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Geographic and Sexual Variations in Body Size, Morphology, and Diet among Five Populations of Green Pythons (*Morelia viridis*)

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ABSTRACT.— Body sizes and morphological traits of animals are often strongly influenced by their diet. Several studies have shown this to be true for snakes and have linked intraspecific differences in these attributes to geographic and sexual variations in prey sizes and diet. To help clarify anecdotal reports of morphological variation among populations of Green Pythons (*Morelia viridis*), we assessed geographic and sexual variations in the body size, morphology, and diet of 908 individuals from five sites in Australia and New Guinea. Body sizes and morphology differed among populations and, although some variation could be explained by sampling biases, we found no significant geographic dietary variation to help explain these differences. Juvenile Green Pythons preyed exclusively on small lizards and adults preyed on mammals, while birds comprised only 2.5% of all dietary records. Within all populations females grow to larger body sizes, although we observed little sexual dimorphism in other traits. Males and females selected the same prey types. However, large females, despite their larger overall size, consumed a greater proportion of small, diurnal prey (lizards and birds) than did males, suggesting a niche divergence. Although the two New Guinean mainland populations of Green Python are the most genetically divergent from one another, they are the most morphologically similar. Our data provide weak evidence to reject nonadaptive processes as creating geographic variations in the body sizes and morphology of Green Pythons and suggest that a better understanding of the relative importance of different prey may elucidate the mechanisms involved.

Intraspecific variation in morphology is widespread among reptiles and may reflect adaptations to local environmental conditions. Morphological variation can result from a number of processes including variation in seasonality and climate (Tracy, 1999; Ashton, 2001; Zuffi et al., 2009), prey sizes and abundance (Forsman, 1991; Pearson et al., 2002; Krause et al., 2003), and random effects (Wassersug et al., 1979). Males and females may also differ in morphology. Large body sizes in males relative to females may result from sexual selection through male-male competition or female mate choice (Darwin, 1871; Cox et al., 2003; Cox et al., 2007). Large female body size may evolve for maximizing the capacity for ovarian development, thus increasing fecundity (Seigel and Ford, 1987; Cox et al. 2007). In addition, ecological factors such as sex-specific niche partitioning may contribute to sex differences in morphology (Shine, 1991; Pearson et al. 2002), and sexual dimorphism may result from sexual variation in growth rates or mortality (Shine, 1990; Brito et al., 2003). Because the factors creating both geographic and sexual variations in morphology may not be mutually exclusive, disentangling the cause of these differences may require multiple explanations.

Green Pythons are medium-sized (<2 m) constricting snakes distributed widely within mainland New Guinea (O'Shea, 1996). In addition, they also inhabit a number of offshore islands as well as a small area of northern Australia (Natusch and Natusch, 2011). They are born either bright yellow or brick red before undergoing an ontogenetic color change to green (Wilson et al., 2006; Natusch and Lyons, 2012a). These vivid colors have made Green Pythons highly sought-after in the captive pet trade, resulting in large numbers being collected from New Guinea annually (Lyons and Natusch, 2011). Anecdotal information from pet collectors has described Green Pythons from islands and from a number of mainland sites to display variations in body size, head shape, tail length, and color (Kivit and Wiseman, 2005; Maxwell, 2005). In support of these observations, it has been shown that ontogenetic color

change varies among populations and that Green Pythons from north and south of New Guinea's central cordillera are genetically deeply divergent (Rawlings and Donnellan, 2003; Natusch and Lyons, 2012a).

Sexual and geographic variations in morphological traits are common in snakes, but the causes of such variation differ greatly among taxa. Perhaps the most commonly cited reason for geographic and sexual differences in snake body and head sizes is attributed to variations in food quantity (Forsman and Lindell, 1991a; Aubret and Shine, 2007), diet (Krause et al., 2003), and prey size (Forsman, 1991; Pearson et al., 2002). Because snakes are gape-limited predators, their diet is constrained by their gape size and, thus, geographic variations in body and head sizes are linked strongly to the size and shape of available prey (Arnold, 1993; Vincent et al., 2004). For example, body size and head shape differences among island and mainland populations of *Boa constrictor* result from local adaptations to mammalian versus avian prey (Boback, 2006; Boback and Carpenter, 2007). Furthermore, Forsman and Shine (1997) showed that head and body size differences in European Adders *Vipera berus* and Grass Snakes *Natrix natrix* are the result of prey differences among populations. For both adders and grass snakes, individuals inhabiting islands with relatively small prey items are smaller than snakes feeding on larger prey (Forsman and Shine, 1997; Madsen and Shine, 1993). Several studies have also revealed significant geographic variation in sexual dimorphism in body and head sizes (as well as the degree of sexual dimorphism in these traits) and have coupled these with sex-specific variation in diet (Shine 1991; Pearson et al., 2002; Krause et al., 2003).

In the present study we examined the body sizes and morphology of a field-based sample of Green Pythons from five populations with the aim of quantifying the anecdotal reports of intraspecific variation in these traits. In addition, we examine whether males and females differ in body and head sizes as well as the degree of dimorphism in these traits among populations. Finally, we aim to qualify any observed variation by analyzing geographical and sexual variation in the diets of Green Pythons from across their range.

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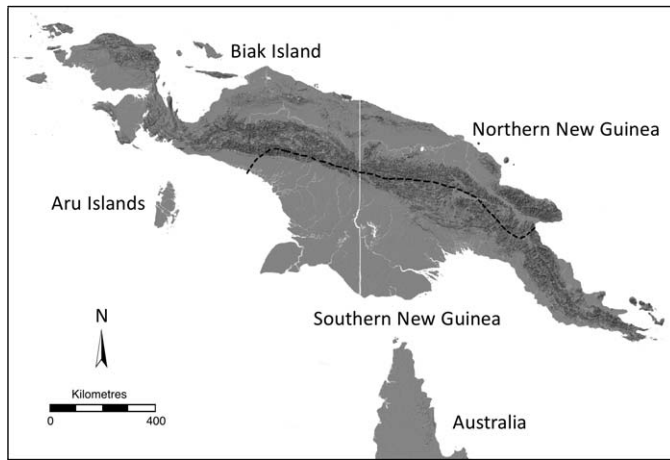


FIG. 1. Geographic distribution of the five populations of Green Pythons examined in the present study. Dashed lines delimited northern and southern mainland populations.

MATERIALS AND METHODS

Study Area and Regional Groupings.—We examined 908 Green Pythons collected from New Guinea and Cape York Peninsula, Australia between November 2007 and April 2011. We collected Australian Green Pythons by surveying areas of closed forest habitat at night using a hand-held spotlight (Natusch and Natusch, 2011). All individuals captured in Australia were released immediately after measurements were recorded. All New Guinean Green Pythons were measured after being opportunistically collected by villagers for the pet trade (Lyons and Natusch, 2011). We divided Green Pythons into five populations for analysis based upon geographic separation and known genetic structure. All island populations were treated as independent groups (Aru, Australia and Biak; Fig. 1). In addition, we treated specimens from northern New Guinea and southern New Guinea separately (Fig. 1) because the central cordillera is a known barrier to gene flow (Beehler, 2007; Deiner et al., 2011) and Green Pythons from north and south of the central range are genetically deeply divergent (Rawlings and Donnellan, 2003). Although the rainforest habitats at each site are superficially similar, the environmental and climatic conditions experienced by the populations differ subtly. The environmental characteristics of each population are summarized with data taken from Van Balgooy (1996), Prentice and Hope (2007), the Australian Bureau of Meteorology (2012), and the Indonesian Meteorological, Climatological and Geophysical Agency (2012) (Table 1).

Examination of Snakes.—We measured the snout–vent lengths (SVL) of all Green Pythons to the nearest 0.5 cm using a steel ruler. Head length and width was measured using digital calipers to the nearest 0.1 mm, from the tip of the snout along

the dorsal midline to the base of the skull, and at the widest point, respectively. We measured body mass to the nearest 1 g using Pesola spring scales and sex was determined by inserting a blunt probe into the cloacal bursa and recording the depth. We recorded prey types captured by Green Pythons either by direct observation of predation events or examination of stomach contents and fecal samples. For Australian samples, prey species were identified using the reference collections in the Queensland Museum.

Data Analysis.—We included only adult Green Pythons in our analyses of body sizes and morphology. Previous studies of Green Pythons have used the minimum sizes at sexual maturity provided by the museum-based sample of Shine and Slip (1990) to distinguish between juvenile and adult snakes. However, in the present paper we deem mature males and females to be 91 cm and 112 cm SVL, respectively (for details of this justification see Natusch and Lyons, 2012a) because of the uncertainties involved with SVL measures from preserved museum specimens (Natusch and Shine, 2012). We included both juveniles and adults within our descriptive analysis of diet; however, because juveniles prey exclusively on reptiles, we thus restricted subsequent analyses of geographic and sexual variations in diet to individuals large enough to consume mammalian prey (>70 cm SVL, sensu Natusch and Lyons, 2012a).

We analyzed all data using Minitab® 16 software (State College, Pennsylvania, USA). All continuous variables were \log_{10} -transformed prior to analysis to fit assumptions of normality and homogeneity of variance required for parametric tests. We analyzed morphological data from Green Pythons (i.e., mass, head shapes) using two approaches: analysis of covariance (ANCOVA) and general linear regressions on residual scores of \ln -transformed variables on \ln SVL. Our statistical comparisons relied on the more robust approach of ANCOVA (where the independent variable was included as a covariate) whereas residual scores were used in figures to aid graphical representation.

RESULTS

Body Sizes.—In each of the populations we studied, female Green Pythons grew to significantly larger body sizes than did males (Table 1). Mean adult body sizes also differed significantly among populations (two-factor analysis of variance [ANOVA] with sex and population as factors and \ln SVL as the dependent variable; $F_{4,396} = 16.73$, $P < 0.001$). Pairwise comparisons revealed that Australian Green Pythons are smaller than pythons from all other localities while those from southern New Guinea are larger (Table 1). To avoid biases because of size differences between the sexes at sexual maturity, we repeated the two-factor ANOVA using the SVL of the largest 20% of our adult sample. A significant two-way interaction between population and sex ($F_{4,83} = 5.06$, $P = 0.001$) revealed that females are consistently larger than males in maximum

TABLE 1. Location and environmental characteristics for five Green Python populations used in this study.

Study site	Aru Islands	Australia	Biak Island	Northern New Guinea	Southern New Guinea
Latitude	6°S	13°S	1°S	7–0°S	5–10°S
Longitude	134°E	143°E	136°E	130–147°E	138–148°E
Mean min/max temp (°C)	24–32	22–30	23–31	24–32	22–30
Mean rainfall (mm)	2,078	2,112	2,816	2,000–4,000	2,000–4,000
Seasonality	Moderate	High	Low	Low	Moderate

TABLE 2. Sample sizes and sexual dimorphism in adult SVL for Green Pythons from five populations in New Guinea and Australia. Standard errors appear within parentheses.

	Aru	Australia	Biak	Northern New Guinea	Southern New Guinea
Total number (juveniles, females, and males)	63	208	420	176	41
Adult males					
N	26	43	58	60	19
Mean (SE)	115.4 (1.8)	105.2 (1.4)	114.5 (1.7)	114.9 (1.4)	126.5 (2.4)
Min/max of largest 20%	125–138	115.5–123.5	124–160	125–139	141–142
Adult females					
N	26	46	53	54	12
Mean (SE)	128.2 (2.3)	125 (1.2)	133.1 (2.1)	132 (1.8)	141.3 (4.5)
Min/max of largest 20%	137–151.5	134–145	149–172	148–160	145–160
SSD ^a % difference	11	18.8	16.2	14.8	11.6

^a SSD = sexual size dimorphism.

body size, but the magnitude of sexual dimorphism varied among populations (Fig. 2). We quantified the degree of sexual dimorphism using the method of Lovich and Gibbons (1992). Data from populations with the largest sample sizes suggest that mean body sizes are 15% larger for females compared to conspecific males, and sexual dimorphism in maximum body sizes may be even greater (Table 2; Fig. 2).

Geographic and Sexual Variations in Morphology.—Are there sexual or geographical differences in the morphological traits of Green Pythons, or are any observed variations simply related to overall differences in body sizes between the sexes or among populations? We analyzed this question using a two-factor ANCOVA with sex and population as factors, morphological traits as the dependent variables (ln mass, head length, and width), and body size (ln SVL) as a covariate. If interaction terms were nonsignificant we deleted such terms to increase the power of our analysis and look for differences in main effects. We assessed the same data using an analysis of residual scores (Fig. 3).

(a) Body mass relative to SVL: The ANCOVA detected no significant interaction terms but did reveal a significant main effect of population on relative body mass ($F_{4,460} = 34.1$, $P < 0.001$). Inspection of residual scores (of ln mass vs. ln SVL) showed that this effect is because of heavier snakes from Australia and lighter snakes from the Aru Islands compared to other populations (Fig. 3a).

(b) Head length relative to SVL: After deletion of a nonsignificant three-way interaction, the ANCOVA revealed two significant two-way interaction terms: between population and SVL ($F_{4,474} = 48.8$, $P < 0.001$) and between sex and SVL ($F_{1,474} = 5.31$, $P = 0.022$). Snakes from Biak had longer relative heads than did conspecifics from other populations, and males from Australia had longer heads than did females (Fig. 3b).

(c) Head width relative to SVL: The ANCOVA detected no significant interaction terms but did reveal a significant main effect of population on relative head width ($F_{4,474} = 68.1$, $P < 0.001$). Green Pythons from Australia and Biak having wider

TABLE 3. Numbers and prey types recorded from Green Pythons from four populations in Australia and New Guinea (no prey items were recovered from Aru Islands pythons).

Prey type	Australia	Biak	Northern New Guinea	Southern New Guinea
Reptiles				
Scincidae				
Unknown spp.	17	33	2	1
<i>Emoia</i> spp.		15 ^a		
<i>Emoia longicauda</i>	8			
<i>Eremiascincus pardalis</i>	2 ^b			
<i>Glaphyromorphus nigricaudis</i>	3 ^a			
<i>Glaphyromorphus pumilus</i>	1			
<i>Lygisaurus sesbrauna</i>	1 ^b			
<i>Carlia sexdentata</i>	5			
<i>Bellatorias frerei</i> (Major Skink)	1			
Birds				
Unknown spp.	3	1		
Mammals				
Unknown spp.	5	7 ^a	14 ^a	2
Muridae				
<i>Melomys capensis</i> (Cape York Melomy)	14 ^b			
<i>Rattus leucopus</i> (Cape York Rat)	7 ^b			
Peramelidae				
Unknown spp.			2	
<i>Echymipera kalubu</i> (Common Spiny Bandicoot)		3 ^a		
<i>Echymipera rufescens</i> (Rufous Spiny Bandicoot)	4 ^b			
Total	71	59	18	3

^a Examination of gut contents.

^b Observed predation event.

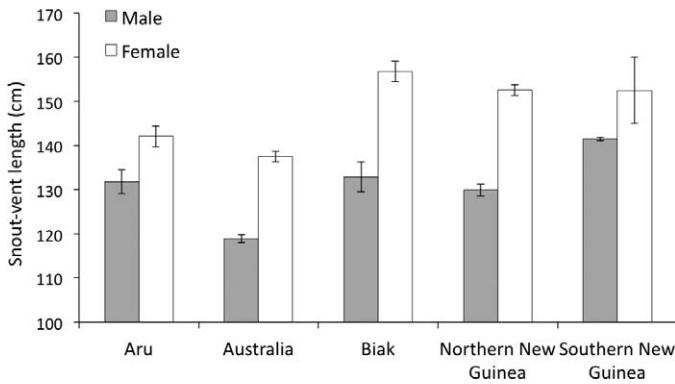


FIG. 2. Body size comparisons for the largest 20% of male and female Green Pythons from five sites in New Guinea and Australia.

heads compared to other populations are likely driving this effect (Fig. 3c).

Diet.—Invertebrate remains were recorded from juvenile and adult Green Pythons on 26 occasions; however, they were always accompanied by the remains of other prey species and were considered to be the gut contents of those prey species (Table 3). Restricting analyses to adult snakes, there was little divergence between the sexes in the types of prey consumed; however, a two-way ANOVA (with sex and prey type as factors and \ln SVL as the dependent variable) showed that the mean body size of snakes eating mammalian prey was greater than those consuming reptiles and birds (main effect of prey type, $F_{2,79} = 17.9$, $P = 0.001$; Fig. 4), and the mean body sizes of snakes consuming all prey types was greater for females than for males (main effect of sex $F_{1,79} = 6.82$, $P = 0.01$; Fig. 5). Table 3 suggests the proportion of prey types consumed by Green Pythons differs among populations. However, given the known ontogenetic diet shift, are these differences merely sampling biases towards snakes of different sizes or does dietary composition actually vary among populations? Our results suggested the former interpretation; mean body sizes of Green Pythons consuming mammalian prey were greater compared to those consuming reptiles, but snakes from different populations exhibited similar patterns in this respect (interaction term between population and prey type in two-factor ANOVA with \ln SVL as the dependent variable, $F_{2,73} = 2.39$, $P = 0.09$). The ANOVA thus showed that body size was the main determinant of prey type ($F_{2,73} = 29.1$, $P = 0.001$), with diet varying among populations because of differences in the size distribution of Green Pythons among samples.

DISCUSSION

Within the five populations studied we found significant sexual dimorphism while among populations we found significant variation in the body sizes and head shapes of Green Pythons. However, there are few clear patterns in the direction or degree of these variations, and understanding their significance (if any) is difficult. For example, although the large size of snakes from southern New Guinea is likely to be related to small samples sizes, Green Pythons from Australia are significantly smaller than other populations, particularly within males (Table 2; Fig. 2). However, is their small size related to stochastic (random) effects (e.g., founder effects, genetic drift) or phenotypic plasticity to variable food resources, or is a small body size adaptive in this population? It may generally be the

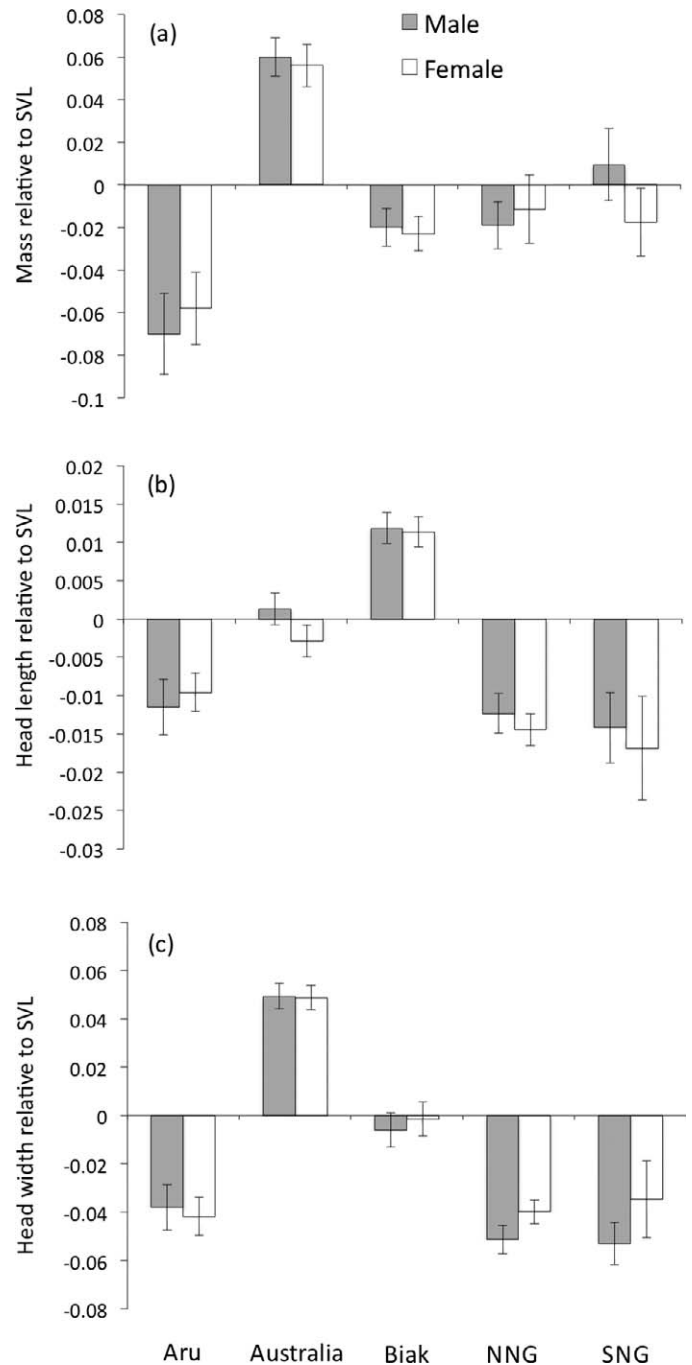


FIG. 3. Morphological comparisons between the sexes and among five populations of Green Pythons. The graphs show mean values and associated standard errors for residual scores from general linear regressions of \log_{10} -transformed variables: a) body mass relative to SVL; b) head length relative to SVL; and c) head width relative to SVL. More-positive values indicate longer or larger traits whereas more-negative values represent shorter or smaller traits; see text for statistical analysis of these data.

case that snakes grow bigger, and have larger relative head sizes, in populations where prey sizes are correspondingly large (e.g., Forsman and Lindell, 1991b; Forsman and Shine, 1997). The process creating such variation in snakes has been shown to be adaptive in some cases but merely the result of phenotypic plasticity in growth rates related to available prey resources in others (Boback and Carpenter, 2007). Our analyses did not

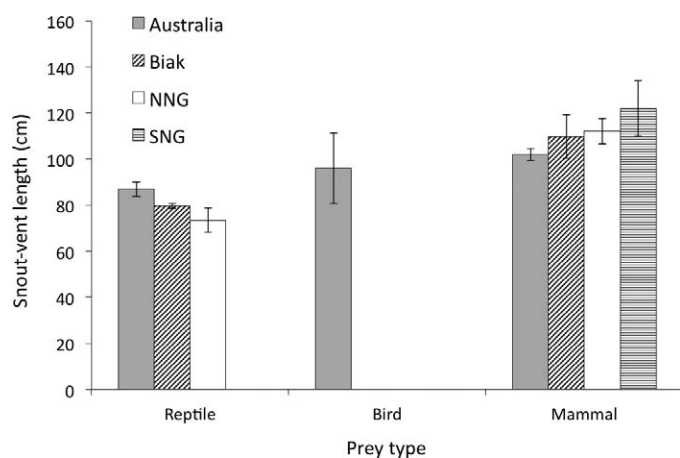


FIG. 4. Mean SVL (and associated standard errors) of Green Pythons from five sites recorded to select various prey types.

reveal any clear variation in diet among populations to explain these variations and are limited for two reasons: 1) absence of suitable reference material for New Guinea's wide range of (sometimes undescribed) reptilian and mammalian fauna precluded our identification of many of the species consumed by Green Pythons, and 2) data on the number of prey types consumed provide no information on the relative importance of those prey for Green Pythons.

Nevertheless, our data may provide some information to help clarify these variations. For example, variation in relative body mass is possibly related to collection biases among populations. Australian Green Pythons were measured immediately after capture in the field whereas individuals from the Aru islands may have lost condition because of the long period needed to transport snakes from their point of capture to the collector located in the main port on the far side of the Aru archipelago (*sensu* Lyons and Natusch, 2011). Several authors have suggested that longer heads may be an adaptation to saurophagy (Lillywhite and Henderson, 1993). Henderson and Binder (1980) found that Vine Snakes (genera *Ahaetulla*, *Oxybelis*, *Thelotornis*, *Uromacer*) that specialize on lizards have longer snouts compared to those that specialize on frogs. However, our data provide no evidence for a greater proportion of lizards in the diets of Green Pythons with relatively longer heads. Nevertheless, although it is difficult to infer the processes at work in generating intraspecific morphological variation within Green Pythons, we are reluctant to rule out diet as a contributing factor despite our inconclusive results. The direction and degree of morphological divergence in Green Pythons may provide weak evidence to reject nonadaptive processes as the cause of such variation. For example, Green Pythons from either side of New Guinea's central cordillera have been separated for approximately 4.5 million years (Rawlings and Donnellan, 2003). Despite this long period of separation, morphological divergence was least pronounced between these populations. In fact, our results suggest striking morphological convergence, suggesting similarities in ecological niche. By contrast, Green Pythons from Biak and Australia exhibited the greatest morphological variation, despite being only recently separated and genetically closely related to their mainland conspecifics (Voris, 2001; Rawlings and Donnellan, 2003; Natusch and Natusch, 2011).

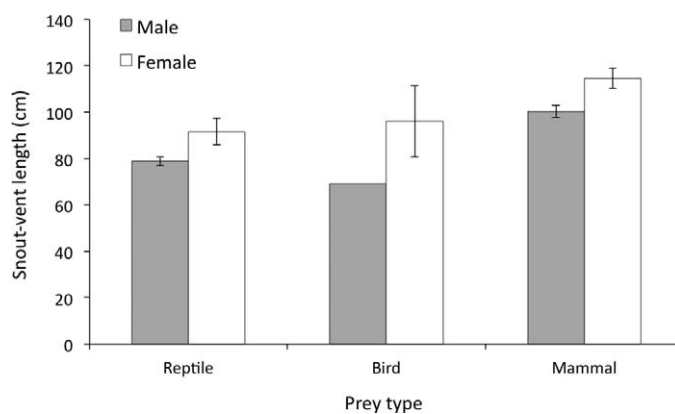


FIG. 5. Mean SVL (and associated standard errors) of male and female Green Pythons selecting different prey types.

Sexual dimorphism in average and maximum body sizes was broadly similar to those reported for other Australian pythons (Shine and Slip, 1990). Wilson et al. (2006) found that, at similar body sizes, females had longer and wider heads than males, although the opposite was true for head length in our study. The reason for this is unclear, but may arise because the present study analyzed only data from adult snakes, and juveniles and adults are known to differ in head dimensions (Natusch and Lyons, 2012a). The larger body sizes of female Green Pythons may be caused by fecundity selection favoring large body size because of enhanced reproductive output (Seigel and Ford, 1987). In keeping with this hypothesis, clutch sizes in other pythons of the genus *Morelia* increase with body size (Slip and Shine 1988; Natusch and Lyons, 2012b). Although the degree of sexual size dimorphism (SSD) was found to differ among populations, the magnitude of SSD was not substantial. Males and females selected the same prey types; however, the relative proportion of those prey items did differ somewhat and is corroborated by our raw data. Despite their larger body sizes, females consumed higher proportions of small-bodied, non-mammalian prey than did males. In fact, large males prey almost solely upon mammals whereas large females fed upon larger numbers of lizards and a few birds. As Green Pythons grow, males begin to hunt exclusively at night while females continue to hunt during the day (Wilson, 2007). This may explain the higher proportions of diurnal prey in the females' diet, which could be related to increasing body condition prior to reproduction (Wilson et al., 2007). These data, together with those of Wilson (2007), suggest a possible niche divergence between the sexes of Green Pythons.

In contrast to the claims of historical and contemporary authors and the popular literature, birds are relatively uncommon in the diets of arboreal snakes (Shine, 1983; Shine et al., 1996). By comparison, birds made up only 2.5% of all diet records for Green Pythons (Table 3). In addition to our dietary analyses this was also confirmed during fieldwork. We observed large adult Green Pythons (up to three at one time) at five sites (in Australia and New Guinea) hunting beneath emergent canopy trees laden with the nests of Metallic Starlings (*Aplonis metallica*). Although other snakes were observed climbing the trees to feed on newly hatched bird chicks (*Boiga irregularis* [Brown Tree Snake], *Liasis fuscus* [Water Python], *Morelia amethistina* [Scrub Python], and *Stegonotus cucullatus* [Slaty-grey Snake]), Green Pythons waited in ambush on the

forest floor, preying on small mammals attracted to seeds dropped by the birds above (Natusch, pers. obs.).

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