Patterns of sexual dimorphism and mating systems

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Abstract

Of the 216 species of phyllostomid bats, fewer than 10% have had their mating systems studied in any great detail; however, some species exhibit mating systems ranging from apparent monogamy to extreme polygyny. Paternity studies reveal that the social mating system is generally indicative of the genetic mating system although in some cases, subordinate males father some offspring. These findings suggest that mate selection can involve both male competition and female choice. To estimate the strength of precopulatory and postcopulatory sexual selection, we use measures of sexual dimorphism in relative body mass and canine length as indicators of direct male competition, and relative testes mass as a proxy for sperm competition. We then evaluate the influence of aggregation size and permanence of the roosting structure on the intensity of sexual selection using phylogenetically-informed analyses. Even though females are often larger than males, male-biased sexual dimorphism for relative mass and canine length is widespread and associated with large roosting aggregations. In contrast, sperm competition is greatest in species with intermediate sized aggregations. These patterns of sexual dimorphism are largely consistent with what is known about phyllostomid mating systems, but exceptions provide potential opportunities for future study.

Keywords: sexual selection, male competition, canines, sperm competition, female choice

INTRODUCTION

Bats exhibit a diverse range of mating systems from monogamy to extreme polygyny (McCracken and Wilkinson 2000). Describing a species' mating system typically requires a long-term study to determine the spatial distributions and behavioral interactions among males and females, in addition to assigning parentage. Relatively few phyllostomid species have been studied in such detail, but the available evidence suggests that species in the family exhibit much of the mating system variation present in the order. In the absence of additional studies, patterns of mating behavior can be inferred by examining variation in traits likely to influence male mating success before and after mating.

Socio-ecological factors can offer insight into expected mating systems because they influence the spatial and temporal distribution of resources and the females that depend on them. When resources or females are spatially clumped and limiting, they become defensible, thus promoting resource or female defense polygyny (Emlen and Oring 1977). Bats form aggregations ranging from a few to thousands of individuals (Kerth 2008) and occupy a range of roost structures that vary in size and longevity (Kunz et al. 2003). Both roost abundance and permanence are known to affect social associations (Chaverri and Kunz 2010), such that species that roost in abundant but ephemeral roosts, such as foliage or leaf tents, tend to have more fluid social structures with short term associations (Chaverri and Kunz 2010; Chaverri et al. 2007; Sagot and Stevens 2012). By contrast, species in less abundant but more permanent structures, such as caves or hollow trees, exhibit more stable social associations (Brooke 1997; McCracken and Bradbury 1981; Wilkinson 1985a), often amidst a much larger assemblage of individuals.

When resources or females are defensible, males are expected to compete to control them (Emlen and Oring 1977). Because male mammals are largely liberated from the demands of parental care, they are free to invest in competition to maximize mating opportunities (Trivers 1972), and thus most mammals exhibit some form of polygyny (Clutton-Brock 1989). In both female and resource defense polygyny, selection typically favors large, aggressive males that can compete effectively to control access to females (Andersson 1994; Clutton-Brock et al. 1977; Plavcan and van Schaik 1997). Thus, precopulatory sexual selection has been inferred to be the primary cause of male-biased sexual size dimorphism (SSD) in mammals (Lindenfors et al. 2007; Lindenfors et al. 2002; Plavcan and van Schaik 1997; Weckerly 1998). Alternative explanations based on ecological differences between the sexes have also been proposed (Isaac 2005; Ralls 1977), but have typically received less empirical support. Among bats, however, females are often larger than males (Ralls 1976). One explanation for why female bats are larger is to carry additional weight during and after pregnancy given that bat litters can approach 50% of maternal body mass at birth (Kunz and Kurta 1987). This idea is commonly referred to as the Big Mother hypothesis (Ralls 1976; Stevens et al. 2013). Therefore, even modest male-biased sexual dimorphism may be indicative of strong sexual selection in bats.

In addition to body size, precopulatory sexual selection often promotes the development of weapons (Andersson 1994; Darwin 1871). Unlike large terrestrial mammals that wield obvious weapons, such as horns or antlers, bats are constrained by aerodynamics given their need to fly, which leaves their canine teeth, and possibly their thumbs, as potential weapons. Primates and carnivores also use their canines as weapons and the degree of sexual dimorphism in canine length is associated with differences in their mating behavior (Gittleman and Van Valkenburgh 1997; Kappeler 1996; Plavcan 2012; Plavcan and van Schaik 1992). Among carnivores, canine sexual dimorphism is greatest in polygynous species with single-male, multi-female groups (Gittleman and Van Valkenburgh 1997). A similar pattern is seen among many primates in which increasing canine dimorphism is correlated with increasing levels of intrasexual aggression (Plavcan and van Schaik 1992), although lemurs and lorises are an exception (Kappeler 1996). Therefore, sexual dimorphism in canine length can serve as an additional indicator of the strength of precopulatory sexual selection.

In situations where males cannot control female mating, precopulatory sexual selection can result from females choosing traits that reflect attributes of male quality other than fighting ability, such as the amount of carotenoid pigment (Blount 2003) or the length of feathers (Andersson 1982). There is evidence that female choice occurs in some bat species and has resulted in sexually dimorphic traits used for signaling, such as the enlarged rostrum of male hammer-headed bats, *Hypsignathus monstrosus* (Bradbury 1977), the wing-sacs of some male emballonurid bats (Bradbury and Vehrencamp 1977; Voigt and von Helversen 1999), and the complex songs produced by some male molossid bats (Smotherman 2016). The role of female choice is largely unexplored among phyllostomid species; the presence of sexually dimorphic features that can act as signals may reveal candidates worthy of further study.

Reproductive success is not guaranteed by acquiring copulations, because multiple mating by females creates opportunities for postcopulatory sexual selection via sperm competition (Ginsberg and Huck 1989). In many taxa, including bats (Wilkinson and McCracken 2003), there is a strong positive correlation between the opportunity for female promiscuity and size of the testes (Harcourt et al. 1995; Moller and Briskie 1995; Stockley et al. 1997), as males with larger testes are able to produce more sperm (Moller 1988) and are thus more likely to successfully sire offspring. Given the challenges of observing copulations of bats in the wild, measures of relative testis size can provide insight into the degree of female promiscuity and the resulting sperm competition among species of phyllostomids.

Information on roosting habits, particularly aggregation sizes and the structures used for roosting, is more readily available than detailed observations of mating behavior. Therefore, the aim of this chapter is to examine how roosting habits may shape mating systems by influencing opportunities for precopulatory and postcopulatory sexual selection. We infer the strength sexual selection from measures of sexual dimorphism and testis size using both museum collections and live, wild bats. Finding strong associations will improve our ability to predict mating behavior from simple observations of roosting behavior. We hypothesize that increasing aggregation size increases opportunities for male-male competition and thus promotes precopulatory sexual selection for larger, heavier males with longer canines. Additionally, we expect larger aggregations to facilitate opportunities for multiple mating by females, thus increasing postcopulatory selection for larger testes. Whether or not such postcopulatory selection occurs depends on whether males can control females within aggregations. When roosts are ephemeral, social groups are likely to be more labile, which may decrease direct competition among males but could increase sperm competition. Therefore, as roost permanence decreases, we expect sexual dimorphism in body mass and canine length to become less prominent and testes mass to increase. Because the Phyllostomidae include several groups of species that have undergone recent radiations (Rojas et al. 2016), we incorporate phylogenetic similarity (Pagel 1999) into our analyses to determine if relationships among traits or factors are due to recent selection or are the result of gradual evolutionary change that occurred in proportion to the time since a common ancestor. We further examine how the patterns uncovered in our analyses align with what is known about the subset of phyllostomid bats whose mating behavior has been studied.

METHODS

Data Collection

To evaluate the role of roost permanence and aggregation size on precopulatory and postcopulatory sexual selection we utilized data from several sources. We downloaded 212,823 phyllostomid specimen records from VertNet (http://www.vertnet.org) and then added 29,721 records from the United States National Museum of Natural History (USNM, http://collections.nmnh.si.edu/search/mammals/). We used species names provided by Simmons and Cirranello (Chapter 4). From these records we extracted sex, lifestage, forearm length, mass, testis size and capture location whenever it was available. We supplemented these data with direct measurements of canine length or testes that we made on specimens at the USNM, the American Museum of Natural History, the University of Kansas Museum of Natural History, and the Carnegie Natural History Museum. For each species, we selected at least 10 adult skulls of each sex that showed little or no evidence of tooth wear to measure the length of the left canine to at least 0.05 mm using calipers. When available, we measured specimens from the same collecting excursion to a single country. We measured length and width of one testis either from fluid specimens or from live animals that either DMA or GSW captured in Trinidad, West Indies, or Costa Rica. After eliminating records without useable data or irreconcilable species names, our dataset contained 60,338 specimen records on 154 species including 149 phyllostomids, two species of *Noctilio* and three mormoopids (Table S13.1). We then examined the range of measurements for each trait and removed obvious outliers, i.e. greater than ± 3 SD from the mean, to ensure that data entry errors did not distort mean values. In Table 13.1 we summarize the number of species and number of specimens for each character in the dataset.

To measure sexual dimorphism in canine length and body size, we first perform a phylogenetic size correction (Revell 2009) because canine length and body mass are not independent of body size. Using phylogenetic generalized least squares (PGLS), as implemented in CAPER for R (Orme et al. 2013), we regressed species mean canine length on mean forearm length. Because PGLS operates on species means rather than sex-specific means, we used the resulting coefficients and the sex-specific trait means to calculate the sex-specific residuals. We then measured sexual dimorphism as the residual male trait – residual female trait divided by the average value of the trait multiplied by 100, so that each dimorphism measure would represent the percent difference in the trait between the sexes independent of body size. We calculated percent difference in mass similarly, after excluding pregnant females, except that we estimated residuals from the PGLS of log mass on log forearm to account for the nonlinear relationship between mass and forearm. All phylogenetic analyses are based on the phylogeny of Davalos, Velazco, and Rojas presented in Chapter 6.

Following Wilkinson and McCracken (2003), we used relative combined testes mass, estimated as double the volume of a prolate spheroid divided by body mass multiplied by 100, to measure intensity of postcopulatory sexual selection. To compensate for the fact that testes regress during the nonbreeding season and expand during the breeding season, we used the 90% quantile of relative combined testes mass to represent an average breeding male for each species. This correction likely still underestimates maximum testes mass. For example, average combined testes mass for 174 *Phyllostomus discolor* was 0.597 g while the 90% quantile was 1.053 g and the maximum was 1.868 g. To normalize this distribution, we used log relative combined testes mass. Finally, we only used measures of dimorphism or testes in subsequent analyses if there were three or more measurements per sex per species.

We used information from the literature or from museum records to score each species with regard to the degree of permanence of a roosting site and the relative number of individuals typically found in a roosting site (Table S13.1). For each species, we scored roost permanence on an ordinal scale with (1) foliage or roots, (2) tents, (3) hollow trees, logs or excavated termite nests, and (4) caves, culverts, mines or buildings according to reports (Arita 1993; Eisenberg 1989; Kunz et al. 2003; Reid 1997; Tuttle 1976). We calculated the average roost score for species that have been observed in multiple types of roosts. We also scored aggregation size on an ordinal scale with (1) small or family groups less than 10, (2) groups containing 11-25 individuals, (3) small colonies of 25-100, (4) large colonies greater than 100 based on comments in Reid (1997), Eisenberg (1989), Goodwin and Greenhall (1961), or in a Mammalian Species Account (mspecies.oxfordjournals.org; see Table S13.1 for references). In cases where sources differed, we again used the average of the ordinal scores.

Following McCracken and Wilkinson (2000), we also used information from the literature to characterize the mating system as either single male/single female (SM/SF), single male/multi-female (SM/MF), or multi-male/multi-female (MM/MF). In addition, in cases where paternity studies have been conducted, we required harem male paternity to exceed 60% before characterizing a species as SM/MF. As a consequence, some species that were previously described as harem-forming or SM/MF are now scored MM/MF here (Table S13.1). We made this change because reduced paternity means that sperm competition is likely to be greater and precopulatory selection on body mass or canine length is likely to be lower in such species.

Statistical analyses

To determine the extent to which sexual dimorphism for a trait in any extant species is due to phylogenetic history, i.e. closely related species are more likely to exhibit similar degrees of dimorphism, we estimated Pagel's lambda (λ) using CAPER (Orme et al. 2013). This parameter ranges from 0 to 1, such that $\lambda=0$ represents no phylogenetic signal and $\lambda=1$ represents strong phylogenetic signal consistent with gradual evolution via a Brownian motion model (Harvey and Pagel 1991; Pagel 1999).

We used phylogenetic generalized least squares (PGLS), implemented in CAPER (Orme et al. 2013) to examine the effects of aggregation size and roost permanence on measures of dimorphism and testes mass. As before, we used the recent noctilionoid tree by Davalos, Velazco, and Rojas (Chaper 6). In the context of PGLS, λ represents the degree to which the phylogeny influences the regression, which may differ from the phylogenetic signal of a particular trait (Symonds and Blomberg 2014). We used AICc for model selection to evaluate the candidate models (Burnham and Anderson 2002), such that the model with the lowest AICc is preferred and models with $\Delta\text{AICc} < 2$ are considered equivalent. Because the number of species for which we have data differs depending on which traits are considered, we use only those species for which we have complete data during model selection, but then apply the selected model to all possible species.

RESULTS

We find that different traits vary in the degree to which phylogenetic similarity has an effect (Table 13.1). Average forearm length has a high lambda value, indicating it is highly influenced by phylogenetic relationships. By contrast, forearm sexual dimorphism has a low lambda value, indicating that SSD varies independently of phylogenetic relationships, i.e. has evolved rapidly among phyllostomid bats. Sexual dimorphism in both mass and canine length exhibits moderate phylogenetic signal, while relative testes mass is also influenced by phylogeny, an observation consistent with the large family-level differences in relative testes mass reported by Wilkinson and McCracken (2003). In addition to these morphological traits, both roost permanence and aggregation size are influenced by phylogeny, with aggregation size having a lambda value not significantly different from 1. Similarities between related species could be due to genetic constraints or to similar patterns of selection; regardless, this finding highlights the need to control for phylogeny rather than assume species values represent independent observations in comparative analyses.

Patterns of dimorphism

Phyllostomid bats vary greatly in body size as measured both by length and sexual dimorphism of forearms. One of the smallest bats in the group, *Ametrida centurio*, exhibits the greatest female-biased sexual size dimorphism (SSD, male forearm (mean ± SD): 25.56 ± 0.48

mm, female forearm: 31.95 ± 0.76 mm, % difference: -22.22%). By contrast, the largest bat, *Vampyrum spectrum*, exhibits only weak SSD (male forearm: 105.56 ± 2.98 mm, female forearm: 104.33 ± 3.02 mm, % difference: 1.17%). Rensch's rule predicts that among species with male-biased SSD, larger species will show greater degrees of SSD, while among female-biased species, larger species will show less dimorphism (Rensch 1959). We did not find support for this predicted pattern among either female-biased species (PGLS: $F_{1,38} = 0.04$, $p = 0.84$, $\lambda=0.00$) or male-biased species (PGLS: $F_{1,88} = 3.12$, $p = 0.08$, $\lambda=0.31$; Fig. 13.1).

Sexual dimorphism in mass ranges from extreme female bias in *Macrophyllum macrophyllum* (-20.76%), to minimal sex bias in *Diphylla ecaudata* (-0.01%), to extreme male bias in *Monophyllus redmani* (20.67%). Similarly, canine sexual dimorphism ranges from moderately female-biased (*Centurio senex*: -7.51%) to strongly male-biased (*Phyllonycteris poeyi:* 23.24%), with males possessing relatively longer canines than females in most species. Additionally, canine sexual dimorphism is positively associated with mass sexual dimorphism (PGLS: $F_{1,80} = 4.68$, $p = 0.03$, $\lambda = 0.65$, $R^2 = 0.06$; Fig. 13.2).

Although Phyllostomidae tend to have smaller testes than other bat families (Wilkinson and McCracken 2003), they still span a broad range from 0.07% of body mass (*Leptonycteris yerbabuenae*) to 3.67% of body mass (*Diaemus youngi*) indicating that postcopulatory sexual selection is likely important for many species. Relative testes mass decreases with increasing body size (PGLS: $F_{1,99} = 6.31$, $p = 0.01$, $\lambda=0.82$), but does not covary with measures of mass sexual dimorphism (PGLS: $F_{1,88} = 0.05$, $p = 0.82$, $\lambda = 0.77$) or canine dimorphism (PGLS: $F_{1,77} = 1.11$, $p = 0.29$, $\lambda = 0.71$).

Effect of roosting ecology on sexual dimorphism and testis size

As expected, variation in both canine sexual dimorphism and mass sexual dimorphism is best explained by species' aggregation sizes (Table S13.2), but measures of roost permanence do not improve model fits, as per AICc. Species that form large aggregations are more likely to exhibit male-biased mass dimorphism (PGLS: $F_{1,69} = 20.41$, $p < 0.001$, $R^2=0.23$, $\lambda=0.00$, Table 13.2, Fig. 13.3). Similarly, canine dimorphism increases with aggregation size (PGLS: $F_{1,59} = 12.25$, $p < 0.001$, $R^2=0.17$, $\lambda=0.58$, Table 13.2, Fig. 13.3).

The two best-fit models that explain variation in relative testes mass show negative quadratic relationships with aggregation size and roost permanence (Table S13.2). The model with the lowest AICc score includes only the effect of aggregation size, but the model including both aggregation size and roost permanence is equivalent. Upon examination of the effect sizes (Table 13.2), it is clear that aggregation size has a stronger effect on relative testes mass than roost permanence. Species with moderate aggregation sizes tend to have larger testes for their body size than species that form very small or very large aggregations (Fig. 13.4). However, there is considerable variation among species that roost in small groups, with combined testes mass ranging from 0.07% to 2.90% of body mass.

DISCUSSION

Dimorphism as a signature of precopulatory selection

We hypothesized that both larger aggregations and more permanent roosting structures would promote competition among males for access to reproductive females and thereby select for larger body mass and longer canines in males relative to females. We found that as roost aggregations increase in size, males become heavier and have longer canines for their size, thus supporting our hypothesis of greater competition in larger groups. We did not, however, find such support for the effect of the roost structure permanence.

For 18 of the 149 species included in our analyses we have more detailed information on mating behavior and can thus examine where these species lie in the family-wide patterns we have found for sexual dimorphism. Two of the least dimorphic species are *Vampyrum spectrum* and *Chrotopterus auritus,* both of which roost in small groups in hollow trees or caves. *V. spectrum* is socially monogamous and the roosting group typically consists of a single male and female along with recent offspring that have not yet dispersed (Vehrencamp et al. 1977). *C. auritus* also appears to be socially monogamous as accounts indicate roosting groups consist of family groups similar to those of *V. spectrum* (Reid 1997). How pairs form in either species is still unknown, but the lack of sexual dimorphism suggests very limited direct competition between males.

Several species show no sex bias or female bias in dimorphism, including *Uroderma bilobatum*, *Ectophylla alba*, and three of the four *Artibeus* species for which some information on mating system is available (*A. watsoni, A. literatus, A. phaeotis*). These species all roost in small groups and construct leaf tents, except *A. literatus,* which often roost in foliage, or occasionally in hollow trees or caves. Leaf tents cannot accommodate the large aggregations found in more permanent roosting structures, such as hollow trees, caves, and buildings. Additionally, the limited life span of tents requires movement between roosts, which may limit the stability of social groups (Sagot and Stevens 2012). Both of these attributes would limit opportunities for direct competition among males. However, precopulatory sexual selection may act on males if females are choosing a mate based on his tent. Kunz and McCracken (1996) suggest that tent roosts are a defendable resource and thus likely to be constructed by males to attract females. Observations of *A. watsoni* support this claim. Male *A. watsoni* construct and defend leaf tents and roosting groups generally consist of a single male with multiple females, which suggests a mating system based on resource-defense (Chaverri and Kunz 2006). Although males invest in tent construction, they do not restrict themselves to a single tent and both males and females frequently switch among roost sites (Chaverri and Kunz 2006). By contrast, *E. alba* roost in mixed-sex groups (Brooke 1990) and both males and females engage in tent construction, with multiple individuals making modifications to a single tent (Rodríguez-Herrera et al. 2011). How group composition and tent construction influence individual mating success is still unknown, but the lack of male-biased dimorphism in mass or canine length among these species implies that small aggregations limit opportunities for direct male-male competition.

The other tent-roosting bats, *A. phaeotis, U. bilobatum, Vampyriscus nymphaea* and occasionally *Artibeus jamaicensis,* appear to form small harem groups consisting of a single male with multiple females. These species exhibit female-biased mass dimorphism, but *V. nymphaea* and *A. jamaicensis* have male-biased canine dimorphism. Little is known about the details of *V. nymphaea*'s mating behavior, but *A. jamaicensis* has been well-studied (Kunz et al. 1983; Morrison 1979; Ortega and Arita 1999, 2000, 2002; Ortega and Maldonado 2006; Ortega et al. 2003). *A. jamaicensis* roosts in a variety of structures ranging from leaf tents to caves and, as a result, aggregation sizes also vary (Kunz et al. 1983). Dominant males aggressively defend groups of females from other males (Ortega and Arita 2000), but the composition of the female groups is labile (Ortega and Arita 1999). In large harems, the dominant male tolerates the presence of a subordinate male, whose presence allows the dominant male to maintain control of the large female group in exchange for a fraction of the paternity (Ortega and Arita 2002; Ortega et al. 2003). The males' enlarged canines are presumably valuable for female defense. Our measures of dimorphism are based on species averages, but given the widespread geographic range of this species along with the diversity of roosting structures and aggregation sizes, a within-species examination of variation in mass and canine length could reveal interesting patterns. Population differences in relative testes mass has already been reported for this species (Wilkinson and McCracken 2003) and geographic variation in sexual dimorphism is known in two other phyllostomids (Willig and Hollander 1995).

Male *Lophostoma silvicolum* also build roosts to attract females, but rather than modify leaves, they excavate the underside of arboreal termite nests. The size of these roosts constrains aggregation size, but they are more permanent than most leaf tents. Roost construction appears to be under sexual selection as only males perform the excavation and reproductive success is greater for males with roosts (Dechmann and Kerth 2008). Unlike tent-making bats, males are larger than females and have larger canines. Moreover, males with roosts are heavier than those without roosts and females prefer to associate with larger roost holders (Dechmann and Kerth 2008). While these observations have been interpreted as a consequence of female choice, the patterns of dimorphism are consistent with a history of male-male competition.

Another species in which female choice may be important is *Erophylla sezekorni,* which forms labile mixed-sex groups with lek-like mating behavior. Males perform multimodal displays that involve visual wing flapping and display flights, vocalizations, acoustic wing buzzes, and olfactory signals (Murray and Fleming 2008). Similar to classic lekking species, *E. sezekorni* males often perform these displays in small aggregations within the cave. According to our analyses, *E. sezekorni* males and females have a similar body mass, but males have much larger canines (Fig. 13.2). However, Murray and Fleming (2008) found that males are heavier and in better condition than females. This difference may be to due to population differences or seasonal variation. Regardless, their large aggregation size and male-biased canine dimorphism suggest the presence of precopulatory sexual selection, but how mass and canine size play a role in mating success remains to be determined.

The species with the greatest degree of mass and canine dimorphism for which mating behavior has been reported are *Phyllostomus hastatus*, and the two outgroup species, *Noctilio leporinus* and *N. albiventris.* All three of these species form harem groups often within larger colony aggregations (Brooke 1997; McCracken and Bradbury 1981; Schad et al. 2012). In both *P. hastatus* and *N. leporinus* female aggregations are remarkably stable over several years and remain intact despite turnover of the harem male. When in residence, the harem male fiercely defends the group by aggressively driving away any approaching males (Brooke 1997; McCracken and Bradbury 1981). This guarding behavior enables the harem male to secure most of the paternity within the group, thus making harem defense critical to reproductive success (McCracken and Bradbury 1977). In turn, competition among males to obtain harem status is expected to be fierce and observations of *P. hastatus* males with injuries during the breeding season support this expectation (personal observation). Large body mass and long canines are thus a likely advantage in these competitive interactions. Less is known about the mating behavior of *N. albiventris*, but its similarity to both to *P. hastatus* and *N. leporinus* in dimorphism, testes mass, and roosting ecology suggests it is similar with respect to mating system.

Overall as aggregation size increases, sexual dimorphism becomes increasingly male-biased. However, within a narrow range of aggregation sizes we still find variation in the degree of dimorphism, particularly among species with small aggregation sizes. Thus, even basic knowledge of roosting aggregations can provide insight into the degree of precopulatory selection a species may have experienced, and simple measures of sexual dimorphism can improve inferences. However, comprehensive understanding of the mating system and precopulatory selective pressures still requires long-term careful observation.

Testes mass as a signature of postcopulatory selection

We expected species that use more ephemeral roosts to have larger testes due to increased opportunities for multiple mating. Additionally, roosting in large aggregations might provide females access to more potential mates and make it more difficult for males to defend their mates, resulting in increased post-copulatory sexual selection. We found that aggregation size has a greater effect on testes mass than does roost permanence. In our analysis, moderate aggregations have higher levels of postcopulatory competition as indicated by the negative quadratic relationship between relative testes mass and increasing aggregation size. However, an additional pattern emerges when we examine the variation within each aggregation level. In doing so, we see that species known to have MM/MF groups have consistently larger testes than SM/MF groups, which in turn have larger testes than SM/SF species (Fig. 13.4). This observation is consistent with previously reported patterns for the entire order (Wilkinson and McCracken 2003).

Of the species for which we have mating system information, some of the largest testes relative to body size are found in *E. alba*, *A. watsoni,* and *L. silvicolum*. As described above, these three species occur in small groups in roosts constructed from leaves or termite mounds. The relatively large testes of *E. alba* are consistent with multiple mating by females and strong sperm competition, which may be expected in their mixed-sex roosting groups. Interestingly, after parturition the composition of roosting groups changes; groups of nursing females associate only with a single adult male, while males form separate aggregations (Brooke 1990). To date, no studies have examined paternity in *E. alba*, so it is unknown what proportion of the pups in a group are sired by the resident male. Both *A. watsoni* and *L. silvicolum* form groups that appear to be harems (Chaverri et al. 2008; Dechmann et al. 2005); however, females do not remain loyal to a single male and frequent roost switching creates opportunities for multiple mating. As a consequence, less than 30% of the pups in an *A. watsoni* tent are sired by the resident male (Chaverri et al. 2008). Similarly, less than half of the pups in a *L. silvicolum* termite roost have been sired by the resident male or by a male the female was known to roost with previously (Dechmann et al. 2005). Harems with labile female membership are also observed in *P. discolor* (GSW, personal observation) and *C. perspicillata* (Fleming 1988; Porter 1979), and males of both species also have relatively large testes. Such flexible harems create opportunities for multiple mating and thus sperm competition; as a consequence, selection is expected to favor males with larger testes (Fig. 13.4). In *C. perspicillata,* bachelor males are able to successfully sneak copulations further increasing the degree of sperm competition (Fasel et al. 2016).

Both *E. sezekorn*i and *D. rotundus* form large multi-sex aggregations, but appear to have small testes relative to the other multi-male/multi-female species. Small testes may be expected in lekking species because females can exercise mate choice freely and the remating rate is expected to be low; however, studies of lekking birds reveal that females may mate multiply even when able to choose freely (Hess et al. 2012; Lank et al. 2002; Petrie et al. 1992). The testes of *E. sezekorni* are relatively small which supports the hypothesis that remating rates are low when females are able to choose. However, paternity analyses reveal that reproductive skew is relatively weak and thus this species does not conform to a classic lek (Murray and Fleming 2008). These observations do not preclude low female remating rates, but further research is needed. *D. rotundus* also has moderately sized testes for a species with MM/MF groups. Unlike many bats, *D. rotundus* reproduction is asynchronous and year-round (Wilkinson 1985b). Increasing asynchrony may allow males to sequentially defend preferred females to reduce remating and limit sperm competition (Emlen and Oring 1977). This hypothesis is consistent with their substantial canine length sexual dimorphism, although behavioral observations indicate that females sometimes remate or reject males (Wilkinson 1985b).

Relative to species with MM/MF mating systems, the seven species known to form polygynous (SM/MF) groups tend to have smaller testes. The three species that form larger aggregations, *P. hastatus, N. leporinus,* and *N. albiventris*, all have relatively small testes, which is expected given the stability of female groups and the intensity with which males defend those groups. *P. hastatus* harem males are able to successfully exclude most intruders and secure 70-100% paternity of pups born in their harems (McCracken and Bradbury 1977).

As expected, the two monogamous species, *V. spectrum* and *C. auritus*, have relatively small testes. Pair bonding and low population densities drastically reduce opportunities for sperm competition, thus selection should not favor large testes. *Centurio senex* also has small testes and roosts in small aggregations suggesting weak or absent sperm competition. Additionally, females are also relatively heavier and have relatively larger canines than males, suggesting weak sexual selection on males, but little is known about their mating behavior. The other species with small testes include several nectar feeders (*Anoura cultrata, Leptonycteris yerbabuenae,* and *Monophyllus redmani*), which roost in a range of aggregation sizes. While little is known about their mating behavior, sexual dimorphism in canine length is substantially male-biased in all three species (14.35% - *A. cultrata*, 15.22% - *L. yerbabuenae*, 12.27% - *M. redmani*) suggesting that males likely fight to control access to groups of females.

In addition to variation in testis size, postcopulatory sexual selection could be influenced by how sperm are stored or utilized by females for fertilization (Orr and Zuk 2014). Many bats are well known for being able to store sperm for unusually long periods (Racey and Entwistle 2000). Consequently, some of the variation in testis size could be related to species differences in sperm storage or fertilization. For example, *Noctilio albiventris* can delay fertilization (Badwaik and Rasweiler 2000; Rasweiler 1979) which should increase the opportunity for sperm competition. Similarly, *Glossophaga soricina* can delay implantation (Badwaik and Rasweiler 2000; Rasweiler 1979), which should allow females to bet-hedge by mating with multiple males before committing to a pregnancy. Finally, at least three phyllostomids (*Artibeus jamaicensis*, [Fleming 1971], *Carollia perspicillata* [Rasweiler and Badwaik 1997; Roellig et al. 2011], *Macrotus californicus* [Bleier 1975]) can delay development, which could allow females to compare developing embryos and only invest in the most successful one. This could favor multiple mating if each embryo was fathered by a different male. Given that females of these species typically give birth to a single pup, this scenario would also require selective embryo resorbtion, which has been reported in some bats (van der Merwe and Rautenbach 1987). The extent to which females use some form of reproductive delay to manipulate postcopulatory sexual selection is an interesting topic worthy of further investigation.

Other consequences of sexual selection: signaling and mate choice

Sexual selection can lead to some of the most elaborate ornaments and armaments (Darwin 1871) and while most bats are drab in color and their morphology is constrained by the demands of flight, several species possess sexually dimorphic traits and behaviors that may function as signals in agonistic interactions or for mate attraction. Vocalizations are a common sexual signal in many taxa and several studies have documented vocalizations for courtship and territory defense in bats (Behr and von Helversen 2004; Bradbury 1977; Davidson and Wilkinson 2004). Among phyllostomids, two species known to use vocalizations are *E. sezekorni* and *C. perspicillata*, both of which perform multimodal displays. As mentioned previously, *E. sezekorni* males perform a visual display consisting of wing movements and short display flights, which are accompanied by acoustic signals produced both vocally and percussively by vibrating the wings. These signals are directed toward females, suggesting a role in mate attraction; however, the importance of these signals for acquiring mates is unclear because as noted above, reproductive skew is low (Murray and Fleming 2008). *Carollia perspicillata* males also perform wing displays, which include poking with the wings and hovering flights, along with a courtship-specific trill vocalization. These trills exhibit acoustic differences among individuals (Knörnschild et al. 2014), but again, how these calls influence male reproductive success is still not fully understood. An additional set of vocalizations are used in aggressive contexts (Knörnschild et al. 2014) and playback experiments demonstrate that males are able to discriminate individuals by their aggressive calls, which may mitigate conflict between territorial neighbors (Fernandez et al. 2014; Porter 1979).

Olfactory signals are common among bats (Bloss 1999), but their role in mate defense or courtship is poorly understood. The best-studied example is the wing-sac odor of *Saccopteryx bilineata*, an emballonurid bat (Caspers et al. 2008; Voigt et al. 2005; Voigt and von Helversen 1999), but there is evidence that phyllostomid bats also employ olfaction in both competitive and courtship interactions. Some species have sexually dimorphic scent-producing structures, while others have monomorphic structures with dimorphic chemical profiles. Within the subfamily Phyllostominae, adult males of multiple species have a glandular throat sac that is absent or rudimentary in females (*Phyllostomus discolor* [Holler and Schmidt 1993], *Phyllostomus hastatus* [McCracken and Bradbury 1981], *Chrotopterus auritus* [Medellin 1989], *Phylloderma stenops* [Nowak 1994]). In both *P. discolor* and *P. hastatus*, males rub this gland on their roost site and *P. hastatus* males also rub the gland on their harem females. Holler and Schmidt (1993) report that *P. discolor* males are able to discriminate their own scent from that of other males, which implies utility in territorial defense; furthermore, females can discriminate the scent of familiar and unfamiliar harem males suggesting a potential role in mate recognition or choice. Similarly, the chemical composition of *P. hastatus* gland secretions indicates that males possess individually distinct scent profiles that could facilitate discrimination (DMA, unpublished data). The chemical profile also reflects variation in social status as either a bachelor or harem male, but further work is needed to determine how individuals respond to these signals.

Many chemical signals are associated with a visual component, such as swellings or hairs specialized for disseminating the odor (Fig. 13.5c, d). In two nectar-feeding bats, *Leptonycteris curasoae* and *L. yerbabuenae,* males create a visible patch between their shoulder blades by smearing secretions from various glands on their backs during the mating season (Munoz-Romo and Kunz 2009; Nassar et al. 2008). In *L. curasoae,* the presence of this dorsal patch is correlated with larger testes, lower body condition, and fewer ectoparasites (Munoz-Romo and Kunz 2009; Munoz-Romo et al. 2012). The secretion mixture contains compounds that act as natural insecticides in other taxa, which might contribute to the lower parasite load, but this causal relationship is yet to be confirmed (Munoz-Romo et al. 2012). Although little is known about the mating system of this species, this visual and chemical signal is expected to serve a role in either mate attraction or choice, as females preferentially associate with odors from males with a dorsal patch over odors from males without a patch (Munoz-Romo et al.

2011). In both species, males are relatively heavier and possess longer canines than females, but have small testes, with *L. yerbabuenae* having the smallest testes (0.07% of body mass) of the phyllostomid bats for which we have data. This implies strong precopulatory competition but weak postcopulatory competition among males despite large aggregations.

Males and females of several *Sturnira* species possess epaulettes, tufts of hair on the shoulders that are associated with underlying sebaceous glands (Fig. 13.5). There is no sexual dimorphism in the structure of these epaulettes (Scully et al. 2000), but there is significant sexual dimorphism in the bacterial colonies present in these glandular regions (Gonzalez-Quinonez et al. 2014). Bacteria play an important role in olfactory communication by altering chemical signals through the metabolism of secretory products, and as a result, odor can serve as a signal of condition or infection status (Penn and Potts 1998; Zala et al. 2004).

Some of the most bizarre sexually dimorphic traits in bats are found among the short-faced bats within the family Stenodermatinae. For example, male *Pygoderma bilabiatum* have glandular tissue around their eyes, under their chins, and on their wrists that undergo seasonal swelling (Tavares and Tejedor 2009; Fig. 13.5c), during which time males emit a subtle musky odor (R. L. M. Novaes, personal communication). Their small testes and weak female-biased size dimorphism suggest that sexual selection is weak, but the function of these structures and the behavior of this species are largely unknown. Close relatives of *P. bilabiatum* also possess a variety of intriguing facial structures. Male *Sphaeronycteris toxophyllum*, appropriately named the visored bat, have a large sexually dimorphic outgrowth on their foreheads (Fig. 13.5a, b). In addition to the forehead protrusion, males also have a fleshy flap under their chin which can be raised to cover their faces (Nowak 1994). Unfortunately, little is known about the behavior of this species, but we can infer there is some element of male-male competition due to the strong male bias in relative mass, despite weak sexual dimorphism in skeletal and canine size.

In addition to choosing males based on morphological features and behavioral displays, females may also select mates based on the quality of the roosts they construct. As described above, males of several species construct roosts from leaves or termite mounds and these roosts may serve as an extended phenotype (Schaedelin and Taborsky 2009). Because roosts are an essential resource for females, they may prefer males that are able to build suitable roosts. Furthermore, roosts may signal male quality. However, this requires that the resident male roosts only in tents that he has constructed. While this is clearly the case for *L. silvicolum* males that excavate termite nests (Dechmann and Kerth 2008), it is unlikely to be true for many tent-making bats that frequently switch between several roosts at any given time.

CONCLUSION

Even though females have larger forearms than males in 69% of phyllostomid species, males have relatively longer canines than females in 85% of species and males have relatively greater body mass than females in 57% of species. These patterns of sexual dimorphism are consistent with strong precopulatory sexual selection acting via male competition for access to mates. Moreover, these two measures of sexual dimorphism are correlated with each other and both are better predicted by size of roosting aggregations than by the degree of permanence of the roosting site. These results indicate that proximity within a roost facilitates male competition and likely enables males to defend larger groups of females. Postcopulatory sexual selection appears to operate independently of precopulatory sexual selection as relative testis size is uncorrelated with sexual dimorphism in either relative canine length or mass. In contrast to our predictions, postcopulatory sexual selection is not positively related with aggregation size. Instead, species that form relatively small to intermediate sized aggregations exhibit some of the largest testes, although considerable variation in testis size is unexplained. Variation in reproductive delay among species might explain some of that variation.

The patterns of sexual dimorphism we observed are consistent with what is known about the mating systems of phyllostomid bats. Species that form single-male, multi-female (or harem) groups exhibit some of the most extreme male-biased sexual dimorphism for canine length and body mass while species that form single-male, single-female or multi-male, multi-female groups typically show much less sexual dimorphism for these traits. In contrast, relative testis size tends to be largest in species that form multi-male, multi-female groups in various sized aggregations. The sexually dimorphic traits of the stenodermatine species, such as extended brow ridges, swollen eye tissue, or glandular tissue in males, may be used by females for mate selection; unfortunately, too little is known about their mating systems, but this possibility is certainly worthy of further study.

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Table 13.1. Phylogenetic signal and sample sizes for each trait

Character	No. Species (No. Specimens)	Pagel's λ	(CI)
Forearm Length	137 (17,999)	0.98	(0.92, 1.00)
Forearm Dimorphism (% difference)	129 (17,974)	0.00	(0.00, 0.55)
Mass Dimorphism[2]	110 (17,990)	0.60	(0.29, 0.83)
Canine Dimorphism[1]	87 (2,111)	0.86	(0.55, 0.98)
Relative Testes Mass[3]	100 (6,234)	0.83	(0.56, 0.95)
Roost permanence	105	0.60	(0.33, 0.82)
Aggregation size	83	0.96	(0.85, 1.00)

[1] percent difference of sex-specific residuals from regression on forearm length

[2] percent difference of sex-specific residuals from regression on ln(forearm length)

[3] ln(combined testes mass as % of body mass)

Table 13.2. Effect sizes of roost permanence and aggregation size on measures of dimorphism and testes mass from phylogenetic generalized least squares models

Response	Predictor	Estimate ± SE	t	p
Mass dimorphism	Aggregation	3.74 ± 0.83	4.52	<0.001
Canine dimorphism	Aggregation	3.20 ± 0.91	3.50	<0.001
Testes mass	Roost	1.48 ± 0.83	1.79	0.079
	Roost^2	-0.29 ± 0.15	-1.89	0.064
	Aggregation	1.37 ± 0.55	2.50	0.015
	Aggregation^2	-0.33 ± 0.11	-3.02	0.004
Testes mass	Aggregation	1.15 ± 0.51	2.26	0.027
	Aggregation^2	-0.31 ± 0.11	-2.92	0.004

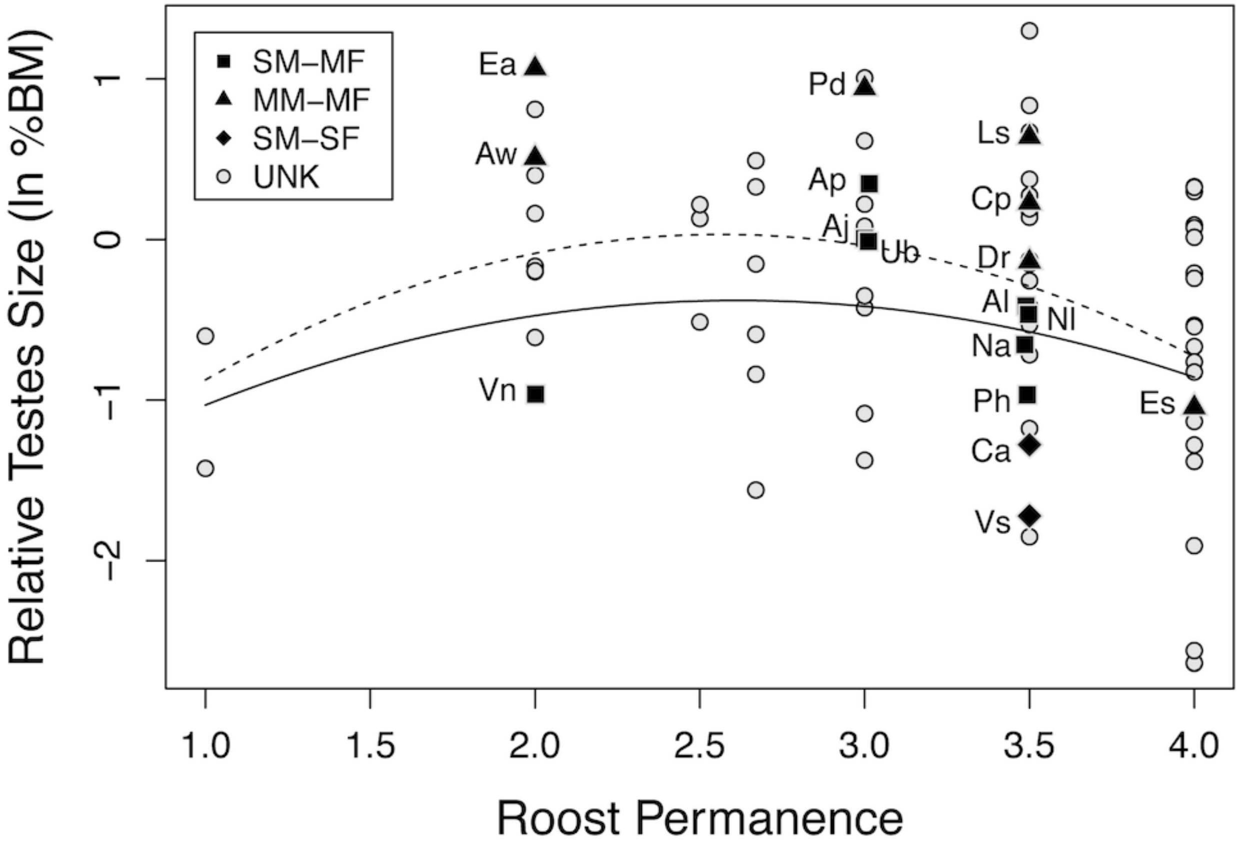
Figure 13.1. Relationship between sexual size dimorphism (SSD) and body size for 129 species. SSD is measured as the difference in forearm length between males and females expressed as a percentage of the species average. Symbols represent mating system types and species labels indicate genus and species as follows: *Aj – Artibeus jamaicensis, Ap – A. phaeotis, Aw – A. watsoni, Cp – Carollia perspicillata, Ca – Chrotopterus auritus, Dr – Desmodus rotundus, Ea – Ectophylla alba, Es – Erophylla sezkorni, Ls – Lophostoma silvicolum, Mc – Macrotus californicus, Nl – Noctilio leporinus, Na – N. albiventris, Pd – Phyllostomus discolor, Ph – P. hastatus, Ub – Uroderma bilobatum, Vn – Vampyriscus nymphaea, Vs – Vampyrum spectrum.*

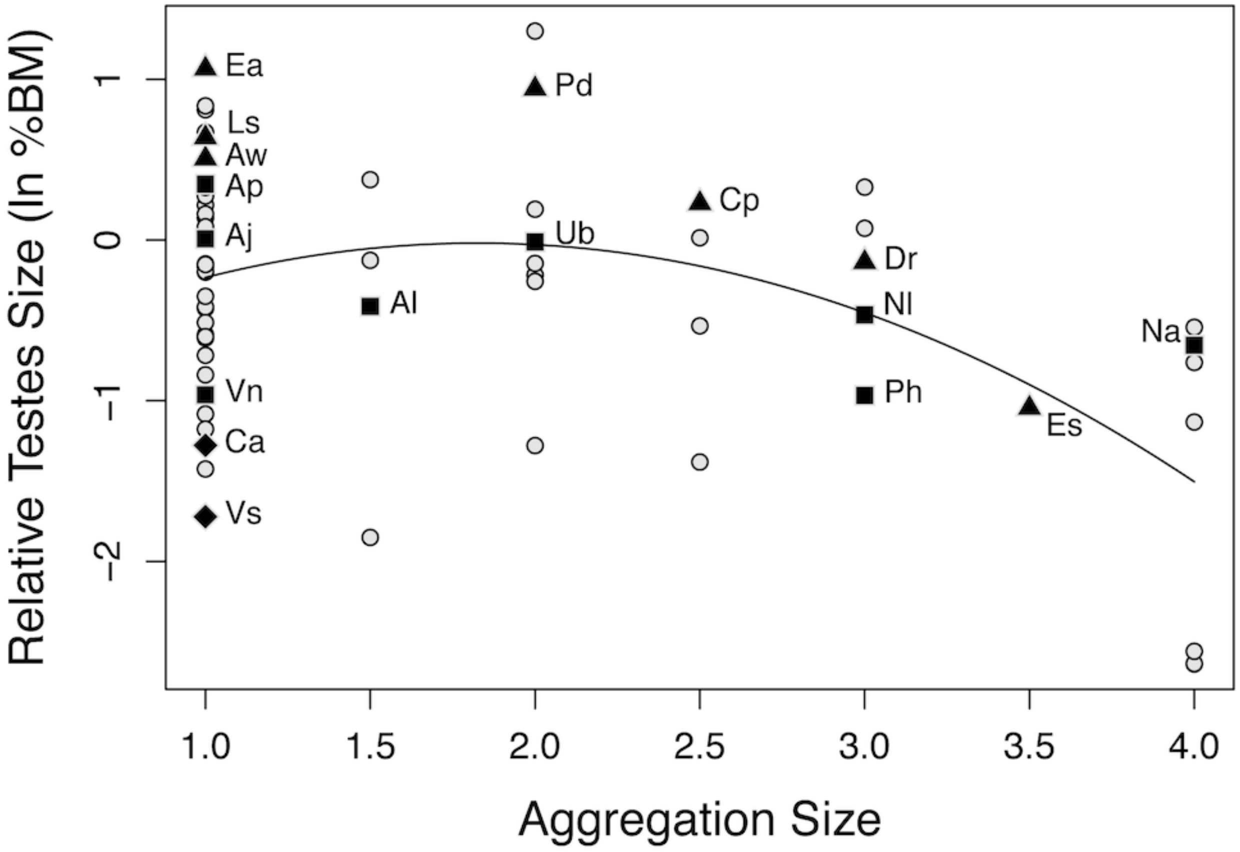
Figure 13.2. Relationship between measures of sexual dimorphism in canine length and mass among 82 species. Lines are fit by ordinary least squares (dashed) or phylogenetic generalized least squares (solid). Symbols represent mating system types and species labels indicate genus and species as in Fig. 1.

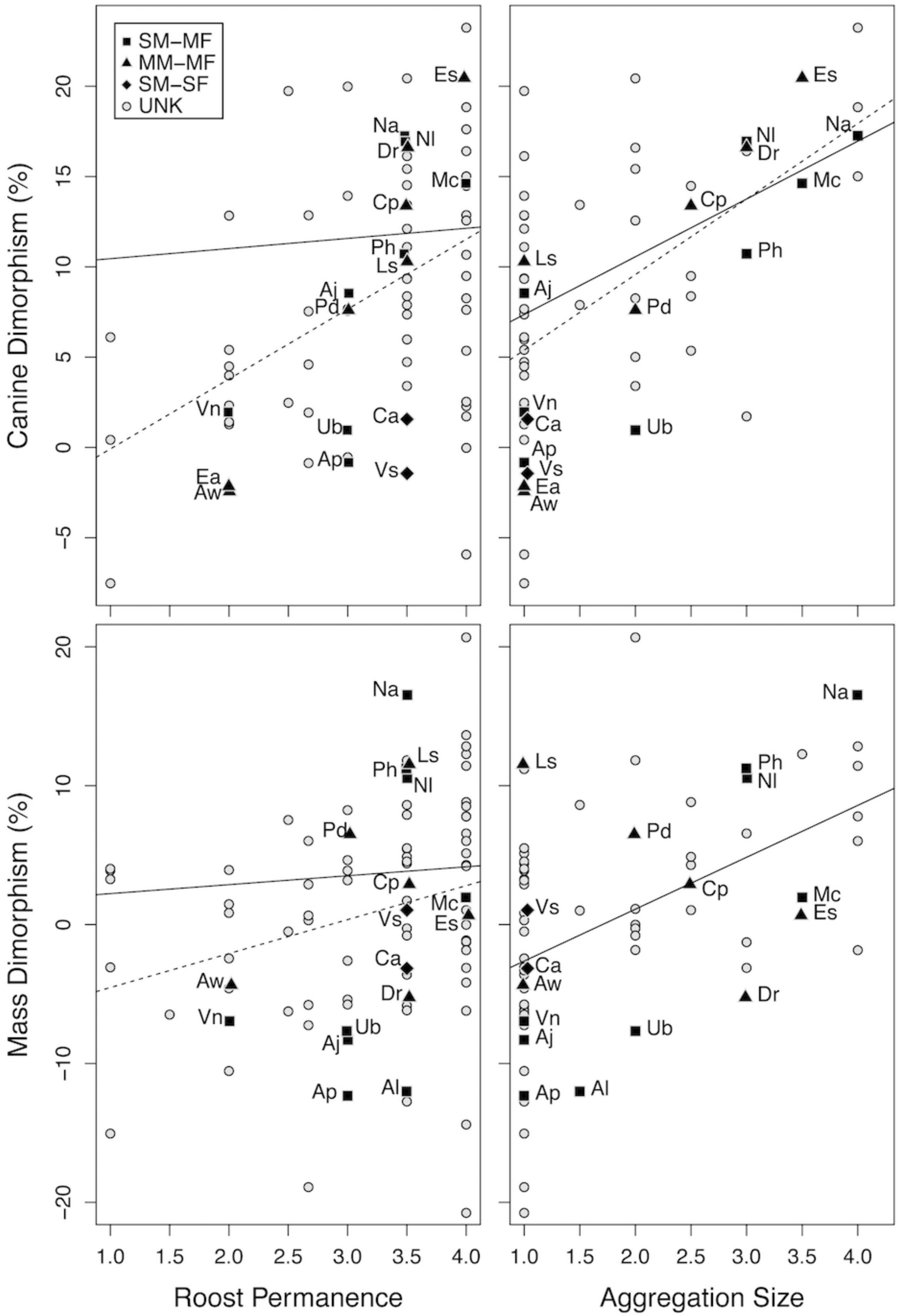
Figure 13.3. Sexual dimorphism for weaponry and weight increase with opportunity for male-male competition due to roost permanence and aggregation size. Canine dimorphism plotted against (A) degree of roost permanence for 73 species and (B) aggregation size category for 61 species. Mass dimorphism plotted against (C) degree of roost permanence for 90 species and (D) aggregation size category for 71 species. Lines are fit by ordinary least squares (dashed) or phylogenetic generalized least squares (solid) and are identical when lambda is zero. Model details available in Table S3. Symbols represent mating system types and species labels indicate genus and species as in Fig. 1.

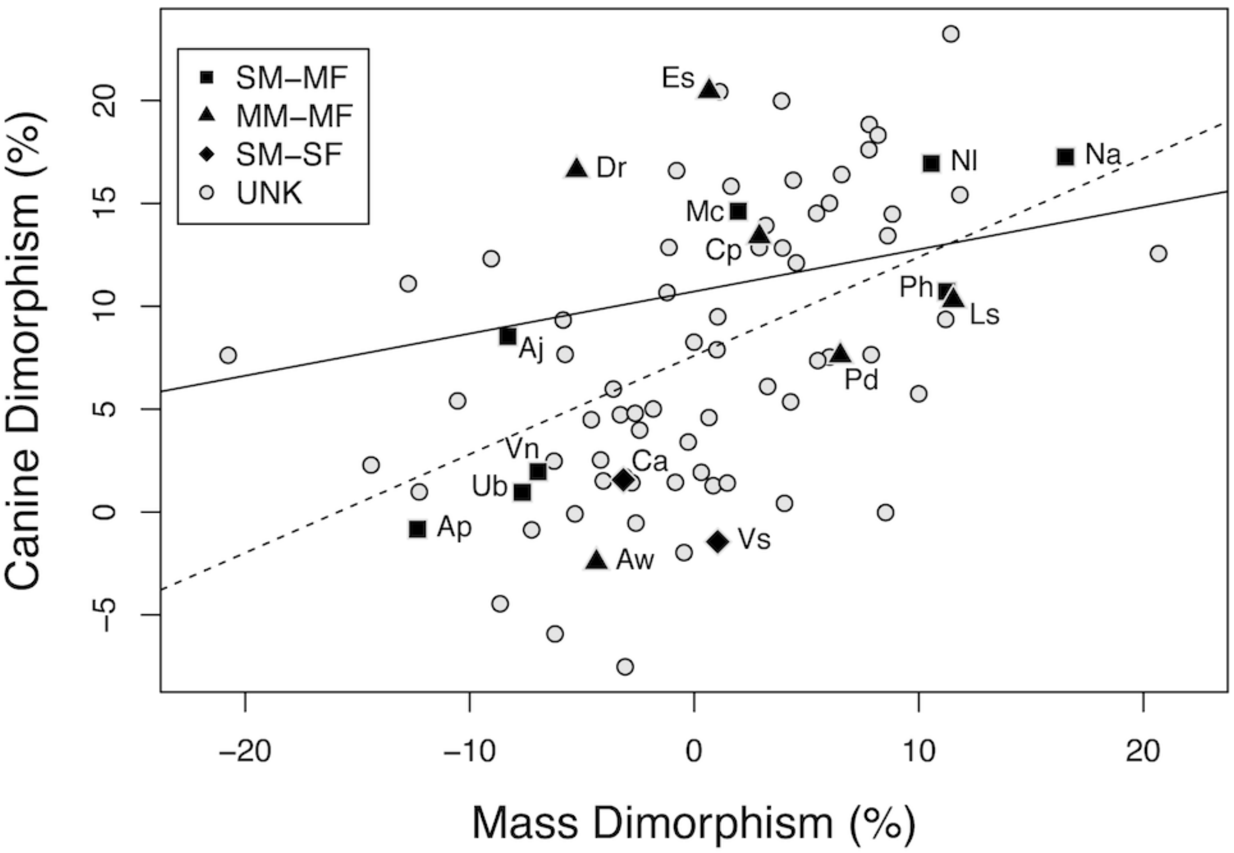
Figure 13.4. Species that roost in structures of intermediate permanence and in intermediate aggregation sizes have the largest testes. (A) Testes mass, shown as the logarithm of the percent of body mass, plotted against roost permanence for 83 species. (B) Testes mass, shown as the logarithm of the percent of body mass, plotted against aggregation size for 65 species. Lines fit by ordinary least squares (dashed) and phylogenetic generalized least squares (solid) are identical when lambda is zero. Symbols represent mating system types and species labels indicate genus and species as in Fig. 1. Additional model details available in Table S4.

Figure 13.5. Examples of sexually dimorphic traits in phyllostomids. A) Male *Sphaeronycteris toxophyllum* with enlarged browridge. B) Female *Sphaeronycteris toxophyllum* without pronounced browridge. C) Male *Pygoderma bilaboatum* with swollen tissue surrounding the eyes. Males also have swollen tissue around their wrists. D) Male *Sturnira tildae* with shoulder epaulettes caused by glandular secretions. Photos courtesy of Rodrigo Medellin (A, B), Roberto L. M. Novaes (C), and Merlin Tuttle (D).

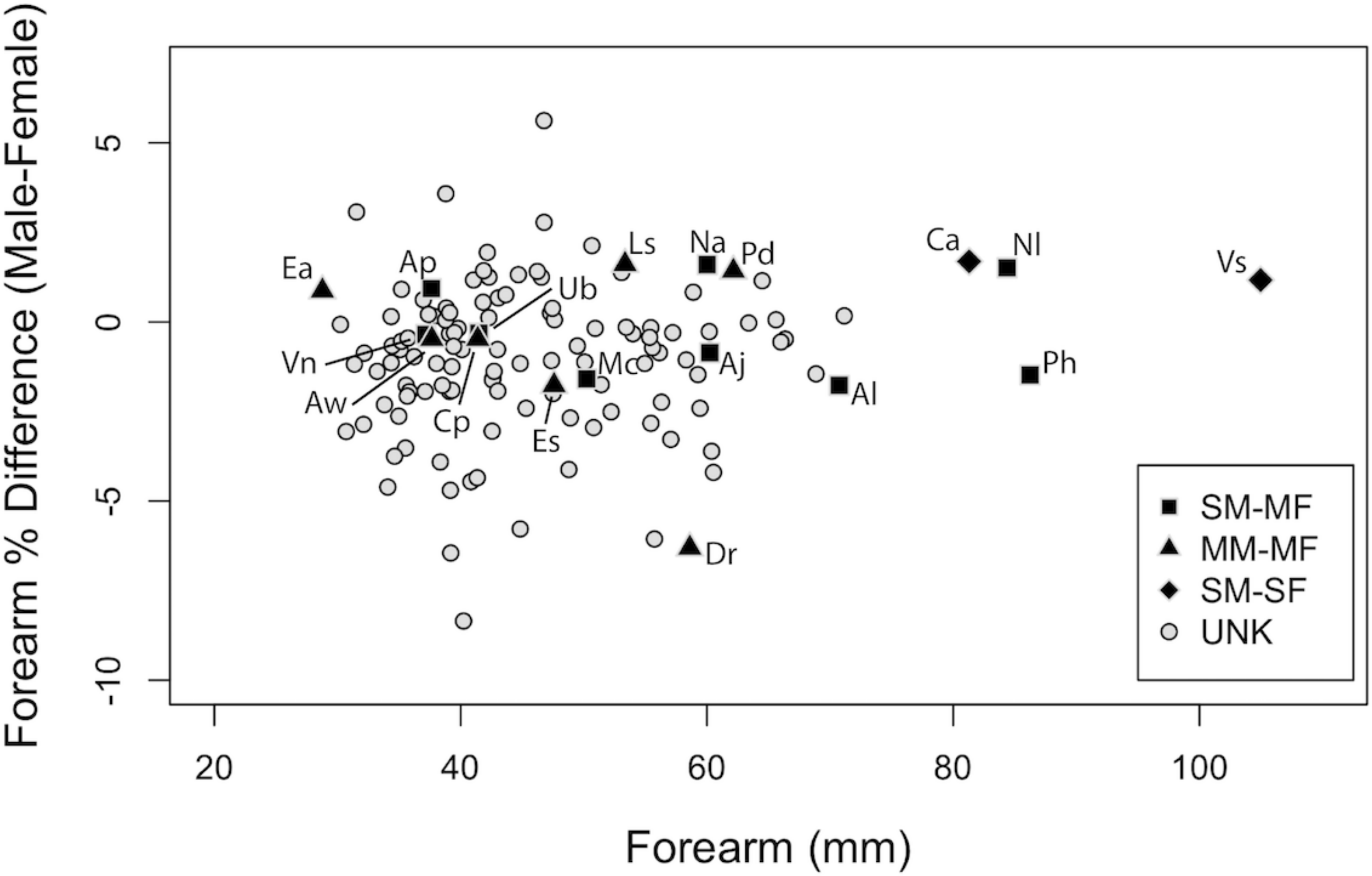

SM–MF
MM–MF
SM–SF
UNK
Ea
Aw
Vn
Pd
Ap
Aj
Ub
Ls
Cp
Dr
Al
Nl
Na
Ph
Ca
Vs
Es
Relative Testes Size (ln %BM)
1
0
−1
−2
1.0
1.5
2.0
2.5
3.0
3.5
4.0
Roost Permanence

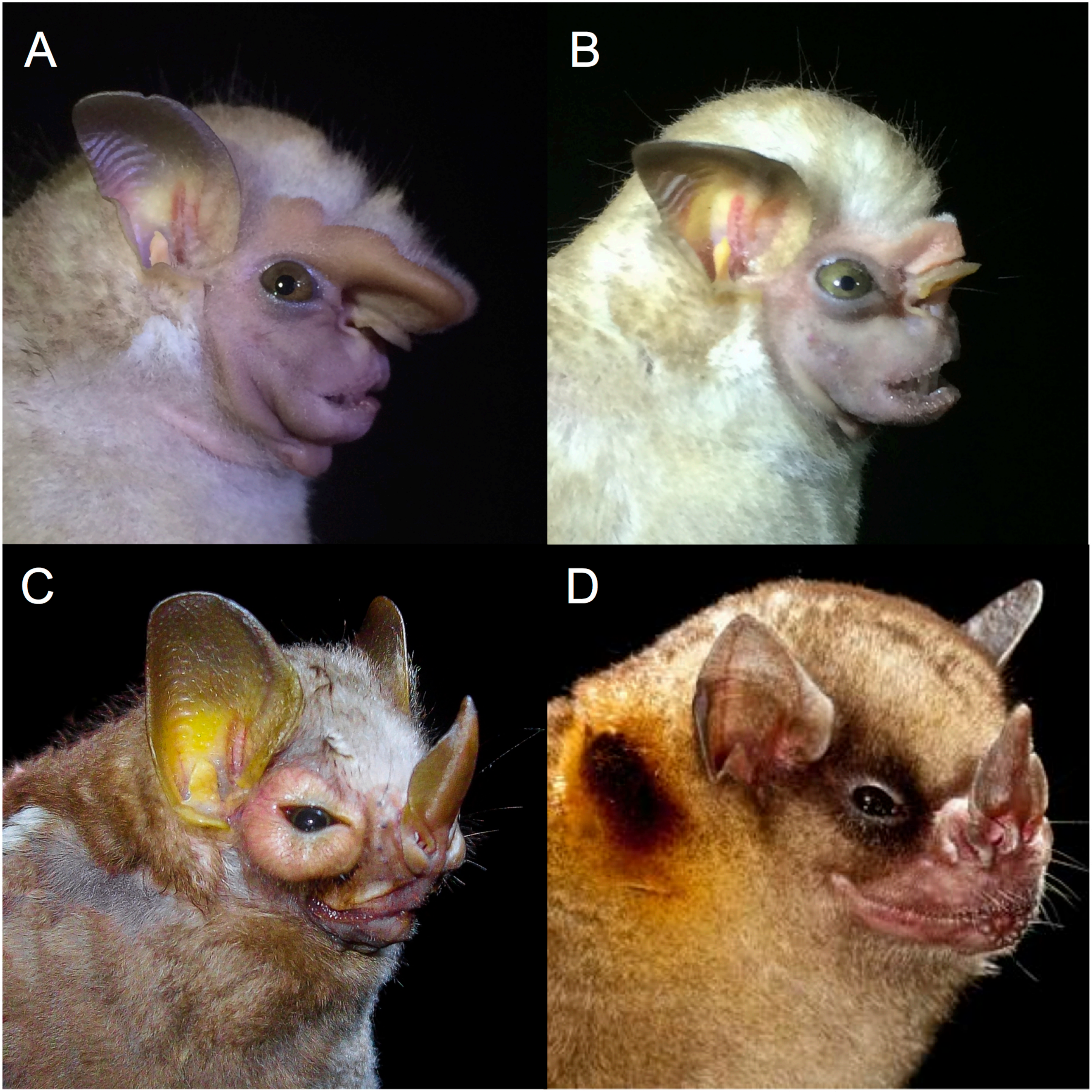

Ea
Ls
Aw
Ap
Aj
Vn
Ca
Vs
Al
Pd
Ub
Cp
Dr
Nl
Ph
Es
Na
Relative Testes Size (ln %BM)
1
0
−1
−2
1.0
1.5
2.0
2.5
3.0
3.5
4.0
Aggregation Size


SM–MF
MM–MF
SM–SF
UNK
Canine Dimorphism (%)
Mass Dimorphism (%)
Roost Permanence
Aggregation Size
1.0
1.5
2.0
2.5
3.0
3.5
4.0
−5
0
5
10
15
20
−20
−10
Es
Na
Nl
Dr
Mc
Cp
Ph
Ls
Aj
Pd
Vn
Ub
Ca
Ap
Vs
Ea
Aw
Al



■ SM–MF
▲ MM–MF
◆ SM–SF
○ UNK
Es
Dr
Nl
Na
Mc
Cp
Ph
Ls
Aj
Pd
Vn
Ca
Ub
Ap
Vs
Aw
Canine Dimorphism (%)
Mass Dimorphism (%)
−5
0
5
10
15
20
−20
−10
0
10
20


Forearm % Difference (Male-Female)
Forearm (mm)
5
0
-5
-10
20
40
60
80
100
Ea
Ap
Ls
Na
Pd
Ca
Nl
Vs
Ub
Vn
Aw
Cp
Es
Mc
Aj
Al
Ph
Dr
■ SM-MF
▲ MM-MF
◆ SM-SF
○ UNK


A
B
C
D