

Bats and Balls: Sexual Selection and Sperm Competition in the Chiroptera

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Introduction

Darwin (1871) recognized that competition between individuals for access to mates can lead to the evolution of exaggerated ornaments or weapons when these traits influence mating success. He referred to this process as sexual selection and distinguished two mechanisms—male competition and female choice—by which it could occur. Recognition that sexual selection can also operate after mating was not widely appreciated until Parker's (1970) seminal work led to the realization that competition among mates can occur after copulation.

Some of the earliest and subsequently most consistent evidence for sexual selection by sperm competition has come from comparisons of testes size between species that differ in mating system. If sperm are costly to produce (e.g., Dewsbury 1982; Nakatsura and Kramer 1982; Olsson et al. 1997), and a male's probability of fertilization is proportional to the relative representation of his sperm in the female reproductive tract, as appears to be true for many mammals (Martin et al. 1974), then sexual selection should favor greater sperm production capability—that is, larger testes—when females are promiscuous. In internally fertilizing species, larger testes are predicted when females have opportunities to mate with multiple males, while smaller testes are expected in monogamous or highly polygynous species in which one male controls access to a female or group of females. These predictions have been upheld for many vertebrate groups, including primates (Harcourt et al. 1981, Short 1979), whales (Brownell and Ralls 1986), other mammals excluding bats (Kenagy and Trombulak 1986), birds (Møller 1988), and fishes (Stockley et al. 1997).

Sexual selection by sperm competition might be expected to be intense in bats for several reasons. In most other mammals, sperm are capable of fertilizing eggs for only a few days after copulation (Birkhead and Møller 1993; Gomendio et al. 1998). A short sperm lifespan sets a narrow window of time during which females must mate with more than one male for sperm competition to occur. In contrast, many female bats are capable of storing viable

sperm for up to 6 mo (Racey 1979). Although sperm storage was first observed in a hibernating temperate species (Wimsatt 1942), sperm storage is now known to occur in a variety of tropical and temperate species (Racey and Entwistle 2000). Many bats also exhibit seasonal variation in testes size (Gustafson 1979, Heideman et al. 1992; Krutzsch 1979; O'Brien 1993) with changes up to 40-fold in mass (Racey and Tam 1974). Only males in good body condition initiate spermatogenesis (Entwistle et al. 1998, Speakman and Racey 1986). These observations are consistent with an energetic cost to sperm production and suggest that sperm is limiting for males, a necessary requirement for sexual selection to operate on sperm production.

Several lines of evidence suggest that female bats also remate often enough, at least in some species, for sperm to compete. Estimates of roost aggregation size positively covary with relative testes mass across 31 microchiropteran (Hosken 1997b) and 17 megachiropteran bat species (Hosken 1998b). These results have been interpreted as indicating that testes have become larger relative to body size in those species that form large colonies because sperm competition risk increases with group size in bats (Hosken 1997b, 1998b). Although few direct observations are available, females of several species have been observed to mate with multiple males during estrus, including *Desmodus rotundus* (Wilkinson 1985), *Tadarida brasiliensis* (A. Keeley and B. Keeley, unpublished manuscript), and *Phyllostomus discolor* and *Molossus ater* (Rasweiler 1987). Females of some sperm-storing species also may mate both before and during hibernation, for example, *Corynorhinus townsendii* (Pearson et al. 1952), *Myotis lucifugus* (Thomas et al. 1979), and *Nyctalus noctula* (Gebhard 1995). Sperm genotyping has demonstrated that females of *N. noctula* may have sperm from up to five males in their uteruses prior to conception (F. Mayer, personal communication), consistent with genetic evidence for multiple paternity (Mayer 1995). Paternity also differs from observed mating patterns in at least two species, *M. lucifugus* (Watt and Fenton 1995) and *Nyctophilus geoffroyi* (Hosken 1998a), as might be expected if ejaculate size, the competitive ability of sperm, or female storage/use of sperm differs across males. Thus, there is clearly opportunity for sperm competition to occur in bats.

While there has been substantial research on bat mating systems (reviewed in McCracken and Wilkinson 2000), sperm competition has received little study in bats (Fenton 1984; Hosken 1997b, 1998b) compared to the attention it has received in other mammals (Ginsberg and Huck 1989; Gomendio et al. 1998; Møller and Birkhead 1989). As yet, no one has tested if mating system influences testes size in bats. In this chapter we compile measurements of bat testes mass from published sources, capture records made by ourselves or colleagues, or measurements of museum specimens. Because testes mass covaries with body mass in other mammals (Kenagy and Trombulak 1986), we

determine if the allometric relationship between testes mass and body mass in bats differs from other groups of mammals. Using information compiled in McCracken and Wilkinson (2000), we then categorize species according to male-female association and potential for female promiscuity to test whether variation in testes size among species is consistent with the sexual selection hypothesis. In addition, we consider several alternative explanations for testes size including colony size (Hosken 1997b, 1998b), breeding seasonality (Hosken 1998b; Kenagy and Trombulak 1986; Stockley and Purvis 1993), sperm storage (Hosken 1997b), and genetic potential for gametic dysfunction (Cohen 1967, 1973; Manning and Chamberlain 1994). Finally, we compare testes size between populations for two species of bats to determine if intraspecific differences exist and could be consistent with sexual selection.

Methods

We obtained testis mass from either direct measurements or estimation of testicular volume. Testicular volume was approximated as a prolate spheroid, that is: $(4/3)\pi r^2 \times \text{length}/2 = 0.5236 \times \text{length} \times \text{width}^2$ (Myers 1977). The product-moment correlation between mass and estimated volume for seven *Myotis* testes was $r = 0.996$ (Myers 1977) and for nine bat species $r = 0.964$ (Hosken 1998b). We obtained mass and volume estimates for testes from five species—*Lasiurus ega*, *Eptesicus furinalis*, *Pteropus tonganus*, *Eidolon helvum*, and *Mops condylura*—which range in body mass from 7.5 to 570 g. The correlation between \log_{10} testis mass and \log_{10} testis volume for these five species was also 0.996 ($P < 0.001$). Furthermore, the regression equation was \log_{10} testis mass = $0.021 (\pm 0.054) + 1.024 (\pm 0.051) \log_{10}$ testis volume, indicating that testis volume can be used as an unbiased estimate of testis mass. For some species, only testis length was reported. From 10 species, we calculated the average testis width to be $0.66 \times$ testis length, and then used this factor to estimate testis width from testis length when direct measurements of testis width were not available.

Pronounced seasonal variation in the size and visibility of the testes (Gustafson 1979; Krutzsch 1979) complicates comparative study of testes size in bats. Therefore, when seasonal variation in testes size was available (e.g., *Myotis albescens*, *M. nigricans*, *Eptesicus furinalis*, *Lasiurus ega* [Myers 1977]; *Nyctalus noctula* [Racey 1974], *Plecotus auritus* [Entwistle et al. 1998], *Pipistrellus pipistrellus* [Racey and Tam 1974], *Coleura afra* [McWilliam 1987], *Mops condylura* [Vivier and van der Merwe 1996], *Haplonycteris fischeri* [Heideman 1989], *Anoura geoffroyi* [Heideman et al. 1992], and *Pteropus poliocephalus* [McGuckin and Blackshaw 1991]), we report mean testis mass from the period of maximal testicular size. When such information was not available, we only measured

scrotal testes, which often indicates spermatogenesis (Entwistle et al. 1998; Hosken et al. 1998). We include sample sizes when available for each species.

To allow comparison with previous allometric studies (Kenagy and Trombulak 1986), we doubled testis mass to estimate the combined mass of a pair of testes and used body mass of the same males scored for testis mass whenever possible. Because testes mass covaried allometrically with body mass, we use the residuals from a regression of \log_{10} combined testes mass (CTM) on \log_{10} body mass (BM) to test alternative hypotheses regarding testes size evolution. Sperm storage was scored from reviews of bat reproductive biology (Bernard 1989; Bernard and Cumming 1997; Gustafson 1979; Krutzsch 1979; Racey 1979; Racey and Entwistle 2000). We assume that females do not store sperm if spermatogenesis or copulations coincide with ovulation. Annual reproductive opportunities were categorized as one, two, or continuous (Bernard and Cumming 1997; Krutzsch 1979). Two sources (Baker 1979; Hsu and Benirschke 1977) were consulted for chromosome complement number. Estimates of colony size were taken from papers on sperm competition in microchiropteran (Hosken 1997b) and megachiropteran (Hosken 1998b) bats.

To determine if mating system influences testes size, we use two variables to categorize bat mating systems: (1) number of females associating with males during mating periods and (2) female opportunity for multiple mating. The number of females roosting with or visiting males was categorized into single-male/single-female, single-male/multiple-female, or multiple-male/multiple-female associations. Female mating opportunities were dichotomized as promiscuous or not. Single-male/single-female systems include those species in which male-female pairs typically roost together for extended periods during and beyond the mating period, as in *Vampyrum spectrum* (Vehrencamp et al. 1977) and *Lavia frons* (Vaughan and Vaughan 1986). Single-male/multiple-female systems include species typically classified as harem-holding systems, for example, *Phyllostomus hastatus* (McCracken and Bradbury 1981) and *Saccopteryx bilineata* (Bradbury and Emmons 1974), in which males associate with and defend a group of females for extended periods. This category also includes species in which female group associations are more labile, for example, *Carollia perspicillata* (Fleming 1988; Williams 1986), *Artibeus jamaicensis* (Kunz et al. 1983; Morrison 1979), and *Pipistrellus pipistrellus* (Gerell and Lundberg 1985; Lundberg and Gerell 1986), and species in which multiple females visit and mate, but do not roost, with displaying males, for example, epomophorine bats (Bradbury 1977, 1981). Multiple-male/multiple-female groups include species in which males and females roost together during the mating period, as in *Myotis lucifugus* (Thomas et al. 1979), *Rhynchonycteris naso* (Bradbury and Vehrencamp 1976), and *Pteropus poliocephalus* (Nelson 1965). We classified the mating system of 45 species into one of these three categories based on roosting association (table 3.1).

Table 3.1. Male body mass (BM), combined testes mass (CTM), roosting associations, opportunity for promiscuity (Prom.), sperm storage by sex, number of reproductive events per year (R/yr), and diploid chromosome complement (2n) for bats used in the study

Family/Species	BM (g)	CTM (mg)	% BM	N	Roost Assn.	Prom.	Sperm Store	R/yr	2n	References
Emballonuridae:										
<i>Coleura afra</i>	10.5	60	0.57	...	SM-MF	No	n	2	...	McWilliam 1987
<i>Rhinonycteris naso</i>	3.8	17	0.45	4	MM-MF	No	n	1	...	Plumpton and Jones 1992
<i>Saccopteryx bilineata</i>	7.4	11	0.14	26	SM-MF	No	n	1	...	C. Voigt, personal communication
<i>Saccopteryx leptura</i>	4.1	25	0.61	6	SM-SF	No	n	1	...	N. Simmons, personal communication
<i>Topiazous georgianus</i>	30.0	76	0.25	m	1	...	Jolly and Blackshaw 1988; Kitchener 1973
<i>Topiazous fildaeardae</i>	33.0	138	0.42	4	f	1	...	McWilliam 1988b
<i>Topiazous longimanus</i>	36.0	77	0.21	C	42	...	Singh 1997
<i>Saccolaimus peli</i>	100.0	575	0.58	2	SM-SF	1	...	G. Wilkinson, AMNH
Megadermatidae:										
<i>Carollia cor</i>	26.0	80	0.31	12	SM-SF	2	...	G. Wilkinson, AMNH
<i>Lasia frons</i>	23.4	26	0.11	12	SM-SF	No	...	1	...	G. Wilkinson, AMNH
<i>Microderma givns</i>	108.0	168	0.16	1	1	...	G. Wilkinson, AMNH
<i>Megaderma lyra</i>	38.6	155	0.40	5	1	...	G. Wilkinson, AMNH
<i>Megaderma spasma</i>	22.6	113	0.50	10	1	...	G. Wilkinson, AMNH
Molossidae:										
<i>Mormopterus phainopepla</i>	8.0	185	2.32	4	SM-MF	...	f	Krutzsch and Crighton 1987
<i>Otonops natteriensis</i>	45.0	143	0.32	76	SM-MF	No	...	1	...	Mutere 1973
<i>Tadarida aegyptiaca</i>	14.9	132	0.89	Hosken 1997b
<i>Tadarida brasiliensis</i>	11.1	91	0.81	146	MM-MF	Yes	n	1	48	A. Nicklack, personal communication
<i>Myotis conditira</i>	27.9	138	0.49	8	n	2	...	Vivier and van der Merwe 1996
<i>Chiroptera pumila</i>	10.8	38	0.36	1	SM-MF	No	n	C	...	G. Wilkinson
Mormoopidae:										
<i>Pteronotus damyi</i>	9.2	174	1.89	2	Adams 1989
Noctilionidae:										
<i>Noctilio albiventris</i>	31.2	64	0.21	7	SM-MF	...	n	1	34	Hoed and Pitocchi 1983
<i>Noctilio leporinus</i>	64.8	177	0.27	18	SM-MF	No	n	1	...	A. Brooke, personal communication
Phyllostomidae:										
<i>Anoura cultrata</i>	17.1	99	0.58	n	...	30	Jamsitt and Nagorsen 1982
<i>Anoura geoffroyi</i>	15.1	50	0.33	12	n	...	30	Heideman et al. 1992
<i>Artibeus nichollsi</i>	16.9	99	0.58	n	...	30	Jones and Genoways 1973
<i>Artibeus jamaicensis</i>	47.6	314	0.66	15	SM-MF	...	n	2	30	Taft and Handley 1991
<i>Artibeus jamaicensis</i>	40.0	51	0.13	32	SM-MF	No	n	2	30	J. Ortega, personal communication
<i>Artibeus littratus</i>	79.0	229	0.29	2	30	G. Wilkinson
<i>Artibeus phaeotis</i>	12.0	50	0.42	32	Timm 1985
<i>Brachyphyllax cavernum</i>	40.1	64	0.16	20	Swanepoel and Genoways 1983
<i>Carollia perspicillata</i>	18.5	125	0.68	...	SM-MF	No	...	2	28	Fleming 1988
<i>Centurio senex</i>	22.9	80	0.35	...	SM-SF	2	28	Snow et al. 1980
<i>Chiropterus auritus</i>	92.1	182	0.20	4	SM-SF	1	28	G. Wilkinson, AMNH
<i>Desmodus rotundus</i>	33.7	83	0.25	68	SM-MF	No	n	C	28	G. Wilkinson, personal communication
<i>Lctophylla alba</i>	5.5	79	1.45	25	SM-MF	...	n	2	30	A. Brooke, personal communication
<i>Glossophaga leachii</i>	8.4	29	0.35	...	SM-MF	...	n	...	32	Webster and Jones 1984
<i>Leptonycteris curasoae</i>	29.0	263	0.91	n	2	...	T. Fleming, personal communication
<i>Macroretus vaterhousi</i>	16.0	37	0.23	n	...	46	Krutzsch et al. 1976
<i>Monophyllus plethodon</i>	15.5	42	0.27	n	...	32	Homan and Jones 1975
<i>Phyllostomus discolor</i>	44.9	649	1.45	56	SM-MF	No	n	2	32	G. Wilkinson
<i>Phyllostomus hastatus</i>	91.8	308	0.34	10	SM-MF	No	n	1	32	G. Wilkinson
<i>Sturmia bidens</i>	17.5	58	0.33	n	...	30	Molinari and Soriano 1987
<i>Sturmia lilium</i>	20.4	121	0.59	11	n	2	30	Gannon et al. 1989
<i>Tonatin caribaei</i>	23.0	409	1.78	4	SM-MF	...	n	...	26	McCarthy et al. 1992
<i>Uroderma bilobatum</i>	14.9	98	0.66	...	SM-MF	...	n	2	44	Baker and Clark 1987
<i>Vampyressa caraccioli</i>	26.9	332	1.24	2	n	...	30	Whitts et al. 1990
<i>Vampyrus spectrum</i>	158.8	203	0.13	6	SM-SF	No	...	1	...	G. Wilkinson, AMNH
Pteropidae:										
<i>Acerodon maccloti</i>	518.0	6500	1.25	n	Hosken 1998b
<i>Cynopterus sphinx</i>	62.0	173	0.28	...	SM-MF	14	f	C	...	Storz et al. 2000
<i>Dakosmia peroni</i>	224.0	3280	1.46	n	Hosken 1998b
<i>Eidolon helvum</i>	325.0	5800	1.78	20	MM-MF	...	n	1	...	Mutere 1967

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Table 3. 1. (continued)

Family/Species	BM (g)	CTM (mg)	%BM	N	Roost Assn.	Prom.	Sperm Store	R/yr	2n	References
<i>Eonycteris spelae</i>	60.0	1596	2.66	...	MM-MF	...	n	C	...	Hosken 1998b
<i>Epomops auratus</i>	80.0	1800	2.25	...	SM-MF	...	n	2	...	Hosken 1998b
<i>Epomops batikofori</i>	178.0	358	0.20	6	SM-MF	...	n	1	...	Koifrom and Chapman 1994
<i>Hypsignycteris fischeri</i>	18.0	190	1.06	5	n	Heideman 1989
<i>Hypsignycteris monstrosus</i>	310.0	471	0.15	2	SM-MF	...	f	2	35	G. Wilkinson, AMNH
<i>Macroglottus minimus</i>	15.9	574	3.61	f	Hosken 1998b
<i>Macroglottus sobrinus</i>	23.0	634	2.76	n	2	...	Hosken 1998b
<i>Micropteropterus pusillus</i>	32.5	460	1.42	...	MM-MF	Yes	n	2	...	Hosken 1998b
<i>Pteropus aldo</i>	800.0	10200	1.28	...	MM-MF	Yes	n	1	38	Hosken 1998b
<i>Pteropus giganteus</i>	1021.0	16800	1.65	...	MM-MF	...	n	1	38	Hosken 1998b
<i>Pteropus oetus</i>	470.0	11000	2.34	n	1	...	Hosken 1998b
<i>Pteropus poliocephalus</i>	860.0	17000	1.98	7	MM-MF	Yes	m	1	38	McCuckin and Blackshaw 1991
<i>Pteropus scapulatus</i>	400.0	14000	3.50	6	MM-MF	Yes	m	1	...	O'Brien et al. 1993
<i>Pteropus touqianus</i>	568.3	5400	0.95	2	SM-MF	...	n	2	...	A. Brooke, personal communication
<i>Roussettus accipitrinus</i>	142.0	7000	4.93	n	2	...	Hosken 1998b
<i>Roussettus amplexicaudatus</i>	91.8	1480	1.61	n	Hosken 1998b
Rhinolophidae:										
<i>Hipposideros galeritus</i>	6.5	60	0.92	...	SM-SF	...	f	Hosken 1997b
<i>Hipposideros sporis</i>	10.0	80	0.80	f	Hosken 1997b
<i>Rhinolophus chloros</i>	16.2	350	2.16	6	f	Bernard 1983
<i>Rhinolophus hypsiglorus</i>	7.0	38	0.54	f	Hosken 1997b
<i>Rhinomycteris aurantius</i>	9.8	12	0.12	f	Hosken 1997b
Rhinopomatidae:										
<i>Rhinopoma hardwicki</i>	11.0	251	2.28	f	1	...	Karim and Banerjee 1989
<i>Rhinopoma microphallum</i>	31.0	1255	4.05	1	n	1	...	Anand Kumar 1965
Vespertilionidae:										
<i>Antrozous pallidus</i>	32.0	330	1.03	2	f	1	46	Beasley and Zucker 1984
<i>Chalinolobus gouldii</i>	14.0	29	0.21	f	1	...	Hosken 1997b
<i>Eptesicus fernaldis</i>	7.5	154	2.05	12	f	2	...	Myers 1977
<i>Euderma maculatum</i>	15.0	66	0.44	f	1	...	Watkins 1977
<i>Lasius exa</i>	11.9	46	0.39	8	f	1	...	Myers 1977
<i>Lasius seminolus</i>	9.3	13	0.14	f	1	28	Wilkins 1987
<i>Miniopterus australis</i>	7.5	40	0.53	...	SM-MF	No	f	1	...	Medway 1971
<i>Miniopterus minor</i>	7.0	50	0.71	3	MM-MF	Yes	n	1	...	McWilliam 1988a
<i>Miniopterus schreibersi</i>	13.0	76	0.58	9	n	2	...	Kruttsch and Crichton 1990
<i>Myotis adersi</i>	10.0	143	1.43	10	SM-MF	Yes	f	2	...	G. Wilkinson, NMNH
<i>Myotis albescens</i>	5.5	368	6.69	13	MM-MF	Yes	f	2	...	Myers 1977
<i>Myotis bocagei</i>	8.0	80	1.01	2	SM-MF	No	n	G. Wilkinson, NMNH
<i>Myotis evotis</i>	6.8	192	2.83	2	f	Manning and Jones 1989
<i>Myotis lucifugus</i>	6.8	108	1.59	6	MM-MF	Yes	f	1	...	Gustafson and Damassa 1985
<i>Myotis nigricans</i>	4.0	26	0.65	22	SM-MF	No	n	C	...	Myers 1977
<i>Nyctalus noctula</i>	28.0	540	1.93	2	SM-MF	Yes	f	1	...	Racy 1974
<i>Nyctophilus geoffroyi</i>	6.5	46	0.71	f	1	...	Hosken 1977b
<i>Nyctophilus gouldii</i>	14.0	217	1.55	1	f	1	...	Phillips and Inwards 1985
<i>Nyctophilus major</i>	13.5	60	0.44	f	1	38	Hosken 1997b
<i>Pipistrellus nanus</i>	3.6	53	1.47	f	1	...	Bernard et al. 1997; Happold and Happold 1990
<i>Pipistrellus nanus</i>	3.5	31	0.90	7	SM-MF	Yes	f	1	...	Happold 1990
<i>Pipistrellus pipistrellus</i>	5.0	230	4.60	...	SM-MF	Yes	f	1	...	Racey and Tam 1974
<i>Pipistrellus ruscicus</i>	4.0	310	7.75	7	f	1	...	van der Merwe and Rautenbach 1990
<i>Pipistrellus subflavus</i>	5.0	59	1.18	3	f	1	30	Kruttsch and Crichton 1986
<i>Pteropus ariatus</i>	7.2	44	0.62	55	MM-MF	...	f	1	...	Entwistle et al. 1998
<i>Cephalophanes rufovespuiti</i>	9.0	754	8.38	...	MM-MF	Yes	f	1	...	Pearson et al. 1952
<i>Rhogeessa tumida</i>	5.1	77	1.51	1	n	G. Wilkinson
<i>Scotophilus bebbianicus</i>	22.0	290	1.32	1	n	1	...	G. Wilkinson
<i>Scotophilus heathii</i>	45.0	387	0.86	6	f	1	...	Singh and Kristina 1996
<i>Tubonactis pachypus</i>	4.1	140	3.41	...	MM-MF	Yes	f	1	...	Medway 1972
<i>Tubonactis robustula</i>	8.4	200	2.38	...	MM-MF	Yes	f	1	...	Medway 1972

Note: MM-MF = multiple males roosting with multiple females; SM-MF = single male roosting with multiple females; SM-SF = single male roosting with single female; n = neither; m = male; and f = female; AMNH = American Museum of Natural History; NMNH = National Museum of Natural History. Ellipses dots indicate variables for which no data were available.

We would prefer to classify promiscuous systems as those in which females routinely mate with multiple males. However, such information is not available for most bats. Therefore, we operationally classified a species as promiscuous when available evidence indicates that females do not maintain consistent association with a single male at a roost throughout the mating period. Promiscuous mating occurs in many species of vespertilionid bats in which males will mate with females before hibernation in the fall and while females are in torpor during the winter, as in *Myotis lucifugus* (Thomas et al. 1979) and *Nyctalus noctula* (Gebhard 1995), but it has also been observed in nonhibernal mating species, such as *Tadarida brasiliensis* (A. Keeley and B. Keeley, unpublished manuscript). Promiscuous mating also occurs in single-male/multiple-female systems in which females move among different males during the mating season, for example, *Pipistrellus pipistrellus* (Gerell and Lundberg 1985; Lundberg and Gerell 1986) and *Pipistrellus nanus* (Happold and Happold 1996; O'Shea 1980), as well as in multiple-male/multiple-female systems. We were able to classify the mating systems of 30 species as promiscuous or not (table 3.1).

Close phylogenetic relationships can confound comparative analyses. If a variable, such as testes size, does not undergo rapid evolutionary change, and species are treated as independent observations in a comparative analysis, then the significance associated with a test result may be overestimated. One of the best methods for dealing with this problem is to compare phylogenetically independent contrasts (Harvey and Pagel 1991) to determine if correlated evolution has occurred. Unfortunately, this method requires a robust phylogeny, preferably with estimated branch lengths, for all species in the analysis. While a well-supported phylogeny for familial relationships has recently been proposed (Simmons and Geisler 1998), no species-level phylogeny is currently available for the order. Therefore, to determine if phylogenetic effects contribute to any association, we conduct three additional analyses. First, we use analysis of covariance (ANCOVA) to determine if bat families exhibit different allometric relationships between testes size and body size and to quantify the extent to which familial relationships contribute to observed associations between testes size. Second, we identified, a priori, and compared multiple species within genera or subfamilies that differ in mating system or degree of female promiscuity. We then use species averages within these groups in a paired comparison to determine if there is associated change in testes size. Third, for two species, *Artibeus jamaicensis* and *Tadarida brasiliensis*, we obtained data on testes size for two or more populations. Independent evidence indicates that these populations may differ in opportunities for multiple mating by females, either as a consequence of female movement patterns or mating assemblage size. Thus, this final comparison allows us to determine if intraspecific variation in testes size shows patterns of change that would be predicted by sexual selection due to sperm competition.

Results

Allometric Relationships between Testes Mass and Body Mass

We obtained or estimated testes mass from a total of 104 species of bats (table 3.1), including 84 species from nine families of microchiropteran bats and 20 species of megachiropteran bats (family Pteropodidae). Male body mass varied from 3.8 g for *Rhynchonycteris naso* to 1,021 g for *Pteropus giganteus*. Expressed as a percentage of body mass, combined testes mass ranged from 0.12% for *Lavia frons* to 8.4% for *Corynorhinus rafinesquii* (see also fig. 3.1).

Body mass explained 61% of CTM variation ($F = 159.9$, $df = 1, 102$, $P < 0.0001$) among bat species (fig. 3.2). In most mammals, larger species have progressively smaller testes, relative to body size, that is, the exponent in the allometric relationship of combined testes mass (CTM) on body mass (BM) is less than 1. In contrast, bat testes increase proportionally with body size—that is, $CTM = (0.009 \pm 0.002)BM^{(0.947 \pm 0.075)}$. The 95% confidence interval on the bat body mass exponent exceeds the exponents for all other orders of mammals (Kenagy and Trombulak 1986): rodents (0.77), primates (0.68), insectivores (0.74), and carnivores (0.59).

Analysis of variance revealed a highly significant effect of family on residual CTM ($F = 6.22$, $df = 9, 94$, $P < 0.0001$) but no significant interaction between family and body mass. Combined testes mass of rhinopomatid, pteropodid, and vespertilionid bats exceeded allometric expectations, while the testes of phyllostomid, noctilionid, megadermatid, and emballonurid bats were smaller than expected for their body sizes (fig. 3.3). Therefore, in the

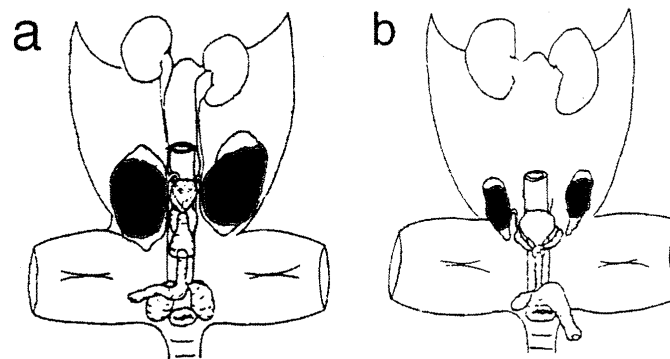


Figure 3.1. Anatomical perspective of the difference in testes size for breeding season males in (a) *Rhinopoma kinneari* (combined testes mass [CTM] approximately 4% body mass) and (b) *Taphozous longimanus* (CTM = 0.02%). (Redrawn from Krutzsch 1979.)

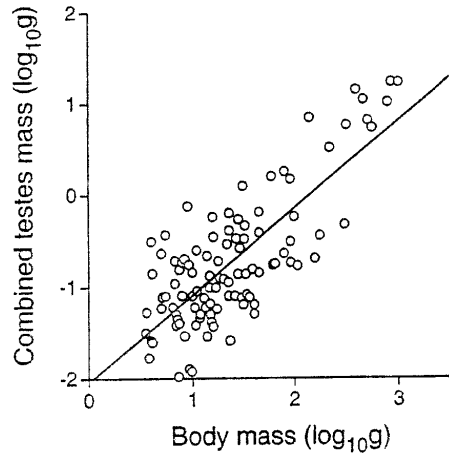


Figure 3.2. Plot of \log_{10} combined testes mass on body mass for 104 bat species.

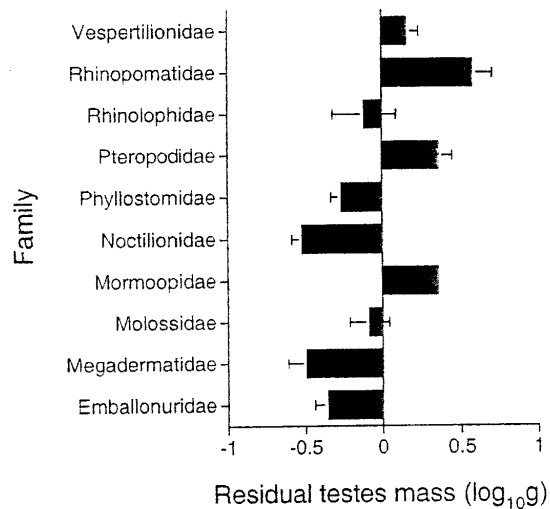


Figure 3.3. Mean \pm SE residual combined testes mass, from the regression in figure 3.2, plotted for each family of bats in the data set.

analyses presented below we remove effects of body size by using the residuals from a regression of \log_{10} CTM on \log_{10} BM for all bat species. Then, if any variable exhibits significant differences in residual CTM, we conduct a two-way ANOVA to determine if the effect remains significant after removing familial differences.

Relative Testes Mass and Mating System

Comparison of residual CTM among the bat mating systems shows strong evidence for sexual selection by sperm competition (ANOVA: $F = 12.9$, $df = 2, 43$, $P < 0.0001$). Species in which multiple males roost with multiple females showed the largest relative testes, single-male/multiple-female species were intermediate in size, and the smallest relative testes occurred in single-male/single-female species (fig. 3.4). Fisher's partial least squares difference post hoc tests revealed that the two single-male categories did not differ from each other ($P = 0.12$), while the multiple-male category differed strongly from the other two ($P < 0.001$, for both comparisons). The effect of mating system appears to be independent of phylogeny, as family was not significant ($F = 1.59$, $df = 7, 36$, $P = 0.17$) while mating system remained significant ($F = 5.04$, $df = 2, 36$, $P = 0.012$) in a two-way ANOVA.

A comparison of residual CTM between promiscuous or non-promiscuous species revealed that promiscuous species have much larger testes ($t = 6.36$,

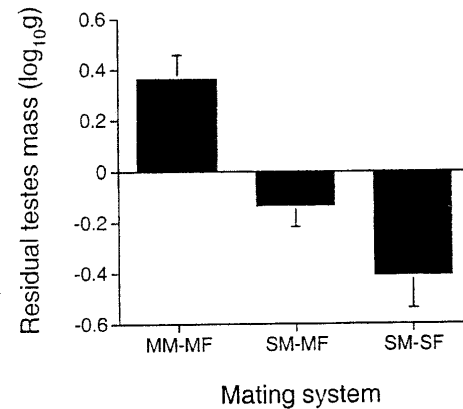


Figure 3.4. Mean \pm SE residual combined testes mass for bats with mating period roosting associations that consist of multiple males and multiple females (MM-MF), single males and multiple females (SM-MF), and single males with single females (SM-SF).

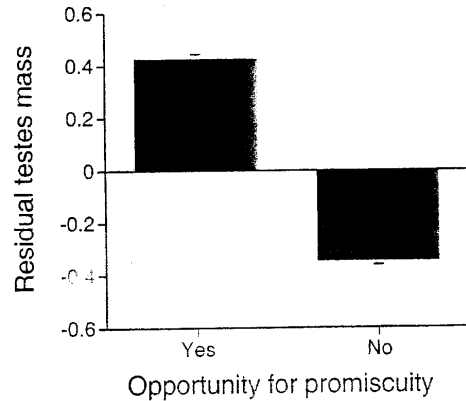


Figure 3.5. Mean \pm SE residual combined testes mass for species categorized by their opportunity for promiscuity. Promiscuity indicates that females do not maintain consistent association with a single male at a roost throughout the mating period.

$P < 0.0001$; fig. 3.5). This result also appears to be independent of phylogeny, given that family was non-significant ($F = 1.03$, $df = 6, 22$, $P = 0.43$) while promiscuity remained significant ($F = 6.55$, $df = 1, 22$, $P = 0.018$) in a two-way ANOVA. Promiscuity appears to be a better predictor of residual testes mass than mating system, as promiscuity ($F = 15.6$, $df = 1, 26$, $P = 0.0005$), but not mating system ($F = 1.16$, $df = 2, 26$, $P = 0.33$), was significant in a two-way ANOVA. Mating system and promiscuity do not, however, occur independently across species. We classified 11 of 12 multiple-male species as promiscuous and 15 of 20 single-male species as non-promiscuous ($\chi^2 = 14.22$, $P = 0.0008$). Thus, any conclusion that residual testes size is influenced more by promiscuity than by mating system must be qualified given that this analysis was dependent on only a few species.

We used eight matched sets of closely related species—that is, either from the same genus or subfamily (table 3.2)—to determine if testes size exhibits correlated change with mating system. We predicted that bats in multiple-male roosting groups should have larger testes than bats in single-male roosting assemblages. In addition, we predicted that species with more stable roosting associations among females should exhibit smaller relative testes than species in which females move more frequently among males. For example, *P. hastatus* form more stable female groups than does *P. discolor* (Wilkinson 1987) and multiple males of *T. robustula* roost with multiple females less often than

Table 3.2. Phylogenetically independent paired comparisons used to test for effect of promiscuity and mating system on testes size

Multiple-Male Group/ More Promiscuous	Single-Male Group/ Less Promiscuous
<i>Rhynchonycteris naso</i>	<i>Saccopteryx leptura</i> , <i>Saccopteryx bilineata</i>
<i>Tadarida brasiliensis</i>	<i>Chaerophon pumila</i> , <i>Otomops martiensseni</i>
<i>Phyllostomus discolor</i>	<i>Phyllostomus hastatus</i>
<i>P. discolor</i> , <i>P. hastatus</i>	<i>Vampyrum spectrum</i>
<i>Pteropus poliocephalus</i>	<i>Pteropus tonganus</i>
<i>Miniopterus minor</i>	<i>Miniopterus australis</i>
<i>Myotis albescens</i> , <i>Myotis lucifugus</i>	<i>Myotis nigricans</i> , <i>Myotis bocagei</i> , <i>Myotis adversus</i>
<i>Corynorhinus rafinesquii</i>	<i>Plecotus auritus</i>
<i>Tylonycteris pachypus</i>	<i>Tylonycteris robustula</i>

Note. Multiple-male group/more promiscuous = either roost in multiple male, multiple female aggregations, or females exhibit less roosting group stability than closely related species. Single-male group/less promiscuous = either roost in single male, single female aggregations, or females show more roosting group stability than closely related species.

in *T. pachypus* (Medway 1972). Despite the relatively small sample size, the paired difference in average residual testes mass was highly significant (paired t -test: $t = 4.16$, $P = 0.0032$; fig. 3.6). Thus, testes size appears to have evolved rapidly in response to change in female opportunity for multiple mating.

Relative Testes Mass and Colony Size

We used estimates of colony size from Hosken (1997b, 1998b) to determine if residual testes mass covaries with roosting aggregation size for 48 species of bats. A least squares regression between \log_{10} colony size and residual testes mass was significant ($F = 6.62$, $df = 1, 46$, $P = 0.013$), but colony size explained only 12.6% of the variation in residual testes size. When family and \log_{10} colony size were included in an ANCOVA, both family ($F = 3.15$, $df = 6, 40$, $P = 0.013$) and colony size ($F = 4.72$, $df = 1, 40$, $P = 0.036$) were significant. Colony size did not, however, explain significant variation in residual testes mass when either promiscuity or mating system was included in a two-way ANOVA (respectively: $F = 0.06$, $df = 1, 10$, $P = 0.81$; $F = 0.80$, $df = 1, 18$, $P = 0.38$). Thus, colony size appears to be less important than the mating system for explaining variation in residual testes mass.

Relative Testes Mass, Sperm Storage, and Seasonality

Testes size might also be expected to increase if females store sperm because stored sperm should have more opportunity to interact. At the same time, if sperm suffer a constant rate of mortality during storage, then the duration of sperm storage should determine the amount of sperm that must be produced independently of any effects of sperm competition. To address these alternatives we used information on sperm storage patterns for 72 species. A comparison of residual testes size among these species reveals that sperm-storing

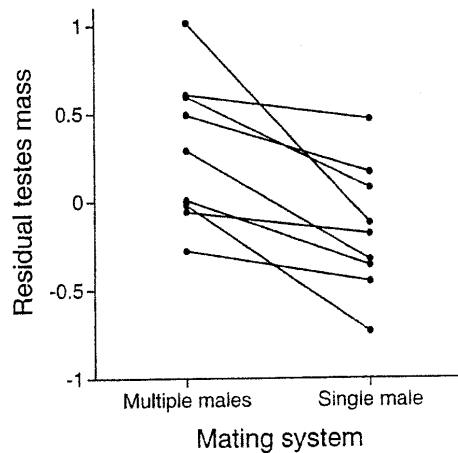


Figure 3.6. Mean \pm SE residual combined testes mass for nine paired comparisons of species that differ in mating system (see table 3.2).

species do have relatively larger testes than species that do not store sperm ($t = 3.10$, $P = 0.003$). But, a two-way ANOVA using family and sperm storage shows that sperm storage is not significant when family is included in the model ($F = 0.81$, $df = 1, 63$, $P = 0.37$). Furthermore, if sperm competition was the only determinant of testes size, then species in which sperm is stored longer in females should have larger testes than species in which sperm is stored longer in males. In contrast, if sperm are produced to counter storage decay, then there should be no difference in testes size between male and female sperm-storing species. Although only three of 36 sperm-storing species exhibit longer male than female sperm storage—for example, *Taphozous georgianus*, in which sperm is produced by males in the fall and then stored in the cauda epididymides until copulation in the spring (Jolly and Blackshaw 1988)—we found no difference in residual testes mass between species with longer male than female sperm storage ($t = 0.46$, $P = 0.65$). Thus, while sperm storage may select for increased testes size, it exhibits strong phylogenetic patterns and does not depend on the sex where most storage occurs.

Males that breed only once per year might be expected to allocate more resources into sperm production and, therefore, testes size than species that breed two or more times per year (Kenagy and Trombulak 1986; Stockley and Purvis 1993). In contrast to this prediction, our information from 72 species re-

veals that the number of breeding episodes per year does not explain a significant fraction of the variation in residual combined testes mass (ANOVA: $F = 0.76$, $df = 2, 69$, $P = 0.47$). Species in which males breed once per year do not differ in residual testes size from those that breed continuously or twice per year.

Relative Testes Mass and Chromosome Complement

Alternatively, perhaps testes are larger in species prone to gamete dysfunction to insure some gametes survive until fertilization (Cohen 1967). One prediction from this hypothesis is that species with higher chromosome complements should produce more sperm to compensate for increased frequencies of recombination-related chromosome damage. Although support for this prediction has been obtained across a diverse assemblage of species (Cohen 1967, 1973; Manning and Chamberlain 1994), we found no evidence for it among bats. For the 31 species for which we have data, the product-moment correlation between diploid chromosome number and residual CTM was 0.134 ($P = 0.46$).

Intraspecific Variation in Testes Size

All of the analyses presented above ignore within-species variation. To test for geographic variation in testes size we compared CTM of *Artibeus jamaicensis* from Mexico (J. Ortega, personal communication) and Panama (Taft and Handley 1991) and of *Tadarida brasiliensis* from four colonies in Texas (A. Keeley, personal communication; fig. 3.7). Length and width of testes were measured on reproductively active males during the breeding season for both species. The *A. jamaicensis* measurements were taken during the mating season in caves on the Yucatan Peninsula, Mexico (Ortega and Arita 1999, 2000) or from a colony that had been captured in Panama and maintained at the National Zoological Park (Taft and Handley 1991). The *T. brasiliensis* measurements were taken between March 21 and March 30, 1998, in southwestern Texas during which time mating was observed.

Both species exhibited highly significant differences in testes size, independent of body size, between populations. *Artibeus jamaicensis* testes in Panama were about six times larger than those in Mexico ($t = 9.25$, $P < 0.0001$; fig. 3.6a). These two populations are approximately 1,600 km apart. The testes of *T. brasiliensis* also exhibited highly significant differences between sites ($F = 26.7$, $df = 3, 142$, $P < 0.0001$; fig. 3.6b). The results of Fisher's partial least squares difference post hoc tests are shown in figure 3.6b. Males at Eckert James River Cave had significantly larger testes than any other site, and Davis Cave males had larger testes than McNeil Bridge males. However, males at Davis Cave did not differ from males at South Grape Creek nor did males at South Grape Creek differ from McNeil Bridge. These caves are within 80 km

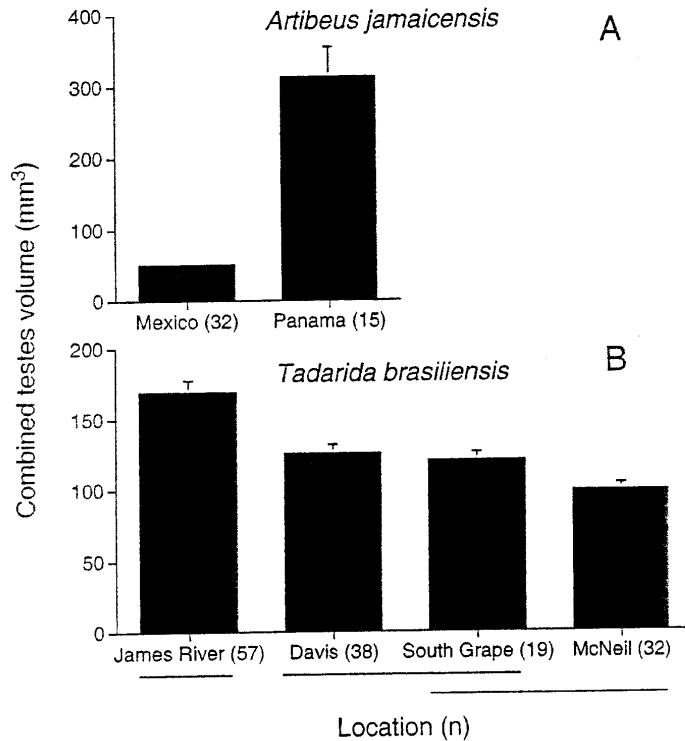


Figure 3.7. Mean \pm SE combined testes volume for (A) two populations of *Artibeus jamaicensis* and (B) four colonies of *Tadarida brasiliensis*. Significant differences between sites according to Fisher's partial least squares differences post hoc comparisons are indicated by discontinuous lines beneath colony names.

of each other with the exception of McNeil Bridge, which is approximately 160 km from EckertJames River Cave, 100 km from Davis Cave, and 150 km from South Grape Creek.

Discussion

The range and maximal size of combined testes mass exhibited by different bat species is extraordinary, ranging from 0.12% to 8.4% of body mass. In a survey

of 133 mammal species, which included only one bat, rodents exhibited the greatest range in testes size—from 0.15% for desert woodrats to 8.4% for gerbils (Kenagy and Trombulak 1986). Primates, which have been widely used as evidence that sexual selection influences testes size (Harcourt et al. 1981; Harvey and Harcourt 1984), exhibit combined testes mass ranging only from 0.02% to 0.75% of body mass. Thus, bats show variation in relative testes size that exceeds any other mammalian order. Allocation of body mass to testicular tissue in *Corynorhinus rafinesquii* not only equals or exceeds any other mammal but also exceeds any bird. The largest testes yet reported for birds occur in the alpine accentor with combined testes mass 7.7% of body mass (Nakamura 1990).

Our results strongly implicate sexual selection by sperm competition as the evolutionary explanation for both the range and maximal size of testes in bats. Species in which multiple males roost with multiple females during the breeding period have much larger testes than those in which single males attend single or multiple females. In addition, the fidelity of females to males at particular roosts has an independent effect on testes size suggesting that females are more likely to mate with multiple males when they move among roosts. The strong effect of promiscuity in our analysis suggests that female behavior facilitates sperm competition and causes sexual selection for testes size in bats.

Although we made considerable effort to obtain testes mass and volume during periods of maximal testes size when spermatogenesis is most likely to occur, little information on the reproductive cycle or mating behavior has been published for single-male/single-female species, such as *Vampyrum spectrum* and *Saccolaimus peli*. Since few specimens of these species were available for measurement, we could have underestimated mean testes size if the specimens we measured were collected during periods of testicular regression. However, we minimized this risk by restricting measurements to specimens with descended testes. Furthermore, residual testes size did not differ between single-male/single-female and single-male/multiple-female species, and the data for many species in the latter category could not have suffered this potential source of measurement error. Thus, while seasonal variation in testes size undoubtedly contributes unexplained variation in our data, it cannot account for the effects of mating system and female promiscuity that we obtained.

Several lines of evidence indicate that evolution of testes size is not constrained by phylogeny. Even though we did not conduct a formal independent contrasts analysis, the effects of the mating system on residual testes size did not disappear when differences among families were removed in the analysis. Furthermore, comparisons of residual testes size using species from the same subfamily or genus indicate that testis size can evolve rapidly and independently of body size (fig. 3.6). These results are consistent with the evolution of testes size occurring in response to the mating system.

Evolution of testes size may also be occurring within species, as indicated by significant variation in testes size between populations of both *Artibeus jamaicensis* and *Tadarida brasiliensis*. The differences between populations of either species cannot be ascribed to measurement bias because the differences are too large (*A. jamaicensis*) or because the same person conducted all of the measurements (*T. brasiliensis*). Within species differences in testes size of *Miniopterus australis* have previously been attributed to seasonal variation caused by altitudinal differences between roost sites (Dwyer 1968). Seasonal variation is not likely, however, to explain the testes size differences we observed, at least for *T. brasiliensis* because measurements were taken over a 9-d period from nearby roosts and persist even when colonies measured on successive days are compared.

Nevertheless, other explanations for intraspecific variation in testes size are possible. For example, maximal testicular volume might be attained at different times at each *T. brasiliensis* colony. Alternatively, males at small colonies may be actively excluded from larger colonies, perhaps because they differ in age. Age has been found to contribute to population differences in relative testes size in the greenfinch, *Carduelis chloris* (Merilä and Sheldon 1999). At the same time, some of the intraspecific differences in testes size are consistent with sexual selection. *Artibeus jamaicensis* in Panama have been reported to form harems in hollow trees (Morrison 1979; Morrison and Morrison 1981). Females show some fidelity to one or more preferred tree cavities, but they also move between cavities. Thus, female groups are labile and a given female may visit more than one male roost during the breeding season. In contrast, in the Mexican cave-roosting population of *A. jamaicensis*, female group composition was stable from March to September through the breeding season (Ortega and Arita 1999). Thus, we expect that opportunities for multiple mating by females are greater in Panama than in Mexico.

The mating system of *T. brasiliensis* has not been well characterized, although males have been observed displaying to females using vocalizations (Lollar 1995), and females have been observed mating with multiple males in the field (A. Keeley, personal communication). The most obvious difference between sites is the size of the roosting population. Eckert James River Cave contains a large maternity colony with an estimated 4–6 million individuals present during the summer. The Davis Cave colony is substantially smaller, perhaps approaching 1 million bats, while South Grape Creek and McNeil Bridge each contain about 100,000 bats. Because testes size increases with colony size across bat species (Hosken 1997b, 1998b), the differences in testes size between these four colonies might also reflect differences in risk of sperm competition.

Bats also exhibit a steeper allometric relationship between testes mass and body mass than any other mammalian order. An explanation for this difference is not obvious. It seems intuitive that testes mass should increase as body

mass increases, but what scaling relationship should be expected? Presumably, the answer depends on the volume in which sperm can interact within the female and how that volume scales with body mass. One possibility is that female bats store more sperm in their reproductive tracts than other mammals relative to body size. Bats store sperm in a variety of locations including the oviduct, uterus, and utero-tubal junction (Fenton 1984; Uchida and Mori 1987). In a study by Gomendio and Roldan (1993), residual sperm number in mammals has been found to correlate positively with uterine horn length, relative to body size. Unfortunately, this study did not include any bats. In contrast, after removing effects of body size, no significant relationship was found between uterine horn width and testes mass in 13 microchiropteran bats (Hosken 1997b) or between uterine horn length and testes mass in seven species of bats (Hosken 1998b). However, a highly significant relationship between body mass and uterine horn length was found with and without phylogenetic correction (Hosken 1998a). Whether the allometric relationship between female reproductive tract size and body size in bats differs from other mammals needs to be ascertained to determine if this factor can account for the difference in testes mass–body mass allometry observed between bats and other mammals.

Sperm storage has been proposed as a mechanism to promote sperm competition or permit selective use of sperm by females (Bernard and Cumming 1997; Birkhead and Møller 1993). Reports of phagocytosis of sperm in the female reproductive tract (Hosken 1997a; Racey et al. 1987; Rasweiler 1987) are, therefore, intriguing. Phagocytosis is often interpreted as a mechanism to remove dead sperm, but it might also function to select sperm. Nonrandom paternity by males (Hosken 1998a; Watt and Fenton 1995) might be due to selective sperm use by females, although other alternatives are also possible. At the same time, we did not find a difference in testes size between species that exhibit longer storage of sperm in females than males. While the relationship between testes size and sperm storage may reflect selection to insure adequate numbers of surviving sperm, the significant effect of family on the relationship between sperm storage and testes size indicates that variation in sperm storage cannot explain differences in testes size between closely related species.

Nevertheless, sperm storage may influence selection on other traits. A number of bat species that store sperm exhibit sperm plugs (Fenton 1984). These are often interpreted as a mechanism for ensuring paternity and reducing sperm competition. For example, sperm plugs may ensure that sufficient sperm are corralled at the cervix to get past this barrier to storage, making subsequent removal impossible. This interpretation seems inadequate given that some species with large residual CTM—for example, *Nyctalus noctula* (table 3.1)—produce sperm plugs and in some species, females are capable of expelling plugs. An interesting proposition that deserves comparative study is that penile and/or bacula morphology represent counteradaptations by male

bats to facilitate sperm or sperm plug removal (Bernard and Cumming 1997; Eberhard 1985).

This review has focused on testes size and ignored the possibility that sperm size might also influence sperm competition. However, bats exhibit variation in sperm morphology across species (Forman and Genoways 1979). In an early study of 232 mammals (Cummins and Woodall 1985), a negative relationship between sperm length and body mass was found for all mammals except bats, where the relationship was positive. The negative relationship was interpreted as indicating a trade-off between sperm size and number because more sperm need to be produced when the female reproductive tract is larger and dilution is greater. However, more recent work has shown that sperm size is independent of body mass in bats (Hosken 1997b), as well as in 300 species of mammals after correction for phylogenetic effects (Gage 1998). Thus, variation in sperm size is not explained by body size and warrants explanation. Hosken (1997b) failed to find a significant relationship between sperm length and estrous duration or group size in microchiropteran bats. He also failed to find a significant relationship between sperm length and uterine horn length, although only five species were used in this analysis (Hosken 1998b). In contrast, sperm length has been shown to correlate with oviduct length across mammals independently of phylogenetic effects (Gomendio and Roldan 1993). Future studies should consider the possibility that sperm length might influence sperm competitive ability or mobility (Birkhead et al. 1999; Gomendio and Roldan 1991; Stockley et al. 1997) and differ among mating systems in bats.

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