Growth, bimaturation, and sexual size dimorphism in wild gray-headed flying foxes (*Pteropus poliocephalus*)

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In many mammals large size is more important for male than female fitness, which may select for bimaturation with males maturing later and attaining a larger size. In bats, however, sexual dimorphism in size tends to be reversed, with females being larger. Exceptions to this can be found, notably in the genus *Pteropus*. I examined growth, maturation, and sexual size dimorphism in free-ranging gray-headed flying foxes (*Pteropus poliocephalus*) to better understand the links between life history, behavior, and ecology of this large, polygynous Australian fruit bat. Juveniles left the colony independently at dusk when their forearm length and body mass exceeded 130 mm and 301 g, or 79% and 39% of mean adult dimensions, respectively. Mean forearm length and mass of these volant juveniles increased by 0.72 mm and 4.9 g per week, independent of sex. However, significant dimorphism and bimaturation were observed: adult males averaged 1.8–4.5% larger for skeletal measurements and 25% heavier than adult females, but 40% heavier at the start of the breeding season. Males also were sexually mature at a larger skeletal size and at a higher mass (604 g) than females (514 g). Sexual size dimorphism in *P. poliocephalus* likely results from prolonged male growth and delayed maturation. Intrasexual selection among males for fighting ability is implicated as the cause for dimorphism, together with a release of female size from the constraints posed by carrying heavy young. Bimaturation likely results from the high costs of maintaining mating territories that confer few reproductive benefits for small males. DOI: 10.1644/09-MAMM-A-157R.1.

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Sexual size dimorphism is more pronounced in species with a polygynous mating system in which males compete for access to breeding females. Sexual size dimorphism is common among birds (Dunn et al. 2001; Owens and Hartley 1998) but is especially common among mammals (Clutton-Brock 1989; Weckerly 1998). In polygynous species sexual selection is expected to favor adaptations that increase success in male–male interactions (Clutton-Brock et al. 1977, 1979; Schulte-Hostedde et al. 2001; Trivers 1972). These adaptations include large size and weaponry such as antlers and canines. For many taxa a positive correlation exists between sexual dimorphism and bimaturation, such that members of the larger sex mature at older ages (Stamps and Krishnan 1997). Life-history theory predicts that the timing of maturation will be affected by the trade-off between the benefits of current reproduction versus ecological, physiological, or behavioral costs (Stearns 1992). When this trade-off differs between sexes it may lead to sexual size dimorphism and bimaturation (Andersson 1994).

Like most other mammal species (Clutton-Brock 1989), the majority of bat species are polygynous (McCracken and Wilkinson 2000). However, sexual size dimorphism tends to be reversed in bats, with females attaining the larger size. This is hypothesized to result from the demands on females that have to carry heavy young during flight (Myers 1978). Several exceptions to this can be found, notably in the genus *Pteropus* (McNab and Armstrong 2001). Many pteropids are polygynous with either single-male–multifemale groups (e.g., *P. tonganus*—Grant and Banack 1999) or multimale–multifemale groups (e.g., *P. giganteus*—Grant and Banack 1999; Neuweiler 1969). Sexual dimorphism in *Pteropus* involves larger male body size (most species), larger male canines (many species), and in some species males with conspicuous skin glands (Hill and Smith 1984; Nowak and Walker 1994).

Despite its relatively widespread distribution, *Pteropus* is poorly studied, which is a problem for the management of this ecologically important genus (Mickleburgh et al. 1992; Pierson and Rainey 1990). The gray-headed flying fox

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(*Pteropus poliocephalus*) is among the best-studied species, yet no detailed published accounts have been made of growth, maturation, and sexual dimorphism. Such information is important for modeling how populations are likely to change under varying conditions (e.g., McIlwee and Martin 2002), which is vital at present given that preservation of *P. poliocephalus* has become a prominent issue (Duncan et al. 1999; Eby et al. 1999; Lunney et al. 2008; Tidemann 2003).

Pteropus poliocephalus is a large (600- to 1,100-g) bat endemic to the forested areas of southeastern Australia, principally east of the Great Dividing Range (Hall and Richards 2000; Mickleburgh et al. 1992; Nelson 1965b; Ratcliffe 1931). At night it flies up to 50 km to eat fruit, nectar, and pollen (Eby 1991, 1996; Fujita and Tuttle 1991; Spencer et al. 1991). During the day it forms large colonies among the foliage and branches of canopy trees (Mickleburgh et al. 1992; Nelson 1965a; Pierson and Rainey 1990; Ratcliffe 1931; Tidemann et al. 1999).

The social system of *P. poliocephalus* involves seasonal harems that consist of a single male and an unstable multifemale group (Welbergen 2005). Beginning in February males hold mating territories in the colonies that are scent-marked and aggressively defended (Nelson 1965a; Welbergen 2005). Larger males have larger harems than smaller males and occupy the more central territories of the colony (Welbergen 2005). During the mating season (mid-March to mid-May—Martin et al. 1995; Nelson 1965a; Welbergen 2005, 2006) females mate repeatedly with the harem male over the course of several days (Welbergen 2005). After conception females gestate for approximately 6 months, and most give birth to a single young (Martin 1999; Nelson 1965a) that is weaned at approximately 4–6 months, just before the next mating season (Martin et al. 1986, 1995; Nelson 1965a).

I examined growth, maturation, and sexual size dimorphism of free-ranging *P. poliocephalus* to better understand the links between life history behavior and ecology of this species. Because *P. poliocephalus* is polygynous, and larger size seems more important for male than for female reproductive success, the species should be sexually dimorphic, with males maturing later and attaining a larger size than females. To test this prediction I used data from 3 seasons of catching individuals from a wild population of *P. poliocephalus* to infer sex-specific patterns of growth and maturation and to determine whether adult males differed from females in body mass, overall size, and weaponry used in territorial disputes.

Materials and Methods

Study area.—This study was conducted in the Dallis Park colony (28°31′S, 153°32′E) on a 2-ha strip of forested wetland in northeastern New South Wales, Australia (for details see Welbergen 2005). In 2002 and 2003 ground and emergence counts provided population estimates of *P. poliocephalus* of 26,500–28,400 between January and February and 26,800–27,800 between April and May (Welbergen 2005). During this period the colony contained both *P. poliocephalus* (~70%)

and the closely related *P. alecto* (~30%—Welbergen 2005). In 1998–2001 between 320,000 and 400,000 *P. poliocephalus* existed in Australia (Threatened Species Scientific Committee—Eby and Lunney 2002), meaning that the colony comprised approximately 5% of the entire species population.

Data collection.—Bats were caught in a 4 × 15-m mist net or a noose trap (Welbergen 2005) 1–3 times each week between January and July in 2001–2003. No individuals were recaptured. All bats ($n = 256$) were weighed to the nearest 10 g using a 2.5-kg Pesola spring balance (Pesola AG, Baar, Switzerland). Forearm length was measured to the nearest millimeter with a stainless steel ruler, and thumb length, thumb claw length, and tibia length were measured to the nearest 0.1 mm with vernier calipers. Molar wear was estimated on a 1–5 scale by visually inspecting teeth (1 = no wear, 5 = worn to gum line) and used as a relative measure of age. Bats were banded on their thumbs with both a numbered metal band (Australian Bird and Bat Banding Scheme, http://www.environment.gov.au/biodiversity/science/abbbs/) and a unique combination of 1–3 colored metal bands to facilitate permanent individual recognition. I followed guidelines of the American Society of Mammalogists for the capture, handling, and care of mammals (Gannon et al. 2007), and all protocols were approved by the Animal Ethics Committee of the New South Wales Department of Agriculture.

Sexually mature females were distinguished from immatures on the basis of worn nipples, indicating that they had suckled young at some time in their life (Nelson 1965b). Sexually mature males were distinguished from immatures based on a fully developed penis and testes > 10 mm in the scrotum or abdomen (Vardon and Tidemann 1998). This method underestimates the proportion of sexually mature females because 1st-time breeders, or breeders that aborted during their previous breeding attempts, exhibit no sign of nipple wear.

Immature individuals were classified as young (<12 months old; i.e., born the previous parturition period) or subadult (12–24 months old). Using the same criteria as Holmes (2002), young were distinguished by their smaller size, narrower shoulders relative to their head, longer legs relatively to their body length, and larger eyes and ears relative to facial area.

Young were designated as volant juveniles if they had been caught alone in the net as they emerged independently from the colony at dusk, whereas young were designated as nonvolant when they were attached to their mother at this time (Welbergen 2006). This classification separates young on a continuum from the onset of volancy to sustained flight and foraging (Kunz and Stern 1995) and is repeatable and relatively easy to assess.

Statistical analysis.—All tests were 2-tailed, employed an alpha value of 0.05, and were carried out in Minitab for Windows (version 14.0; Minitab Inc., State College, Pennsylvania). Means are expressed ± standard error (*SE*), unless otherwise stated. Student's *t*-tests were used to test for

comparing morphometrics and forearm/tibia, forearm/thumb, and forearm/claw ratios between sexes. General linear models (GLMs) were used to evaluate the relationship between body mass, forearm length, and sex in both young and adults, and to determine the relationships of mass and forearm length to time of year and sex. In all cases the distribution of residuals from the GLMs were examined for normality to check for violation of model assumptions. Binary logistic regressions (BLRs) with a logit-link function were used to determine the relationships of both juvenile volancy and maturity versus the main morphometric measurements and sex. The BLR procedure uses an iterative-reweighted least-squares algorithm to obtain maximum-likelihood estimates of parameters (McCullagh and Nelder 1989). For all BLR models, overall confidence that all slopes were not equal to 0 was high (log-likelihood < -10.63; $G_2 > 165.07$, $P < 0.01$), and no evidence existed that models were of insufficient fit (Pearson correlation, $P > 0.87$).

RESULTS

Of the total bats caught, 160 were adults (87 males and 73 females), 4 were subadults (3 males and 1 female), and 92 were young (49 males and 43 females). I found a significant effect of age class on body mass ($F_{2,249} = 422.49$, $P < 0.01$) and on forearm length ($F_{2,253} = 702.08$, $P < 0.01$). Subsequently, age classes were analyzed separately, but subadults were omitted because they comprised such a small part of the sample ($n = 4$; 1.6%). No effect of year of capture on any of the measurements of young was observed (analysis of variance: $0.07 < F_{1,91} < 1.32$; $0.25 < P < 0.79$) and adults ($0.13 < F_{1,159} < 1.32$; $0.25 < P < 0.88$). Therefore, I pooled measurements from different field seasons for each age group.

Captures were not biased with respect to relative age or sex within age groups. The ratio of males to females among captured adults and young did not deviate from chance, assuming a 1:1 sex ratio (cumulative binomial probability = 0.24 and 0.77, respectively). Furthermore, molar wear did not vary significantly between young males and females ($\chi_1^2 = 0.88$, $P = 0.35$) nor between adult males and females ($\chi_4^2 = 1.61$, $P = 0.81$). This means that morphometric differences between males and females are unlikely to be the result of sampling in the colony.

Young morphometrics.—The body mass of young increased significantly with forearm length, independent of sex (GLM [$R^2 = 50.9\%$]—forearm length (covariate): $F_{1,87} = 94.28$, $P < 0.01$; sex [factor]: $F_{1,87} = 0.01$, $P = 0.91$; Fig. 1). All other morphometric measurements were positively correlated ($0.533 < r < 0.824$, $P < 0.01$). No differences between sexes were observed for any morphometric measurements of young (Table 1).

The proportion of young that were volant juveniles increased significantly with forearm length (BLR: $Z = 3.29$, $P = 0.01$) and body mass (BLR: $Z = 2.03$, $P < 0.04$). The BLRs predicted that 50% of young were volant juveniles at a forearm length of 130 mm and a body mass of 301 g, representing 79% and 39% of average adult dimensions,
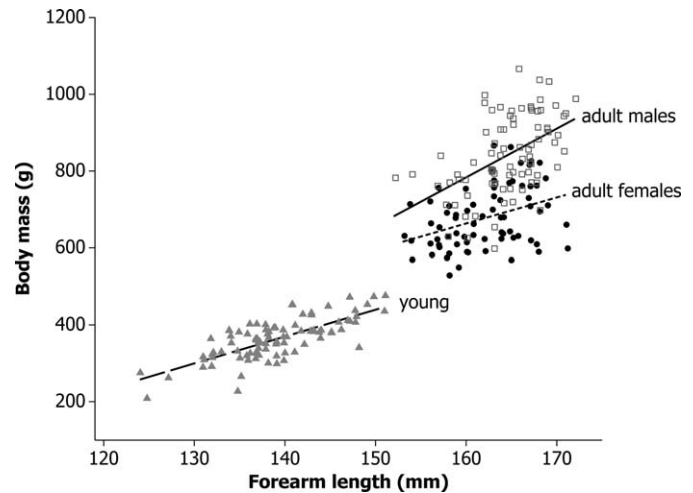

FIG. 1.—Forearm length versus body mass of adult male (open squares), adult female (closed circles), and young (closed triangles) gray-headed flying foxes (*Pteropus poliocephalus*).

respectively (see below). These predicted threshold values closely match the forearm length (131 mm) and mass (295 g) of the smallest juveniles that were found to emerge independently from the colony at dusk.

Body mass of volant juveniles increased significantly with time of year, independent of sex and the interaction between time of year and sex (GLM [$R^2 = 24.5\%$]—time of year [covariate]: $F_{1,78} = 28.43$, $P < 0.01$; sex [factor]: $F_{1,78} = 0.21$, $P < 0.65$; time of year × sex: $F_{1,78} = 0.21$, $P < 0.65$). A linear regression of mass of volant juveniles against number of weeks since the median birthing week (i.e., the week most young *P. poliocephalus* are born in nearby Brisbane—Martin 1999) yielded an average increase in mass of 5.03 ± 0.93 g/week ($= 0.72 \pm 0.13$ g/day) between week 12 and 30 (Fig. 2). Variation around the growth trajectory comes from 2 sources, individual variation among bats born at the same time and differences among bats born at different times.

Forearm length of volant juveniles increased with time of year but was independent of sex and the interaction between time of year and sex (GLM [$R^2 = 38.4\%$]—time of year: $F_{1,80} = 53.85$, $P < 0.01$; sex: $F_{1,80} = 0.22$, $P = 0.64$; time of year × sex: $F_{1,80} = 0.22$, $P = 0.64$). A linear regression relating forearm length to the number of weeks since median birthing week yielded an average increase in forearm length of 0.76 ± 0.10 mm/week ($= 0.109 \pm 0.015$ mm/day) between weeks 12 and 30 (Fig. 2). Again, variation around the growth trajectory represents individual variation among bats born at the same time and differences among bats born at different times.

Maturation.—The proportion of individuals that were sexually mature increased significantly with body mass, and females and males were mature at significantly different mass (BLR, proportion mature versus mass: $Z = 3.89$, $P < 0.01$; sex: $Z = -2.75$, $P < 0.01$; Fig. 3). The BLR predicted a threshold mass at which 50% of individuals were mature of 514.1 ± 6.3 g for females and 604.1 ± 9.1 g for males (difference = 17.5%), or 76% and 71% of the average for adult females and males, respectively.

TABLE 1.—Morphometrics (mean ± SE) of young gray-headed flying foxes (*Pteropus poliocephalus*) caught during 2001–2003.

Young	Body mass (g)	Forearm length (mm)	Tibia length (mm)	Thumb length (mm)	Thumb claw length (mm)
Females (n = 43)	359 ± 8.8	139 ± 0.9	695 ± 5.7	386 ± 3.7	164 ± 1.2
Males (n = 49)	360 ± 7.1	139 ± 0.8	692 ± 5.9	390 ± 2.9	167 ± 1.4
t	−0.09	0.30	0.33	−0.91	−1.12
P	0.93	0.76	0.74	0.37	0.13

The proportion of individuals that were mature also increased significantly with forearm length; however, females and males were mature at similar forearm lengths (BLR, proportion mature versus forearm length: $Z = 4.02$, $P < 0.01$; sex: $Z = 1.50$, $P <$ 0.13; Fig. 3). The BLR estimate for the threshold forearm length at which 50% of individuals were mature was 151.2 ± 0.4 mm for females and 153.6 ± 0.4 mm for males (nonsignificant difference = 1.6%), or 93% and 93% of the average adult
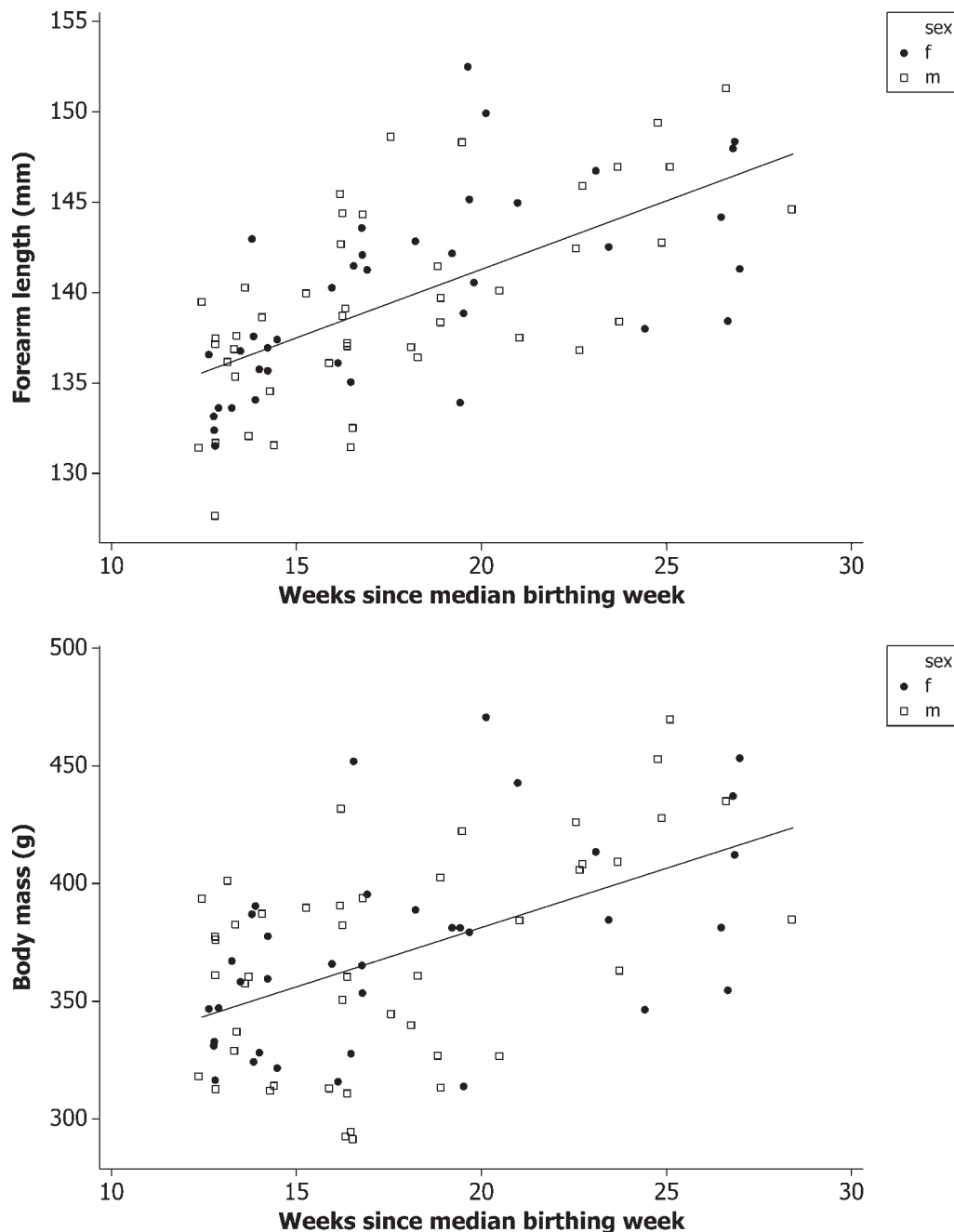

FIG. 2.—Forearm length (top) and body mass (bottom) of volant male (m) and female (f) juvenile gray-headed flying foxes (*Pteropus poliocephalus*) caught in the Dallis Park colony versus the number of weeks since median birthing week (1–8 November = 0).
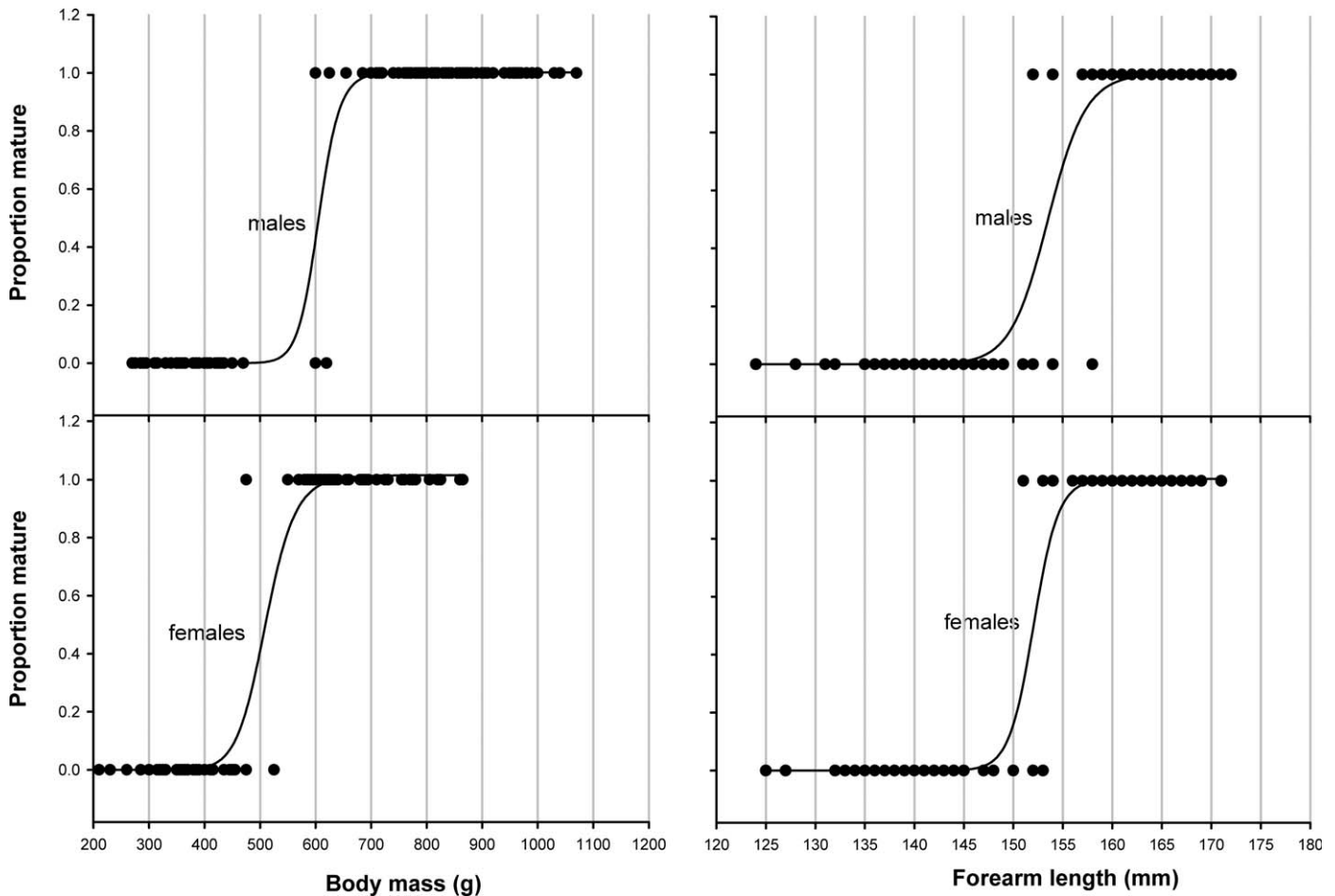
FIG. 3.—Sex-specific transition to maturity based on body mass and forearm length. Binary logistic regression lines illustrate the change in proportion of mature individuals with body mass (females: $x_{50\%} = 514.2$; males: $x_{50\%} = 604.1$; difference $= 17.5\%$) and forearm length (females: $x_{50\%} = 151.2$; males: $x_{50\%} = 153.6$; difference $= 1.6\%$).

female and male dimensions. However, males were mature at significantly greater dimensions of the other skeletal measures (i.e., tibia length, thumb length, and thumb claw length) than females in all cases (BLR, proportion mature versus tibia length: $Z = 2.70$, $P < 0.01$; sex: $Z = 6.78$, $P < 0.01$; versus thumb length: $Z = 7.66$, $P < 0.01$; versus sex: $Z = 2.81$, $P < 0.01$; and versus thumb claw length: $Z = 8.05$, $P < 0.01$; sex: $Z = 2.60$, $P < 0.01$). Furthermore, females were mature at higher forearm/tibia ratios than males (BLR, proportion mature versus ratio forearm length/tibia length: $Z = 3.34$, $P < 0.01$; sex: $Z = 2.21$, $P < 0.03$), and forearm/tibia ratio increased significantly less with the proportion of individuals that were mature in males than in females (interaction forearm length/tibia length $\times$ sex: $Z = 2.20$, $P < 0.03$). Thus, these results indicate that with the exception of forearm length, males mature at greater skeletal measures and body masses than females. Females grow longer forearms relative to other skeletal measures than males, which reduced the difference in this measure between mature males and females.

Adult morphometrics.—Body mass of adults was positively related to forearm length and differed significantly between the sexes (GLM [$R^2 = 54.9\%$]—forearm [covariate]: $F_{1,153} = 39.57$, $P < 0.01$; sex [factor]: $F_{1,153} = 98.81$, $P < 0.01$; Fig. 1). The interaction between forearm length and sex was marginally nonsignificant ($F_{1,153} = 2.91$, $P = 0.09$). The maximum mass of females and males was 865 g and 1,070 g, respectively (difference: 205 g $= 23.7\%$). The maximum forearm length of females and males was 171 mm and 172 mm, respectively (0.6% difference). All other adult morphometric measurements were positively correlated ($0.285 < r < 0.68$, $P < 0.01$), and, in contrast to juvenile bats, adults were significantly sexually dimorphic for all measurements, with males always being larger (Table 2). Adult females had significantly higher forearm/tibia, forearm/thumb, and forearm/claw ratios than adult males ($t_{155} > 2.96$, $P < 0.01$ in all cases), indicating that forearms are longer relative to other skeletal measures in females than in males.

Adult body mass varied with the time of year depending on sex (GLM: [$R^2 = 56.4\%$]—time of year [covariate]: $F_{1,154} = 9.41$, $P < 0.01$; sex [factor], $F_{1,154} = 28.45$, $P < 0.01$; time of year $\times$ sex: $F_{1,154} = 28.31$, $P < 0.01$). Thus, I considered the effect of time of year on body mass separately for the 2 sexes. Female body mass was dependent on time of year and fit a quadratic function between January and July (polynomial regression [$R^2 = 17.3\%$]: $F_{2,70} = 8.51$, $P < 0.01$; linear: $F_{1,70} = 3.13$, $P = 0.08$; quadratic: $F_{1,70} = 13.34$, $P < 0.01$; Fig. 4). The quadratic function predicted a minimum average body

TABLE 2.—Morphometrics (mean ± SE) of gray-headed flying foxes (*Pteropus poliocephalus*) caught during 2001–2003.

Adults	Body mass (g)	Forearm length (mm)	Tibia length (mm)	Thumb length (mm)	Thumb claw length (mm)
Females (f; $n = 73$)	675 ± 9.7	162 ± 0.5	792 ± 3.6	424 ± 3.1	184 ± 1.2
Males (m; $n = 87$)	842 ± 11.0	165 ± 0.4	817 ± 3.2	443 ± 3.2	191 ± 1.2
% dimorphism ((m − f)/f)	24.7	1.8	3.2	4.5	3.8
t	−11.34	−3.91	−5.13	−4.23	−4.14
P	<0.01	<0.01	<0.01	<0.01	<0.01

mass of 636 g on 23 March. Male body mass also was dependent on time of year and fit a cubic function between January and July (polynomial regression [$R^2 = 33.8\%$]: $F_{3,81} = 15.32$, $P < 0.01$; linear: $F_{1,81} = 29.15$, $P < 0.01$; quadratic: $F_{1,81} = 0.20$, $P > 0.65$; cubic: $F_{1,81} = 12.72$, $P < 0.01$; Fig. 4). This function predicted a maximum mean body mass of 921 g on 9 February and a minimum mean body mass of 729 g on 12 May.

DISCUSSION

As predicted, I found clear sexual size dimorphism among adult *P. poliocephalus*, with males being larger than females. The dimorphism is due primarily to prolonged male growth and bimaturation.

Volant juvenile *P. poliocephalus* added about 720 mg/day of body mass. This is similar to the rate reported for other free-ranging pteropids (Thomas and Marshall 1984). I found no evidence for sex differences in growth rates of volant *P. poliocephalus*. This suggests that maternal investment is independent of sex in this species (see also Tuttle 1976)

because *P. poliocephalus* young are weaned up to 6 months (~26 weeks) after birth (Nelson 1965a), which is up to 4 months after they join the evening emergence as independent flyers. Juvenile microchiropteran bats become volant when they attain ~70% of adult mass and 95% of skeletal size and wing dimensions (Barclay 1995; Kunz and Stern 1995). In contrast, megachiropterans typically fly when relative body mass and skeletal size are substantially less than this (Orr 1970). *P. poliocephalus* is no exception because juveniles already were capable of independently emerging from the colony at dusk when they had attained only 39% of average adult mass and ~79% of average adult skeletal dimensions (compared to 35% and 75%, respectively, in the fulvous fruit bat [*Rousettus leschenaultia*]—Elangovan et al. 2002).

The cross-sectional method that I adopted and that was used by many others (e.g., Gopalakrishna and Chaudhari 1977; Stangl et al. 1996; Thomas and Marshall 1984; Vardon and Tidemann 1998) is limited because growth curves based on average measurements of bats by date of capture can underestimate postnatal growth rates; for example, when larger young are better at evading capture than smaller young
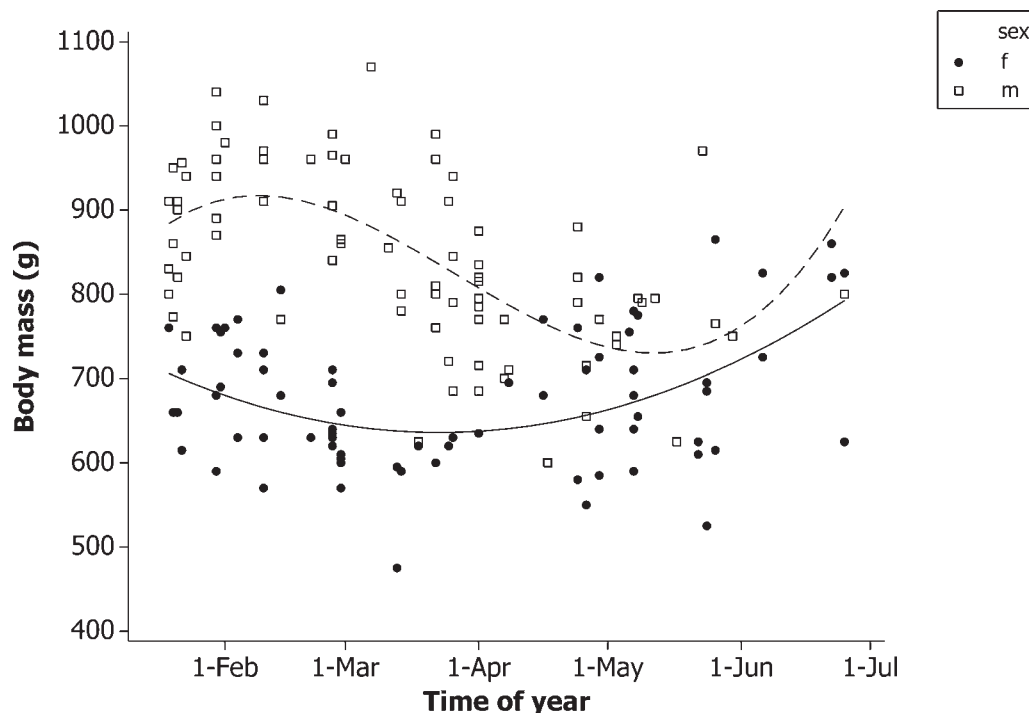
FIG. 4.—Body mass of adult gray-headed flying foxes (*Pteropus poliocephalus*) caught in the Dallis Park colony versus the time of year. Male (open squares) and female (closed circles) have a 3rd- and 2nd-order polynomial regression fitted, respectively (see text).

(Baptista et al. 2000; Kunz 1987). I believe that my results did not underestimate postnatal growth rates in my free-ranging study population. My measurements are similar to those of wild young bats brought into care (D. Pinson, bat rehabilitator, pers. comm.). Furthermore, for the slightly larger *P. alecto* (Vardon and Tidemann 1998), growth curves generated from mean values by capture date in harp traps led to only marginally higher inferred growth rates than for *P. poliocephalus* between approximately 12 and 30 weeks of age. Forearm length of *P. alecto* was predicted to increase by 0.87 mm per week in males and 0.94 mm/week in females, versus the 0.76 mm/week in male and female *P. poliocephalus* that I found.

The body mass at which 50% of individuals were mature was 17.5% higher on average for males than females. Males also were mature at slightly (1.6%) longer forearms on average than females, but this was not significant. Given the small difference between forearms of adult males and females (1.8%; Table 2), the lack of significance likely results from a lack of statistical power. Indeed, males were mature at significantly greater dimensions of all the other skeletal measurements (i.e. tibia length, thumb length, and claw length), in keeping with the greater relative size difference between adults in those measurements (Table 2).

Bimaturation has been reported for several other mega-chiropterans (*Hypsignathus monstrosus* [Bradbury 1977], *Cynopterus sphinx* [Sandhu 1984, 1988; Sandhu and Gopa-lakrishna 1984], *C. brachyotis* [Bumrungsri et al. 2007], *R. leschenaultia* [Gopalakrishna and Chaudhari 1977], *Epomops buettikoferi* [Thomas and Marshall 1984], *Micropteropus pusillus* [Thomas and Marshall 1984], and *P. alecto* [Vardon and Tidemann 1998]). In all but *P. alecto*, bimaturation arises from delayed maturation of males relative to females. Bimaturation in *P. alecto* may be caused by slower growth rates in males (Vardon and Tidemann 1998), although the difference in growth rates between the sexes was not statistically significant. I found no evidence for sex differences in growth rates in *P. poliocephalus*; rather, my data are consistent with the hypothesis that bimaturation is the result of prolonged (as opposed to slower) male growth combined with delayed maturation.

Assuming that mass increases linearly from the onset of volancy (~39% of mean adult mass) to maturity (~74% of mean adult mass), the regression of mass versus number of weeks since median birthing week can be used to generate an estimate of the age by which 50% of males and females are mature. The estimate is 48 weeks (October, year 0) for females and 66 weeks (February, year 1) for males. This corresponds with what is known from captive *P. poliocephalus*. Captive females can conceive during the 2nd breeding season after birth, whereas the testes of many captive males are still growing at that time, and males therefore are unlikely to achieve effective fertility before the 3rd breeding season after birth (Martin et al. 1986; McIlwee and Martin 2002; O'Brien et al. 2003). However, body mass of adults fluctuates seasonally in *P. poliocephalus*. Males attain mean maximum adult mass (921 g) in February, when mating territories form, at which point they are approximately 40% heavier than adult females. As for many other mammals (Michener and Locklear 1990; Mitchell et al. 1976; Wolff 1998), male reproductive success is likely constrained most by body mass at the onset of the mating season; however, males are estimated to reach mean maximum adult mass not before 130 weeks (April, year 3) and are therefore unlikely to be competitive in establishing mating territories until their 3rd year after birth.

Why do males mature later than females? Life-history theory predicts that the timing of maturation is affected by the trade-off between the benefits and costs of early reproduction (Stearns 1992). In the short term the costs are energetic expense (Loudon and Racey 1987), but in the medium and long term reproduction has costs in terms of individual body condition (Clutton-Brock et al. 1989) and survival (Bell 1980). This trade-off is likely to differ between sexes in polygynous species where reproductive success is more variable for males than for females (Andersson 1994). For example, when strong sexual selection acts on males for increased body size, the likelihood of reproducing by small males is low (by definition) and it would benefit males to mature at a larger size. Considerable variance is found in reproductive success among male *P. poliocephalus*. Harem sizes range from 1 to 5 females and change frequently so that some males may mate with more than 20 females during a single mating season (Welbergen 2005). In addition, male mating success is correlated with body size, suggesting sexual selection for increased size (Welbergen 2005). In contrast, little variance is found in reproductive success among female *P. poliocephalus*. Females usually raise a single offspring per year (Martin et al. 1986; Nelson 1965b) and therefore are more likely than males to have evolved a conservative growth strategy to invest resources into provisioning young (Reeve and Fairbairn 2001; Schulte-Hostedde et al. 2001; Trivers 1972).

I have demonstrated that *P. poliocephalus* exhibits the normal mammalian pattern of sexual size dimorphism (Glucksman 1974), with adult males being 1.8–4.5% larger in skeletal measurements and 25% heavier than females on average, but 40% heavier than females at the start of the mating season. This pattern is consistent with the polygynous mating system of this species. Skeletal size measurements that were most dimorphic involved the thumbs (i.e., thumb length and thumb claw length), which are used by male *Pteropus* spp. as weapons during fights with rival males for mating territories (Markus 2002; Markus and Blackshaw 2002; J. A. Welbergen, pers. obs.).

Marked sexual size dimorphism is rare in bats (Hughes et al. 1995), but when it occurs, it tends to be reversed with females being larger than males. This is probably the result of demands placed on females that fly carrying heavy young (Myers 1978). However, *Pteropus* spp. wean their young at a relatively small mass for their size (Barclay and Harder 2003), suggesting that female size is released from the constraints posed by the need to carry heavy young in this group (McNab and Armstrong 2001). Nevertheless, with

nonvolant young weighing up to 38% of adult female body mass, female *P. poliocephalus* are unlikely to be released entirely from these constraints. Compared to males, females had longer forearms relative to their other skeletal dimensions and body mass, which would enable them to carry heavier loads.

As expected, behavioral and ecological differences in males and females are reflected in the ontogeny of sexual size dimorphism in *P. poliocephalus*, with males maturing later and at a greater size. The results implicate sexual selection on males for fighting ability as a cause for sexual size dimorphism, together with a partial release of female size from the constraints posed by the need to carry heavy young. Bimaturation may be an adaptive response to both high relative cost of territory defense and low relative reproductive success of small males.

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