2	1	50
All others	23	0	0
Total	963	66	6.9

Species diversity from Findley, 1993

Table 8.2 Classical zoogeographic regions, species diversity, and information on bat mating systems

Region	Total species	Information on mating systems	
		# species	% total
Neotropical	221	17	7.7
Nearctic	40	4	10.0
Palearctic	85+	6	7.1
Ethiopian	186	21	11.3
Oriental	268	14	5.2
Australian	166	7	4.2

Zoogeographic data from Findley, 1993

'Year-round harems' were described for six species based either on association patterns among adults, or association patterns coupled with long-term observations of marked individuals. Eleven other species were listed as monogamous, but this categorization was a best guess. Discussing this category, Bradbury (1977a) stated that '. . . the existence of monogamous families in any species of bat remains to be proven by year-round studies'. With some exceptions, little or nothing was known about the mating systems of the species that Bradbury placed in his other social structure categories (e.g. 'sexes separate except for mating', 'sexual segregation at parturition; sexes together at other times', 'year-round multi-male, multi-female groups'). In large part, Bradbury's review was a call to the need for more research.

This chapter shows that the call has been answered by a large number of studies. Here, we focus specifically on the mating systems of bats, emphasizing research from the last 20 years. For completeness, we list all species where mating systems were defined by Bradbury, but we discuss only those where there is new information or where additional interpretations are possible. In total, we include information on the mating systems of 66 species of bats in 10 families. Bats from the largest families (Vespertilionidae, Pteropodidae, Phyllostomidae) are best represented in this literature (Table 8.1). In proportion to their species diversity, bats in the Rhinolophidae and Molossidae have received the least attention (Table 8.1). Bats from the zoogeographic regions with the greatest numbers of species (Ethiopian, Neotropical, Oriental) also have received the most study. In proportion to regional species richness, mating systems have been least studied in bats from the Australian and Oriental regions (Table 8.2).

8.2 MATING SYSTEMS IN BATS AND OTHER MAMMALS

Over 90% of the mammal species that have been studied have some form of polygynous mating system in which one male mates with several females (Kleiman, 1977; Clutton-Brock, 1989). In contrast to birds, where about 90% of all species were thought to be monogamous, a view now refuted by numerous molecular studies of bird mating systems (Birkhead and Moller, 1992; Westneat and Webster, 1994), monogamy has been attributed to only about 3% of mammal species (Kleiman, 1977; Whittenberger and Tilson, 1980). Bats conform to the general mammalian pattern. Most bat species are apparently polygynous, while fewer, yet a surprising number, appear to be monogamous.

Polyandrous mating systems have been attributed to very few mammals (e.g. Malcolm and Marten, 1982; Terborgh and Goldizen, 1985). However, there are many mammals where a female mates with several males. Molecular studies have documented numerous examples of multiple paternity in birds (e.g. Gowaty and Karlin, 1984; Burke et al., 1989; Westneat, 1990), but also in some mammals (Birdsall and Nash, 1973; Hanken and Sherman, 1981), including bats (Mayer, 1995; Wilkinson, unpublished data). In some bats, females mate in sequence with several males, and paternity outside of apparent mating groups has been documented in a few species. Available evidence suggests that multiple mating by females is common in bats, and it deserves further study.

Many mammals are promiscuous in that the individuals that mate have no continuing relationship before or after mating (Clutton-Brock, 1989). Many bats are promiscuous, and earlier studies (e.g. Ognev, 1928; Wimsatt, 1945; Pearson et al., 1952) described mating in bats that appeared to be totally anarchic. More recent studies on bats have described mating as both 'promiscuous' and 'random' (Thomas et al., 1979; Fenton, 1984; Wai-Ping and Fenton, 1988), but these terms must not be confused. Promiscuous mating can be highly structured and nonrandom. For example, lek mating in the Hammer-headed bat *Hypsignathus monstrosus* (Bradbury, 1977b) is promiscuous, but highly nonrandom because only a few males mate. There is no convincing evidence that mating in any bat is random.

8.2.1 Categorizing Mating Systems

There are many ways to categorize animal mating systems (e.g. Bradbury and Vehrencamp, 1976, 1977; Emlen and Oring, 1977; Clutton-Brock, 1989), but any

Table 8.3 Bat mating systems

Family	Species	Region	Diet	Day roost	References
I. Single-male/multi-female groups					
I.1. Year-round harems with stable female composition					
Phyllostomidae	*Phyllostomus hastatus*	Neotropical	Omnivore	Caves	Bradbury, 1977a; McCracken and Bradbury, 1977; 1981; McCracken, 1987
Noctilionidae	*Noctilio leporinus*	Neotropical	Insects, fish	Caves, tree hollows	Brooke, 1997
Vespertilionidae	*Myotis bocagei*	Paleotropical (Africa)	Insects	Rolled leaves	Brosset, 1976
Molossidae	*Tadarida pumila*	Paleotropical (Africa)	Insects	Buildings	McWilliam, 1988
Emballonuridae	*Coleura afra*	Paleotropical (Africa)	Insects	Caves	McWilliam, 1987a
I.2. Year-round harems with less stable female composition					
Phyllostomidae	*Artibeus jamaicensis*	Neotropical	Fruit Leaves	Caves, tree hollows, tents	Morrison, 1979; Morrison and Handley, 1991; Kunz et al., 1983; Kunz and McCracken, 1996; J. Ortega, personal communication
	Carollia perspicillata	Neotropical	Fruit	Caves, tree hollows	Williams, 1986; Porter, 1979; Fleming, 1988
	Phyllostomus discolor	Neotropical	Fruit	Tree hollows	Bradbury, 1977a; Wilkinson, 1987
Vespertilionidae	*Tylonycteris pachypus*	Paleotropical (Malaysia)	Insects	Bamboo hollows	Medway, 1969
	Tylonycteris robustula	Paleotropical (Malaysia)	Insects	Bamboo hollows	Medway and Marshall, 1972; Medway, 1969
	Miniopterus australis	Paleotropical (Malaysia)	Insects	Caves	Medway and Marshall, 1972; Medway, 1971
Emballonuridae	*Saccopteryx bilineata*	Neotropical	Insects	Tree holes	Bradbury and Emmons, 1974; Tannenbaum, 1975; Bradbury and Vehrencamp, 1976, 1977; McCracken, 1984
Pteropodidae	*Cynopterus sphinx*	Paleotropical (India)	Fruit	Tents	Bhat and Kunz, 1995; Balasingh et al., 1995; G.S. Grant and S.A. Banack, unpublished
	Pteropus tonganus	Paleotropical (Samoa)	Fruit	Trees	
	Pteropus mariannus	Paleotropical (Guam, Mariana Islands)	Fruit	Trees	Wiles, 1987
I.3. Seasonal single-male/multi-female groups					
Phyllostomidae	*Ectophylla alba*	Neotropical	Fruit	Tents	Brooke, 1990
Vespertilionidae	*Myotis adversus*	Subtropical (Australia)	Insects	Caves	Dwyer, 1970
	Nycticeius humeralis	Temperate (N. America)	Insects	Buildings	Watkins and Shump, 1981
	Nyctalus noctula	Temperate (Europe)	Insects	Tree holes	Bain and Humphrey, 1986; Sluiter and Van Heerdt, 1966; Mayer, 1995
	Pipistrellus pipistrellus	Temperate (Europe)	Insects	Tree holes, bat boxes	Gerell and Lundberg, 1985; Lundberg and Gerell, 1986; Gerell-Lundberg and Gerell, 1994
	Pipistrellus nanus	Paleotropical (Africa)	Insects	Rolled leaves, buildings	O'Shea, 1980; LaVal and LaVal, 1977; Happold and Happold, 1996
	Pipistrellus nathusii	Temperate (Europe)	Insects	Tree holes, bat boxes	Heise, 1982; Gerell-Lundberg and Gerell, 1994
I.4. Other single-male/multi-female groups					
Phyllostomidae	*Vampyressa nymphaea*	Neotropical	Fruit	Tents	Brooke, 1987
	Uroderma bilobatum	Neotropical	Fruit	Tents	Timm and Clauson, 1990; Timm and Lewis, 1991; Lewis, 1992b
	Artibeus cinereus	Neotropical	Fruit	Tents	Kunz and McCracken, 1996; Kunz and McCracken, in prep.

Table 8.3 (continued)

Family	Species	Region	Diet	Day roost	References
Molossidae					
	Tadarida midas	Paleotropical (Africa)	Insects	Rock crevices	Verschuren, 1957; Bradbury, 1977a
	Otomops martiensseni	Paleotropical, temperate (Africa)	Insects	Buildings	Richardson and Taylor, 1997
Pteropodidae					
	Cynopterus brachyotis	Paleotropical (Malaysia)	Fruit	Tents	Tan et al., 1997
	Cynopterus horsfeldi	Paleotropical (Malaysia)	Fruit	Foliage	Tan et al., 1997
	Pteropus seychellensis	Paleotropical (Comoro Islands)	Fruit	Trees	Cheke and Dahl, 1981
	Pteropus rodricensis	Paleotropical (Captivity)	Fruit	Trees	Carroll and Mace, 1988
	Pteropus hypomelanus	Paleotropical (Captivity)	Fruit	Trees	J. Seyjagat, personal communication
	Pteropus vampyrus	Paleotropical (Captivity)	Fruit	Trees	J. Seyjagat, personal communication
	Pteropus pumilus	Paleotropical (Captivity)	Fruit	Trees	J. Seyjagat, personal communication

2. Multi-male/multi-female groups
2.1 Year-round multi-male/multi-female groups that mate at the roost

Family	Species	Region	Diet	Day roost	References
Phyllostomidae					
	Desmodus rotundus	Neotropical	Blood	Caves, hollow trees	Wilkinson, 1985a, b; 1987
Emballonuridae					
	Rynchonycteris naso	Neotropical	Insects	Tree holes, cliffs	Bradbury and Vehrencamp, 1976; 1977
	Balantiopteryx plicata	Neotropical	Insects	Caves	Bradbury and Vehrencamp, 1976; 1977
	Peropteryx kappleri	Neotropical	Insects	Hollow trees	Giral et al., 1991

2.2 Year-round multi-male/multi-female groups that mate away from the roost

Family	Species	Region	Diet	Day roost	References
Pteropodidae					
	Hypsignathus monstrosus	Paleotropical (Africa)	Fruit	Foliage	Bradbury, 1977b
	Epomophorus crypturus	Paleotropical (Africa)	Fruit, flowers	Foliage	G.S. Wilkinson, unpublished observations
	Epomophorus wahlbergi	Paleotropical (Africa)	Fruit, flowers	Foliage	Wickler and Seibt, 1976 Bradbury, 1977a; 1982
	Epomops franqueti	Paleotropical (Africa)	Fruit	Foliage	Bradbury, 1977a; 1982

2.3 Seasonal multi-male/multi-female groups

Family	Species	Region	Diet	Day roost	References
Phyllostomidae					
	Macrotus californicus	Temperate, subtropical (N.America)	Insects, fruit	Caves	Berry and Brown, 1995
Vespertilionidae					
	Myotis lucifugus	Temperate (N.America)	Insects	Caves, buildings	Thomas et al., 1979 Wai-Ping and Fenton, 1988 Watt and Fenton, 1995
	Myotis myotis	Temperate (Europe)	Insects	Buildings	Zahn and Dippel, personal communication
	Miniopterus minor	Paleotropical (Africa)	Insects	Caves	McWilliam, 1990
	Plecotus auritus	Temperate (Europe)	Insects	Buildings	Speakman and Racey, 1987 Speakman et al., 1991 Burland, 1998
Molossidae					
	Tadarida brasiliensis	Temperate (N.America) Neotropical (Captivity)	Insects	Caves, buildings	Lollar, 1995 A. Lollar, personal communication B. French, personal communication
Rhinolophidae					
	Rhinolophus ferrumequinum	Temperate	Insects	Caves, mines	G. Jones, personal communication
Pteropodidae					
	Pteropus poliocephalus	Paleotropical, subtropical (Australia)	Fruit	Trees	Nelson, 1965 Martin et al., 1995

Table 8.3 (continued)

3. Single-male/single-female monogamous groups

Family	Species	Region	Diet	Day roost	References
Phyllostomidae					
	Vampyrum spectrum	Neotropical	Carnivore	Tree hollows	Vehrencamp et al., 1977
Vespertilionidae					
	Kerivoula picta	Paleotropical (S. Asia, India)	Insects	Foliage	Brosset, 1962; Bradbury, 1977a
	Kerivoula harrisoni	Paleotropical (Africa)	Insects	Foliage	Brosset, 1966; Bradbury, 1977a
	Kerivoula papillosa	Paleotropical (Malaysia)	Insects	Bird and wasp nests	Medway, 1969; Bradbury, 1977a
Emballonuridae					
	Saccopteryx leptura	Neotropical	Insects	Tree boles	Bradbury and Vehrencamp, 1976; 1977
	Taphozous peli	Paleotropical (Africa)	Insects	Tree hollows	Kingdon, 1974; Bradbury, 1977a
Megadermatidae					
	Cardioderma cor	Paleotropical (Africa)	Insects	Caves	Vaughan, 1976; McWilliam, 1987b
	Lavia frons	Paleotropical (Africa)	Insects	Foliage	Wickler and Uhrig, 1969; Vaughan and Vaughan, 1986; 1987
Nycteridae					
	Nycteris arge	Paleotropical (Africa)	Insects	Tree hollows buildings	Bradbury, 1977a
	Nycteris nana	Paleotropical (Africa)	Insects	Tree hollows	Bradbury, 1977a
	Nycteris hispida	Paleotropical (Africa)	Insects	Buildings, trees, tree hollows	Bradbury, 1977a
Rhinolophidae					
	Rhinolophus sedulus	Paleotropical (Malaysia)	Insects	Culverts	Heller and Volleth, 1989; Heller et al., 1993
	Rhinolophus luctus	Paleotropical (India)	Insects	Caves, buildings	Bradbury, 1977a
	Hipposideros beatus	Paleotropical (Africa)	Insects	Foliage	Brosset, 1982
	Hipposideros brachyotis	Paleotropical (Sri Lanka)	Insects	Caves	Bradbury, 1977a
Pteropodidae					
	Pteropus samoensis	Paleotropical (Samoa)	Fruit	Trees	Cox, 1983; Pierson and Rainey, 1992

attempt to categorize bat mating systems is a compartmentalization of a continuum. Consequently, all categorizations, simple or complex (e.g. Clutton-Brock, 1989), suffer because many species do not fit neatly into any one category. Having wrestled with diverse categorizations, we opt for simplicity, which we believe enhances, rather than detracts from, the ability to emphasize common themes.

Following Bradbury's approach (1977a), we categorize species according to the structural roosting and mating associations of males and females, and the stability and seasonality of these associations (Table 8.3). Our basic structural association categories are (1) single male/multi-female mating groups, (2) multi-male/multi-female mating groups, and (3) single male/single female mating groups. We subdivide these categories into associations that persist throughout the year versus those that occur only during the mating season, and with regard to the compositional stability of groups (Table 8.3).

Mating groups that consist of a single male and multiple females are typically called harems. This use of the term 'harem' has been criticized for ambiguity and for carrying anthropocentric connotations of male dominance and female subservience (Lewis, 1992a). We intend no such connotations, and find 'harem' useful for ease of discussion in describing the mating systems of many bat species. As we use the term, a harem is a single male/multi-female roosting group of adults in which the resident male has, or appears to have, preferred opportunities for mating and reproducing with those females. In using the term 'harem', we recognize that the preferred reproductive ability of a resident male has been documented for very few species of bats, and that one or both sexes also may mate outside of their harems.

Ambiguity is a separate issue. Mating groups are not called harems if they lack, or appear to lack, the basic criterion of one male reproducing preferentially with a roosting group of multiple females. All single male/multi-female mating groups are not harems. This is illustrated by the African banana leaf-roosting bats Pipistrellus nanus, in which single males establish themselves at ephemeral roosting sites where they are visited briefly for mating by roving females. Males are often visited simultaneously by several females, and some males are visited more frequently by more females than others. However, both males and females appear to mate promiscuously (Happold and Happold, 1996).

Other bat species (e.g. Macrotus californicus, Miniopterus minor and Tadarida brasiliensis) also have mating systems in which single males establish themselves at sites where they are visited by roving females. Although it has been suggested that these species may mate in harems or perhaps leks, we categorize these bats as mating in 'multi-male/multi-female polygynous groups' because mating occurs in mixed-sex colonies and it is not clear whether their mating systems satisfy the criteria for harems or leks. The category 'multi-male/multi-female polygynous groups' is an umbrella for a diversity of mating systems, but we clarify the form of each mating system by subdividing this category and by providing the information that is available for each species.

There are other difficulties in classifying bat mating systems. For example, male Pteropus poliocephalus defend seasonal territories in mixed-sex colonies where some males are polygynous and other males are monogamous. For convenience, we categorize P. poliocephalus as mating in multi-male/multi-female polygynous

groups. Also, we refer to species that typically roost and mate in single male/single female groups as 'monogamous', and place *Saccopteryx leptura* in this category. However, there is evidence that some male *S. leptura* are polygynous. The fact that this diversity of mating systems defies categorization may vex an orderly human mind, but it points to the extensive variability of mating behaviors in bats.

8.3 SINGLE MALE/MULTI-FEMALE POLYGYNOUS GROUPS

Depending on taxonomy, 34 or 35 bat species are reported to mate in groups that consist of a single adult male and multiple adult females (Table 8.3). Almost all of these (i.e. 33 or 34 species) have been cited as mating or possibly mating in harems, but, as discussed above, all of these species do not mate in harems. None the less, current literature suggests that harems are common, perhaps the most common mating system in the Order.

8.3.1 Year-round Harems with Stable Female Composition

Highly stable aggregations of females that remain together for several years have been described for five species of tropical bats (Table 8.3). *Phyllostomus hastatus* forms clusters of 7 to 25 females (Figure 8.1) with an annual group compositional stability of 87% (McCracken and Bradbury, 1977, 1981). The same marked females have remained together for over 10 years (G.F. McCracken and G.S. Wilkinson, unpublished observations) and some females appear to have lifetime associations. Stable associations lasting two or more years also have been documented for groups of three to 10 female *Noctilio leporinus* (Brooke, 1997), and two to seven female *Myotis bocagei* (Brosset, 1976). Groups of three to 21 adult female *Tadarida pumila* showed an annual group compositional stability of 70% (McWilliam, 1988), and females in clusters of two to 20 *Coleura afra* have remained together throughout a 14-month study (McWilliam 1987a).

The stable female groups in all of these species each are attended by a single adult male (Figure 8.1) that aggressively repels intrusions by other males. Paternity studies using allozymes showed that resident males sire between 60 to 90% of the pups born to the females in the harems of *P. hastatus* (McCracken and Bradbury, 1977, 1981). Paternity estimates are not available for the other species.

In all of these species harem male replacements occur without disrupting female roosting associations, suggesting that males attach themselves to existing female groups and that grouping is the result of female gregariousness. In *P. hastatus* and *N. leporinus* females evicted from a roost site remain together at new sites. All-male 'bachelor' clusters can occur in the same roosts as harems in *P. hastatus*, *N. leporinus* and *C. afra*, but McWilliam (1987a) reports that bachelor males in *C. afra* are more likely to roost singly. Singly roosting bachelors also have been reported for *M. bocagei*. Single 'satellite' males may attend larger female clusters in *C. afra*.

Relative age indices based on toothwear show that in *P. hastatus* and *N. leporinus* harem males are on average older than bachelor males, but in both species harem males were not larger than bachelors (McCracken and Bradbury, 1981; Brooke, 1997). Harem males in *N. leporinus* had larger testes and larger areas

Figure 8.1 A harem group of *Phyllostomus hastatus*. The harem male is at the periphery of the group of females (photograph by G.F. McCracken).

covered with subaxial secretions that are used in social communication (Brooke, 1997). There was a correlation between male body size and harem size in *T. pumila*, with larger males attending larger harems (McWilliam, 1988).

In *P. hastatus* and *N. leporinus* female groups consist largely of similarly aged bats, suggesting that female groups form as age cohorts of females born in the same year. This has been documented for *P. hastatus* (McCracken and Bradbury, 1981), but young females also are occasionally recruited into natal groups of both species (Brooke, 1997; Wilkinson, personal observation). The recruitment of females into natal groups led McWilliam (1987a, 1988) to suggest that harems in *T. pumila* and *C. afra* may be kin groups. Genetic information documents low average relatedness (r = 0.037) among harem females in *P. hastatus* (McCracken, 1987). This level of relatedness would result if approximately 15% of the females in a *P. hastatus* harem were half-sisters. The age cohort structure of harems of *N. leporinus* also

suggests low average relatedness within female groups (Brooke, 1997), but relatedness was not estimated. Brosset (1976) did not observe recruitment of female *M. bocagei* into natal groups, but he did observe one harem male that assumed residence in its natal harem after that male's mother had disappeared from the harem.

8.3.2 Year-round Harems with Less Stable Female Composition

Year-round harems have been reported for several other tropical bats, but female group composition is more fluid with females often moving between groups. *Artibeus jamaicensis* (Morrison, 1979; Morrison and Handley, 1991; Kunz et al., 1983; J. Ortega-R., personal communication) and *Phyllostomus discolor* (Bradbury, 1977a, Wilkinson, 1987) both form groups of one male with two to 15 females in hollow trees or caves. Cave-roosting groups of female *A. jamaicensis* with more than 14 females are sometimes attended by two resident males (J. Ortega-R., personal communication). Smaller groups of two to six *A. jamaicensis* also roost in modified leaves ('tents') in associations that suggest harems (Kunz and McCracken, 1996). *Carollia perspicillata* roosts in groups of one male and two to 17 females (Williams, 1986; Fleming, 1988), and *Tylonycteris pachypus* and *Tylonycteris robustula* both roost in apparently year-round groups that typically consist of one male and up to 12 or seven females, respectively (Medway, 1969; Medway and Marshall, 1972; Bradbury, 1977a). Groups with multiple males and females have been reported for both *T. pachypus* and *T. robustula*, but only during the months after weaning, suggesting that these additional males are juveniles (Medway and Marshall, 1972). *Saccopteryx bilineata* roosts on the sides of large trees and in buttress cavities in colonies of one to a few dozen individuals. Colonies consist of a single group or several adjacent groups, each group with one male and up to eight females (Bradbury and Emmons, 1974; Bradbury and Vehrencamp, 1976, 1977). Groups of bachelor males or bachelors roosting singly are found at the same roosts as female groups in *A. jamaicensis*, *C. perspicillata* and *S. bilineata*, and at separate roost sites in all of the above six species.

These roosting associations suggest harems, which have been attributed to all of these species. However, the reproductive success of the males attending female groups has not been documented for any of these bats, and the fluidity of female group compositions suggests that females may mate with multiple males. The presumption of harem mating is supported where it is known that, despite their movements, many of the same females are typically found with the same male.

Female groups of *A. jamaicensis*, in caves in Mexico, had a compositional stability of 65% between October to February, but a compositional stability of 95% from March to September, with the latter period including the mating season (Ortega-R., personal communication). In Panama, many of the same females remained together in the same tree hole for over three months (Morrison, 1979), further indicating that female *A. jamaicensis* show affinity for a site or a roosting group (Wilkinson, 1987). In the wild, female *C. perspicillata* moved between an average of 3.8 harems every six months, but individuals showed greater affinity for particular groups and sites, being at their favored site in 62% of all observations and at their two most favored sites in 82% of all observations (Williams, 1986).

Even so, only 3.3% of the same female pairs were together on 50% or more of all observations. In captivity, female *C. perspicillata* showed a similar pattern of frequent movement between groups but preference for roosting at particular sites (Porter, 1979). Harems of *S. bilineata* censused outside of the November/December mating season every 10 days from April to August consisted of one to four resident females (i.e. the same individuals present in the same group on at least 2/3 of all censuses). However, the annual compositional turnover of females in *S. bilineata* colonies was high, ranging from 80% to 100% (Bradbury and Emmons, 1974; Bradbury and Vehrencamp, 1977). In both *Tylonycteris* species, females changed roost sites frequently and Medway and Marshall (1972) suggested that they may associate randomly. Random associations among females suggest that mating in these *Tylonycteris* species may be promiscuous. Except that compositional turnover among females is high, little has been published about female group stability in *P. discolor* (Bradbury, 1977a). In *S. bilineata* (Bradbury and Emmons, 1974; Bradbury and Vehrencamp, 1976) and *C. perspicillata* (Porter, 1979; Williams, 1986) the male's fidelity to a group's roost site exceeds that of females, suggesting that site or group associations among females are an indicator of resident males' opportunities for reproduction.

Unlike *P. hastatus* and *N. leporinus*, there is no evidence that any of these species form female groups that are age cohorts. Most young female *S. bilineata* disperse widely and there is no evidence that females join natal groups as adults (Bradbury and Emmons, 1974; Bradbury and Vehrencamp, 1976; Tannenbaum, 1975). However, Tannenbaum (1975) reported that 76% of young male *S. bilineata* remained in their natal colonies, where they established territories as adults. Only one of 31 young female *A. jamaicensis* was captured as an adult in the hollow tree where she was born (Morrison and Handley, 1991), but Williams (1986) reported that 58% of yearling female *C. perspicillata* returned to their natal caves.

Using the information available on group stability and dispersal patterns, Wilkinson (1987) modeled the expected kin relationships among females in groups of *P. discolor*, *C. perspicillata* and *A. jamaicensis*. Where the best information was available he concluded that average relatedness among females was low for groups of *C. perspicillata* and *A. jamaicensis* (r = 0.010–0.058 and r = 0.000–0.001, respectively). Wilkinson (1987) thought that relatedness may be higher among groups of *P. discolor* (r = 0.019–0.083). Allozyme genetic assays of *S. bilineata* roosting groups showed no evidence for non-random genetic relationships among adult females (McCracken, 1984). However, these assays revealed non-random allelic distributions among males in different colonies, suggesting that males within *S. bilineata* colonies may be related as a consequence of male philopatry to their natal colonies (McCracken, 1984).

At least three species of Old World fruit bats and one other microchiropteran have been reported to live for all or most of the year in harem groups with labile female composition. Tent roosting *Cynopterus sphinx* in India have two annual breeding periods which coincide with biannual periods of tent construction by the resident males (Balasingh et al., 1995). Single adult males expend considerable effort constructing tents, which are then used as day roosts by the male and variable numbers of adult females. Single tents can be used for a year or more, and adult males have been observed defending tents from intrusions by other bats

(Balasingh et al., 1995; Bhat and Kunz, 1995). Female groups of two to 19 adults per tent varied substantially in size and in their fidelity to particular tents, indicating that harem composition in C. sphinx is labile (Balasingh et al., 1995).

Pteropus tonganus, in American Samoa, roosts in largely defoliated trees in groups of two to 16 females per male (Grant and Banack, 1995; Figure 8.2). Females typically roost about 25 cm apart in group-specific roosting areas defended by individual males using scent marking and aggressive interactions at boundaries. Male bachelor groups and single males roost at the periphery of these colonies. This social structure was maintained throughout the year, except for a two-month period (November–December) when all bats left the study area. Copulations were frequent and observed throughout the study, and pregnant females and lactating females with young were found at all times. Biweekly surveys showed frequent fluctuation in the size of female groups suggesting that group composition is highly labile (Grant and Banack, 1995). Pteropus mariannus in Guam and the Northern Mariana Islands, has a mating system that is similar to that of P. tonganus. Pteropus mariannus lives year-round in groups of two to 15 females per male, has aseasonal reproduction, and groups fluctuate in size over periods of days (Wiles, 1987).

In Malaysia, Miniopterus australis roosts in erosion concavities in caves in highly labile clusters of up to six females with one male (Medway, 1971). These apparent harems exist in October, November, and February to May, spanning the

Figure 8.2 A presumed harem group of Pteropus tonganus (photograph by A.P. Brooke).

mating season, as well as much of pregnancy and lactation. Harems also exist outside of the reproductive season in July, suggesting that they are maintained throughout the year (Medway, 1971). Interestingly, in Australia (Dwyer, 1968) and the New Hebrides (Baker and Bird, 1936) both sexes are together during most of the year, but females are segregated from males in maternity colonies during parturition (Bradbury, 1977a). The contrasting reports about M. australis may reflect problems with taxonomy, or, alternatively, support the notion that within single species mating systems can adapt to local ecological contexts (Clutton-Brock, 1989).

8.3.3 Seasonal Single Male/Multi-Female Groups

A large number of temperate as well as many tropical bat species show a three-phase annual social structure that Bradbury (1977a) termed the 'temperate cycle'. Two phases of this cycle consist of mixed sex associations in winter, and sexually segregated groups at parturition. Bradbury (1977a) pointed out that the third phase of the cycle, mating, was the least known but was largely assumed to be random and promiscuous. Several temperate cycle species are now known to mate in single male/multi-female associations.

The annual cycles and mating systems of three European species are similar. Nyctalus noctula (Sluiter and van Heerdt, 1966), Pipistrellus nathusii (Heise, 1982; Gerell-Lundberg and Gerell, 1994), and Pipistrellus pipistrellus (Gerell and Lundberg, 1985; Lundberg and Gerell, 1986; Gerell-Lundberg and Gerell, 1994) hibernate during the winter in mixed sex groups. After emergence in the spring they roost briefly in mixed sex associations, but during parturition and nursing females form maternity colonies apart from males. All three species form summer roosts in trees and buildings, and studies of these bats were facilitated by their acceptance of boxes as alternative roosts (Heise, 1982; Gerell and Lundberg, 1985; Lundberg and Gerell, 1986; Gerell-Lundberg and Gerell, 1994).

In all three species, single males establish seasonal territories for mating in roost boxes where they roost and mate with multiple females. However, the timing and duration of territory establishment and mating varies among species. Male P. pipistrellus establish territories in June while females are in maternity roosts, and the solitary distribution of males is stable throughout the summer. Mating occurs in August and September with 93% of the male P. pipistrellus remaining at the same box roost from June to September (Gerell and Lundberg, 1985; Gerell-Lundberg and Gerell, 1994). In contrast, male P. nathusi do not establish territories until July, when females are leaving their maternity roosts, and mating occurs shortly afterward in mid-July and August (Heise, 1982; Gerell-Lundberg and Gerell, 1994). Comparing the mating behaviors of these bats in southern Sweden, Gerell-Lundberg and Gerell (1994) suggest that these differences occur because P. nathusi migrates out of the study area in September, and because the locations of maternity roosts and mating sites are stable and predictable from year to year in P. pipistrellus, but not so in P. nathusi. Male N. noctula also do not establish individual territories until later in the summer as the females are leaving their maternity colonies (Sluiter and van Heerdt, 1966; Gerell and Lundberg, 1985). Sluiter and van Heerdt (1966) reported that male N. noctula are solitary and

dispersed earlier in the summer, whereas Gerell and Lundberg (1985) state that male *N. noctula* establish bachelor groups during the nursing period.

In all three species, multiple females aggregate at some male territories. Female group sizes ranged from one to 10, with an average of 2.9 females/territorial male in *P. pipistrellus*, and from one to nine with an average group size of 3.5 females/territorial male in *P. nathusi* (Gerell and Lundberg, 1985; Gerell-Lundberg and Gerell, 1994). The group composition of females at male roost sites changes throughout the mating season (Sluiter and van Heerdt, 1966; Gerell and Lundberg, 1985; Gerell-Lundberg and Gerell, 1994), suggesting that females also may mate with several males. DNA tests show that the twins produced by *N. noctula* are sometimes sired by different males (Mayer, 1995), and that the sperm of one to five different males is present in the uteri of females (Mayer, personal communication). Mayer's studies using DNA suggest that levels of polygamy in female *N. noctula* may be as great as or exceed those of males.

Even though female composition in roost boxes is labile, both male and female *P. pipistrellus* show some fidelity to the same roost sites. Eleven of 13 marked males that attracted females in two successive years did so at the same box, and 25 of 46 marked females returned during these years to the same site. This resulted in some females roosting with the same male in successive years (Gerell and Lundberg, 1985). Female group size did not correlate with male size or age, but there was a significant correlation over years with the number of females that visited particular sites. Transient adult males that had not established territories were often captured in roost boxes, providing additional evidence that males compete for territorial roost sites, and that the number of available sites limits the population of breeding males. It was suspected that these surplus males attempted to 'steal' matings from territorial males (Lundberg, 1990).

In some of the first studies to reveal structured mating systems in bats, Dwyer (1970, 1971) reported seasonal harems in *Myotis adversus*. Mating occurs twice each year, in the fall and again in the spring. The colony of *M. adversus* in an abandoned railroad tunnel varied greatly in size, with few bats present there in winter (Dwyer, 1971). However, when present, males were usually solitary and largely faithful to particular holes in the wall of the tunnel, while females were typically in unisexual groups, or in groups with other females and pups. During the mating seasons, groups of up to 12 females ($\bar{x} = 7.6$), and females with their pups during the spring mating period (Bradbury, 1977a), roosted with the single males at their apparently territorial roost sites. Monthly censuses showed that these associations of females are labile and apparently short-term, occurring only during the mating season (Bradbury, 1977a).

Available evidence suggests that *Nycticeius humeralis* mate in seasonal single male/multi-female groups. In the northern part of its range in Missouri, *N. humeralis* form female-only maternity colonies during the summer (Watkins and Shump, 1981). In the fall, females and young of both sexes gain fat and migrate to unknown southern locations. In Florida, two males alternately roosted and mated with a group of 30 females between October and February (Bain and Humphrey, 1986). Because individual males were resighted, but did not roost together, it appears that males defend females from other males. Throughout the species' range, female *N. humeralis* show natal philopatry (Watkins and Shump, 1981;

Bain and Humphrey, 1986), but the same females use multiple roost sites which may provide mating opportunities for multiple males (Bain and Humphrey, 1986).

Neotropical *Ectophylla alba* appear to mate in seasonal harems (Brooke, 1990), roosting in tents that are occupied during most of the year by mixed sex groups of one to 17 bats (Figure 8.3). After young are born in April, tent groups segregate into small groups consisting of mothers and pups with a single adult male, or into bachelor groups of males only. This change of roosting group composition at birth led Brooke (1990) to suspect a post-partum oestrus and a harem mating system. The same bats roosted together for up to 45 days, and remained together after moving to different tents, suggesting substantial stability in roosting group composition.

Pipistrellus nanus in Africa roost in rolled-up banana leaves as well as in palms, thatch roofs, crevices and culverts (LaVal and LaVal, 1977; O'Shea, 1980; Happold and Happold, 1996). Throughout Africa *P. nanus* are currently recognized as a single species, but O'Shea (cited in Happold and Happold, 1996) has suggested that the thatch-roosting bats, which have a pair of glands on their tails, and the leaf-roosting forms, which lack these glands, might represent different species. The existence of cryptic species cannot be discounted even for well-known bats, as is
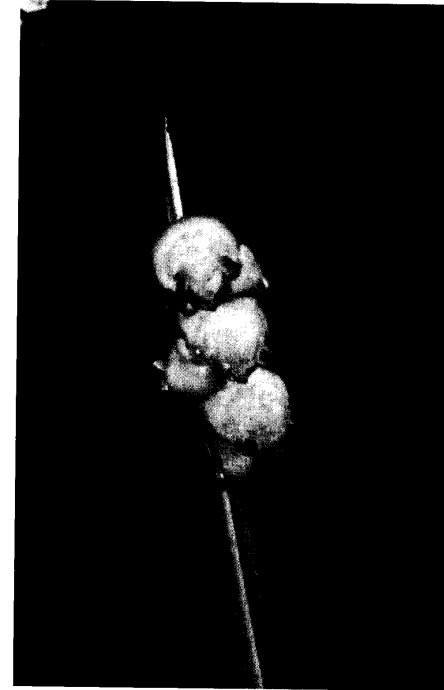
Figure 8.3 *Ectophylla alba* roosting in a *Heliconia* leaf, a bat that apparently mates in seasonal harems (photograph by A.P. Brooke).

illustrated by the recent discovery of two sibling species in what was believed to be *Pipistrellus pipistrellus* (Barlow and Jones, 1997; Barratt *et al.*, 1997).

Two studies have examined mating behaviors in *P. nanus*. One of these studies focused on a thatch-roosting population in Kenya (O'Shea, 1980), the other study on a leaf-roosting population in Malawi (Happold and Happold, 1996). In both studies, the bats roosted alone or in small groups during most or all of the year. Males were almost always solitary or with small groups of females. Females were solitary or in small single- or mixed-sex groups. One difference between the leaf-roosting and thatch-roosting forms is that thatch-roosting *P. nanus* appear to segregate into maternity colonies of 100 or more females and pups between November and January (LaVal and LaVal, 1977; O'Shea, 1980), whereas leaf-roosting forms segregate during the same period into smaller groups consisting of single females roosting alone with their pups or of two to three females with young.

In both studies, mixed-sex clusters were formed after young were weaned, with small groups of females aggregating temporarily around single males at the male roosting sites. Clustering behavior peaked at the beginning of the mating season (May or June to August) and persisted until November. The average size of these mixed sex clusters was small ($\bar{x} = 2.6$ bats (O'Shea, 1980); $\bar{x} = 2.4$ (Happold and Happold, 1996)), but groups of up to 10 or 12 females were occasionally found with single males. Census data from both populations showed that the composition of these female groups was highly labile, with no associations among particular females. In both studies, success in attracting females varied among males.

In the thatch, the average duration of a female's residence with a male was 1.8 days, and females roosted with several different males during the mating season (O'Shea, 1980). However, females showed preferences for particular males, and were found with their favored male 2.6 times more frequently than their next favored male. Of 44 color-banded resident males, the two most successful males accounted for 56% of all visits by females.

In the leaves, 19 males that were monitored repeatedly each roosted with between four to 21 ($\bar{x} = 9.1$) different females (Happold and Happold, 1996). Between May and June, 14 males captured in at least three censuses were found with between one to seven ($\bar{x} = 2.9$) different females, usually with one or two at a time, but sometimes with as many as five. Similarly, seven females that were captured at least three times during this period were found roosting with two to seven ($\bar{x} = 4.3$) different males.

The roost sites used by these two populations differ in important respects, as do the mating behaviors that were observed in the two studies. Significantly, thatch roost sites are stable and persist for years, whereas rolled banana leaf roost sites persist for only one to three days, until the leaf roll opens. In the thatch roosts, males maintained territories throughout the year, and 77% of all marked males were within 1 m of their previous roost site during all censuses. As a banana leaf provides a usable roost for only one to three days, leaf-roosting bats must move frequently to different leaves. However, multiple rolled leaves were always available either on the same banana plant or on nearby clumps of plants, and almost half (44%) of all males were found only in leaves located on the same plant or in leaves on a small number (< 5) of nearby clumps of plants. Such roost site fidelity was not seen in the leaf-roosting females.

Thatch-roosting males also showed obvious territorial behaviors. Calling by males, both in the roost and while flying nearby, was common and most intense during the mating season. Fights among males were common, as were injuries to males that were associated with this fighting (O'Shea, 1980). O'Shea (1980) found a positive correlation between the average number of females with a male and his calling activity.

Evidence for territorial behavior was equivocal in leaf-roosting *P. nanus* (Happold and Happold, 1996). Although males rarely roosted with other males, obvious territorial behaviors, including calling by males and injuries due to fights, were not noted. It appeared that competition among males for leaves or preferred clumps was not necessary because the numbers of rolled leaves and the numbers of clumps of plants with suitable leaf roosts always exceeded the number of males in the population. Roost site fidelity by males increased with an index of roost site 'quality' (assessed as the percentage of surveys in which a clump provided one or more suitable rolled leaves). However, the numbers of females that a male attracted did not increase with this index.

O'Shea (1980) concluded that *P. nanus* has a harem mating system based on territorial defense of roost sites and display behaviors by males. Happold and Happold (1996) argued that unstable groups of roving females that visit multiple males in quick succession are not harems. As leaf roosts provided a resource to the transient groups of females using them, they also argued that this mating system is not a lek. Happold and Happold (1996) suggested that the super-abundance of ephemeral roost sites results in minimal competition among males for resources (i.e. roost sites) needed by females. Thus, possession of a roost is not a reliable indicator of a male's competitive ability or fitness. Happold and Happold (1996) also note that *P. nanus* has a long (two- to three-month) mating season during which females are receptive. They argue that the lack of male–male competition and protracted female receptivity result in a promiscuous mating system, and they propose that levels of polygyny are determined largely by sperm competition.

8.3.4 Other Single-Male/Multi-Female Groups

Harem mating systems have been reported or suspected in at least 13 other tropical bat species (Table 8.3). *Pteropus seychellensis*, from the Comoro Islands, are reported as having harem groups (Cheke and Dahl, 1981), and both in the wild and captivity *Pteropus rodricensis* forms apparent harem groups of one male with up to eight adult females (Carroll and Mace, 1988). Captive groups of several other Old World fruit bats, including *P. hypomelanus*, *P. vampyrus* and *P. pumilus*, appear to mate in small harems in captivity (J. Seyjagat, personal communication). Paternity information obtained using variable microsatellite DNA markers has demonstrated a high level of polygyny in the captive breeding colony of *P. vampyrus* at the Lubee Foundation, Inc. (Comeaux and McCracken, unpublished). Although this colony contained as many as 10 adult males, the DNA studies proved that three of these males sired 25 of the 26 pups that were born in the colony (the three males sired 13, 10 or two pups and the paternity of one pup was not identified). Interestingly, independent assignations of paternity based on observations of the roosting associations of males and females and male dominance were often incorrect,

demonstrating that female *P. vampyrus* often mate outside of their apparent harems (L.B. Comeaux and G.F. McCracken, unpublished).

Kunz and McCracken (1996) hypothesize that many of the bats that live in tents (reviewed in Kunz *et al.*, 1994) have harem mating systems, but little is known about group composition, seasonality, or group stability for most of these bats. In Trinidad, Kunz and McCracken (1996) found groups of two to six adult female *Uroderma bilobatum* roosting with single males, some of the females with pups. If these are harems, information from Costa Rica suggests that female group composition is highly labile (Lewis, 1992b). Seasonal changes in population size at study sites (Timm and Lewis, 1991; Lewis, 1992b) also suggest that female group formation in *U. bilibatum* may be seasonal, and that many roosting clusters may be maternity groups rather than harems (Lewis, 1992b). Ten of 11 roosting groups of *Vampyressa nymphaea* captured by Brooke (1987) contained one adult male with enlarged testes and up to three pregnant or lactating females and their young. The same individuals used the same tent for at least eight days and one tent was used for more than nine months, but there is no information on the compositional stability of groups. Similarly, 12 complete tent roosting groups of *Artibeus cinereus* captured by T.H. Kunz and G.F. McCracken (unpublished) on Trinidad consisted of
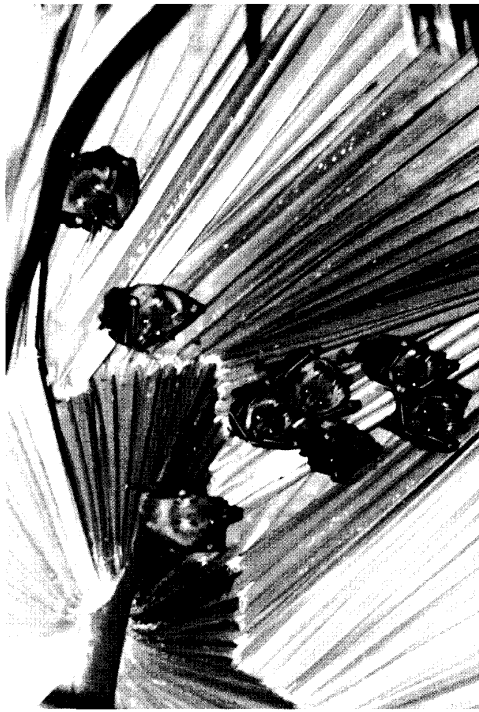
Figure 8.4 Tent-making bats *Cynopterus brachyotis* roosting in a *Livistonia chinensis* palm (photograph by T.H. Kunz).

up to five females ($\bar{x}$ = 1.6 females/group) with a single adult male. In Pennisular Malaysia, *Cynopterus brachyotis* roost alone or in groups in tents formed when bats modify the leaves of palms, orchids, philodendrons and other plants (Tan *et al.*, 1997; Figure 8.4). Individuals roosting alone were always males, while groups consisted of a single adult male and up to four adult females. Harem composition appears stable as the same bats roosted in the same tent for several months. The capture of three subadult females roosting with a subadult male suggests that harems in *C. brachyotis* may form as age cohorts (Tan *et al.*, 1997). A harem mating system also has been suggested for *C. horsefeldi*. Four groups of *C. horsefeldi* that were captured in naturally occurring concavities of epiphytic ferns consisted of one adult male and two or three adult females, some with young (Tan *et al.*, 1998).

In Durban, South Africa, single adult male *Otomops martiensseni* roost with small groups of adult females and their young in buildings (Richardson and Taylor, 1997). Roosting females are spaced 100 to 300 mm apart with the male about 1 m from the female group. Adult males are about 5% larger than adult females and resident males are more aggressive than females; all suggest that *O. martiensseni* may mate in harems (Richardson and Taylor, 1997). In contrast, populations of the same species in Kenya roost tightly packed in caves, and appear to lack sexual dimorphism (Mutere, 1973).

8.4 MULTI-MALE/MULTI-FEMALE GROUPS

Many bats mate in multi-male/multi-female colonies. In many of these species males establish themselves at preferred roosting sites where males may be dominant or territorial. The males at preferred sites may have greater access to females and greater success at mating than males at other sites. Territorial males often call, have display behaviors, and may mark females, their territories, or themselves with glandular secretions. Several other bat species roost in mixed sex colonies, but males establish display sites or territories for mating away from their regular roost sites.

8.4.1 Seasonal Multi-Male/Multi-Female Polygynous Groups

Tadarida brasiliensis, *Myotis myotis*, *Rhinolophus ferrumequinum*, *Macrotus californicus* and *Miniopterus minor* mate in seasonal male territories within mixed-sex colonies. *Tadarida brasilensis* overwinters in mixed sex colonies that either hibernate (*T. b. cynocephala*, Sherman, 1937; *T. b. mexicana*, Cockrum, 1969) or migrate (*T. b. mexicana*, Villa-R., 1956; Villa-R. and Cockrum, 1962; Cockrum, 1969). In summer, females and pups live in largely sexually segregated maternity colonies that include some of the largest aggregations recorded for any mammal (Davis *et al.*, 1962). Until recently, the mating system of *T. brasilensis* has been an enigma. Sherman (1937) reported that in spring all individuals of a nonmigratory population of *T. b. cynocephala* in Florida left their usual roost for a one-week period during which they mated at an unknown site. Others (Villa-R. and Cockrum, 1962; Davis *et al.*, 1962; Constantine, 1967; McCracken *et al.*, 1994) have suggested that mating in migratory populations occurs in winter roosts shortly

before migration, or at sites along their spring migratory routes (Cockrum, 1969; McCracken et al., 1994).

Recent evidence of their mating system comes from observations in captive and wild colonies. Lollar (1995), A. Lollar (personal communication) and B. French (personal communication) report that between November and February males in captive colonies establish small territories in the roost that are visited briefly by multiple females for mating. Male territorial behavior involves aggressive interactions among males, vocalizations and scent marking of territories and females. A. Lollar and B. French both noted differential success among males in attracting females and mating with them.

In the wild, mating was observed during a three-week period between mid-March and early April in caves and under bridges in Central Texas (A. Nicklaus and B. Keeley, personal communication). Nicklaus and Keeley also observed male vocalizations and scent marking, but mating interactions seemed far more chaotic than were observed in captivity. Two distinct copulatory strategies seemed evident: (1) the male aggressively pulled a female from a group, restricted her movements, and mated with her while vocalizing; or (2) the male moved slowly over a female in a group and they quietly mated with no apparent reaction from the female and no male vocalizations. Marked individuals of both sexes mated multiple times, and some of the same individuals engaged in both types of matings. Vaginal plugs that were either ejected or removed from females littered the floors below roosts. Available evidence shows that *T. brasiliensis* is promiscuous, but these observations in captivity and the wild suggest that they may employ as many as three different strategies for mating. This species clearly demands additional research.

Male *Myotis myotis* establish and defend roosting sites of ca. 250 cm^2 in area in attics that may also be occupied by females and juveniles (Zahn and Dipple, personal communication). Males are not faithful to one site, and may roost at different sites on different days. Different males may also use the same sites sequentially. However, the fidelity of males to preferred sites increases from May to August, and peaks during the August–September mating season. Some of the same males used the same sites for up to six years (Zahn and Dipple, personal communication).

Female *M. myotis* visit and mate with males at these sites. Females typically remain with a male for a few days, they visit several different males during the mating season, and may return to visit the same male several times. Males apparently show no obvious behaviors to attract females, but females visit and mate with some males more frequently than with others. During one mating season, five males were each visited by a minimum of four to nine females, and the most successful male accounted for 14 of 31 observed copulations (Zahn and Dipple, personal communication).

While mating in *M. myotis* usually occurs in male roosts with females visiting from different roosts, some males also roost with females at maternity sites. Banding studies and genetic analysis based on a microsatellite locus and mtDNA sequence information indicate that females are philopatric to their natal maternity sites, that males disperse, and that males at maternity sites are not related to the females (Petrie et al., 1997). Microsatellite paternal allelic contributions for 46

mother/pup pairs in a large (ca. 700 adult females) maternity colony in Bavaria showed that no males monopolize paternity. The maximum likelihood of paternity for 19 males that roosted at the maternity site was 0.178 (SD = 0.1), consistent with the conclusion that most females mate with males at other sites (Petrie et al., 1997). Interestingly, the genetic tests suggested that a group of males roosting about 16 km from the maternity site were both more closely related to the females and had higher success at mating with them. The suggestion that female *M. myotis* may selectively mate with related males demands more study (Petrie et al., 1997).

Rhinolophus ferrumequinum appears to have a polygynous mating system that involves male territoriality (G. Jones, personal communication). Beginning in September, male *R. ferrumequinum* in England establish themselves at apparently territorial sites in mines and caves. These sites are marked with brown stains that are presumably from scent marks of males. Multiple females gather at these sites and mating can occur through the hibernation period. Males maintain large testes throughout the winter and secretions from males form a vaginal plug that is shed by females in April, which is presumably the time of fertilization (G. Jones, personal communication).

In September, males in a California population of *Macrotus californicus* establish and defend preferred roosting locations in an abandoned mine that was not their normal roost site (Berry and Brown, 1995). Displays involving wing flapping and vocalizations attract females for copulation and some males were more successful than others in mating. Berry and Brown (1995) also report that in summer small clusters of females and pups are attended by a single displaying male.

In coastal east Africa, McWilliam (1990) reports that male *Miniopterus minor* aggressively compete for access to a dome in the ceiling of a cave every year when their testes are enlarged. Fifteen of 25 males were faithful to the dome from May to July and several returned for three successive years. Males roosting in the dome cover their venters with urine and emit a conspicuous odor during the mating period. At the beginning of the mating period, males occupying the dome were heavier and older than males roosting elsewhere in the cave. Although McWilliam (1990) did not observe copulations, he interprets the competition among males as evidence that mating is concentrated in the dome. During the mating season females move between roosting sites within and between caves and do not roost with males for extended periods. All females sampled were pregnant by the end of July when males abandoned the mating site. Pregnant females leave coastal mating caves and move inland where they give birth in sexually segregated maternity colonies (McWilliam, 1990). Because males appear to aggregate in a traditional location for mating, McWilliam (1990) argues that *M. minor* exhibits a lek mating system. Additional studies including direct observations of copulations or paternity analysis are needed to confirm this conclusion.

During the summer *Plecotus auritus* forms stable mixed-sex colonies of five to 55 ($\bar{x}$ = 16.8) individuals in attics (Speakman et al., 1991). Mating has been observed rarely, but is reported to occur in summer colonies and in transient roosts or hibernation sites in fall and winter. Females store sperm and fertilization occurs in early spring (Speakman and Racey, 1987). Recent paternity testing using six microsatellite loci (Burland, 1998) established that a third of assigned paternities

involved males from the same summer roost sites as their mates, although males from up to 10 km away sired young. The long mating season, absence of a vaginal plug, and sperm storage appear to provide considerable opportunity for sperm competition. Nevertheless, paternal allelic contributions in 86 offspring indicated no skew in male reproductive success.

While both sexes of P. auritus are philopatric, Burland's (1998) genetic data indicate that females are more likely than males to remain in their natal roosts. The average relatedness among females within 23 colonies was 0.009 to 0.042, whereas average relatedness among males was 0.007 to 0.022. Males and females within colonies had average relatedness of 0.002 to 0.039. The presence of related males and females within a colony creates the possibility for inbreeding. Burland (1998) did, in fact, identify four parental pairs with pair-wise estimates of relatedness greater that 0.2; consistent with consanguineous mating. However, all data across all loci showed an inbreeding coefficient of −0.001. Thus, despite natal philopatry by both sexes, inbreeding appears to be avoided in P. auritus.

In several species of Australian Pteropus, including P. alecto, P. gouldi (= alecto), P. poliocephalus and P. scapulatus (Nelson, 1965; Martin et al., 1995), both sexes aggregate in spring at traditional camps located in trees (Figure 8.5). Here, females give birth and raise their young, and males set up territories around females. After copulation, both sexes disperse from the traditional mating sites and may live either in sexually segregated winter camps (Nelson, 1965) or as individual nomads (Martin et al., 1995).

There is little information on mating for most of these species but, in the best-known species, individuals appear to be both monogamous and polygynous. In Pteropus poliocephalus, a male's mating success appears to be related to the location of his territory within a camp. Nelson (1965) reports that males with territories near the center of the camp are polygynous, while males with territories away from the camp's center are monogamous. Males roosting on the periphery of the camp rarely roost with females. Nelson (1965) also noted higher monogamy among males that set up territories around females that were caring for a pup of the previous year (Nelson, 1965).

The case of Myotis lucifugus

Myotis lucifugus has been 'the bat' for many studies on reproduction (Fenton, 1984), and it is the best known temperate cycle species in which mating has been cited as random and promiscuous (Thomas et al., 1979; Wai-Ping and Fenton, 1988). Myotis lucifugus hibernates in mixed sex groups in caves and mines, and is largely sexually segregated in maternity colonies in spring and summer (Fenton, 1969; Humphrey and Cope, 1976). In Ontario, 'swarming behavior' begins in July when groups, mostly of males and nulliparous females, briefly visit the hibernation sites. Hibernating populations begin to build up in August when adults of both sexes and subadults arrive in groups during a second period of swarming (Fenton, 1969). Mating activity peaks in August, but continues even among hibernating bats through the fall, winter and spring (Figure 8.6).

Figure 8.5 A camp of Pteropus poliocephalus in Brisbane, Australia (photograph by G.S. Wilkinson).

Figure 8.6 Myotis lucifugus copulating in August in a mine at Renfrew, Ontario (photograph by M.B. Fenton).

During the peak of mating activity, males visit small crevices or holes in the walls of the roost where they land briefly, and from which they make short, 2 to 10 m, looping flights. Males frequently move to different crevices and holes where they repeat these behaviors. Small groups of bats join males at these sites, and 77% of 90 copulations observed in an abandoned mine occurred at holes (Thomas *et al.*, 1979). However males showed no fidelity to holes, no territorial behavior, and no evidence for displays or social interactions (Barclay and Thomas, 1979; Barclay *et al.*, 1979; Thomas *et al.*, 1979). Copulation occurred immediately upon contact between a male and female. The short looping flights of males could serve to attract females, but there was no apparent relationship between flight activity and the numbers of females attracted to holes. Thomas *et al.* (1979) concluded that mating was indiscriminant. Subsequently, Wai-Ping and Fenton (1988) found no relationship between the size and mass of males that were captured in copula versus those not copulating, providing further support for indiscriminant mating.

Indiscriminant mating in *M. lucifugus* is supported by frequent observations of males copulating with torpid females. Copulating pairs have been found in hibernacula throughout the hibernation period (Wimsatt, 1945; Fenton, 1969), and Thomas *et al.* (1979) observed matings when males that had been disturbed into flight landed on single or grouped torpid bats and attempt to 'force' copulations. At this time, males not only copulate with females, but also with other males (Thomas *et al.*, 1979).

Despite this evidence, the recent examination of DNA fingerprints shows that fertilization in *M. lucifugus* is non-random (Watt and Fenton, 1995). Multilocus DNA fingerprint profiles of mothers and their single nursing pups revealed that the percentage band sharing between pups was significantly greater than the band sharing observed between the mothers or between a cohort of other adult females captured in the vicinity. The closer DNA fingerprint similarity among pups indicates that successful fertilizations were non-random and skewed toward particular males or male lineages. While it seems likely that non-random fertilization is achieved as a consequence of non-random mating, sperm competition in multiply mated females cannot be eliminated (Watt and Fenton, 1995). *Myotis lucifugus* provides an excellent example of the fact that mating systems in bats, and other social interactions as well, can be exceedingly difficult to determine even with careful observational studies.

8.4.2 Year-round Multi-Male/Multi-Female Groups

Groups of eight to 12 adult female vampire bats (*Desmodus rotundus*) roost throughout the year in hollow trees or caves with groups of two to 10 adult males (Wilkinson, 1985a, b; Figure 8.7). Males fight with one another for locations at the top of roosts that contain females, and top males have the highest mating success. In tree hollows, 20 of 42 adult males that were observed in top positions accounted for 16 of 21 observed copulations, with the second highest males achieving two matings, and lower males the remaining three (Wilkinson, 1985b). Females were observed mating with top and lower males on successive days, and females were also known to mate with and have offspring from males of other roosts (Wilkinson, 1985b). Genetic data show that top males sire about 46% of the pups born in their

Figure 8.7 A cave-roosting group of common vampire bats *Desmodus rotundus* (photograph by G.S. Wilkinson).

colony, and that top males sire about two times as many offspring as an average male (Wilkinson, 1985b).

Groups of female vampire bats are stable with a new female entering a group about every two years. Average adult male tenure is 17 months, and adult males move among groups more frequently than do females. Female offspring are recruited into their mother's group, while young males disperse (Wilkinson, 1985a, b). Because of these dispersal patterns, a roosting group of vampire bats consists of adult males that are unrelated, and sets of females that are related through different matrilines. Male movements and high juvenile mortality suggest that it is unlikely that females in groups are related through common paternity. Genetic data show that average relatedness among female group members is 0.02 to 0.03 (Wilkinson, 1985b).

A similar vertical structure in male roost-site location and mating success is seen in *Pteropus giganteus*. In India, *P. giganteus* aggregate in trees in permanent, year-round colonies of several 100 or more bats (Neuweiler, 1969). Adult males are faithful to particular roost site locations, with a vertical rank-order in which dominant males roost higher in the tree than subordinate males. Females and their pups also aggregate in the upper branches of these trees. The higher roost sites of dominant males appear to provide reproductive advantage. During the period from

birth (March) through mating (July) many young males roost in separate trees apart from the major colony.

While they did not detect any relation between roosting position and male dominance, Bradbury and Vehrencamp (1976) suggested that *Rhynchonycteris naso* has a polygynous mating system involving a dominance hierarchy among males. In Trinidad and Costa Rica, colonies typically consist of five to 11 individuals with both sexes in approximately equal numbers. Colonies roost on the exposed boles of trees or on cliffs, with individuals spaced 2 to 4 cm apart, often in a vertical line (Figure 8.8). Male membership in colonies fluctuated over a period of months, but a particular male was always present at each colony. These 'most-constant' males frequently returned to the day roost at night, whereas other males rarely did so. Most-constant males also were often observed foraging at the periphery of female colony-specific foraging areas, and harassing intruders from other colonies. Some males appeared to have preferred access to matings and copulated without interruption from nearby males, while other males were unsuccessful at copulating.

Two other emballonurids, *Peropteryx kappleri* and *Balantiopteryx plicata* roost year-round in mixed sex colonies. Colonies of *P. kappleri* in Costa Rica were found

Figure 8.8 *Rhynchonycteris naso* in their typical 'in a line' roosting configuration (photograph by A.P. Brooke).

in hollow logs and tree boles and averaged 4.3 bats per colony (Bradbury and Vehrencamp, 1976), whereas in Columbia colonies in abandoned mines were substantially larger with five to 147 bats per colony (Giral *et al.*, 1991). A colony of *B. plicata* in a cave in Costa Rica had a population size of 1500 to 2000 bats. Colonies of both species were subdivided into smaller roosting clusters, but the two sexes were interspersed with no evidence for male territoriality or female grouping.

Within clusters, *P. kappleri* maintain the individual spacing of a few cm that is typical of many emballonurids, and the same individuals remained in the same roosting locations throughout a 14-month study (Giral *et al.*, 1991). However, Bradbury and Vehrencamp (1976) reported that *P. kappleri* roost in dorsal-ventral contact except when disturbed, at which time they then assume individual spacing. Bradbury and Vehrencamp (1976, 1977) suspected that *P. kappleri* may be monogamous because clusters sometimes consisted of one or two adult male/female pairs. In the larger colonies in Columbia, adult females always outnumbered adult males with an average colony sex ratio of 1.4 females/male. For this reason, Giral *et al.* (1991) suspected a harem mating system. At present, we can conclude only that *P. kappleri* mate in mixed sex colonies, and that some level of polygyny seems likely.

The colony of *B. plicata* in Costa Rica was divided into clusters of 50 to 200 bats that roosted in cracks, tunnels, and concavities of the cave surface (Bradbury and Vehrencamp, 1976). A similar colony structure was documented in Guerrero, Mexico (Lopez-Forment, unpublished; cited in Bradbury and Vehrencamp, 1976). In contrast to Giral *et al.*'s (1991) observations on *P. kappleri*, colonies of *B. plicata* in both Costa Rica and Mexico showed a consistent male sex ratio bias. Over ten months of censuses, only 23% of the adults captured in the Costa Rica roost were females. In both Costa Rica and Mexico this superbundance of males peaked in the dry season when mating occurs, and thereafter the fluctuating excess of males decreased. This seasonal pattern led both Bradbury and Vehrencamp (1976) and Lopez-Forment (unpublished) to conclude that, while males are always in abundance, male excesses decrease for much of the year because males move away from these sites after the mating season. Bradbury and Vehrencamp (1977) described mating in *B. plicata* as a possible 'mating swarm'.

8.4.3 Multi-Male/Multi-Female Groups That Mate Away From the Roost

Males of several paleotropical fruit bats establish nocturnal display sites where females visit males for mating. Details of this behavior are available for *Hypsignathus monstrosus*, which mates in leks (Bradbury, 1977b), and for *Epomophorus wahlbergi* (Wickler and Seibt, 1976), and *Epomops franqueti* (Brosset, 1966; Bradbury, 1977b). Unpublished observations by G.S. Wilkinson indicate similar behavior in *Epomophorus crypturus*.

Leks are defined by four criteria: (1) absence of male parental care, (2) the mating arena is significantly smaller than the normal home ranges of both males and females, (3) male territories contain no resources, and (4) females have the opportunity to select mates (Bradbury, 1977b; 1982). While the mating systems of many bats satisfy the first two criteria, little is known for many species with regard

to the resources provided by mating sites, such as protection or food, or with regard to mate selection. Thus, in bats, leks have been convincingly documented only for *H. monstrosus* (Bradbury, 1977b).

Hypsignathus monstrosus roosts in trees during the day, mostly as singles of either sex, but also in mixed sex groups of up to 17 individuals. Males typically roost at the periphery of larger groups (Bradbury, 1977b). During biannual breeding seasons that occur in Gabon, males fly at dusk to traditional display areas. There, males establish hanging sites in trees from which they call with loud, repetitive vocalizations. Male sites are spaced approximately 10 m apart, and individual males use the same site each night. Display areas that were studied in detail during the peak of the July mating season ranged between 1.6 to 6.4 ha in size, and included the hanging sites of 25 and 132 males, respectively. Different display areas were located 5 to 18 km apart, all in riparian forest along major streams or rivers. All of the display areas were traditional sites that had been used for many years.

Females enter the display area and hover near the calling male. Females visit some males much more frequently than others, and males respond to female visits by greatly accelerating the rate of their calling, giving a 'staccato buzz'. After several visits, the female lands and copulates with a chosen male. By monitoring the frequencies of staccato buzzes, Bradbury (1977b) determined that males at sites located near the centers of the display areas receive 10 to 20 times more visits from females than males at more peripheral sites. Direct observation of 50 copulations indicated high polygyny, with 6% of the males accounting for 79% of the observed matings.

Studies on the distribution of food resources and the foraging movements of males and females demonstrate that, except for a mate, the male display areas do not provide resources to females. *Hypsignathus monstrosus* also show obvious evidence of the strong sexual selection that is typical of other species with lek mating systems (Bradbury, 1982). *Hypsignathus monstrosus* has the most extreme sexual dimorphism of any bat. Males are almost twice the weight of females, and males have a large hypertrophied larynx that fills more than half of their body cavities.

Epomophorus wahlbergi roosts in palm leaves or thatch roofs in mixed sex colonies of three to over 100 individuals (Wickler and Seibt, 1976). Except for female-pup pairs, individuals are spaced a minimum of 2.5 cm apart. They maintain this roosting configuration year-round, and consistently maintain preferred roosting locations, but there are no apparent associations between males and females. Observations during two successive January mating seasons showed that individuals leave the roost independently at dusk, and males fly various distances from the roost, calling audibly as they fly. Males continue to call from apparently traditional hanging sites that are in or close to their feeding areas, but rarely closer than 30 m from the calling site of another male. Other bats, presumably females, are attracted to calling males and hover in front of them as males increase the repetition rate of their calls and evert their whitish yellow epaulets. Males and visitors were observed touching noses and licking, but copulations were not observed.

Like *Epomophorus wahlbergi*, single male *E. crypturus* and *Epomops franqueti*

call from roost sites that are more dispersed than those of *H. monstrosus*. Bradbury (1977b) also observed female or juvenile *E. franqueti* feeding near the territory of a calling male, suggesting that male territories may provide females or juveniles with other resources. Male *Epomophorus crypturus* call from roosts in trees that are spaced about 50 m apart along rivers. Calling males are visited by other bats that are presumably females, but mating was not observed (G.S. Wilkinson, unpublished observations). With the information available, the mating systems of *E. wahlbergi*, *E. crypturus* and *E. franqueti* do not fulfill the definitional requirements for a lek. There is no information on levels of polygyny in *E. wahlbergi*, *E. crypturus* or *E. franqueti*.

8.5 SINGLE MALE/SINGLE FEMALE GROUPS

Since Bradbury's (1977a) review, monogamy has been reported for five other bat species: *Pteropus samoensis* (Cox, 1983; Pierson and Rainey, 1992), *Rhinolophus sedulus* (Heller and Volleth, 1989; Heller *et al.*, 1993), *Cardioderma cor* (Vaughan, 1976; McWilliam, 1987b), *Saccopteryx leptura* (Bradbury and Vehrencamp, 1976; 1977), and questionably, *Peropteryx kappleri* (Bradbury and Vehrencamp, 1977). Additional information is available for two of the 11 species listed by Bradbury as monogamous: *Vampyrum spectrum* (Vehrencamp *et al.*, 1977; A.P. Brooke, G.F. McCracken, and G.S. Wilkinson, unpublished observations) and *Hipposideros beatus* (Brosset, 1982), and for *Lavia frons* (Wickler and Uhrig, 1969; Vaughan and Vaughan, 1986, 1987), a species that Bradbury discussed as monogamous, but did not include in his table. Thus, monogamy has been reported for a total of 17 bat species (Table 8.3).

Lavia frons and *C. cor* are sit and wait predators that hang from low branches on trees or bushes, listening for prey that are usually on the ground. Both species approach and attack prey in short flights from habitual roosting sites that are within feeding territories. In *L. frons*, male/female pairs roost in the same territory during the day, and pair-specific roost sites and foraging areas remain stable for at least several months (Wickler and Uhrig, 1969; Vaughan and Vaughan, 1986, 1987).

In contrast, *C. cor* roost by day in colonies of 80 or more individuals in hollow trees (Vaughan, 1976) or caves (McWilliam, 1987b). In the evening these bats leave their day roosts for habitual hanging sites where the bats sing and maintain foraging territories. Working in inland southern Kenya, Vaughan and Vaughan (1986) reported that singing was seasonal, occurring only during the March–April wet season. Vaughan and Vaughan (1986) reported individual, but not pair-specific territories. At a different site in coastal Kenya, McWilliam (1987b) found that singing was exclusively a male behavior that occurred primarily in the long dry season. At the coastal site, pairs were observed together from June to November, often sharing the same hanging site in close contact, and showing joint circling flights. Pregnant or lactating females and juveniles were present throughout the year, but peak pregnancy occurred in December.

Vampyrum spectrum is the only bat known to form long-term pair-bonds and to live in extended family groups. Adult pairs have roosted together in the same hollow tree for over a year, and the apparent offspring of up to three successive

reproductions have remained with their parents (Vehrencamp et al., 1977; A.P. Brooke and G.F. McCracken, unpublished observations). *Vampyrum spectrum*, which is carnivorous and the largest bat in the neotropics, apparently forages alone, mostly on colonial roosting birds, but also on rodents and other bats (Vehrencamp et al., 1977).

Saccopteryx leptura roost on the sides of trees in small groups. Group size in Trinidad ranged from one to five ($\bar{x}$ = 2.6) individuals (Bradbury and Emmons, 1974), whereas group size in Costa Rica ranged from two to nine ($\bar{x}$ = 4.6) individuals (Bradbury and Vehrencamp, 1976). At both sites, pairs consisting of a male and female were most common, suggesting that monogamous pairs are the basic social unit of this bat (Bradbury and Emmons, 1974; Bradbury and Vehrencamp, 1976, 1977; McCracken, 1984). Groups larger than two appear to consist of two or more adult pairs or pairs with offspring which may be retained in the parental group for up to a year (Bradbury and Vehrencamp, 1976). This group configuration was maintained throughout the year at both sites, but some individuals shifted roosting trees. When larger groups split, the same male/female pairs typically remained together.

Roosting groups of *S. leptura* share colony-specific foraging areas. Most foraging was by solitary bats using separate but adjacent beats, but colony members also foraged in groups, and groups actively defended foraging areas from bats belonging to other colonies. Volant juveniles up to three months old sometimes foraged with their mothers (Bradbury and Vehrencamp, 1976).

Brosset (1982) reported on a population of *Hipposideros beatus* that roosted opportunistically in traps that were set in a grid to capture chevrotains. The regular dispersion of these roost sites over a small island suggested territoriality, and the same sites were occupied continuously by male/female pairs throughout a three year study. Marked pairs of *H. beatus* remained together throughout one year, but new pairs were formed at the beginning of each annual mating season. Yearlings associated in territories with adult pairs that were not their parents (Brosset, 1982).

Less information is available for *Pteropus samoensis, Taphozous peli* and *Rhinolophus sedulus*. *Pteropus samoensis* roosts and forages in pairs in primary rainforest. Repeated observations of single males and females roosting together, interacting at roost sites, and sharing the same foraging areas leads to the conclusion that they pair-bond (Cox, 1983; Pierson and Rainey, 1992). Similarly, monogamy is suspected in *R. sedulus* because it also typically roosts in pairs (Heller and Volleth, 1989; Heller et al., 1993). Further evidence for monogamy in *R. sedulis* is provided by DNA fingerprint profiles that demonstrate an extremely high probability of paternity for an adult male that was captured roosting together with a lactating female and non-volant, nursing young (Heller et al., 1993).

Monogamy implies that males can contribute to the survival of females or pups. The only evidence for male parental care in bats comes from *V. spectrum* and *L. frons*. In *V. spectrum*, at least one adult or older offspring remains in the roost with the most recent juvenile, while the other bats in the group forage. Foragers bring prey to the roost, and the energy content of these prey may exceed the needs of the solitary forager. Thus, it appears that both adults and the older offspring share in 'guarding' young and in provisioning the bats that remain in the roost (Vehrencamp et al., 1977). Provisioning has been documented both in the wild, where a male brought prey to a juvenile in his roost (G.S. Wilkinson, personal observation), and in a captive breeding pair, where the male frequently provided food to the female that was caring for a pup (cited in Vehrencamp et al., 1977).

In *L. frons*, the single juvenile remains closely associated with both parents at roost sites and on the foraging area for up to 50 days after young become volant (Vaughan and Vaughan, 1987). During this period, juveniles frequently huddle with and nurse from the mother at the roost site. The mother remains within a few meters of her young on the foraging grounds, the young frequently follows its mother on foraging flights, and she allows it to replace her at her roosting sites. Fewer interactions were observed between the juvenile and the male, but the male also allowed the young to take over his roosting sites (Vaughan and Vaughan, 1987).

The unusual foraging habits of *V. spectrum, L. frons,* and probably *C. cor*, appear to involve an extended period during which young must learn to forage. The extended period of parental involvement with the young, and, in the case of *V. spectrum*, the ability of the males to provision females and offspring, evidently select for monogamy in these bats (Vehrencamp et al., 1977; Vaughan and Vaughan, 1987).

8.6 ECOLOGICAL DETERMINANTS OF MATING SYSTEMS IN BATS

While there has been substantial progress in describing bat mating systems, there has been considerably less progress toward understanding the ecological factors responsible for their evolution and maintenance. The conventional view holds that female dispersion patterns are primarily influenced by resource distribution while male dispersion patterns are primarily determined by female dispersion (Bradbury and Vehrencamp, 1977; Emlen and Oring, 1977). In mammals without paternal care, mating systems can be defined by what males defend, i.e. either females (female defense) or resources needed by females (resource defense). Leks are often considered a default mating system, adopted when males cannot defend either females or resources because resources are too finely distributed and females range too widely in unstable groups (Bradbury and Vehrencamp, 1977; Bradbury, 1981).

In bats, female defense polygyny has been attributed to *Phyllostomus hastatus* (McCracken and Bradbury, 1977, 1981) and *Tadarida pumila* (McWilliam, 1988). The similar mating systems of *Myotis bocagei* (Brosset, 1976), *Coleura afra* (McWilliam, 1987a), and *Noctilio leporinus* (Brooke, 1997) suggest that single males may defend stable groups of females in these species. Resource defense polygyny has been attributed to *Carollia perspicillata* (Williams, 1986), *Artibeus jamaicensis* (Morrison, 1979; Morrison and Handley, 1991), *Pipistrellus pipistrellus* (Gerell and Lundberg, 1985; Lundberg and Gerell, 1986), *Pipistrellus nathusii* (Gerell-Lundberg and Gerell, 1994) and several tent-roosting species of bats (e.g. *Artibeus jamaicensis, Artibeus cinereus* and *Uroderma bilobatum*, Kunz and McCracken, 1996; *Cynopterus sphinx*, Balasingh et al., 1995; *Cynopterus horsefeldi*, Tan et al., 1999) where preferred or limited roost sites may be defended from other males and used by groups of females. Resource defense polygyny has also been attributed to *Saccopteryx bilineata* (Bradbury and Vehrencamp, 1976,

1977) because males defend foraging areas utilized by multiple females, and to *Pipistrellus nanus*, where males may also defend foraging areas used by females (O'Shea, 1980).

These attempts to identify underlying ecological causes place important focus on understanding the evolution of diverse mating systems, but there are problems. One problem is the difficulty of inferring causation from correlation. Once females form groups at a fixed site, then males can either defend locations preferred by those groups or they can defend the groups directly. Related to this is the problem that the distribution of potential mates and their resources are linked, and both may be objects of defense (Ostfeld, 1987). While correlations between food dispersion, female dispersion, and mating systems have been documented in epomophorine (Bradbury, 1981) and emballonurid (Bradbury and Vehrencamp, 1977) bats, experimental evidence supporting causal factors influencing mating system variation is lacking for bats and for most other mammals (Davies, 1991). Lundberg and Gerell's (1986) experiments of adding new roost boxes to manipulate the resources available to *Pipistrellus pipistrellus* are a notable exception. These experiments appear to confirm resource defense polygyny in *P. pipistrellus*.

Some studies on bats have recognized the above problems. McWilliam (1988) suggested that the female defense mating system of *Tadarida pumila* may also involve resource defense because roosting sites are defendable. Kunz *et al.* (1983) suggested that harem polygyny may be best described as resource defense where *Artibeus jamaicensis* roost in limited available tree holes (Morrison, 1979; Morrison and Handley, 1991), but as female defense where this same species roosts in abundantly available erosion concavities in caves.

If mating systems are determined by what males can defend, it might be assumed that females have little opportunity to assess and choose mates. While female mate choice is clearly important in determining the extreme mating skew that occurs among lekking males (Bradbury, 1977b), leks are thought to result when males can defend neither females nor their resources. Indeed, it has been argued that polygynous territorial mating systems driven by female choice, such as have been proposed for birds (Verner, 1964; Orians, 1969), are inappropriate for most mammals because female mammals are often philopatric to their natal area, female groups often persist over seasons, and males often impose themselves on pre-existing female groups (Clutton-Brock, 1989).

These arguments clearly do not apply to many bats. As described above, seasonal male mating territories have been observed in many temperate cycle bats as well as several tropical species. In many of these species (e.g. *Pipistrellus pipistrellus*, *P. nathusi*, *P. nanus*, *Nyctalus noctula*, *Macrotus californicus*, *Tadarida brasiliensis*, *Saccopteryx bilineata*) males produce audible vocalizations which are often accompanied by aerial displays. *Saccopteryx bilineata* also differs from many other mammals in that females, not males, disperse from their site of birth (Bradbury and Vehrencamp, 1976). In all of these species, females do not form stable groups and frequently move between males during the mating season. While experimental work is needed to determine if females visit males to gain access to roosting sites or to preferred mates, these examples indicate that female choice is likely to be more important in determining male mating success in bats than in most groups of mammals.

Just as opportunities for female mate choice should be inversely related to female group stability, a male's opportunity to monopolize paternity within female groups should also be associated with the stability of female social groups. None the less, even in *Phyllostomus hastatus* which exhibits the highest level of female group fidelity known for bats, at least 10% of the offspring born to harem females are sired by males from outside of the harem (McCracken and Bradbury, 1977; 1981). Information on levels of polygyny and polyandry is lacking for almost all bats. However, the many examples of seasonal male mating territories, and the many examples of year-round social groups in which female group composition is unstable (Table 8.3), suggest that females mate with multiple males in many and probably most species of bats.

Multiple mating by females, as well as features of the reproductive physiology of bats (Racey, 1975; 1979; Racey and Entwistle, this volume) suggest that sperm competition is an important and underappreciated factor in the evolution of bat mating systems (Fenton, 1984; Hosken, 1997). Fenton (1984), Hoskin (1997), Crichton (this volume) and Racey and Entwistle (this volume) review the incidence of sperm storage in bats and consider the significance of sperm competition for the evolution of bat reproductive systems. Notably, the longevity of viable sperm correlates with the length of oestrus and female receptivity. Also, male testes mass correlates with the size of roosting or social groups over a wide range of bat taxa (Hosken, 1997). Testes mass is an index of the numbers of sperm produced, and group size an index of the risk of sperm competition (Hosken, 1997). It is likely that male mating success depends on sperm competition in *Myotis lucifugus* (Fenton, 1984; Watt and Fenton, 1995), and in banana leaf roosting *Pipistrellus nanus* (Happold and Happold, 1996). In one species, *N. noctula*, molecular studies have demonstrated that female reproductive tracts may contain sperm from up to five males, strongly supporting the significance of sperm competition (F. Mayer, personal communication). The role of sperm competition deserves major attention in future studies of bat mating systems.

The incidence of monogamy varies greatly among mammalian taxa, being the most common mating system in canids (Bekoff *et al.*, 1984) and known or suspected in 22% of primates species (Wrangham, 1987). The 18 possibly monogamous bat species comprise about 25% of the known mating systems in the Order (Table 8.3), so the frequency of monogamy in bats may be well above the mammalian average (Kleiman, 1977). Monogamy in other animals is associated with biparental care (Davies, 1991). Among bats, only *Vampyrum spectrum* and *Lavia frons* have been reported to exhibit male parental care. While these two species are similar to canids in being both monogamous and carnivorous, they differ in being monoestrous. Consequently, female reproductive rate is not obviously increased by male parental care. Alternative advantages of monogamy in bats might be that male parental care increases female survival, or that provisioning the young by males permits the female to resume reproduction more rapidly than would be possible if she were the sole source of nutrition for the offspring.

The recent discovery of male milk production in *Dyacopterus spadiceus* (Pteropodidae) (Francis *et al.*, 1994) demonstrates that some male bats lactate. However, male milk production could be due to factors such as phytoestrogen

consumption, rather than an evolved participation in parental care. If male lactation allows biparental nursing, it is most likely to occur in monogamous species.

With the exceptions of *Vampyrum spectrum* and *Lavia frons*, the remaining examples of monogamy in bats (Table 8.3) have been inferred from observations of mixed sex pairs in species which feed on insects or fruit. While these observations are consistent with monogamy in which a male defends the range of a single female, other more complicated mating systems, such as sequential polyandry, cannot be excluded. Roost observations to determine the presence and extent of male parental care, tracking studies to determine overlap and persistence of male and female ranges, and molecular studies to determine paternity are all needed. Given the unusually high frequency of monogamy in bats as compared to other mammals, such studies are long overdue.

Only a few of the pre-1977 studies on mating systems in bats involved marking of individuals (Dwyer, 1970; Bradbury and Emmons, 1974; Bradbury, 1977a, b) or otherwise identifying individuals (e.g. '. . . by the patterns of bullet holes in the wing membranes', Nelson, 1965), thereby allowing observations of known individuals. There has been an increasing number of such studies since 1977, both for free-ranging and captive bats. Advances in radio-telemetry and night vision and low light observational techniques have all contributed greatly to documenting the mating systems of many bat species. We expect the next 20 years to provide even more information as these techniques are applied more widely.

Compared to work on other taxa, such as birds, research on bat mating systems has lagged considerably in the use of molecular gene markers. Although the first molecular analysis of a bat mating system dates from over 20 years ago (McCracken and Bradbury, 1977), there are still fewer than 10 such published studies on mating in bats. The advent of molecular markers based on DNA amplification (PCR) has eliminated many of the logistic problems (i.e. limited allelic diversity and the need for cryogenic storage of substantial blood or muscle samples) that were inherent in earlier applications based on allozymes (McCracken and Wilkinson, 1988). The development of hypervariable microsatellite markers now provides single-locus genetic markers that typically provide an order of magnitude more variability than is available with allozymes (Quellar *et al.*, 1993). Sufficient DNA for these analyses can be obtained from minimally invasive sampling of even the smallest bats, and samples can be stored indefinitely at room temperatures (Worthington Wilmer and Barratt, 1996). It is even possible to investigate multiple insemination from DNA analysis of sperm in female reproductive tracts (Mayer, 1995). Combined with detailed field studies, the immediate future will see an increasing emphasis on the use of these new molecular methods to resolve the big issues in bat mating systems. In our opinion, these issues are questions of apparent monogamy, the significance of multiple mating by females, and the roles of female choice and sperm competition.

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