Slow growth and delayed maturation in a Critically Endangered insular flying fox (*Pteropus natalis*)

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Flying foxes (family Pteropodidae) have distinct life histories given their size, characterized by longevity, low reproductive output, and long gestation. However, they tend to decouple the age at which sexual maturity is reached from the age at which they reach adult dimensions. We examined growth, maturation, and reproduction in the Critically Endangered Christmas Island flying fox (*Pteropus natalis*) to determine the timing of sex-specific life cycle events and patterns of growth. We estimated that juvenile growth in forearm length and body mass increased at a mean rate of 0.029 ± 0.005 mm/day and 0.33 ± 0.07 g/day for both males and females alike. Using these growth rates, we determined that the birth of pups occurs between December and March, with young becoming volant between June and August. The age at maturation for *P. natalis* is one of the oldest among all bat species. Juvenile males began to mature 15 months after birth and reached maturity 27 months after birth. Females reached maturity 24 months after birth at a significantly smaller body mass (3.6%) and forearm length (1.4%) than males. Significant sexual dimorphism and bimaturation was observed, with juvenile males being 1.5% and adult males being 1.9% larger on average than females for skeletal dimensions only. Growth and maturation are even slower in *P. natalis* than in the few other *Pteropus* species studied to date. The slow growth and delayed maturation of *P. natalis* imply slower potential population growth rates, further complicating the recovery of this Critically Endangered single-island endemic.

Key words: bats, Chiroptera, Christmas Island, developmental milestones, fruit bats, island conservation, life history, Pteropodidae, sexual dimorphism

There is an enormous diversity in life history strategies across mammalian species; however, all species can be placed along a "fast–slow" continuum (Read and Harvey 1989) along which life history traits vary predictably with body size (Stearns 1983, 1992; Harvey 1989; Read and Harvey 1989; Promislow and Harvey 1990). Most smaller mammals have evolved on the "fast" side of the continuum, having short life spans, producing large litters of small, rapidly growing and early maturing offspring that require little care. In contrast, most larger mammals represent the "slow" side of the continuum, having long life spans and producing few large offspring that develop slowly and mature late, and require extensive parental care. Bats,

however, are quite unusual for mammals of smaller size (Racey and Entwistle 2000) in that they exhibit many of the life history traits normally found in larger mammals. Bats are long-lived and have low fecundity, usually producing only a single offspring annually (or twins in some species) that matures slowly. However, juvenile bats reach adult dimensions well before reaching reproductive maturity, suggesting a decoupling of maturation from the otherwise slow life history traits (Jones and MacLarnon 2001; Barclay et al. 2003).

Bats comprise the 2nd largest mammalian order after rodents, but despite this, their unique lifestyles are poorly represented in life history studies (Barclay 1994). One genus,

Pteropus (family Pteropodidae), has been particularly underrepresented in the literature. Only a handful of studies of the gray-headed flying fox (*Pteropus poliocephalus*) and the black flying fox (*Pteropus alecto*) have provided detailed accounts of *Pteropus* life history, identifying aspects of growth, maturation, and sexual dimorphism (Vardon and Tidemann 1998; Welbergen 2010; Welbergen 2011). Most research conducted on *Pteropus* has focused on estimating population size, identifying foraging or roosting resource use, and identifying threats, leaving important questions about life history variation in this genus unanswered.

In addition to furthering our understanding of the broader variation and evolutionary drivers of mammalian life histories, life history information can be used as an important tool for conservation at the genus and species level. Life history information can be crucial for determining population health and for modeling population viability under varying conditions and management interventions (McGraw and Caswell 1996; McIlwee and Martin 2002).

Of all *Pteropus* species, Australia's flying foxes are by far the most studied, with the exception of the Christmas Island flying fox (*Pteropus natalis*). Research on this single-island endemic is limited to: 1) an internal report on the biology and ecology conducted over 33 years ago (Tidemann 1985), 2) a 2010 health assessment (Hall et al. 2014), 3) research on the species' genetic diversity (Phalen et al. 2017), and 4) recent efforts aimed at estimating population size and monitoring trends (Woinarski et al. 2014b; Parks 2016). Urgency in research needs of *P. natalis* has been prioritized, as the species became listed as Critically Endangered in Australia in 2014 (Threatened Species Scientific Committee 2014). It is now the last surviving native mammal on the island (Andrews 1909; Gibson 1947; Woinarski et al. 2014a) following the extinctions of the Christmas Island rat (*Rattus macleari*), the bulldog rat (*Rattus nativitatis*), and the Christmas Island shrew (*Crocidura trichura*) during the 20th century, and the recent extinction of the Christmas Island pipistrelle (*Pipistrellus murrayi*) in 2009 (Lumsden 2009).

Pteropus natalis is a medium-sized (up to 550 g) flying fox endemic to Christmas Island, Australia. Currently, the taxonomic status of *P. natalis*, whether it is a subspecies of extralimital *P. melanotus* or a distinct species, appears to be an area of much confusion (see Jackson and Groves 2015). Following the taxonomy of Chasen (1940), Simmons (2005) and the current listing under the IUCN Red List (Hutson et al. 2015) recognize it as a subspecies within the *P. melanotus* group. Studies published subsequent to Simmons (2005), however, including the most recent taxonomic publication by Jackson and Groves (2015), recognize it as a unique species following the original taxonomy by Thomas (1887). Overall, *P. natalis* maintains a degree of genetic diversity that suggests it may represent a unique species (Phalen et al. 2017); however, further resolution is required at the genetic level. On balance, therefore, we follow the most recent nomenclature by Jackson and Groves (2015) which regards *P. natalis* as a unique species, but note that the taxonomic status remains to be resolved.

Research conducted in 1984 estimated the population of *P. natalis* at 6,000 individuals (Tidemann 1985). The most recent surveys estimate the population at $2,100 \pm 563$, a decline of between 56% and 74% over a period of 24 years (Parks 2016). While different methods were used to estimate the population size between sampling years, any errors associated with the different sampling methods are highly unlikely to account for such a steep decline. The cause of this decline is not fully understood but is suggested to be a result of habitat loss, a decline in food resources, extreme weather and climate events (cyclones and drought), disease and environmental contamination, and the impact of invasive species, most notably feral cats (*Felis catus*) and yellow crazy ants (*Anoplolepis gracilipes*—Parks 2014). Management of the species is clearly warranted but is hindered by the significant gap in our knowledge of the biology and ecology of *P. natalis*. Our study provides key life history information to aid with effective management decisions aimed at conserving this species.

In this study, we examined growth, maturation, and the timing of mating and parturition to identify and construct a time line of the important life cycle events for *P. natalis*. Over the course of 3 years, we collected morphological and observational data from free-ranging *P. natalis* for each calendar month of the year, enabling us to infer sex-specific patterns of growth and maturation, determine the timing of mating and parturition, and identify sexually dimorphic morphological characteristics. We also compared the life history strategies of *P. natalis* to existing data on other *Pteropus* species, as our data add to a much-needed larger data set regarding *Pteropus* and mammalian life histories in general.

Materials and Methods

Study location.—Christmas Island, a territory of Australia, is located in the Indian Ocean at 105°40′E and 10°25′S. It is approximately 380 km south of Java, Indonesia, and 1,500 km west of the Australian mainland. It is a small, 135-km² island composed of tertiary limestone overlying volcanic andesite and basalt that rises steeply from the ocean floor, reaching 361 m above sea level. Its topography consists of a series of limestone terraces separated by cliffs (Tidemann et al. 1994).

Christmas Island's climate is tropical with temperatures ranging from 22°C to 28°C. Mean annual rainfall is $2,183 \pm 143$ mm. It is monsoonal with most rain falling during the wet season, November to June, during which the mean monthly mean rainfall is 239 ± 25 mm/month. During the dry season, from July to October, mean rainfall is 68 ± 14 mm/month.

Data collection.—Our research protocols followed the guidelines of the American Society of Mammalogists for research on live mammals (Sikes et al. 2016) and were approved by the Animal Care and Ethics Committee of Western Sydney University (Project Protocol No. A11140). Permits to capture, handle, measure, and band bats were issued by the Christmas Island National Park (Permit No. CINP-2015-6-1).

Bats were caught using 3.2 × 12 m nylon mist nets with a 45 × 45 mm mesh size (Ecotone, Gdynia, Poland) or an

aluminum anglers' landing net with a 64 × 56 cm dimension. Netting was conducted at both foraging and roost sites (Fig. 1) between August 2015 and November 2017. Capture locations were chosen as randomly as circumstances would allow. Although we could not randomly select the location of our roost sites, net location within each roost site was randomly selected. Foraging sites were chosen by conducting driving surveys at night. A random starting location for the driving surveys was chosen and routes were driven until foraging bats were found. Fruiting trees selected as a capture site were random on any given night, as ripe fruits were usually consumed within a night, forcing flying foxes to find new foraging trees from night to night.

All captured bats were banded on their thumbs using both a numbered metal band (Australia Bird and Bat Banding Scheme, https://www.environment.gov.au/science/bird-and-bat-banding) and a unique combination of 3 colored metal bands to facilitate permanent individual recognition (Welbergen 2010).

Bats were weighed to the nearest 1 g using a 5-kg digital scale (Breville, Sydney, New South Wales, Australia). Forearm length, thumb length, thumb claw length, tibia length, and testes (length and width) were measured to the nearest 0.1 mm with calipers (Just Tools, South Melbourne, Victoria, Australia). Testes volume (V) was calculated using the formula $V = 0.51 * L * W^2$, a measurement usually used for measuring egg volume (Preston 1974; Hoyt 1979). A body condition index was calculated from an ordinary least squares regression of body mass on forearm length, which is a widely used metric for estimating body condition and fat content in mammals (Schulte-Hostedde et al. 2005). Adults that scored high on this index were considered to be in better condition and to have more fat reserves than individuals that scored low (Lunn and Boyd 1993; Huot et al. 1995). The ratio of body mass/forearm length is commonly used as an alternative condition metric in flying fox research, husbandry, and rehabilitation (Pinson 2009). Our body condition index and the ratio of body mass/forearm length were highly correlated ($r = 0.95$, $P < 0.001$) and the results are

qualitatively similar and significant irrespective of the choice of metric.

Bats were aged and classified into 4 groups (adults, subadults, juveniles, and nonvolant). Adult males were identified based on a fully developed penis (Vardon and Tidemann 1998; Welbergen 2011) and testes > 25 mm³. Females were classified as adults if they had dark, keratinized, protruding nipples, indicating that they had previously lactated a young (Racey 2009; Oleksy et al. 2015). Females with small nipples, showing no evidence of prior suckling, were classified as subadult or juvenile (Nelson 1965). This method underestimates the proportion of sexually mature females because 1st-time breeders, or females that aborted during their previous breeding attempts, exhibit no sign of nipple wear (Welbergen 2010). Juveniles (< 12 months of age) were further distinguished from subadults (12–24 months of age) by their smaller size and proportions (i.e., large eyes and ears relative to facial area, longer legs relative to body length), and an undeveloped penis and undescended testes in males (Holmes 2002; Welbergen 2010). We did not capture any nonvolant young during this study; therefore, we extracted measurement data on nonvolant individuals collected by Tidemann (1985) using the program Data Thief III, version 1.7 (Trummers 2006), which allowed for the accurate extraction of data from published figures. These data were used to estimate a growth curve from parturition to maturation.

Molar wear is commonly used as a measure of age (Wood 1958); however, we found that it varied little among *P. natalis*, except for a few extreme cases where the molars were worn to the gum line. Tidemann (1985) also found that tooth wear was a poor indicator of age other than in extreme examples. Molar wear was therefore not incorporated into age determination in the present study.

Growth rates.—We estimated growth rates using both a longitudinal and cross-sectional approach. From 30 recaptured individuals, we used repeat measurements from 17 unique individuals (35 total measurements) that were initially captured as juveniles and a longitudinal approach to calculate the mean daily growth rate for forearm length and body mass. The unused measurements ($n = 13$) were from individuals captured as adults and subsequently showed no growth between captures. We then used a cross-sectional approach, plotting a linear regression relating forearm length to the number of days since volancy, to assess our growth rate estimates of forearm length derived from the longitudinal approach. There were no differences between "sex" and "year" in the estimated growth rates for forearm length (sex: $t_{1,16} = 1.07$, $P > 0.293$; year: $t_{1,16} = 1.73$, $P > 0.099$) and body mass (sex: $t_{1,16} = 0.1.46$, $P > 0.158$; year: $t_{1,16} = 0.69$, $P > 0.499$); therefore, we pooled all individuals for the growth rates analyses. Similarly, there was no effect of "year" on the estimated testes growth rate ($t_{1,15} = 0.41$, $P > 0.691$); therefore, all males were pooled to calculate the mean daily growth rate of testes.

We then used the mean rate of growth for forearm length only to estimate the timing of volancy and used the mean rate of growth for testes volume to estimate the timing of the onset of maturity and the duration of maturity to adulthood, with the equation:
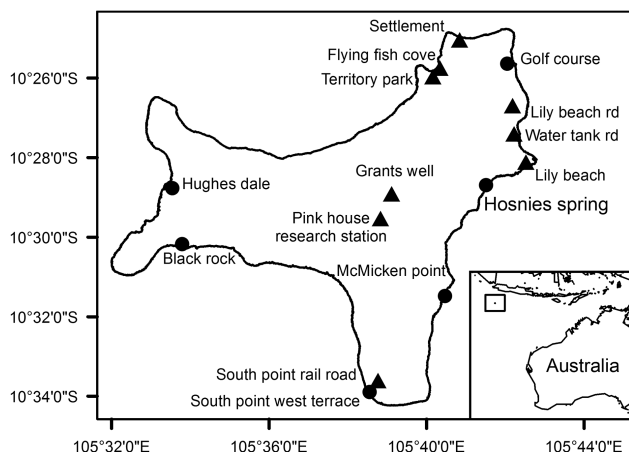
Fig. 1.—The locations of 9 foraging (▲) and 6 roost (●) sites on Christmas Island where flying foxes (*Pteropus natalis*) were captured during this study between August 2015 and November 2017.

$$y = a + bx$$

where y = forearm length or testes volume at time of capture; a = forearm length at time of volancy, testes volume = 0 for onset of maturity and 25 mm³ for adults; b = growth rate coefficient; x = number of days since time of volancy, onset of maturity or adulthood.

We used the smallest measurement of forearm length from a captured volant juvenile that was still receiving care by the mother at the roost (verified by resighting of ID bands) for forearm length at time of volancy (a). We subtracted x (number of days since time of volancy or onset of maturity) from the Julian day at time of capture for all juveniles to identify the time of year in which individuals reached volancy and identify the onset of maturity and when individuals reached adulthood. The timing of parturition and mating was estimated by subtracting a 4-month weaning period and a 5-month gestation period, typical of most *Pteropus* species (Nelson 1965), from the estimated timing of volancy. We decided not to use change in body mass to estimate the timing of these life history events as body mass can fluctuate throughout the year depending on available food resources (McNab 1976; Racey 1982).

Statistical analysis.—All tests were 2-tailed, employed an alpha value of 0.05, and were conducted in R (R Core Team 2017). Means are expressed ± *SE*, unless otherwise stated. Analysis of variance (ANOVA) and Tukey's honest significance difference (Tukey's HSD) were used to test for differences in morphometrics between age classes. Multivariate analysis of variance (MANOVA) was used to test for differences in morphometrics between years and according to time of year. General linear models (GLMs) were used to test the effects of sex and time of year for changes in body condition and testes volume in males. We examined the distribution of residuals from the GLMs to check for violation of model assumptions. A Rayleigh test of uniformity was used to test the unimodal distribution of the estimated timing of mating, parturition, and volancy derived from estimates of growth rates. Binary logistic regressions (BLRs) with a logit-link function were used to determine the relationship of juvenile volancy and maturity versus body mass and sex. We used the R package "Overlap" (version 0.3.0—Meredith and Ridout 2017) to identify the percentage of overlap for forearm length, thumb length, claw length, tibia length, and body mass among juvenile, subadult, and adult *P. natalis*.

RESULTS

Of the 608 *P. natalis* captured, 575 were captured once, and the additional 33 captures consisted of 30 recaptured individuals for which morphological measurements were taken at each recapture (1 recapture, $n = 27$; 2 recaptures, $n = 3$). Of the 575 unique individuals captured, 172 were adults (110 males and 62 females), 82 were subadults (61 males and 21 females), and 321 were juveniles (192 males and 129 females).

There was a significant effect of age class only among juveniles for forearm length ($F_{2,572} = 264.4$, $P < 0.001$), thumb length ($F_{2,545} = 10.29$, $P < 0.001$), claw length ($F_{2,566} = 200.00$,

$P < 0.001$), and tibia length ($F_{2,572} = 189.00$, $P < 0.001$), and a significant effect among all age classes for body mass ($F_{2,572} = 454.80$, $P < 0.001$; Tukey's HSD; juvenile–subadult $P < 0.001$; juvenile–adult $P < 0.001$; subadult–adult $P < 0.001$). We observed a considerable amount of overlap in forearm length, thumb length, claw length, and tibia length among juveniles, subadults, and adults (see Supplementary Data SD1). There was a significant effect of year of capture and time of year of capture on all morphological measurements taken on juveniles (see Supplementary Data SD2). Among subadults there was a significant effect of year of capture for forearm length, thumb length, tibia length, and body condition, and for time of year for claw length, body mass, and body condition (see Supplementary Data SD2). No significant effect of year of capture for any of the morphological measurements taken on adults was observed; however, there was a significant effect of the time of year for mass and body condition (see Supplementary Data SD2).

Young and juvenile morphology.—Adult females were captured or observed with newborn pups under their wing between the months of December and March ($n = 12$), with the highest frequency occurring in February ($n = 8$). The forearm length and mass of a newly born *P. natalis* pup was 49.21 mm and 55.08 g, approximately 38.1% and 13.9% of the mean adult measurements, respectively. Juveniles are estimated to reach volancy at a forearm length and body weight of 111.9 mm and 163 g, representing 86.3% and 41.2% of mean adult dimensions. This was based on the smallest free-ranging individual captured during our study. All morphological measurements were positively correlated and increased significantly with body mass (see Supplementary Data SD3). Juvenile males and females were sexually dimorphic, with males being larger for all measurements except body mass (Table 1).

Using all of the individuals captured in this study and the nonvolant individuals sampled by Tidemann (1985), we fitted a growth curve with an asymptotic regression, spanning parturition through to adulthood (Fig. 2). Early growth of *P. natalis* in the pre-asymptotic phase is primarily invested in skeletal development, with the greatest rate of growth among nonvolant young and juveniles. Skeletal growth then reaches a plateau at the age of maturity, shifting to an increase in body mass.

Juvenile morphology: growth rates.—The longitudinal approach estimated a mean daily growth rate for forearm length and body mass of $0.029 ± 0.005$ mm/day and $0.33 ± 0.07$ g/day. Daily growth rates varied considerably for forearm length (range = 0.011–0.045 mm/day) and body mass (range = 0.11–0.77 g/day). The cross-sectional approach yielded an average daily increase in forearm length of $0.034 ± 0.003$ mm/day, further lending support of our estimate for forearm length derived from the longitudinal approach.

Using the mean growth rate for forearm length and the smallest measurement of a volant juvenile, we estimated that the majority of individuals reached volancy between the months of June and November (Rayleigh test of uniformity: $X^2_{1,8} = 37.89$, $P < 0.001$; Fig. 3). We estimated the timing of parturition to predominately occur between the months of January and April

Table 1.—Morphometric measurements (mean ± *SE*, range in parentheses) of juvenile Christmas Island flying foxes (*Pteropus natalis*) sampled between August 2015 and November 2017. *P*-values in bold indicate sexually dimorphic differences in morphology.

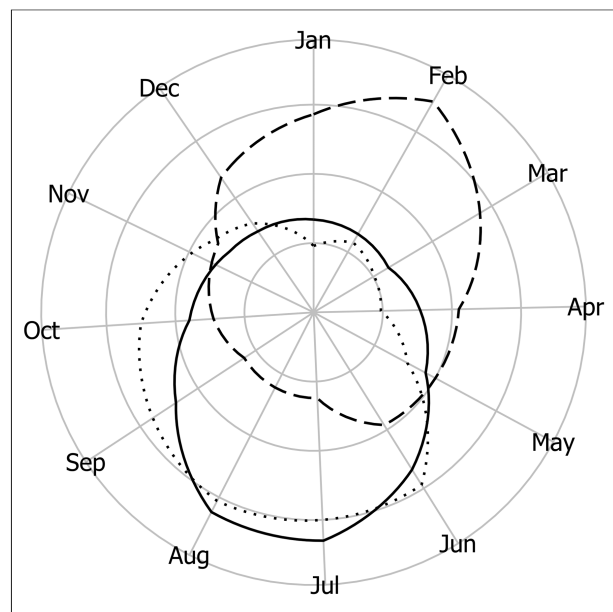| Juveniles	Forearm length (mm)	Thumb length (mm)	Claw length (mm)	Tibia length (mm)	Body mass (g)
Females ($n = 129$)	122.46 ± 0.33	32.87 ± 0.11	14.19 ± 0.05	62.47 ± 0.18	281.58 ± 2.64
	(113.80–133.40)	(29.60–35.60)	(12.70–15.70)	(57.00–69.40)	(194.00–367.00)
Males ($n = 192$)	123.41 ± 0.20	33.50 ± 0.08	14.34 ± 0.04	63.99 ± 0.17	288.37 ± 2.53
	(111.90–132.70)	(30.34–36.10)	(12.50–15.70)	(54.10–69.30)	(163.00–398.00)
t	2.10	4.78	2.13	5.90	1.80
P	**0.036**	**<0.000**	**<0.034**	**<0.000**	0.073
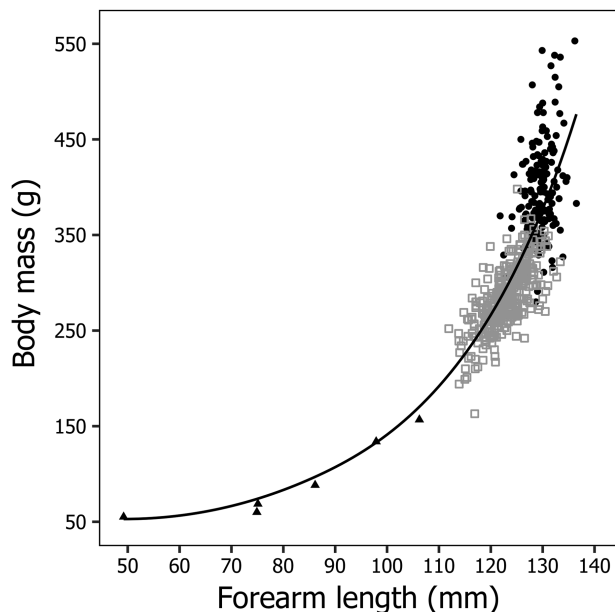
Fig. 2.—Growth curve for forearm length versus body mass of nonvolant (▲—Tidemann 1985), juvenile (□), and adult (●) Christmas Island flying foxes (*Pteropus natalis*) sampled between August 2015 and November 2017, and fitted with an asymptotic regression. Equation of the curve: $\text{mass} = 38.78 + 1.96 \times e(0.04 \times \text{forearm})$, $R^2 = 64.64\%$.

Fig. 3.—The estimated proportion of Christmas Island flying foxes (*Pteropus natalis*) that mated (—), gave birth (– – –), and reached volancy (▪ ▪ ▪) throughout the year.

with the peak frequency of births occurring in February and March and conception occurring between June and August (Rayleigh test of uniformity—parturition: $X^2_{1,8} = 37.74$, $P < 0.001$; mating: $X^2_{1,8} = 34.54$, $P < 0.001$; Fig. 3). However, mating, parturition, and volancy were not limited to these peak periods and occurred with appreciable frequencies throughout much of the year (Fig. 3).

Juvenile morphology: maturation.—Males and females transitioned from their skeletal growth to increasing body mass at a forearm length of $124.08 ± 1.39$ mm, a claw length of $14.32 ± 0.31$ mm, and a tibia length of $63.59 ± 0.96$ mm, and at approximately 95.7%, 92.6%, and 94.4% of the mean adult skeletal dimensions (Fig. 4). There were no significant differences between sexes for each of the morphological measurements at time of transition (forearm: $t_{1,491} = 0.68$, $P > 0.498$; claw: $t_{1,474} = 0.34$, $P > 0.731$; tibia: $t_{1,488} = 0.51$, $P > 0.611$).

Testes volume increased significantly with body mass in males (GLM; $R^2 = 18.08\%$, $t_{1,104} = 5.08$, $P < 0.01$). The proportion mature also was positively related to body mass for both sexes combined (BLR; $Z = 7.23$, $P < 0.01$), but differed

between the sexes ($Z = 154.78$, $P < 0.001$). From the recaptured males ($n = 15$) we estimated a testicular growth rate of $0.067 ± 0.02$ mm³/day. Based on this growth rate, we estimated testicular development to begin in May, approximately $315 ± 24.8$ days after volancy at a forearm length and body mass of $128.65 ± 0.76$ mm and $307.33 ± 11.44$, respectively. The BLR predicted a threshold body mass at which 50% of individuals were mature at $366.98 ± 1.87$ g for males and $353.88 ± 2.60$ g for females (difference = 3.57%), or 92.57% and 89.06% of the mean for adult males and females, respectively (Fig. 5).

Adult morphology.—Body mass of adults was positively correlated with all morphological measurements (see Supplementary Data SD4). Adults were sexually dimorphic for most morphological measurements, with males being significantly larger than females, except for forearm length and body mass (Table 2).

Adult morphology: seasonal variation.—Adult body condition varied with time of year (MANOVA; $F_{11,145} = 4.45$, $P < 0.001$) and sex (GLM; $t_{1,171} = 32.88$, $P < 0.001$). Therefore, we considered the effect of time of year on body condition separately for each sex. Body condition of males was dependent on time of year and best
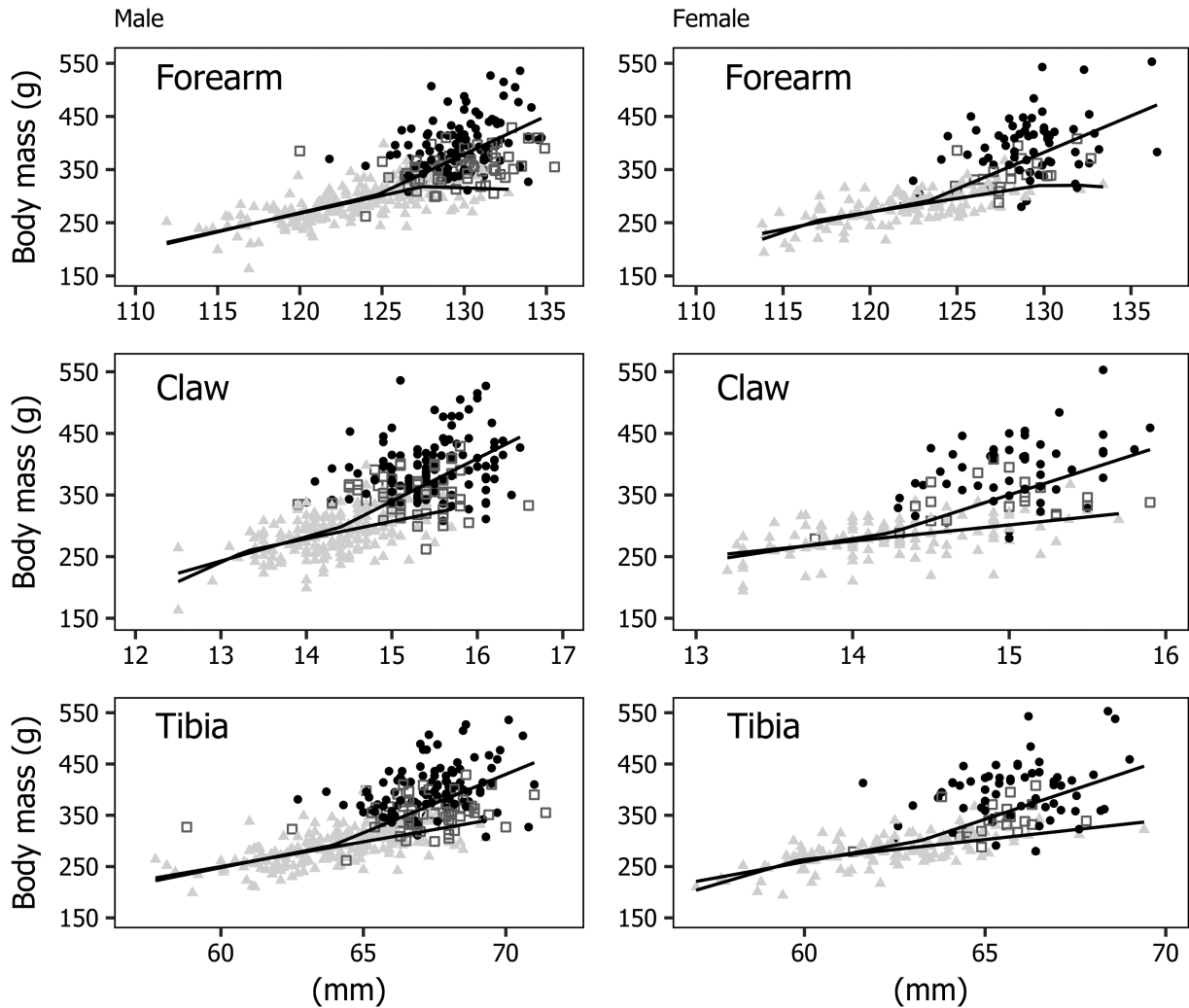
Fig. 4.—Body mass versus the morphological measurements of forearm length, claw length, and tibia length, showing the transition from increasing skeletal dimensions to increasing body mass among juvenile (▲), subadult (□), and adult (●) male and female Christmas Island flying foxes (*Pteropus natalis*) sampled between August 2015 and November 2017.

fit a cubic function (polynomial regression: $R^2 = 33.98\%$; linear $F_{1,105} = 2.11$, $P > 0.149$; quadratic $F_{1,105} = 43.89$, $P < 0.001$; cubic $F_{1,105} = 8.06$, $P < 0.006$; Fig. 6). The cubic equation predicted a minimum mean body condition of −27.13 on 20 November and a maximum mean body condition of 50.67 on 10 May. Body condition of females was also dependent on time of year and best fit a quadratic function (polynomial regression: $R^2 = 34.91\%$; linear $F_{1,50} = 3.29$, $P > 0.075$; quadratic $F_{1,50} = 24.46$, $P < 0.001$; Fig. 6). This quadratic equation predicted a minimum body condition of −22.25 on 7 January and a maximum body condition of 28.90 on 21 July.

Testes volume varied positively with time of year (GLM: $R^2 = 31.76\%$; $t_{1,86} = 3.27$, $P < 0.002$). The change in testes volume fit a quadratic function (polynomial regression: $R^2 = 21.48\%$; linear $F_{1,86} = 3.79$, $P > 0.054$; quadratic $F_{1,85} = 18.09$, $P < 0.001$; Fig. 7). This quadratic function predicted a mean maximum testes volume of 86.6 mm³ on 29 May and a minimum mean testes volume of 51.35 mm³ on 1 December.

DISCUSSION

Pteropus natalis exhibited overall patterns of development similar to those of other Chiroptera species, characterized by fast skeletal growth followed by a delayed onset of maturity, and patterns of sexual dimorphism common among other *Pteropus* species. However, skeletal growth was much slower, and the age at maturity was much later in *P. natalis* than in any other *Pteropus* species studied to date (see Vardon and Tidemann 1998; Barclay et al. 2003; Welbergen 2010).

Compared to young terrestrial mammals, bats are born and wean their young at a significantly larger mean body mass relative to adult size. Young terrestrial mammals give birth and wean their young at a mean 6% and 37% of their mothers' body mass (Millar 1977). Although there is great variation across all bat species, in general pups average 23% of their mothers' body mass at the time of birth and average 75% and 91% of their mothers' body mass and forearm length at the time of volancy (Barclay 1994; Barclay et al. 2003). *Pteropus natalis* pups, however, are born at an average 14% of their mothers' mass and reach volancy, at an average of 41% of their mothers' mass

and an average 86% of their mother's forearm length. This is in line with *P. poliocephalus* that reaches volancy at an average 39% of their mothers' mass and an average 79% of their mother's forearm length (Welbergen 2010). Furthermore, this is similar to other free-ranging pteropodids that are born at an average 18% of their mothers' body mass and become volant at an average 54% of their mothers' body mass and 84% of their mothers' forearm length (Barclay 1994; Barclay et al. 2003). The difference in weaning mass would be much larger in bats than other mammals since females continue to nurse their young after they first fly (Jones 1967; Kunz 1973; Tuttle and Stevenson 1982; Brown et al. 1983; Koehler 1991). Similar to bats, birds fledge their young when they are of adult skeletal size (Ricklefs 1973). This large skeletal size at independence is found in all flying vertebrates, and suggests that it is an evolutionary requirement imposed by the need for fully calcified wing bones required to withstand the forces of flight (Swartz et al. 1992; Barclay 1994; Racey and Entwistle 2000), which

in turn allows for independent feeding (Jones and MacLarnon 2001).

Growth appears to be slower in *P. natalis* than other *Pteropus* species that have been studied. The longitudinal approach we used to assess rates of postnatal growth in volant *P. natalis* yielded a growth rate of 0.33 g/day in mass and 0.029 mm/day in forearm length, respectively, and was similar for males and females alike, suggesting maternal investment is independent of offspring sex (Tuttle 1976; Welbergen 2010). The growth rates of *P. natalis* are lower than the growth rates estimated for forearm length and body mass of *P. poliocephalus* (0.11 mm/day and 0.72 g/day—Welbergen 2010) and *P. alecto* (0.19 mm/day and 2.40 g/day—Vardon and Tidemann 1998), both of which were assessed using a cross-sectional approach. However, for their relative mean adult body mass, *P. natalis* increased 0.08% g/day (2.53% g/month), which is equivalent to the growth rates estimated by Welbergen (2010), for *P. poliocephalus*, but considerably lower than the 0.33% g/day (10.28% g/month) estimated by Vardon and Tidemann (1998) for *P. alecto*. The percent increase in forearm length per day relative to mean adult forearm length is much smaller for *P. natalis* (0.02% mm/day)
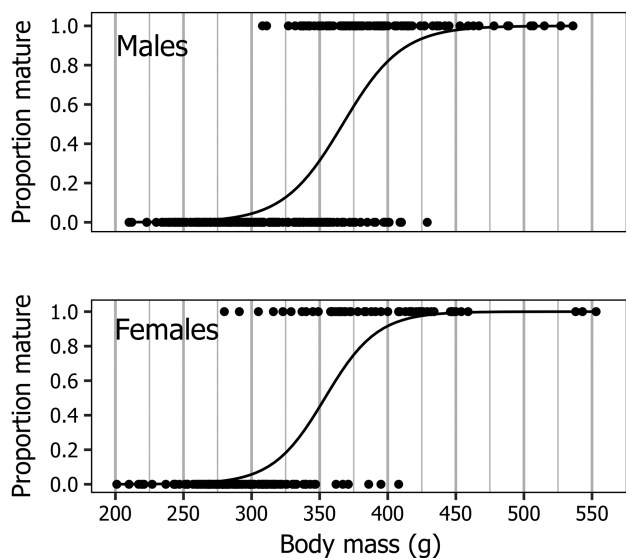
Fig. 5.—Sex-specific transition to maturity based on body mass of the Christmas Island flying foxes (*Pteropus natalis*) sampled between August 2015 and November 2017. Binary logistic regression lines illustrate the change in proportion of mature individuals with body mass (males: $X_{50\%} = 366.98 \pm 1.87$; females: $X_{50\%} = 353.88 \pm 2.60$; difference = 3.57%). Maturity was based on a fully developed penis and a testes size > 25 mm^3 in males and dark, keratinized, protruding nipples in females.
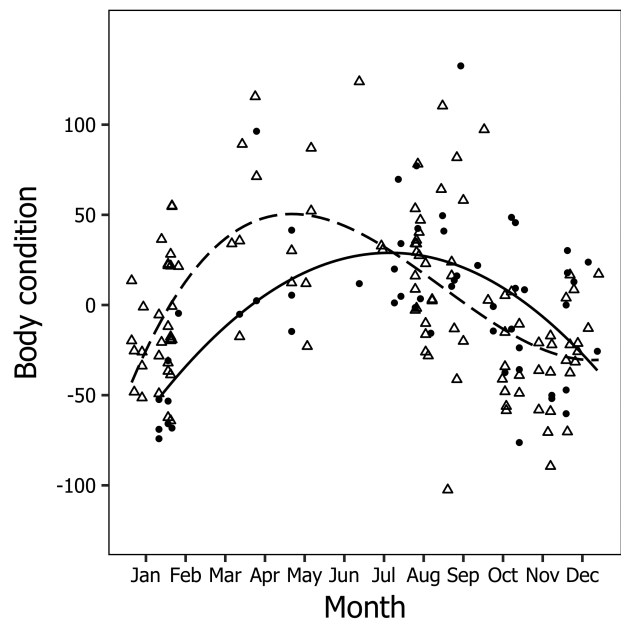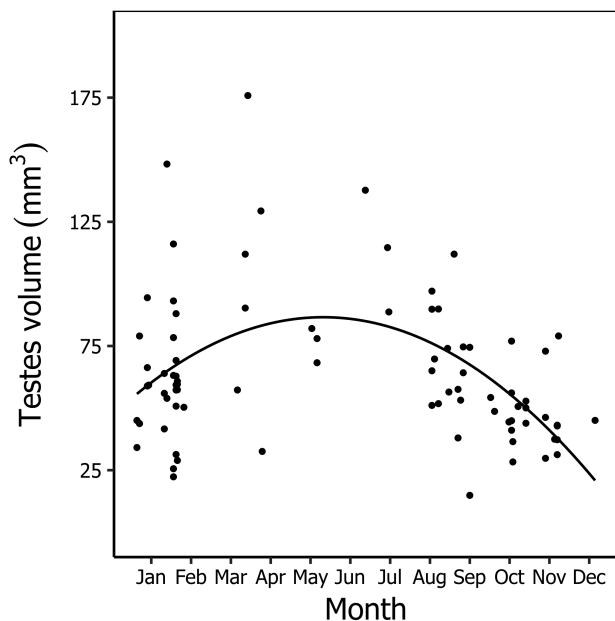

Fig. 6.—Body condition of adult Christmas Island flying foxes (*Pteropus natalis*) sampled between August 2015 and November 2017 versus time of year. Male (Δ – – –) and female (●—) are fitted with a 3rd- and 2nd-order polynomial regression.

Table 2.—Morphometric measurements (mean ± *SE*, range in parentheses) of adult Christmas Island flying foxes (*Pteropus natalis*) sampled between August 2015 and November 2017. *P*-values in bold indicate sexually dimorphic differences in morphology.

Adults	Forearm length (mm)	Thumb length (mm)	Claw length (mm)	Tibia length (mm)	Body mass (g)
Females (*n* = 62)	129.27 ± 0.33	33.35 ± 0.15	15.01 ± 0.06	65.95 ± 0.21	397.35 ± 6.91
	(122.48–136.50)	(30.70–36.27)	(14.00–16.10)	(61.62–69.90)	(280.00–553.00)
Males (*n* =110)	129.69 ± 0.21	33.86 ± 0.10	15.46 ± 0.05	67.36 ± 0.14	396.44 ± 4.55
	(121.80–134.70)	(31.50–36.40)	(14.00–16.50)	(62.70–71.00)	(308.00–536.00)
t	0.25	8.00	24.36	22.82	0.03
P	0.618	**<0.006**	**<0.000**	**<0.000**	0.852

Fig. 7.—Testes volume of adult male Christmas Island flying foxes (*Pteropus natalis*) sampled between August 2015 and November 2017 versus time of year, fitted with a 2nd-order polynomial regression.

compared to both *P. poliocephalous* (0.07% mm/day—Welbergen 2010) and *P. alecto* (0.10% mm/day—Vardon and Tidemann 1998). The estimates we obtained using the cross-sectional approach were similar to those obtained using the longitudinal approach. Furthermore, a comparison of the longitudinal and cross-sectional approaches was conducted by (Clark et al. 2007), which yielded similar results using both methods; therefore, the differences in the estimated growth rates among these 3 species are not a function of the analysis methods used. Insular species are exposed to their own set of evolutionary rules (Van der Geer et al. 2011; Kolb et al. 2015) and as a result tend to have slower life histories, including slow development and delayed maturation (Köhler and Moyà-Solà 2009; Köhler 2010; Jordana and Köhler 2011; Jordana et al. 2012). The slow forearm growth rates of *P. natalis* further support this trend. However, body mass growth rates are correlated to body size in both homeotherms and poikilotherms (Blueweiss et al. 1978), and given that *P. natalis* is half the size of *P. poliocephalus* and *P. alecto*, the difference in the estimated skeletal growth rates between the 3 species may be confounded by the differences in body size. A larger sample size from a wider range of *Pteropus* species is needed to test these hypotheses.

Growth in *P. natalis* fits an asymptotic curve (Fig. 2) and could be described as "Determinant Growth Type I" (Sebens 1987), in which the growth trajectory and asymptotic size are genetically determined, with only minor environmental modification. Growth is therefore limited during the life span of an individual, so that the organism reaches a maximum size after which growth ceases (Lincoln et al. 1992). Early growth of nonvolant young and juveniles focused primarily on skeletal development (Fig. 2), until juveniles reached an average 95% of their adult skeletal dimensions, at which point growth

transitioned to the accumulation of body mass (Fig. 4). Such growth allows for the development of skeletal strength prior to the accumulation of body mass (Lindstedt and Calder 1981) and may also reduce the stresses of wing loading that are high among pteropodids (Hayssen and Kunz 1996).

There was a substantial amount of overlap between juveniles and adults among *P. natalis* in forearm length (30%), thumb length (87%), claw length (40%), and tibia length (40%) (see Supplementary Data SD1). The small difference (1.2%) between mean thumb length in juveniles and adults suggests that early development of the thumb is important for movement in trees and during social interactions in juvenile *P. natalis* prior to flight. The overall high overlap in morphological measurements observed in *P. natalis* could be related to the seasonal or yearly differences in resource availability during the early and critically energy-demanding period of juvenile development (Barclay 1994, 1995). Asymptotic growth is moderated by energetics in such a way that differentiation in body size among the population, through restricted gene flow, may produce "habitat-dependent" patterns in body size. Animals growing under low food availability, for example, reach a size asymptote at a smaller size than do those under a similar physical regime but with greater food availability (Sebens 1987). The fact that some individuals are born in all seasons of the year (Fig. 3) may also contribute to the differentiation and overlap observed between skeletal measurements of juveniles and adults.

Like many bats species, *P. natalis* exhibited a delayed onset of maturity (Barclay 1994; Racey and Entwistle 2000; Jones and MacLarnon 2001; Barclay et al. 2003). Our estimates of testicular growth suggest that testicular development in juvenile males, and thus the transition to becoming a subadult, began approximately 315 days (10 months) after volancy at a mean forearm length of 128.65 ± 0.76 mm and a mean body mass of 307.33 ± 11.44 g. Furthermore, this growth rate suggests that subadult males reached adult testicular size of 25 mm^3 approximately 688 days (23 months) after volancy, coinciding with the peak mean testes volume of adult males around the time of observed mating and territorial defense. Newly pubescent males were 12% smaller in body mass than an average-sized adult, which may place them at a disadvantage when competing against older, larger males for females (see also Welbergen 2010). The exact onset of maturity and the duration of maturation length in females could not be predicted in this study as we only used external cues (keratinized protruding nipples and pregnancy) to distinguish between age classes of females. We estimated that 50% of females were mature at a body mass of 353.88 ± 2.60 g, and because growth rates of males and females did not differ, this suggests that females reach maturity at 19 months after volancy and are able to become pregnant at 28 months in June of the 3rd year after birth.

The body mass and forearm length at which 50% of *P. natalis* individuals were mature was 3.57% and 1.37% higher on average for males than females. Males were also mature at slightly longer claw lengths (1.88%) and tibia lengths (3.02%), but this difference was not significant. We also found evidence of sexual dimorphism in both juveniles and adults with males

being larger than females most notably in regards to claw length (2.9%) and tibia length (2.1%). These findings are similar to those for *P. poliocephalus* (Welbergen 2010). Sexual dimorphism, resulting in larger males, is common among *Pteropus* species (McNab and Armstrong 2001) and in polygynous mating systems in which male–male competition is necessary for successful reproduction (Orians 1969). The selection for larger claws would be useful for fighting and defending territories when forming harems and selection for larger tibia length would be advantageous in attaining sexual position during mating.

Our growth estimates suggest that *P. natalis* reach mean adult skeletal dimensions approximately 19 months after volancy, just prior to attaining full sexual maturity. There was no evidence to suggest that skeletal measurements increased beyond sexual maturity. As observed for *P. poliocephalus* (Welbergen 2011), the body mass and testes size of adult *P. natalis* varies seasonally. Males attain a maximum mean body condition and testes volume in May, coinciding with observed mating behavior and territorial defense, whereas females attain maximum body condition in July. We expected to see females attain maximum body condition much later in the year, just prior to parturition; however, our finding may be an artifact of the small sample size of adult females during the February to July period. The minimum body condition (20 November) and testicular size (1 December) in males occurred just prior to the minimum body condition in females (7 January), which coincides with the start of the parturition period when females are unlikely to be able to conceive. Yearly cycles of testicular recrudescence and involution are common in many species of bats including *Pteropus* (Baker and Baker 1936; Nelson 1965; McGuckin and Blackshaw 1991; O'Brien et al. 1993; Welbergen 2011), and are matched by cycles in plasma testosterone concentrations (McGuckin and Blackshaw 1991) that have been shown to be important for the ability of males to maintain harems (Klose et al. 2009). Not taking into account the seasonal fluctuations in body mass, maximum body mass of adults (> 550 g) would be attained at a minimum of 38.4 months, in their 4th year after volancy.

The timing and duration of major life cycle events (parturition, volancy, maturation, and copulation) for *P. natalis*, derived from our estimates of growth rates for forearm length, body mass, and testes growth, correspond well with our observational data. Young female *P. natalis* reach maturity approximately 24 months after the mean birth period, whereas male *P. natalis* reach sexual maturity 27 months after the mean birth peak. These estimates are much later than those for *P. poliocephalus* that is estimated to reach sexual maturity at 11 months (females) and 16 months (males) after the peak birth period (Welbergen 2010). In fact, the age at maturation for *P. natalis* is one of oldest among all Chiroptera species (see Barclay et al. 2003). Males of both species, however, reach sexual maturity just prior to the mating season, yet they both reach sexual maturity at a lower average body mass than a fully mature adult (12% in *P. m. natalis* and 28% in *P. poliocephalus*—Welbergen 2010). Mating success is therefore likely constrained by this lower body mass and males are unlikely to be competitive in

establishing mating territories until the following mating season, in the 3rd year after birth for *P. poliocephalus* (Welbergen 2010) and the 4th year for *P. natalis*.

Delayed maturation may be beneficial for both males and females. For example, female greater horseshoe bats (*Rhinolophus ferrumequinum*) that delay maturation and breed later have higher survival rates than females that breed earlier in life (Ransome 1995). In polygynous mating systems where males compete with other males for access to females, mating success is correlated with body size and the largest males were in their 2nd to 4th breeding season (4 to 6 years old—Welbergen 2005). Late maturation allows males to grow larger enabling them to compete against rival males for females during the mating season and defend food resources.

What would cause further postponement of maturation in *P. natalis*? Charnov (1991) suggests that selection will act to maximize an individuals' lifetime reproductive success in the face of mortality rates imposed by the extrinsic environmental factors, and that such success is optimized by altering the age and size at which sexual maturity is reached. Furthermore, it has been suggested that the adaptation of flight in bats and birds reduced the risk of predation, and hence mortality, allowing for delayed maturation (Racey 1974; Barclay et al. 2003). *Pteropus natalis* evolved on Christmas Island in a predator-free environment; if reduced mortality does in fact alter the age of maturity, then it is possible that in an environment void of predation, maturation could be delayed even longer. *Pteropus natalis* already exhibits unique behaviors as a result of the absence of predators. Firstly, it is highly diurnal, leaving its roost as early as 1300 h to forage, and secondly, it displays a tranquil demeanor, or naïveté, allowing humans, and potentially predators, to approach within a close distance before they climb away (Tidemann 1985).

Like many species of Chiroptera, development in *P. natalis* is initially heavily focused on skeletal growth. Individuals reach almost full adult skeletal dimensions prior to volancy, which is followed by a delayed onset of maturity. However, the delayed age at maturity observed in *P. natalis* is even more pronounced, especially among males, than in other species. We suggest as a hypothesis that this is an evolutionary adaptation resulting from a predator-free environment and thus reduced mortality. *Pteropus natalis* can therefore optimize the age at which maturity is reached in favor of prolonged growth, maximizing an individuals' lifetime reproductive success. The intermittent birthing of pups throughout the year, combined with the high amount of overlap in skeletal dimensions between juveniles and adults suggests that limiting food resources moderate reproduction and early development (fetal and post-natal), a period that is critically energetically demanding.

Evolutionary adaptation toward slow reproductive rates that we hypothesize has occurred in *P. natalis* would reduce the population's capacity to recover from disturbance, and such loss of resilience could thus have serious consequences, especially in the context of introduced predators. Extinctions caused by introduced predators are much more frequent on islands and are often attributed to predation of island species

that have not evolved in the presence of predatory mammals (Atkinson 1989). The absence of direct antipredatory behavior combined with slow reproductive rates, behaviors observed in *P. natalis*, are known to predispose other island species to extinction (Simberloff 1995).

The information provided here on the timing of reproductive events and sex-specific patterns of growth can serve as a baseline for future studies aimed at assessing changes in the health of the *P. natalis* population, and can be used in conjunction with other data sets (e.g., seasonal availability of food resources) to understand better the effects of extrinsic stressors on population viability. More studies detailing the life history parameters of *Pteropus* species are needed, however, to facilitate interspecific species comparisons. *Pteropus* spp. already have a very slow rate of population increase (McIlwee and Martin 2002), and while *P. natalis* exhibited overall patterns of development similar to that of other pteropodids, skeletal growth was much slower, and the age at maturity was much later in *P. natalis* than in any other *Pteropus* species studied to date. The slow population growth rate of *P. natalis* further complicates the recovery of this Critically Endangered insular species in the face of numerous anthropogenic threats.

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SUPPLEMENTARY DATA

Supplementary data are available at *Journal of Mammalogy* online.

Supplementary Data SD1.—Percent of overlap for forearm length, thumb length, claw length, tibia length, and body mass for juvenile, subadult, and adult Christmas Island flying foxes (*Pteropus natalis*).

Supplementary Data SD2.—Multivariate analysis of year and time of year for forearm length, thumb length, claw length, tibia length, and body mass for juvenile, subadult, and adult Christmas Island flying foxes (*Pteropus natalis*).

Supplementary Data SD3.—Pearson's correlations on the morphological measurements of juvenile Christmas Island flying foxes (*Pteropus natalis*).

Supplementary Data SD4.—Pearson's correlations on the morphological measurements of adult Christmas Island flying foxes (*Pteropus natalis*).

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