

Body size and sexual size dimorphism in primates: influence of climate and net primary productivity

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Abstract

Understanding the evolution of body size and sexual size dimorphism has been a longstanding goal in evolutionary biology. Previous work has shown that environmental stress can constrain male-biased sexual size dimorphism at the population level, but we know little about how this might translate to geographical patterns of body size and sexual size dimorphism at the species level. Environmental constraints due to a highly seasonal, resource-poor and/or variable environment have often been cited to explain the unusual lack of sexual size dimorphism among Madagascar's diverse and numerous primate taxa; however, empirical tests of this hypothesis are lacking. Using a phylogenetic approach and a geographical information system platform, we explored the role of seasonality, interannual variability and annual measures of temperature and rainfall, and net primary productivity on patterns of body size and sexual size dimorphism across 130 species of primates. Phylogenetically controlled comparisons showed no support for a role of environmental constraints in moderating sexual size dimorphism at the interspecific level, despite significant associations of environmental variables with body mass. Results suggest that the focus of discussions that have dominated in the last two decades regarding the role of environmental constraints in driving patterns of monomorphism of Madagascar's lemurs should be reconsidered; however, the conundrum remains.

Introduction

Understanding causes and consequences of body size and sexual size dimorphism (sexual divergence in body size) has been a critical goal in evolutionary ecology since the time of Darwin (1874). An organism's optimal body size is influenced by multiple, often opposing forces of selection acting on both survival and reproduction (Arnold & Wade, 1984). The direction and magnitude of these combined forces ultimately shape body size and the degree of sexual size dimorphism (Dale *et al.*, 2007), which, as a result, vary greatly across taxa. Although there have been a multitude of

studies using diverse taxa that identify selection pressures resulting in sexual size dimorphism (Fairbairn *et al.*, 2009), few studies have examined environmental factors that might lead to patterns of constrained sexual divergence in body size across taxa (but see Plavcan *et al.*, 2005). Understanding forces that may constrain sexual divergence may allow a better understanding of global patterns of sexual size dimorphism.

At the population level, there is evidence that environmental constraints can moderate both body size and sexual size dimorphism (Wikelski & Trillmich, 1997; Lehman *et al.*, 2005; Stillwell & Fox, 2009; Amarello *et al.*, 2010). As absolute metabolic energy requirements scale positively with body size (McNab, 1971), larger individuals are expected to experience higher mortality when resources are scarce (Forsman, 1996; Beaupré, 2002). Thus, small body size may confer a selective advantage under conditions of low resource availability

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(Stemberger & Gilbert, 1985), high temporal variation in resource availability (McLain, 1993; Badyaev & Ghalambor, 1998; Lehman *et al.*, 2005) and/or high levels of resource competition (Amarillo-Suárez *et al.*, 2011). One of the clearest examples of this is with the marine iguanas of the Galapagos (Wikelski & Trillmich, 1997; Wikelski *et al.*, 1997; Wikelski, 2005). There is strong sexual selection for large male body size on all islands due to a mating system involving lekking, but iguanas are smaller and less sexually dimorphic on islands that experience intense periods of resource scarcity. During such periods, large males experience the brunt of the population-level mortality, resulting in reduced levels of both sexual size dimorphism and overall body size. Another example comes from comparisons of ungulates from island and mainland systems (Raia & Meiri, 2006). Sexual size dimorphism is lower on islands without predators where presumably resource competition may constrain body size relative to mainland habitats where predation limits populations.

Although there is evidence for a negative relationship between the expression of sexually selected traits and environmental stress at the population level (through genetic, epigenetic or plastic response; Badyaev & Ghalambor, 1998; Stillwell & Fox, 2009), how environmental stress relates to interspecific patterns of sexual size dimorphism is less clear. We should not simply assume that interspecific patterns are driven by the same microevolutionary mechanisms that control population-level patterns, although they are certainly likely to interact (Chown & Gaston, 1999). Interspecific patterns can also be driven by species sorting and replacement (Maitner *et al.*, 2012), in some cases leading to opposite clinal patterns of traits found at the intra- and interspecific level (Chown & Klok, 2003).

Interspecific studies of the relationship between habitat productivity and sexual size dimorphism in seabirds and shore birds have yielded mixed results, with one study showing a strong positive relationship between habitat productivity and male-biased size dimorphism (Fairbairn & Shine, 1993) and other studies showing no relationship (Székely *et al.*, 2004; Serrano-Meneses & Székely, 2006).

There may be trade-offs between sexually selected traits such as large male size and resistance to environmental stress, because maintaining sexually selected traits is energetically costly (McLain, 1993; Badyaev & Ghalambor, 1998). Thus, evolution of such traits may be constrained in environments with unpredictable resources (Wikelski & Trillmich, 1997; Wikelski *et al.*, 1997; Wikelski, 2005), and species may rely on mating strategies that require less investment (Emlen & Oring, 1977; Dunham & Rudolf, 2009). For such mechanisms to constrain sexual size dimorphism at an interspecific level, however, the sporadic selection in time and space caused by environmental variability would need to be

sufficient to counteract potentially strong sexual selection among many polygynous taxa.

Alternatively, other authors have argued that periodic resource scarcity should not constrain sexual size dimorphism, but in contrast should select for larger body size because of a greater fasting endurance (Lindstedt & Boyce, 1985). If being small is disadvantageous in times of scarcity, constraints would thus be on the minimum size and the evolution of male-biased sexual size dimorphism would not be constrained. This idea has been used as one of many explanations of Bergmann's rule (Bergmann, 1847; Murphy, 1985), which predicts greater body size in higher latitudes where periodic resource scarcity is more common.

Primates represent a model system for studying patterns of sexual size dimorphism because they are among the best-characterized of all vertebrate orders and exhibit the highest level of sexual size dimorphism among mammals (males larger than females), yet there are several species lacking any kind of sexual size dimorphism across both suborders (Haplorrhini and Strepsirrhini; Weckerly, 1998). Intrasexual selection on male size appears to be the primary driver of sexual size dimorphism in primates (Clutton-Brock *et al.*, 1977; Gaulin & Sailer, 1984; Harvey & Harcourt, 1984; Mitani *et al.*, 1996). However, there are also many polygynous species lacking sexual size dimorphism, which cannot be explained by social structure or operational sex ratios (Kappeler, 2000; Kappeler & Schaffler, 2008; Dunham & Rudolf, 2009). Lack of size dimorphism is most apparent within the strepsirrhines (including Madagascar's lemurs), which exhibit among the lowest levels of sexual size divergence among mammals (Weckerly, 1998).

The evolutionary pressures leading to sexual size monomorphism and other unusual traits in Madagascar's lemurs have been debated repeatedly over the last two decades (Jolly, 1984; van Schaik & Kappeler, 1996; Wright, 1999; Pochron & Wright, 2002; Dunham, 2008; Kappeler & Schaffler, 2008; Dunham & Rudolf, 2009). The majority of hypotheses invoke environmental constraints on body size imposed by seasonality, limitation and/or unpredictability of resources (Jolly, 1984; Leigh & Terranova, 1998; Wright, 1999; Plavcan, 2001), which we define here jointly as the *environmental-constraints hypothesis*. If true, environmental constraints are expected to influence geographical patterns of sexual size dimorphism across taxa; however, this has not been empirically tested (Dunham & Rudolf, 2009).

Our goal was to test whether environmental conditions are associated with body size or sexual size divergence across primate taxa. We used phylogenetically controlled statistical analyses to examine the associations of sexual size divergence with climatic characteristics and variability, seasonality and net primary productivity (NPP) across the primate order.

Materials and methods

Data collection

We compiled a database of male and female body mass for 190 species of primates. Data on mating system and body mass were recorded from 'All The World's Primates' database (<http://alltheworldsprimates.org/>), which summarizes from the literature comprehensive information on morphological, behavioural and ecological characteristics of all known species of primates and is written by specialists of each species (Rowe & Myers, 2012). When numerous estimates of body mass were reported, we took the average of all estimates in the database that were based on at least five individuals. When measurements were available from both captive and wild populations, we excluded estimates from captive populations. When body mass measurements were not found in the database, we took them from the literature (Gaulin & Sailer, 1984; Harvey & Clutton-Brock, 1985; Ford, 1994; Smith & Jungers, 1997; Weckerly, 1998; Dunham & Rudolf, 2009; Estes, 2012). We used the log-transformed ratio of the average male vs. female body mass as a measurement of sexual size dimorphism.

Ranges of all primate species were taken from the IUCN RedList database (IUCN, 2012) and mapped onto a geographical information system (GIS) using ArcView GIS 3.3 (Environmental Systems Research Institute Inc., Redlands CA, USA). Average NPP for each species' range was derived from a global map created with the Carnegie Ames Stanford Approach carbon-model by Imhoff *et al.* (2004). Primate ranges were overlaid onto a global map of climatic data from the WorldClim database (Hijmans *et al.*, 2005). We extracted climatic data for each species by averaging across all 1-km² pixels within each species' range. Analyses focused on annual rainfall, annual mean temperature, degree of seasonality of rainfall and temperature, and interannual variability in rainfall and temperature based on records from 1960 to 2010. As resource availability is difficult to directly measure, and particularly across multiple taxa, we used rainfall and average NPP as proxies for relative levels of food resources available to species in a given region (Previtali *et al.*, 2009). Seasonality of climatic variables were calculated as the average annual coefficient of variation of monthly rainfall and temperature (Murphy, 1985). Interannual variability of rainfall and temperature was calculated as the coefficient of variation of annual measures.

Statistical analysis

Using data extracted from the GIS platform, we investigated potential associations of sexual size dimorphism and male body size of primates with individual environmental variables (annual rainfall, annual mean temperature, degree of seasonality of rainfall, degree of

seasonality of temperature, interannual variability in rainfall, interannual variability in temperature and NPP).

Shared ancestry can yield potential confounding effects in comparative studies because individual species cannot necessarily be considered independent observations (Felsenstein, 1985; Pagel, 1992). Thus, we accounted for potential nonindependence among species using general linear models with log-likelihood statistics corrected for phylogeny with the software PHYLO.GLM V0.7 for SAS (Grafen, 1989, 2006). This method employs phylogenetic degrees of freedom to correct for phylogenetic relationships between species. The phylogeny used in the analysis was by Perelman *et al.* (2011) with branch lengths following those authors' best date estimates. This phylogeny was created using comparative genomic analyses and represents a well-resolved tree that included 130 of the 190 species in our database. As body size is a significant covariate with sexual size dimorphism in primates (Dunham & Rudolf, 2009), the log of male body mass was used as a covariate on all analyses to control for allometry. A sequential Bonferroni adjustment was applied to the multiple tests to limit type I error. For all analyses, log transformations were carried out when necessary to achieve normality of data.

We also performed a phylogenetically corrected principal component analysis (PCA; Revell, 2009) to reduce the full set of environmental variables to a smaller set of uncorrelated variables (phytools package in R, Revell, 2012). The PCA was used to determine how suites of environmental variables might influence the variation in sexual size dimorphism and male body mass and to deal with the issue of potential collinearities between environmental variables, which may obscure patterns in the data. We retained three principal components with an eigenvalue > 1 (Kaiser-Guttman criterion, Peres-Neto *et al.*, 2005). These three components explained 66% of the total variation in the original seven variables. We assessed the influence (loadings) of predictor variables on the remaining PCA scores and then tested whether they could explain significant variation in sexual size dimorphism and male body mass across primates using phylogenetic contrasts (described previously).

Results

Bivariate analyses

Our data set revealed significant differences in sexual size dimorphism patterns across major geographical regions (GLM with male body mass as a covariate, $F_{3,186} = 18.301$, $P < 0.001$, Fig. 1), including unusually low levels of dimorphism in Madagascar's primates relative to those in other regions ($F_{1,186} = 8.360$, $P = 0.004$; Fig. 1). In our phylogenetically controlled bivariate analyses, we found no significant associations between

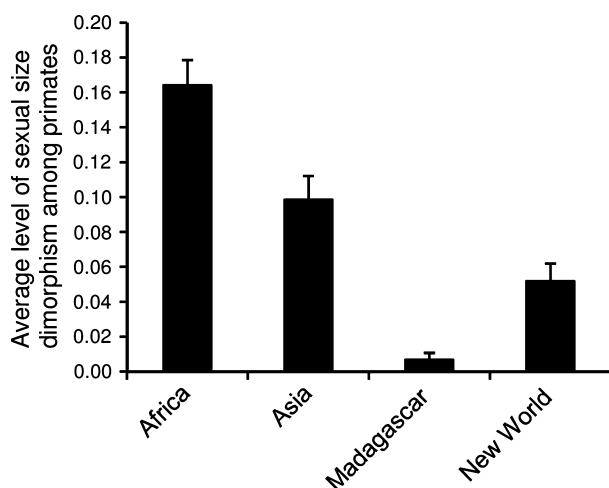


Fig. 1 Average levels of sexual size dimorphism among primate taxa in different regions. Error bars represent standard error.

sexual size dimorphism and net primary-productivity or any climatic variables including temperature, rainfall, seasonality and interannual variability in temperature or rainfall (Table 1, Fig. 2a–f). Madagascar's primates were found to experience levels of interannual variability of rainfall that exceeded all other primates (see tail of distribution in Fig. 2c).

We found a relationship between male body mass and seasonality of temperature ($r = 0.355$, $F_{1,126} = 6.356$, $P = 0.013$); however, this relationship did not remain significant after a Bonferroni adjustment for multiple comparisons ($\alpha = 0.007$). Associations between male body mass and all other climatic factors were non-significant (Table 2).

Multivariate analyses

In our phylogenetically corrected PCA, PC-1 explained 29.3% of the variance among predictor variables, PC-2 explained 19.4%, and PC-3 explained an additional 17.6% of the variance. For PC-1, the largest loadings

Table 1 No associations were observed between environmental variables and sexual size dimorphism across primates with log of male body mass as a covariate.

Environmental variable	Regression coefficient	$F_{1,126}$	P
Average annual rainfall	-1.245E-6	0.005	0.943
Average annual temperature	0.002	0.579	0.448
Seasonality of rainfall	-0.002	0.009	0.923
Seasonality of temperature	-0.072	2.461	0.119
Interannual variation of rainfall	0.031	0.060	0.807
Interannual variation of temperature	0.088	1.301	0.256
Net primary productivity	4.214E-6	3.820	0.053

were seasonality of temperature (positive sign) followed by average annual rainfall and temperature (negative signs; Table 3). For PC-2, the largest loading was for NPP. For PC-3, the largest loadings were seasonality of rainfall and interannual variability in temperature which had opposite signs. The three environmental PCA scores did not explain significant variation in sexual size dimorphism (PC-1, $r = 0.078$, $F_{1,126} = 1.586$, $P = 0.210$; PC-2, $r = 0.073$, $F_{1,126} = 0.865$, $P = 0.354$; PC-3, $r = -0.066$, $F_{1,126} = 0.662$, $P = 0.417$). Interspecific variation in male body mass was associated with PC-1 (PC-1, $r = 0.430$, $F_{1,125} = 5.125$, $P = 0.025$) but not with PC-2 or PC-3 (PC-2, $r = -0.046$, $F_{1,125} = 0.038$, $P = 0.846$; PC-3, $r = -0.200$, $F_{1,125} = 0.654$, $P = 0.420$).

Discussion

Previous work has suggested that resource-poor and highly variable environments can moderate the expression of sexual size dimorphism at the population level (Wikelski & Trillmich, 1997; Isaac, 2005; Stillwell & Fox, 2009); however, very little is known about how environmental factors may affect such patterns on a larger taxonomic scale. Two decades of literature have hypothesized that the lack of sexual size dimorphism in Madagascar's primates is due to environmental constraints on male size due to the island's hypervariable, seasonal and resource-poor environment (Jolly, 1984; Wright, 1999; Simmen *et al.*, 2010; MacLean *et al.*, 2012). However, a review of the literature reveals a paucity of empirical tests. We predicted that if the environmental-constraints hypothesis was true, then we should see patterns of sexual size dimorphism across global distributions of primate taxa that vary with climatic factors and levels of NPP. However, with phylogenetically controlled analyses, we found no associations of sexual size dimorphism with rainfall, temperature, interannual variability or seasonality of temperature or rainfall (see Plavcan *et al.*, 2005, for similar results regarding seasonality), or with NPP. The inability of environmental variables to explain interspecific patterns of sexual size dimorphism was supported by both bivariate contrasts with individual environmental variables and with reduced predictor variables created using a phylogenetically controlled PCA. Interspecific patterns of body mass, however, were associated with climatic factors. Most apparent was that larger-bodied primates are associated with environments with more seasonal temperatures.

Proxies for resource availability: Rainfall and NPP

Large body size has an energetic cost, and thus, resource availability has been suggested as a potential constraint affecting geographical patterns of sexual size dimorphism (Wright, 1999; Amarello *et al.*, 2010).

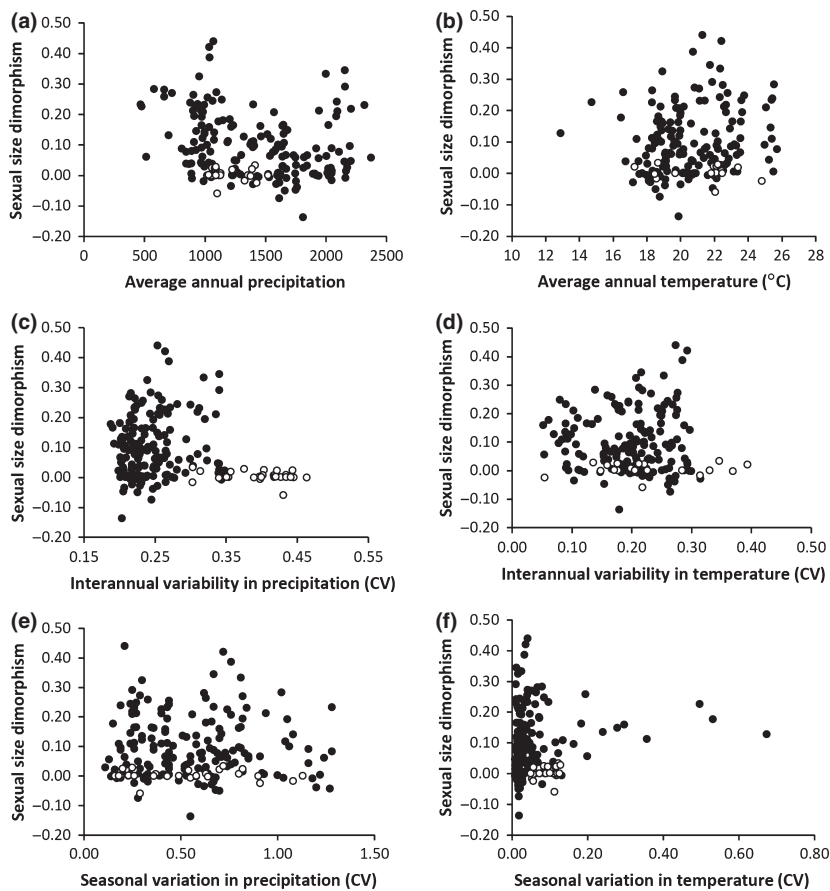


Fig. 2 Associations between climatic variables (a–f) and sexual size dimorphism (log of the ratio between male and female body mass). No significant associations were found. Interannual variability was calculated as the coefficient of variation of monthly values within each species' range. Seasonal variation was calculated as the coefficient of variation of monthly averages of temperature and rainfall. Open circles represent Madagascar's lemurs. Black circles represent all other primates in the database.

Table 2 Associations between environmental variables and log of male body mass. No associations remained significant after a Bonferroni adjustment.

Environmental variable	Regression coefficient	$F_{1,125}$	P
Average annual rainfall	−0.001	2.911	0.090
Average annual temperature	−0.007	1.528	0.219
Seasonality of rainfall	−0.037	0.545	0.462
Seasonality of temperature	0.355	6.356	0.013
Interannual variation of rainfall	−0.548	1.889	0.172
Interannual variation of temperature	0.192	0.670	0.415
Net primary productivity	−9.474E-8	0.0002	0.989

Rainfall and NPP are important indicators of the density and availability of food resources in an environment (Ernest *et al.*, 2003); thus, conditions of low rainfall and/or NPP might be expected to result in constraints on body size and sexual size dimorphism (Boyce, 1978). However, we found no association of sexual size dimorphism or body size with average annual rainfall or NPP in our study of interspecific patterns across a diverse taxa group (Tables 1, 2).

At the population level, Huston and Wolverton (2011) found that the level of primary productivity during the growing season (so-called ecologically relevant NPP or NPPe) was associated with larger body sizes within species of multiple taxa. They argue that NPPe may be a more relevant measure of resource

Table 3 Factor loadings from phylogenetically controlled principal component analysis.

Independent variable	Average annual rainfall	Average annual temperature	Seasonality of rainfall	Seasonality of temperature	Interannual variation of rainfall	Interannual variation of temperature	Net primary productivity
PC-1	−0.688	−0.624	−0.165	0.898	−0.451	−0.356	−0.143
PC-2	−0.199	0.518	−0.518	−0.017	−0.090	−0.502	0.723
PC-3	−0.043	0.484	0.568	−0.101	−0.451	−0.552	−0.395

availability than NPP, with the idea that in seasonal environments, NPP may be concentrated into a few months, allowing organisms to grow during plentiful times and save energy the rest of the year by reducing respiration. The importance of NPPe for determining interspecific patterns of body size or sexual size dimorphism remains to be tested.

Although we found no association of rainfall with body mass, recent coarser scale studies of Madagascar's primates have reported a pattern of larger species occurring in wet forests than in dry habitats (Plavcan *et al.*, 2005; Razafindratsima *et al.*, 2013). We suspect that this pattern is likely a by-product of community structure changes after a recent large-scale extinction of the largest lemurs on the island that occurred in the late Holocene, coinciding with the arrival of humans on the island (Razafindratsima *et al.*, 2013). Isotopic evidence strongly suggests that these large, extinct species were primarily adapted to living in dry environments (Crowley *et al.*, 2011), suggesting a recent relative size-distribution change in Madagascar's dry forests.

Our results were also in contrast to population- and genus-level studies of mammals which have found patterns of larger body size or sexual size dimorphism associated with higher rainfall (Quin *et al.*, 1996; Lehman, 2007; Gordon *et al.*, 2013). It is important to consider, however, that trait patterns at the interspecific level (as in our study) are subject to sorting and assembly processes, which may explain why ecogeographical patterns of body size are not static across all taxonomic levels.

Environmental seasonality

Strong seasonality has been suggested to select against prolonged growth because organisms must reach foraging competence before the beginning of the season of scarcity (Peterson *et al.*, 1998). A prolonged growth period is thought to allow for greater sexual bimaturism (differences in development time between the sexes), which may reduce metabolic risks of accelerated growth rates for males. Thus, it has been proposed that highly seasonal environments with short growing seasons may reduce the opportunity for male ontogeny to respond to pressures of sexual selection and that extreme environmental seasonality experienced by lemurs may have driven the evolution of sexual size monomorphism in these taxa (Leigh & Terranova, 1998). Others have suggested strong seasonality may result in short mating seasons and overlapping oestrus periods of females reducing the potential for polygyny and thus selection pressures for large male size (Shuster & Wade, 2003; Isaac, 2005).

However, our data and previous work (Plavcan *et al.*, 2005) on primates do not support environmental seasonality as a predictor for the degree of sexual size

dimorphism in primate taxa (Table 1, Fig. 2e,f). Interestingly, however, the degree of seasonality of births of primates has been shown to be predictive of reduced male-biased size dimorphism in skull size, but not body size using phylogenetic contrasts of multimale group living species (Plavcan *et al.*, 2005). Birth seasonality is high for Madagascar's lemurs, and breeding seasons are short; however, they do not have synchronous oestrus periods which can preclude polygyny (Dunham & Rudolf, 2009). Environmental seasonality alone is likely to be insufficient to constrain the evolution of sexual size dimorphism (Zeh, 1987). This is emphasized by the observation that in temperate systems, where seasonality is extreme, male-biased sexual size dimorphism is stronger than found in tropical systems (Blanckenhorn *et al.*, 2006). The relationship between birth seasonality and skull dimorphism in primates (Plavcan *et al.*, 2005), however, begs a more detailed look at other dimensions of seasonality and other factors that may constrain female receptivity periods, breeding season lengths and conditions for polygyny.

The degree of seasonality in temperature showed a positive relationship with male body mass across primate taxa (although nonsignificant after a Bonferroni adjustment) and was the only environmental variable we tested that independently had any predictive value on body size. It has long been argued that seasonality selects for larger body size (Lindstedt & Boyce, 1985), but direct examinations at the interspecific level have been limited (but see Kamilar *et al.*, 2012; Clauss *et al.*, 2013). Mechanisms proposed include increased resource availability per individual because of high seasonal mortality and increased fasting endurance of larger individuals (Lindstedt & Boyce, 1985). The association observed in our data with the degree of temperature seasonality was unexpected given that the primate order is restricted primarily to tropical regions where high seasonal mortality related to temperature is unlikely and where seasonality of rainfall may offer a better predictor of intra-annual resource variation.

Interannual variability in rainfall and temperature

An important component of the environmental-constraints hypothesis is the idea that sexual size dimorphism may be constrained in species that are subject to high levels of unpredictability in resource availability as a result of environmental stochasticity (Leigh & Terranova, 1998; Wright, 1999). This is the most common explanation for the prevalence of sexual size monomorphism in lemurid primates in the literature but has not previously been tested across primate taxa. Although we did observe extremes in interannual rainfall and temperature variability in habitats occupied by Madagascar's primates (Fig. 2c,d), phylogenetic contrasts revealed no relationships of environmental variability with body size or sexual size dimorphism across

primates. If a threshold of interannual variability exists that constrains sexual size dimorphism, then we are unable to detect the effect using phylogenetically controlled analyses because there are no non-lemur primates that live with comparable levels of interannual variability in rainfall.

Conclusions: Madagascar's lemur conundrum

It is often assumed that mechanisms driving population-level patterns of selection will be reflected in interspecific patterns of traits. Our results question the predictive value of this approach. Interspecific patterns are a by-product of both optimizing morphology within species but also optimizing trait combinations within communities. For example, trait patterns of species within a community may be constrained by the environment or may involve optimizing niche and therefore trait differences or may represent a balance between these forces. Thus ecogeographical patterns of traits at the interspecific level will not necessarily reflect population-level patterns of selection.

Results from this study suggest that we should redirect current focus away from the environmental-constraints hypothesis to explain interspecific patterns of sexual size dimorphism, particularly in primates. The hypothesis stemmed from observations of ecogeographical trait patterns within species and the general lack of obvious sexual size dimorphism across Madagascar's diverse strepsirrhine primates, comprising over 100 extant and 18 extinct lemur species (IUCN, 2012).

Previous work on primates has shown a strong link between reduced sexual size divergence and copulatory plug use (a solid sperm plug placed in the vagina of a female) in primates, thought to be a passive strategy for mate guarding that does not involve selection for large male size (Dunham & Rudolf, 2009). However, this may be a proximate rather than ultimate mechanism of reduced or absent sexual size divergence; further work is necessary to understand what conditions might favour such passive strategies of mate guarding and their implications for body size evolution.

Primates are a model taxon for better understanding the evolution of body size and sexual size dimorphism generally, because they are so well characterized as a group; but they are also critical for our understanding of human evolution. However, the long-standing conundrum of the evolution of monomorphism in Madagascar's lemurs remains. With 91% of lemurs categorized as at risk of extinction, they may be one of the most endangered groups of vertebrates on Earth (IUCN, 2012; Ratsimbazafy *et al.*, 2013). As habitat loss, hunting and climatic changes continue to put their populations at risk (Dunham *et al.*, 2008, 2011; Barrett & Ratsimbazafy, 2009; Jenkins *et al.*, 2011), evolutionary and ecological studies of them are becoming urgent.

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