Morphological and Roosting Variation in the Dwarf Chameleon *Brookesia stumpffi* Between Primary, Secondary, and Degraded Habitats in Nosy Be, Madagascar

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Abstract.—Morphological, behavioral, and genetic variation of a species in different habitats is central to understanding how and if a species will survive the demands of habitat change. It is well known that the morphology and behavior of ectotherms can diverge due to ecological variation, but there is limited research on chameleons, and their habitat is under threat by deforestation in Madagascar. I aimed to identify if *Brookesia stumpffi*, a dwarf chameleon from northern Madagascar, differed in their morphology and roosting behaviors in primary, secondary, and degraded habitats. I and volunteers conducted surveys at night by recording the type of substrate and the height at which adult *B. stumpffi* were roosting. Measurements of the morphology of chameleon were then taken using analog calipers. I found that *B. stumpffi* roosted on higher perches in secondary and degraded habitats compared to primary forests. Furthermore, there was a significant divergence in chameleons morphology between the habitat types. I conclude that *B. stumpffi* have diverged between habitats and that deforestation may be responsible.

Key Words.—anthropogenic factors; conservation; deforestation; divergence; habitat degradation

Introduction

Variation of species in different habitats is central to understanding how and if a species will survive the demands of habitat change (Da Silva et al. 2013). It is well known that species can adapt to cope with a change in ecosystem (Orr and Smith 1998; Measey et al. 2011; Langin et al. 2015). Some species of lizards are highly adaptive, and thus natural selection can enable the survival of these species in many habitats by changing their morphology to maximise fitness (Darwin 1871; Losos et al. 1997; Hopkins and Tolley 2011; Da Silva et al. 2013; Collins et al. 2015). Ecological divergence demonstrates the plasticity of a species, and if they are likely to survive a sudden change in habitat (Losos et al. 1997; Bickel and Losos 2002; Losos 2009; Measey et al. 2011; Da Silva et al. 2013).

A study by Losos et al. (1997) demonstrated how readily adaptable *Anolis* lizards are by placing *A. sagrei* on islands with different habitats. After only 10–14 y, the researchers found that the morphology of the lizards had changed significantly in relation to the type of habitat. Lizards within a leafy environment had bigger toe pads allowing them to stick to the leaves while lizards in a densely clustered environment had smaller toe pads and limbs allowing them to balance on the substrate (Losos et al. 1997, for a similar and more recent study see Collins et al. 2015). This demonstrates how natural selection changes the morphology of animals to enable survival in new habitats.

Deforestation can change a habitat dramatically as degraded habitats can occupy different prey, predators, microhabitats, roosting availability, and thermal requirements compared to primary habitats (Vitt et al. 1997; Keren-Rotem et al. 2006; D' Cruze and Kumar 2011; Shirk et al. 2014). Any or all of these factors can affect the morphology of species. Measey et al. (2009) showed that two ecomorphs of the Cape Dwarf Chameleon (*Bradypodion pumilum*) had formed due to being either in an open or closed habitat. In open habitat, males had larger head measurements than males in closed habitat. However, Da Silva and Tolley (2013) studied morphological differences in five phenotypic forms of *Bradypodion* and found that chameleons in closed forested areas developed larger heads compared to chameleons in open grassland habitats. Dietary shifts could explain these different results because Herrel et al. (2008) found that with the Italian Wall Lizard (*Podarcis sicula*), a change in habitat was associated with a change in diet, which can ultimately influence head morphology.

Although many herpetofaunal taxa such as anole lizards (Losos et al. 1997), skinks (Melville and Swain 2000), chameleons (Meseay et al. 2009), geckos (Collins et al. 2015), and snakes (Aubret et al. 2004) have been recorded to phenotypically diverge due to exposure to different habitats, the rate of deforestation may be occurring too fast for some species. Shirk et al. (2014) found a dramatic decrease in chameleon populations in the Usambara Mountains in Tanzania due to habitat loss, suggesting that morphological change

FIGURE 1. A Leaf Plated Chameleon (*Brookesia stumpffi*) in primary habitat on Nosy Be, Madagascar. (Photographed by Richard Bloomfield).

may not occur fast enough to allow survival of some species. Similarly, D' Cruze and Kumar (2011) found that lizard abundance had decreased in deforested areas. Additionally, deforestation can change the biocenosis of a habitat. Vitt et al. (1998) found that although clearing forests in the Amazon rainforest had caused heliothermic lizard species to become more abundant, this limited the resources for other ectotherms.

Madagascar is a biodiversity hotspot, with many endemic species of flora and fauna (Myers et al. 2000). It is home to 85 species of endemic chameleons (Uetz, P., P. Freed, and J. Hošek. 2017. The reptile database. Available at http://reptile-database.reptarium.cz/adva ncedsearch?Taxon=chameleonidae&location=Madag ascar&submit=Search [Accessed 15 June 2017]). The deforestation of Madagascar is increasing with the use of techniques such as slash and burn and logging, which limits chameleons roosting microhabitats and potentially puts them at greater risk of predation (Raxworthy 1991). Furthermore, these deforestation techniques clear the forest of vegetation and alter the thermal environment (Vitt et al. 1998; Lawrence and Vandecar 2015; Longobardi et al. 2016) affecting ectotherms. Allnutt et al. (2012) found that in northeastern Madagascar, anthropogenic habitat disturbance was considerably higher in 2011 compared to 2005. At the same time, many of the Madagascan chameleons are increasingly becoming endangered (International Union for the Conservation of Nature [IUCN] 2016).

The genus *Brookesia* is a clade of dwarf chameleons that appear terrestrial in behaviour compared to other chameleons, and are found mostly in the leaf litter

during the day and roosting on small saplings during the night (Glaw and Vences. 2007). These chameleons are endemic to Madagascar (Raxworthy 1991; Glaw and Vences. 2007) with 30 currently recognized species, although 24 are categorized as Near Threatened to Critically Endangered on the IUCN Red List of Endangered Species (IUCN 2016). Due to the difficulty in finding endangered or near threatened species, I studied the Plated Leaf Chameleon (*Brookesia stumpffi*; Fig.1), a species listed as Least Concern by the IUCN, as they are commonly found in all habitat types (see Raxworthy 1991, for a description of *B. stumpffi*). Like most *Brookesia* species, *B. stumpffi* forage for small insects, and at a total length (including tail) of up to 100 mm, *B. stumpffi* is one of the larger species of *Brookesia* (Crottini et al. 2012).

Any knowledge gained from this species could be used as guidance for other ecologically similar species of *Brookesia*. I aimed to identify if *B. stumpffi* differs in their morphology and roosting behaviors in primary, secondary, and degraded habitats. If the chameleons have diverged, this research will lead to hypotheses about why, and if not, it could suggest that *B. stumpffi* is not very plastic and that deforestation may reduce their population.

MATERIALS AND METHODS

I studied chameleons on Nosy Be, an island northwest of Madagascar. *Brookesia stumpffi* are commonly found in primary, secondary, and degraded habitats on this island (Andreone et al. 2003). Primary habitat refers to untouched forest with minimal anthropogenic disturbance and an almost complete canopy cover. Secondary habitat refers to the natural regrowth of cleared forest over 30 y, with occasional anthropogenic disturbance, and partial canopy cover. Degraded habitat refers to a cleared forest with no canopy cover. In this survey, the degraded habitats suffered from intense logging and a large amount of anthropogenic disturbance. Google Earth images show the degraded habitats as experiencing habitat loss and anthropogenic disturbance for at least 12 y (Google Earth 2015).

I carried out the fieldwork along with field assistants between early May and late July 2016, the dry season. All data collection was conducted at night, 1900–2230, to identify the chameleons roosting height and substrate. I established two 200 m transects in each habitat type; thus, six transects were surveyed in total (Fig. 2). I only surveyed for adult chameleons (snout to vent length [SVL] > 30 mm, Raxworthy 1991; Crottini et al. 2012) to ensure their full development in head morphology. I collected data on 25 *B. stumpffi* in each habitat type. I and the other surveyors relied on death feigning to measure the individuals in the field and any individuals

Figure 2. Approximate layout of six transects used to census Plated Leaf Chameleons (*Brookesia stumpffi*) on Nosy Be, Madagascar. The letter P reflects the two primary transects, S the two secondary transects, and D the degraded transects. (Image from Google Earth 2015).

that did not naturally death feign were placed back to ensure minimal stress to the individuals.

Using a 3 m tape measure, I took measurements of the roosting height of individual chameleons and I recorded the roosting substrate. I grouped the substrate into four categories: Shrub, Sapling, Leaf Litter, and Other. Other included a branch and a fallen palm frond. I handled all chameleons and while the chameleons were death feigning, I measured the morphology of the lizard using analog calipers accurate to 0.1 mm. I marked the chameleons with a non-scented marker to ensure independent samples. I collected snout-vent length (SVL), tail length (TaiL), crest head height (CHH), head length (HL), head width (HW), and jaw length (JL; Bickel and Losos 2002; Hopkins and Tolley 2011). Volunteers measured SVL but I made all head measurements of chameleons. I measured HW across the head at the lowest part of the head armour, CHH from the highest point of the crest to the lower jaw, JL from the front of the mouth back to the join of the mouth, and HL by drawing a perpendicular line from the front of the mouth to the back of the head, close to the jaw line (Fig. 3). I compared morphological and roosting data (height, substrate) among the three habitat types: primary (n = 25), secondary (n = 25), and degraded (n = 25).

I found that the variable Roosting Height did not meet the assumptions for parametric analysis despite log transforming. Therefore, I used Kruskal-Wallis to compare differences between roosting heights and habitats. If significant, I made pairwise comparisons with the Mann-Whitney U test for which I used the adjusted P values. The adjusted significance levels were given by multiplying the unadjusted significance values by the number of comparisons, setting the value to 1 if the product was greater than 1. I used Chi-square with the likelihood ratio to compare substrates (See McHugh 2013 on using the likelihood ratio).

When analyzing the morphology measurements, I first conducted a Pearson's Product Moment Correlation to determine if any of the variables were correlated. None of the variables were highly correlated ($r < 0.6$). When testing for parametric assumptions for the morphological variables, only SVL and CHH met parametric assumptions (Shapiro Wilks test > 0.10,
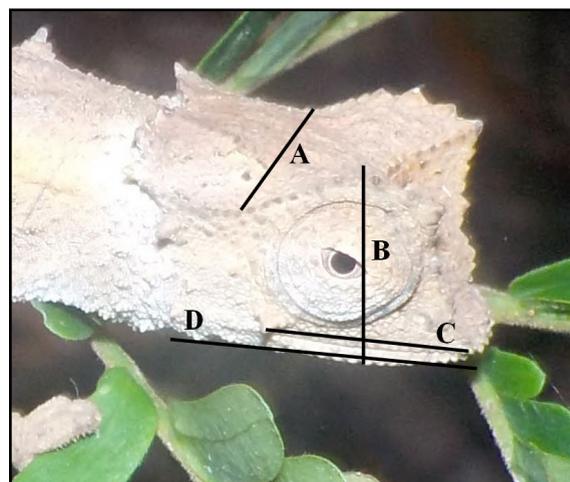

Figure 3. Head morphological measurements of Plated Leaf Chameleons (*Brookesia stumpffi*) on Nosy Be, Madagascar: Head Width (A), Crest Head Height (B), Jaw Length (C), and Head Length (D).
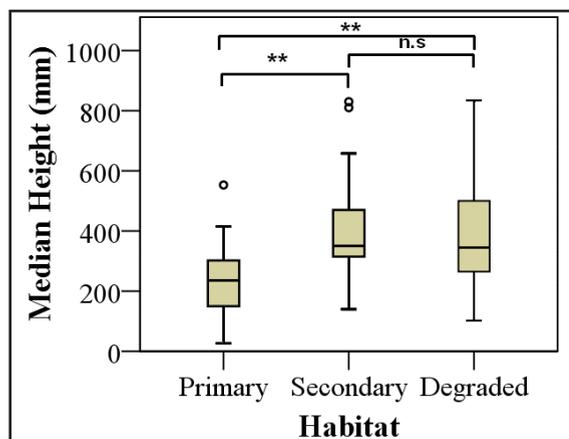
Figure 4. Median roosting heights (mm) of Plated Leaf Chameleons (*Brookesia stumpffi*) on Nosy Be, Madagascar, in primary, secondary, and degraded habitats. The open circles indicate probable outliers and the asterisks indicate the significant level between the habitat types (** = $P < 0.01$, n.s = no significant effect).

Levene's test > 0.08). I used ANOVA to compare these two variables to the different habitat types, using habitat as a fixed factor. I tested the other variables using Kruskal-Wallis. Again, I used Mann-Whitney U tests for the pairwise comparisons of significant results, and I used adjusted P values. For all tests, $\alpha = 0.05$.

RESULTS

Roosting selection.—I found *B. stumpffi* roosting as low as 2.67 cm and as high as 83.40 cm above the ground (Fig. 4). The median height of roosting was 34.50 cm in degraded habitat, 35 cm in secondary habitat, and 23.50 cm in primary habitat (Fig. 4). Roosting heights differed significantly among the three habitats ($H = 14.90$, df = 2, $P = 0.001$). Chameleons roosted at a significantly lower level in primary habitats compared to secondary ($U = -21.96$, $P = 0.001$) and degraded habitats ($U = -18.90$, $P = 0.006$). However, there were no significant differences between secondary and degraded habitats ($U = 3.060$, $P = 1.000$; Fig. 4). Of the four types of substrates on which *B. stumpffi* roosted, Saplings were the most used across the habitat types (Table 1). The use of roosting substrates by chameleons was not significantly different among the habitat types ($\chi^2 = 11.50$, df = 6, $P = 0.074$).

Table 1. The number of roosting substrates used by 75 Plated Leaf Chameleons (*Brookesia stumpffi*) along six transects in three habitat types on Nosy Be, Madagascar.

Substrate	Primary	Secondary	Degraded
Sapling	20	24	18
Shrub	3	1	6
Other	2	0	0
Leaf Litter	0	0	1

Table 2. Mean (± standard deviation) of morphological measurements (in mm) of Plated Leaf Chameleons (*Brookesia stumpffi*) in three habitat types on Nosy Be, Madagascar. Abbreviations are SVL = snout-vent length, CHH = creast head height, TaiL = tail length, HW = head width, HL = head length, JL = jaw length.

Measurement	Primary	Secondary	Degraded
SVL	40.17 ± 4.36	39.30 ± 5.09	37.75 ± 4.37
CHH	8.38 ± 0.75	8.04 ± 0.61	8.56 ± 0.96
TaiL	35.08 ± 3.85	33.47 ± 3.89	30.44 ± 5.72
HW	8.33 ± 0.63	7.92 ± 0.53	8.33 ± 1.05
HL	12.42 ± 0.97	11.67 ± 0.93	11.19 ± 1.26
JL	9.70 ± 0.77	9.60 ± 0.80	8.89 ± 1.09

Morphological measurements.—The mean SVL of *B. stumpffi* varied from 40.17 to 37.75 among habitats (Table 2) but differences were not significant ($F_{2,72} = 1.77$, $P = 0.177$). The mean morphological measurement CHH varied from 8.56 to 8.04 among habitats and also did not differ significantly ($F_{2,72} = 2.76$, $P = 0.070$). The other morphological measures did differ significantly among habitats (TaiL, $H = 8.45$, df = 2, $P = 0.015$; HW, $H = 6.15$, df = 2, $P = 0.046$; HL, $H = 14.67$, df = 2, $P = 0.001$; JL, $H = 8.89$, df = 2, $P = 0.012$). The measures TaiL, HL, and JL, were significantly smaller in degraded habitats compared to primary habitats (Table 3), and HL was also significantly smaller in degraded than in secondary habitats (Table 3).

DISCUSSION

Ecological differences in available habitats may have influenced the selective forces shaping *B. stumpffi* roosting behavior and morphology. Chameleons living in primary, secondary, and degraded habitats varied

Table 3. Results of Mann-Whitney U pairwise comparisons between the morphological measurements of Plated Leaf Chameleons (*Brookesia stumpffi*) and habitat types on Nosy Be, Madagascar, using adjusted P values. Abbreviations are TaiL = tail length, HW = head width, HL = head length, JL = jaw length. Significant values are $P < 0.05*$, $P < 0.01**$, $P < 0.001***$.

Morphology Measurements	Degraded-Secondary	Degraded- Primary	Secondary- Primary
TaiL	$U = 9.90$, $P = 0.325$	$U = 17.88$, $P = 0.011*$	$U = 7.98$, $P = 0.586$
HW	$U = -11.82$, $P = 0.165$	$U = 2.46$, $P = 1.000$	$U = 14.28$, $P = 0.061$
HL	$U = 6.12$, $P = .962$	$U = 22.80$, $P = 0.001**$	$U = 16.680$, $P = 0.020*$
JL	$U = 13.80$, $P = 0.075$	$U = 17.40$, $P = 0.014*$	$U = 3.60$, $P = 1.000$

in their roosting behavior. Individuals in degraded and secondary habitats roosted significantly higher compared to primary habitats. Due to less canopy cover in secondary and degraded habitats, it is likely that vegetation grows faster in these areas compared to primary habitats, reducing the number of smaller saplings. Additionally, the thermal environment would be different in degraded and secondary habitats compared to primary forest (Smith and Ballinger 2001; Reisinger et al. 2006), and this could create a divergence in roosting height, as well as more abundant nocturnal ground dwelling predators, such as certain species of snakes (Raxworthy 1991). Despite these findings, there were no significant differences between the habitat types and substrate *B. stumpffi* were roosting on, suggesting there is similar vegetation in each of the habitat types.

Brookesia stumpffi has not only diverged in roosting behaviors, but I also found morphological differences across the habitat types. In contrast to Measey et al (2009), but similar to Da Silva and Tolley (2013), the head length and jaw length of *B. stumpffi* were smaller in degraded habitats compared to primary habitats. Head shape is frequently influenced by diet (Hjelm et al. 2002; Aubret et al. 2004; Herrel et al. 2008), and lizards therefore may be responding to differences in prey size distributions between habitats. Smaller head length and jaw length measurements indicate a weak bite force (Huyghe et al. 2005; Measey et al. 2009; Measey et al. 2011; Da Silva et al. 2013), which can be due to smaller or softer prey items (Hofer et al. 2003; Aubret et al. 2004). This may be occurring on Nosy Be in degraded habitats where selection may favor smaller-headed *B. stumpffi*, which are exploiting a novel food source. Further research should be conducted to quantify the items *B. stumpffi* is eating in each habitat.

Tail length in *B. stumpffi* was longer in primary habitats. Tail length is often related to locomotion and performance in chameleons (Tsuji et al. 1989; Hopkins and Tolley 2011; Measey et al. 2009). Brickel and Losos (2002) found a difference in tail lengths depending on whether chameleons were terrestrial or arboreal. Although all *Brookesia* are terrestrial chameleons (Brickel and Losos 2002), this finding could still suggest that they have less use for their prehensile tail in degraded habitats.

In 2000 and 2010, laws were passed in Madagascar to stop logging of rosewood (*Dalbergia*) and ebony (*Diosryros*) trees; however, this activity is still ongoing (Innes 2010). My research could lead to future studies investigating if these chameleons are adapting to deforestation. If this species is adapting to deforestation, *B. stumpffi* may be of least concern for extinction rates because they can rapidly diverge more than other *Brookesia* species. However, these roosting and morphological differences could also be due to

fixed genetic differences or non-adaptive plasticity. My research demonstrates that *B. stumpffi* have diverged in roosting behaviors and morphology between primary, secondary, and degraded habitats and has led to intriguing patterns worthy of further study. A better understanding of why these chameleons are diverging may be a useful model of how ectotherms might fare in a rapidly changing world.

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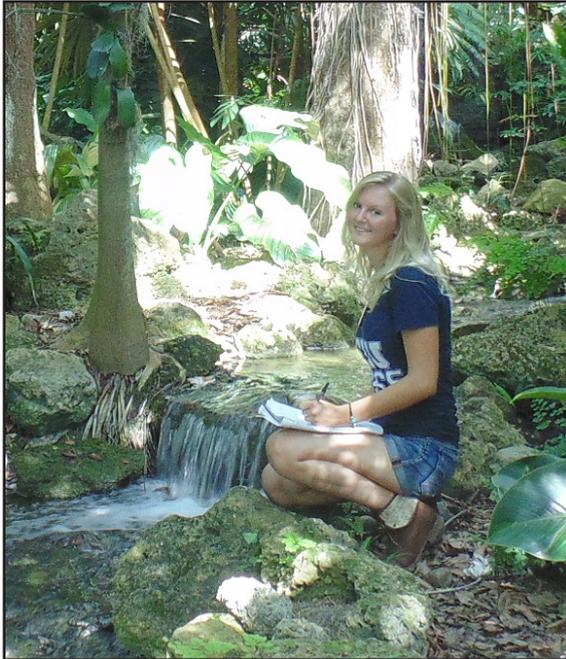
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