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Does delayed fertilization facilitate sperm competition in bats?

Teri J. Orr · Marlene Zuk

Abstract Reproductive delays between mating and birth may provide a previously unconsidered avenue for post-copulatory sexual selection in mammals. In particular, delayed fertilization could provide an enhanced opportunity for sperm competition by extending the time for ejaculates to interact in the female reproductive tract. We tested the prediction that species with delayed fertilization exhibit greater degrees of sperm competition than those without delays by examining testis volume (a proxy for sperm competition) in 38 species of bats. Examination of fluid-preserved museum specimens of bat species with and without delays revealed that species with delays (in particular those with delayed fertilization) had significantly larger testes than species without them. Although it predicts the presence of delayed fertilization, hibernation did not predict relative testis size. We conclude that, once they evolve, reproductive delays may facilitate sperm competition.

Keywords Chiroptera · Delayed fertilization · Hibernation · Sperm competition · Sexual selection · Testes size

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Introduction

Reproductive delays occur when the sequence of events from insemination to birth is interrupted, either (1) after copulation but before fertilization (delayed fertilization), (2) after fertilization but before the blastocyst implants (delayed implantation), or (3) during gestation (delayed development) (Daniel 1970; Sandell 1990). Such delays are quite common, but while their evolutionary origins have been studied (Sandell 1990; Bernard and Cumming 1997; Lindenfors et al. 2003; Ferguson et al. 2006), their role in enhancing the opportunity for post-copulatory sexual selection has not been examined. Because some reproductive delays provide a longer time window for processes leading up to fertilization, they may increase the opportunity for sperm competition and cryptic female choice (Birkhead and Møller 1993; Orr 2012). Nearly half of all mammal species that possess delays are bats, and bats are the only group exhibiting all three types of delay (Bernard and Cumming 1997). Given that some female bats can store sperm from several months (Racey and Entwistle 2000), the opportunity for sperm competition is expected to be greater in bat species with delayed fertilization than in those without (Birkhead and Møller 1993; Orr 2012).

It has been suggested that bats are able to store sperm (delay fertilization) because of use of hibernation (Wimsatt 1960). Indeed, both torpor (pronounced depressed body temperatures and basal metabolic rates) and hibernation (several days of torpor with occasional arousal) are observed in many bat species (Geiser and Stawski 2011). However, not all species that store sperm (delay fertilization) undergo hibernation (Racey and Entwistle 2000, Table 1), and indeed, many are tropical or subtropical in distribution.

Sperm are costly to produce (Dewsbury 1982), but because the probability of fertilizing an egg is correlated with sperm production (Martin et al. 1974), males are expected to invest resources in sperm in a way that increases their

Table 1 Sources of data used in analyses

Species	Common name	N	TV	BM	FA	Delay type	Delay cite	Hibern.	Hibern. cite
Vespertilionidae: Antrozous pallidus	Pallid bat	1	0.04 (NA)	20 (NA)	49.46 (NA)	DF	Orr 1954	H	Oxberry 1979; Ramm et al. 2008
Corynorhinus townsendii	Townsend's big-eared bat	8	0.06 (0.01)	11.74 (1.58)	43.82 (1.24)	DF	Pearson et al. 1952	H	Pearson et al. 1952; Webb et al. 1996
Eptesicus furinalis	Argentine brown bat	2	0.047 (0.02)	11.90 (1.27)	35.15 (2.53)	DF	Myers 1977; Racey 1982	No (N)	Myers 1977
E. fuscus	Big brown bat	8	0.19 (0.11)	21.51 (3.09)	47.06 (1.26)	DF	Gates 1936	H	Hamilton and Barclay 1994
Lasiurus borealis	Western red bat	5	0.04 (0.01)	10.82 (1.28)	39.27 (1.78)	DF	Racey 1982; Shump and Shump 1982 Hayssen et al. 1993; Cryan et al. 2012	H	Shump and Shump 1982
Lasiurus cinereus	Hoary bat	2	0.02 (0.01)	23.40 (3.41)	50.53 (0.08)	DI	Druecker 1972; Hayssen et al. 1993; Cryan et al. 2012	H	Willis et al. 2006
Lasiurus ega	Southern yellow bat	6	0.02 (0.01)	13.11 (0.94)	45.15 (1.39)	DF	Myers 1977	N "Tropical" maybe no hibernation[a]	Myers 1977; Racey and Etwistle 2000
Lasiurus xanthinus	Western yellow bat	5	0.02 (0.01)	7.18 (2.21)	44.47 (0.48)	DF[a]	See Cryan et al. 2012	H[a] implied	Other temperate Lasiurines hibernate, implied
Lasionycteris noctivagans	Silver-haired bat	6	0.04 (0.01)	13.57 (2.93)	40.60 (1.59)	DF (followed by short DI)	Layne 1958; Druecker 1972	H	Webb et al. 1996
Miniopterus australis	Little long-fingered bat	6	0.02 (0.01)	9.78 (0.72)	39.53 (0.47)	DI	Richardson 1977	T[a] in genus (see below)	—
Miniopterus schreibersii	Schreiber's long-fingered bat	1	0.03 (NA)	19.50 (NA)	48.53 (NA)	DI	Richardson 1977; Crichton et al. 1989	T	Crichton et al. 1989
Myotis albescens	Silver-tipped myotis	10	0.16 (0.05)	7.82 (0.57)	35.10 (0.86)	DF	Myers 1977; Racey 1982	H	Myers 1977
Myotis californicus	California myotis	2	0.029 (0.01)	6.5 (0.71)	33.83 (0.59)	DF	Krutzsch 1954	H	Webb et al. 1996
Myotis daubentonii	Daubenton's bat	2	0.03 (0.02)	37.39 (1.17)	10.3 (0.14)	DF	Racey 1982	H	Dietz and Kalko 2006
Myotis lucifugus	Little brown bat	5	0.13 (0.04)	7.72 (0.56)	36.27 (1.59)	DF	Racey 1982	H	Webb et al. 1996
Myotis nigricans	Black myotis	1	0.02 (NA)	5.9 (NA)	34.61	DF	Myers 1977	(N)[a] T	Wilson and Laval 1974
Myotis velifer	Cave myotis	11	0.09 (0.07)	10.14 (1.02)	42.51 (0.78)	DF	Krutzsch et al. 1982	H	Webb et al. 1996
Nyctalus noctula	Common noctule	1	0.03 (NA)	29.0 (NA)	52.09 (NA)	DF	Racey 1982	H	Racey 1974
Parastrellus hesperus	Western pipistrelle	3	0.01 (0.00)	4.13 (0.12)	30.06 (0.79)	DF	Krutzsch 1975	H	Krutzsch 1975
Pipistrellus nanus	Banana pipistrelle	4	0.02 (0.01)	4.65 (0.19)	27.06 (0.79)	DF	Bernard et al. 1997	N (T)	Bernard et al. 1997
Pipistrellus pipistrellus	Common pipistrelle	6	0.037 (0.01)	5.45 (0.64)	31.31 (0.94)	DF	Racey 1982	H	Wilde et al. 1999
Perimyotis subflavus	Eastern pipistrelle	1	0.01 (NA)	6 (NA)	24.16 (NA)	DF	Guthrie 1933	H	Webb et al. 1996
Scotophilus dinganii	African yellow bat	3	0.03 (0.01)	21.17 (0.29)	51.26 (1.83)	DI	Okia 1987	N (T)	Geiser and Stawski 2011

Table 1 (continued)

Species	Common name	N	TV	BM	FA	Delay type	Delay cite	Hibern.	Hibern. cite
Scotophilus heathi	Greater Asiatic yellow bat	4	0.03 (0.01)	21.60 (11.23)	50.19 (6.97)	DF	Racey 1982	N (T)	Srivastava and Krishna 2008
Tylonycteris robustula	Greater bamboo bat	4	0.02 (0.07)	8.23 (0.17)	30.03 (0.48)	DF	Racey 1982	N[a] "tropical"	Racey and Entwistle 2000
Natalidae: *Natalus stramineus*	Mexican funnel-eared bat	1	0.01 (NA)	7 (NA)	36.81 (0.37)	DD[a]	Racey 1982; Mitchell 1965	N[a] 'tropical'	–
Phyllostomidae: *A. jamaicensis*	Jamaican fruit-bat	8	0.14 (0.05)	44.31 (9.11)	59.30 (2.48)	DD	Fleming 1971	N (T)	Ortega and Castro-Arellano 2001
Carollia perspicillata	Seba's short-tailed fruit bat	17	0.12 (0.05)	24 (4.26)	42.26 (2.03)	DD/N	Rasweiler and Badwaik 1997	N but stress-induced can occur	Audet and Thomas 1997
Desmodus rotundus	Common vampire bat	9	0.12 (0.07)	34.97 (7.19)	59.94 (2.41)	DD/N[a, c]	Fleming et al. 1972; Quintero and Rasweiler 1974	N	Lyman and Wimsatt 1966
Glossophaga soricina	Palla's long-tongued bat	15	0.047 (0.24)	11.94 (1.05)	35.45 (0.92)	DD[a]	Rasweiler 1972; Hayssen et al. 1993	N[a] (T) 'tropical'	–
Macrotus californicus	California leaf-nosed bat	5	0.01 (0.01)	15.56 (1.56)	50.13 (1.10)	DD	Bradshaw 1962	H 'semi-hibernating'	Racey and Entwistle 2000
U. bilobatum	Tent-making bat	3	0.11 (0.05)	23 (1.14)	42.85 (0.87)	N[b]	Baker and Clark 1987	N[a] (T) 'tropical'	–
Rhinolophidae: *Hipposideros caffer*	Sundevall's bat	6	0.01 (0.01)	11 (2)	47.72 (2.75)	DD	Racey 1982;	N	Racey and Entwistle 2000
Rhinolophus ferrumequinum	Greater horseshoe bat	2	0.03 (0.03)	26.15 (4.45)	57.19 (0.58)	DF	Racey 1982	H	Park et al. 2000, Webb et al. 1996
Emballonuridae: *Saccopteryx bilineata*	Greater sac-winged bat	5	0.03 (0.01)	13.0 (1.17)	46.14 (2.31)	DD	Bradbury 1979	N[a] (T) 'tropical'	–
Pteropodidae: *C. sphinx*	Greater short-nosed fruit bat	5	0.35 (0.19)	59 (6.56)	69.62 (1.81)	DD	Racey 1982; Krishma and Dominic 1983	N[a] (T) 'tropical' and not commonly noted in group	–
Eidolon helvum	Straw-colored fruit bat	3	12.96 (17.65)	280 (0)	124.77 (3.12)	DI (note: DD implicated)	Mutere 1967; Fayenuwo and Halstead 1974; Funmilayo 1979	N[a]	DeFrees and Wilson 1988; Racey and Entwistle 2000
Haplonycteris fischeri	Philippine pygmy fruit bat	1	0.07 (NA)	23.00 (NA)	49.08 (NA)	DD	Heidman 1989	N[a] (T) 'tropical' and not commonly noted in group	–

Standard errors are in *parentheses* and delay type listed with abbreviations *DF*, delayed fertilization; *DI*, delayed implantation; *DD*, delayed development; *N*, no delay

[a] Indicates the biology is implied

[b] *Uroderma bilobatum* is inferred to not have delays given short gestation for its body size (~4 months (Hayssen et al. 1993)). This short gestation is equivalent to the entire period of delay observed in some related species like *A. jamaicensis* (Fleming 1971; Ortega and Castro-Arellano 2001)

[c] *D. rotundus* is inferred to have delayed development given it's slow progression of pregnancy (i.e., long period of gestation, ~9 months). However, this may be a stress-induced delay. In any case, it does not appear to have delayed fertilization from accounts, and its physiology is likely similar to closely related species (Quintero and Rasweiler 1974). Columns list hibernation (Hibern.) (*H* for yes), or only torpor known (*T*), versus neither of these (*N*). Two letters appear in cases where the evidence is unclear (for example T(N)). A species was considered to hibernate if it experienced several weeks of ambient body temperatures without arousal. Our presentation of thermal biology analyzes species with hibernation (1) versus torpor or none (0)

chances for successful fertilization. In cases where females mate multiply, males have a decreased certainty of fertilizing eggs, and thus, more investment in sperm may help males increase their chances of a successful fertilization. The result is sperm competition, a battle between sperm from more than one male for fertilization (Parker 1970). Evidence of sperm competition can be seen in larger relative testes size, specialized sperm morphology (Hosken 1997; Pitnick et al. 2009), different chemical components in seminal fluid (Ramm et al. 2008), and penile morphology (Eberhard 1985). The most commonly used index of sperm competition is relative testes size. Larger testes produce more sperm (Amann 1970; Parker 1970), and species with increased risk of sperm competition have larger testes (Kenagy and Trombulak 1986; Wilkinson and McCracken 2003; Dixson and Anderson 2004). We used testis size as a proxy for sperm competition in bat species with and without reproductive delays to test the hypothesis that species with delays experience a greater risk of sperm competition than species without delays. Our guiding hypothesis was that, because males with larger testes would benefit from increased sperm production, species with greater intensities of sperm competition (i.e., bats with delayed fertilization) would have relatively large testes. Thus, species with delayed fertilization were predicted (1) to have the greatest degree of sperm competition (largest testes) relative to species without delayed fertilization (no delay, delayed implantation, or delayed development). We also predicted (2) bats might have different testes sizes relative to clade membership or phylogeny. Finally, (3) hibernation might be an alternative driver of testes size (for example smaller testes due to disjoint spermatogensis (Crichton 2000)).

Methods

Data collection

To find reports of bats with reproductive delays, we performed a literature search in SciSearch using the key words reproductive delay, diapause, and Chiroptera and supplemented this with data from mammalian species accounts and Asdell's Patterns in Mammalian Reproduction (Hayssen et al. 1993) (Table 1). Only species confirmed to have one of the three types of delays or for which it was evident from the literature (often detailed physiological data) that delays were absent were included in our sampling. Delays were coded two ways: delayed fertilization (presence or absence) and by delay type (four categories: delayed fertilization, implantation, development, and no delays). Delayed implantation (DI) was assigned for species where the blastocyst remains un-implanted in the female's reproductive tract for extended periods of time (>20 days). This differs from species with delayed development (DD), such that,

in the latter, the blastocyst has implanted before the delay occurs whereby after implantation development pauses or is greatly slowed. Delays that occur during the primitive streak stage and or when the trophoblast has formed (e.g., *Artibeus jamaicensis* (Fleming 1971)) were considered DI or DD depending at what stage the delay occurs (free-floating blastocyst for DI or after implantation for DD). Because published data on testis size were limited, we measured fluid specimens of bats with intact and preserved testes.

Most bats for which we know the mating system (less than 6 % of all species) are polygynandrous, with both males and females mating multiply (McCracken and Wilkinson 2000). The number of times females mate in the field is not known for more than a few species (Hosken 1998a; Heckel and von Helversen 2002). In the few species for which there are data on both reproductive physiology and mating system, females mate more than once, suggesting that this mating pattern is widespread (Ortega et al. 2003; also see McCracken and Wilkinson 2000). Additionally, multiple paternity has been documented in some of the few twinning species such as *Eptesicus fuscus* (two males father offspring in one litter) (Vonhof et al. 2006; Fox et al. 2008). However, genetic evidence of multiple mating will remain elusive because generally only one pup is born per reproductive event (Kurta and Kunz 1987). Even in cases where twins are born, different paternities of siblings may be attributed to male or female post-copulatory processes. Given the known relationship between testes size and sperm competition risk (Wilkinson and McCracken 2003), we focus on sperm competition rather than cryptic female choice or other post-copulatory processes.

We examined testis volume of 187 individuals from 38 species in relation to reproductive delays, testing the prediction that testes are larger in species with delayed fertilization compared with species with delays occurring later in a pregnancy (delayed implantation or development). Because related species may resemble each other due to evolutionary relationships (Garland et al. 2005), we incorporated phylogenetic comparative methods (Lavin et al. 2008).

We dissected male bats from the Los Angeles County Museum, the Museum of Vertebrate Zoology in Berkeley, California, and the American Museum of Natural History. We sampled approximately 6 (range, 1–17; mean, 5) reproductive adults from the same population and date (when possible). Male reproductive condition was approximated from known seasonal trends of spermatogenesis, i.e., during the spring with disjunctive mating in winter for temperate species, bimodal and simultaneous spermatogenesis, and mating in tropical species (Racey and Entwistle 2000). Reproductive condition was then assigned based on examination of individual specimens (Racey 2009).

We measured testis linear dimensions to the nearest 0.03 mm with digital calipers. Body mass was recorded for

dry patted specimens to the nearest 0.1 g. We used the formula for a prolate spheroid volume to estimate testis volume (Myers 1977).

$$TV = (4/3)\pi r^2 \times 1/2 = 0.5236 \times 1 \times W^2$$

Testis volume (TV) can thus be calculated from linear measurements of testis length (l) and width (w). The resulting number was multiplied by two in cases where only one testis was measured to yield total testis volume. To test for possible testis asymmetry, we measured both sides of a subset of bats and found that left and right testes were not significantly different in volume ($F_{1,42}=0.091$, $p=0.764$); however, there was a slight but insignificant trend for the left testis to be larger than the right. Testis volume can be used as an unbiased proxy for testis mass (Wilkinson and McCracken 2003).

Body mass was used as a measure of body size. However, because mass was measured on wet and potentially altered bat carcasses, our values may have been higher than if we had measured animals pre-preservation. Hosken (1998b) found no significant differences in integrity of similar tissues before or after extended preservation. However, to evaluate this possible bias in our data, we compared data from museum records pre-preservation (field notes and museum tags) to our measurements. We found no significant difference (t-test, $N=28$, $p>0.53$). Additionally, because all of our data on body mass come from fluid-preserved specimens, any effects of preservation should be consistent among individuals.

Data analysis

We evaluated the relationship of testis size to delay type (scored two different ways, see above) and clade membership (Pteropodidae versus non-Pteropodidae, two categories, see below), with body mass as a covariate, using both conventional and phylogenetic analyses performed using the Matlab Regressionv2.m program (Lavin et al. 2008; Gartner et al. 2010). Data for body mass and testis volume were $\log_{10}$-transformed.

While it has been noted that bats from species that tend to roost in larger groups may have correspondingly larger relative testes sizes compared with those that live in smaller groups (Hosken 1997, 1998b), we suggest females are likely to mate multiply in mixed-sex groups but not necessarily with correspondingly more mates with increasing group size. For this reason, we did not use group size as a covariate in our analyses as most bats roost in mixed-sex groups.

We used ordinary least squares (OLS) to fit analysis of covariance (ANCOVA) models, which effectively assume a "star" phylogeny (Garland et al. 2005; Lavin et al. 2008). For phylogenetic models, we used the Binninda-Emonds supertree (Bininda-Emonds et al. 2007, Fig. 1) with estimates of branch

lengths in million years. We used phylogenetic generalized least squares (Lavin et al. 2008; Gartner et al. 2010) ANCOVA models and also ANCOVA models in which the residual trait variation is modeled using an Ornstein-Uhlenbeck (OU) process (Lavin et al. 2008). We used maximum log-likelihoods and corrected Akaike information criterion (AICc) to compare model fits (Burnham and Anderson 2002), and we report model coefficients of determination (r^2), the OU parameter (d), and F statistics from models fitted by restricted maximum likelihood (Lavin et al. 2008).

In our phylogenetic tree, the family Pteropodidae was basal. We were interested in exploring if membership in this group had implications for testis size. Our category 'clade' was binary, coding for species membership in the Pteropodidae (1) or not (0). This split, although consistent with the categories Megachiroptera versus Microchiroptera was based on our tree topology. While these previously split groups appear to differ biologically, some data suggest that other bats may be more closely related to members of the Pteropodidae than other Microchiroptera. This has resulted in the use of the categories Yinpterochiroptera and Yangochiroptera (Teeling et al. 2005). We do not ignore this controversy, but focus on "basal," i.e., Pteropodidae bats relative to other bats, to give a natural clade division of our tree (Fig. 1).

Finally, given the hypothesized importance of heterothermy to delayed fertilization (Wimsatt 1960), we scored it as a binary variable (true hibernation=1, or no hibernation and/or daily torpor=0). We evaluated the role of heterothermy in our models and examined the a priori expectation that hibernation predicts the presence of delayed fertilization (Wimsatt 1960). We implemented phylogenetic logistic regression (Ives and Garland 2010) to examine delayed fertilization (two categories) because our dependant variable was binary and therefore less appropriate for analysis using ANCOVA models (Ives and Garland 2010).

Results

As expected, log testis volume was strongly correlated with log body mass (Fig. 2; Table 2, $p<0.0001$ in all simple allometry models). Based on AICc, the best fit was obtained by an OLS model that included delay as a binary independent variable (indicating delayed fertilization ($N=21$) or no delayed fertilization ($N=17$) (i.e., delayed implantation, development, and the absence of delays)) and clade (Pteropodidae versus non-Pteropod) (Fig. 2), supporting our prediction. We did not find that other types of delays had intermediate levels of testes sizes (see Table 2). However, the relative testes sizes of species with delayed fertilization were larger than the testes of species with no delays or delays occurring after fertilization (delayed implantation and delayed development).

Hibernation was a significant predictor of delayed fertilization (two categories) for both conventional (star) and
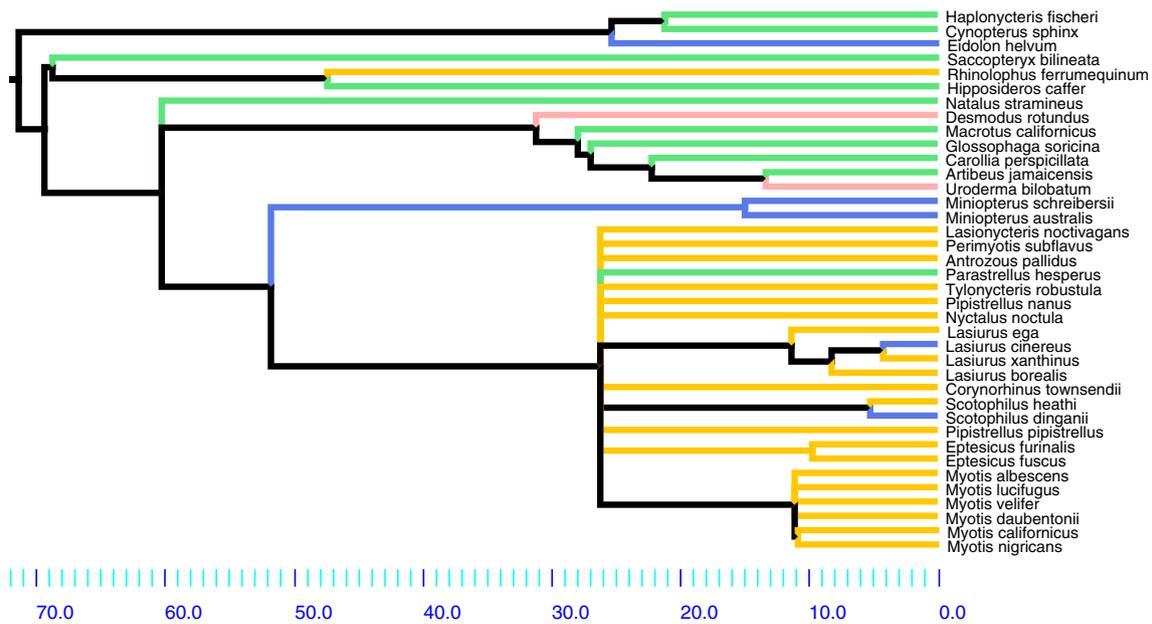
Fig. 1 The phylogenetic tree used in our testes and delay analyses. The tree used in our analyses was a smaller version of the Bininda-Emonds tree (Bininda-Emonds et al. 2007). Species with delayed fertilization are in *orange*, delayed implantation in *blue*, delayed development in *green*, and those with no delay in *pink*. *Numbers* illustrated below the tree indicate million-year divergence times

phylogenetic models (p=0.004 conventional (star) logistic regression, p=0.007 phylogenetic logistic regression). We included hibernation in our models (all possible combinations were considered including the simplest: body mass+-hibernation to the fullest models (body mass+hibernation+-delay (two categories)+clade). Hibernation was in the fourth best model (body mass+hibernation+clade+delay (two categories)). However, hibernation was not a significant predictor of testis size in any model (including this low AICc model, Table 1).

Discussion

Species with reproductive delays (delayed fertilization) have larger testes, suggesting that delays facilitate sperm competition, perhaps by providing more time for the sperm of males to compete inside the female before fertilization. Although our best model did not include phylogeny as an explanatory variable, members of the Pteropodidae tended to have larger testes than non-Pteropods. This pattern suggests the mating system of these bats includes multiple mating by females or consistent with the observations of Towers and Martin that similar to humans some Pteropod species may always be receptive to mating (Towers and Martin 1985). Another possibility is that this group has potential for as of yet unverified delayed fertilization. Indeed, many of these species roost in large colonies inhabited by both competing males and potential female mates. Additionally, *Macroglossus minimus* (the

long-tongued nectar bat) has been suggested to have delayed fertilization (sperm storage) (Hood and Smith 1989). However, their observations of sperm in the female's reproductive tract may be due to other causes such as extended female receptivity, remating, or even the presence of unviable sperm (also see Racey and Entwistle 2000). Interestingly, another Pteropod, *Cynopterus sphinx*, has also been suggested to store sperm (Krishna and Dominic 1983), but detailed histology and breeding studies are needed. Our top three models all included clade followed by simpler models that only included body mass and delayed fertilization (0,1) indicating both variables predict testis size. Although we did not include the analyses of delays after delayed fertilization, one might expect that species with delayed development experience the least amount of sperm competition and species with delayed implantation are intermediate between the extremes of delayed fertilization and delayed development. Species with delayed implantation might be able to fertilize additional eggs in the presence of an unimplanted blastocyst which could be reabsorbed; however, the physiological mechanism of this process might be complicated if females return to a peri-ovulatory state after the termination of a delay (prior to parturition, i.e., via re-absorption).

Our result of larger testis volume in bats with delayed fertilization is consistent with competition between sperm of different males for fertilization or preferential storage by the female. The percentage of sperm stored relative to sperm received is small in mammals, and females generally receive sufficient sperm for fertilization from a single copulation
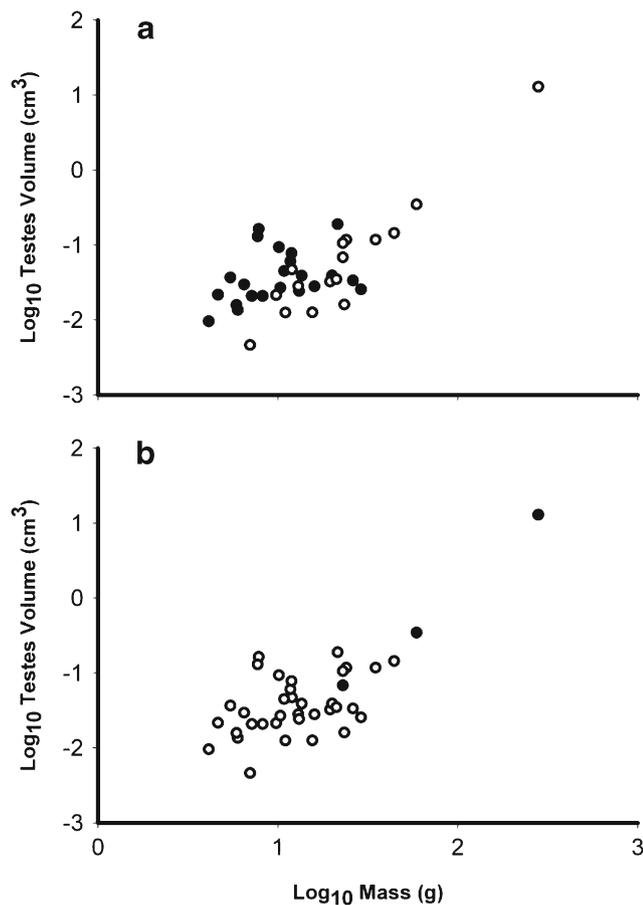
Fig. 2 Testes mass and mass relative to **a** delay type and **b** clade membership. Plots of $\log_{10}$ testes mass versus $\log_{10}$ body mass in relation to **a** delay type (delayed fertilization (*solid circles*) and no delayed fertilization (*open circles*)), and **b** in relation to clade (Pteropodidae (*solid circles*) versus non-Pteropods (*open circles*))

(Neubaum and Wolfner 1999). Thus, selection for larger testes is likely due to sperm competition rather than longer storage time, although this has not been empirically tested in bats. Alternative explanations for our observed patterns in testes size include: differences in breeding cycles (and associated testicular physiologies/morphologies), extended female receptivity for reasons beyond the act of sperm storage, and/or differences relating to sperm survival in the female's reproductive tract. Indeed, females may exert extensive control of post-copulatory processes, and this is an important future avenue worth exploration (see below). We are able to make some predictions regarding un-sampled bats in the context of our results. We expect other species with delayed fertilization to have relative larger testes than those with delays later in reproduction. However, species with delays later in a pregnancy may have larger testes if they belong to the Pteropodidae or have mating systems with particularly high sperm competition risk (Hosken 1997, 1998b; Wilkinson and McCracken 2003). While the use of hibernation appears unimportant in predicting testes size, it does predict the presence of delayed fertilization.

Many temperate species have sperm storage (Racey and Entwistle 2000). Several of these species are temperate bats that have minimal pre-copulatory sexual selection opportunities because of separate migration routes for the sexes and hence uncertain mating opportunities, or because females are mated while they are torpid (Wai-Ping and Fenton 1988). Thus, if females are unable to exert pre-copulatory choice, they may benefit from storing sperm and relying on sperm competition as their main mode for determining paternity.

Table 2 Relationships between testis size and presence of delays, with and without phylogenetic corrections from Regressionv2.m analyses

Model	ln ML	AICc	r^2	Predictors	F for predictors	p for predictors	DF
Mass (simple allometry)							
Phylogeny OU transform (d=0.249)	−16.014	41.241	0.509	Mass	40.664	<0.0001	1, 36
Mass+delay (two categories: delayed fertilization versus no delayed fertilization (no delay and delays post-fertilization))							
Conventional (OLS)	−15.139	39.490	0.596	Mass	49.065	<0.0001	1, 35
				Delay	4.692	0.0372	1, 35
Mass+delay (two categories)+clade (two categories: Pteropoidae versus non-Pteropods)							
Conventional (OLS)	−12.798	37.472	0.643	Mass	26.34	<0.0001	1, 34
				Delay	5.68	0.0229	1, 34
				Clade	4.46	0.0421	1, 34
Mass+delay (two categories)+hibernation (two categories: hibernation or not (regarding none or just torpor))+clade							
Conventional (OLS)	−12.333	41.63	0.624	Mass	25.28	<0.0001	1, 33
				Delay	3.56	0.0680	1, 33
				Hibernation	3.10E-07	>0.50	1, 33
				Clade	3.854	0.0581	1, 33

Best model results from each analysis of covariance model implemented in Regressionv2.m Matlab program (Lavin et al. 2008). Model with lowest AICc (indicating best fit) is in. r^2 is not comparable between conventional and phylogenetic models. Note that with the exception of the simple allometry model (regarding body mass, OU), the best models were always the OLS model (i.e., conventional statistics that did not include phylogeny)

Table 3 Specimens examined listed with sample size, month, year collected, and location (country, counties, or equivalent)

Species	Common name	N	Month collected	Collection location
Vespertilionidae: *Antrozous pallidus*	Pallid bat	1	April 1987 (1)	USA, TX, Val Verde Co. (1)
C. townsendii	Townsend's big-eared bat	8	July 1969 (1), December 1959 (1), October 1960 (5), November 1961 (1)	USA, CA, Mono Co. (1), USA, PA, Union Co. (1), USA, WV, Pendleton Co. (6)
E. furinalis	Argentine brown bat	2	December, 1977 (2)	Mexico, Chiapas (2)
E. fuscus	Big brown bat	8	June 1969 (4), July 1969 (4)	Mexico, Chihuahua (8)
L. borealis	Western red bat	5	August, 1976 (5)	USA, MS, Tishomingo Co. (5)
L. cinereus	Hoary bat	2	May 1961 (2)	Mexico, Chihuahua (2)
Lasiurus ega	Southern yellow bat	6	April 1973 (2), September 1973 (2), May 1971 (1), August 1963 (1)	Paraguay, Reco Leta (4), Costa Rica, Puntarenas Prov. (2)
L. xanthinus	Western yellow bat	5	April 1996 (1), June 1998 (1), October 1995 (1), November 1990 (1), September 1993 (1)	USA, CA, Riverside Co. (4), USA, CA, San Diego Co. (1)
L. noctivagans	Silver-haired bat	6	July 1939 (1), October 1985 (1), September 1985 (1), October 1984 (1), October 1990 (1), August 1972 (1)	USA, MT (1), USA, CA, Butte Co. (2), USA, CA, Alameda Co. (1), USA, CA, Shasta Co. (1), USA, CA, El Dorado Co. (1)
M. australis	Little long-fingered bat	6	June (1), July 1959 (2), April 1953 (3)	Australia, Queensland (3), Papua New Guinea (3)
M. schreibersii	Schreiber's long-fingered bat	1	October, 1961 (1)	Australia, South Australia (1)
M. albescens	Silver-tipped myotis	10	May, 1984 (4), November (2), July 1973 (3), Unk (1)	Peru, Madre de Dios Dept (4)., Paraguay, Presedento Hayes Dept. (5), Unk (1)
M. californicus	California myotis	2	July 1936 (2)	USA, UT, San Juan Co. (2)
M. daubentonii	Daubenton's bat	2	August 2004 (2)	France, Haute-Savoie Prov. (2)
M. lucifugus	Little brown bat	5	August, 1962 (3), July 1947 (1), July 1978 (1)	USA, PA, Center Co. (3), USA, NV, Mineral Co. (1), USA, NY, Sullivan Co. (1)
M. nigricans	Black myotis	1	July 1972 (1)	Guatemala, Sta Rosa Dept. (1)
M. velifer	Cave myotis	11	June 1969 (2), August 1974 (5), May 1940 (1), June 1937(1), September 1939 (1), July 1967 (1)	Mexico, Chihuahua (2), Mexico, Sonora (5), USA, AZ, Santa Cruz Co. (2), USA, AZ, Yavapai (1), USA, AZ, Pima Co. (1)
N. noctula	Common noctule	1	February 1961 (1)	Nepal, Jhapa Dist. (1)
P. hesperus	Western pipistrelle	3	July 1937 (3)	USA, AZ, Navajo Co. (3)
P. nanus	Banana pipistrelle	4	January 1946 (1), June 1947 (3)	Liberia, W. Africa (4)
P. pipistrellus	Common pipistrelle	6	August–September 1950 (6)	"Czechoslovakia" (6)
P. subflavus	Eastern pipistrelle	1	March 1952 (1)	USA, FL, Jackson Co. (1)
S. dinganii	African yellow bat	3	July 1984 (3)	Botswana, Ngamiland (3)
S. heathi	Greater Asiatic yellow bat	4	October 1982 (3), August 1988 (1)	Zambia, Eastern Prov. (3), China, Yunnan Prov. (1)
T. robustula	Greater bamboo bat	4	June 1967 (4)	Malaysia (4)
Natalidae: *N. stramineus*	Mexican funnel-eared bat	1	January 1963 (1)	Costa Rica, Guanacaste Prov. (1)
Phyllostomidae: *A. jamaicensis*	Jamaican fruit-bat	8	March, 1980 (1), March 1968 (1), January 1984 (3), November 1984 (3)	Mexico, Chiapas (1), Mexico, Colima (1), Dominican Rep, Altagracia Prov. (3) Costa Rica, Puntarenas Prov. (3)

Table 3 (continued)

Species	Common name	N	Month collected	Collection location
C. perspicillata	Seba's short-tailed fruit bat	17	May 1964 (6), June 1961 (3), October 1967 (4), October 1993 (2), September 1985 (2)	Costa Rica, Alajuela Prov. (6), Mexico, Vera Cruz (3), Panama, Darien Prov. (4), Brazil, Espirita Santo (2), Peru, Dept. Iunin (2)
D. rotundus	Common vampire bat	9	September 1962 (4), January 1972 (5)	Brazil, Sao Paulo, Itapica (4), Mexico, Oaxaca (5)
G. soricina	Palla's long-tongued bat	15	May 1961 (6), May 1974 (6), June 1963 (3)	Mexico, La Cuhcara (6), Mexico, Sonora (6), Costa Rica, Puntarenas Prov. (3)
M. californicus	California leaf-nosed bat	5	July 1960 (2), January 1940 (3)	USA, CA, Riverside Co. (2), USA, CA, Imperial Co. (3)
U. bilobatum	Tent-making bat	3	September 1985 (1), June 1970 (2)	Bolivia, La Paz, St. Anade (1), Peru, Dept. Cuzco (2)
Rhinolophidae: *H. caffer*	Sundevall's bat	6	March 1972 (3), August 1961 (3)	Angolia, Benguela (3), Somalia, Banaadir (3)
R. ferrumequinum	Greater horseshoe bat	2	November 1933, December 1954	Croatia (1), "Czeckslovakia" (1)
Emballonuridae: *S. bilineata*	Greater sac-winged bat	5	October 1965 (1), September 1965 (2), August 1983 (2)	Bolivia, Dept. Beni (5)
Pteropodidae: *C. sphinx*	Greater short-nosed fruit bat	5	August 1967 (1), Unk. (2), June 1971 (2)	Malaysia, Kelantan (1), India, W. Bengal, Calcutta (2), Thailand (2)
E. helvum	Straw-colored fruit bat	3	Unk. (3)	Sudan (2), D.R. Congo, New Beni (1)
H. fischeri	Philippine pygmy fruit bat	1	May 1983 (1)	Philippines, Mindoro (1)

Dates and locations are listed in the same (corresponding order). Sample sizes are listed in parentheses if bats were taken from several locations or dates

Males that produce more sperm should be better able to outcompete other males for fertilization opportunities (Parker 1970). Specifically, species with delays during fertilization are expected to have increased sperm competition and thus larger testes. However, other aspects of male reproductive morphology (including sperm morphology, seminal fluid composition, and genital morphology) may have also evolved in conjunction with reproductive delays and are worth further exploration. While we made every attempt to sample males during spermatogenesis (Table 3), future studies would benefit from histological analysis of testes to verify testicular state. Furthermore, DNA barcoding of species used in future comparative studies of bat testes size would be important verification of species identification for those species such as members of the genus *Miniopterus* that has been revised several times in recent years (Miller-Butterworth et al. 2007; Rodrigues et al. 2010).

Finally, it is of interest that females may exert control on mating events as well through cryptic female choice or other processes (sperm dumping, genetic incompatibility avoidance (see Eberhard 1996)). Females may even benefit through delayed fertilization by eliciting sperm competition which might result in her bearing offspring from highly competitive fathers. Future studies may benefit from considering these female processes and would do well to investigate twining species such as *E. fuscus* to determine which sex controls post-copulatory events.

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