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# HABITAT SELECTION AND POPULATION DENSITY OF THE WORLD'S SMALLEST CHAMELEON, *BROOKESIA MICRA*, ON NOSY HARA, MADAGASCAR

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**Abstract.**—The recently described species *Brookesia micra* is endemic to the islet of Nosy Hara in northern Madagascar, and is the smallest chameleon species that has been described. Here, I present the first quantitative data on density, behavioral, habitat selection, and natural history on *B. micra*. I observed 117 *B. micra* from 10–23 April 2015. Estimated density was 3,100 individuals/ha (assuming 70% detection), and through satellite image analysis of Nosy Hara, I estimated that the population size was between 100,000–150,000 individuals. I found adult males to have a significantly larger snout-vent length (SVL) than adult females, and juvenile males to have significantly larger SVL than juvenile females. I also found no significant difference in roost height between males and females of all age classes, but I did find a positive correlation between SVL and roost height. I found individuals significantly closer to tsingy outcroppings than to trees during night and day, indicating that this is a tsingy-associated species. I support the International Union for the Conservation of Nature designation of near-threatened due to the high population density, but threats due to tourism and small range size could pose problems for the conservation of the species.

**Key Words.**—habitat; karst; microendemic; natural history; population; reptile; roost height

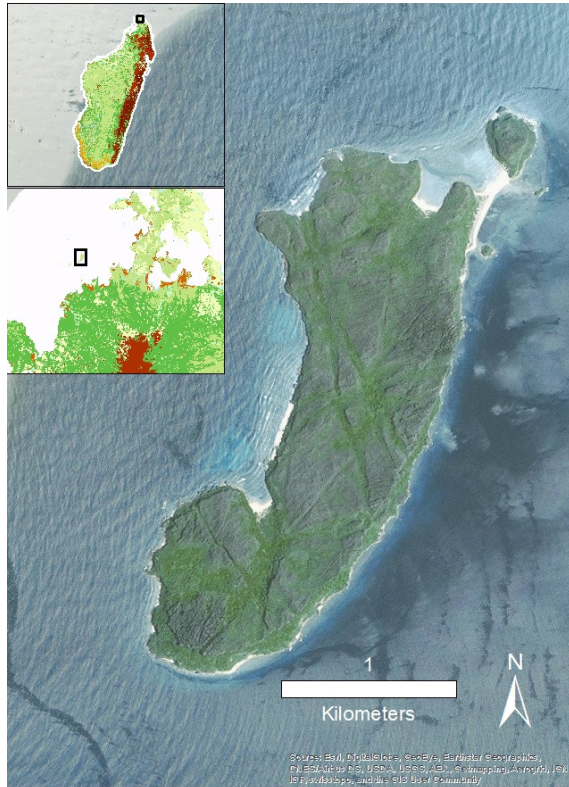
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## INTRODUCTION

Reptiles are one of the most diverse and endemic groups of fauna on Malagasy, and are at high risk due to habitat degradation and climactic shifts; up to 39% of species are at risk of extinction (Jenkins et al. 2014). In addition to lemurs and amphibians, many reptiles in Madagascar are miniaturized and microendemic (Wilmé et al. 2006; Townsend et al. 2009; Glaw et al. 2012). Some patterns of microendemism on Madagascar have been hypothesized to be the result of watershed retreat or mountain refuges (Wilmé et al. 2006), with subsequent effects of low vagility, genetic isolation, and low gene flow in small, isolated land area (Gaston 1996; Townsend et al. 2009; Glaw et al. 2012). The leaf chameleons (genus *Brookesia*) display extremes within the realm of microendemism and miniaturization, with around half of species known from single locality inventories only and exhibiting patterns of miniaturization in proportion with range (Townsend et al. 2009; Carpenter and Robson 2005; Glaw et al. 2012). As a result, many species of *Brookesia* are considered threatened or endangered under the International Union for Conservation of Nature (IUCN) Red List and the entire genus is listed under the Convention on International Trade in Endangered Species of Flora and Fauna (CITES) Appendix II due to small ranges, preference for undisturbed habitat, and specialized niche-filling (Carpenter and Robson

2005; Glaw et al. 2012). *Brookesia* miniaturization is a unique trait in Madagascar chameleons, mirrored by the dwarf African chameleon genera *Rhampholeon* and *Rieppeleon* (Glaw et al. 2012), and most likely developed to exploit specific niches in small, isolated habitat ranges (Gaston 1996).

The recently described species *Brookesia micra* (Glaw et al. 2012) is a charismatic and poorly known member of this chameleon group with a known range restricted to a single Malagasy islet Nosy Hara (Glaw et al. 2012). *Brookesia micra* belongs to the *B. minima* group, currently consisting of 11 small and cryptic species restricted to the northern half of Madagascar (Glaw et al. 2012). The genetic divergences between species in this group are quite deep, being of Eocene to Miocene origin, indicating long-term isolation of populations (Glaw et al. 2012). *Brookesia micra* are exclusively endemic to the small island of Nosy Hara made of limestone karst (locally called tsingy). As of yet, *B. micra* has not been found on the mainland or surrounding islets in the Nosy Hara archipelago. A previous herpetological survey carried out in 2000 (Metcalfe et al. 2007) within the archipelago and on Nosy Hara failed to detect *B. micra*, probably due to the extreme cryptic nature and small size of *B. micra* or because of the absence of trails on the interior of the island at the time. *Brookesia micra* was discovered in litter and tsingy mosaic forest only in the southern valley with a temporary stream on Nosy



**FIGURE 1.** Nosy Hara (main image) is an island off the coast of Madagascar (top insert image). The bottom inset image shows the relative location of Nosy Hara (square) to the main island of Madagascar. Red indicates humid forest, green indicates dry western forest. Satellite imagery of Nosy Hara is a base map from ArcMap v. 10.3, accessed 29 December 2015. Map of Madagascar courtesy of the CEPF Madagascar Vegetation Mapping Project, available from <http://www.vegmad.org/> [Accessed 2 March 2016]. (Map created by Andrew R. Villeneuve).

Hara, and was collected and observed either active in the litter or roosting in bushes (Glaw and Vences 2007; Glaw et al. 2012). I set out to document the habitat, spatial preferences, and behavior of *B. micra* on Nosy Hara. I also determined initial density and abundance estimates and evaluated the actual distributional range of the species on the island.

## MATERIALS AND METHODS

**Study location.**—Nosy Hara (study basecamp at 12°14.885'S 49°00.464'E; Fig. 1) is a limestone karstic island of about 270 ha lying 6 km offshore of the northwest coast of Madagascar in the Baie du Courier, Diana Province, Antsiranana Region. The island and surrounding archipelago lie completely within the Parc National Marin Nosy Hara. The island is dominated by xerophytic vegetation on the higher, more exposed limestone massifs and dry deciduous forest on valley floors. The deciduous valley forest was selectively

logged in the past before the creation of the park, and so while some large softwood trees (*Ficus* spp.) grow in the southern valley, the forest is in a late secondary growth phase. I collected data in the early dry season 10–23 April 2015.

There is no permanent fresh water on the island, but a dry stream bed that holds water during the rainy season exists in the south, where it drains the southern valley onto the southern beach. A trail constructed in 2007 runs the length of the streambed before climbing the eastern limestone massif. Two sets of concrete stairways (about 100 m and 50 m long) were laid down on sections of the trail that entered the dry stream bed. These stairways have destroyed a large portion of the stream bed. There are painted stone cairns every 50 m to mark the trail.

I used this trail as the central transect line for a majority of transects and quadrats in this project. In addition, there exists the Chauve-Souris trail, which climbs an isolated tsingy outcrop in the middle of the southern valley from where I undertook exploratory searches for *B. micra*. A third path covers the entire northern length of the island over tsingy massifs and into forested valleys, and I conducted a second exploratory search for *B. micra* in two of these valleys.

**Field methods.**—I took habitat use, behavior, and population data of *B. micra* on Nosy Hara using modified survey techniques after Jenkins et al. (1999, 2003), Razafimahatratra et al. (2008), and Lowin (2012). I used intensive transects and opportunistic searching in known *B. micra* range to quantify abundance, behavior, morphological characteristics, and microhabitat preferences, and I used quadrats in the same known range to understand habitat changes within the valley. I also used exploratory searches on other parts of the island to extend known *B. micra* range on the island.

Diurnal and nocturnal transects allowed me to gather density, morphological, sex, size class, microhabitat and spatial behavior data. I laid down fourteen 5 m transect lines, each 50 m along the trail, perpendicular to the trail at least 1 m into the forest to eliminate edge effects and ecotone changes (Lowin 2012; Jenkins et al. 1999). I took GPS coordinates and altitude at each transect using a eTrex Vista HCx (Garmin, Canton of Schaffhausen, Switzerland) and left for 24 h before I recorded data to ensure minimal disturbance to existing *B. micra* on transect (Lowin 2012). A single researcher carefully crawled the transects on hands and knees, searching 30 cm of either side of the line (60 cm total) as intensively as possible in the leaf litter during the day and low-lying twigs at night (Jenkins et al. 1999). This gave an area surveyed of 42 m<sup>2</sup>. During the day, I carefully turned over leaf litter abutting tsingy outcroppings and trees with a stick, and at night I used a headlamp to find *B. micra* roosting in low vegetation (Raxworthy 1988).

All night transects took place between 1700 and 2100. Crawl speed varied with vegetation density, and usually ranged from 0.20–0.25 m/min. I measured the snout-vent length (SVL) to the nearest 1 mm of every *B. micra* detected on the transect line using a Vernier caliper. I determined the sex of adults and juveniles by looking for the hemipenial bulge at the base of the tail of males. Juvenile males have a much less defined hemipenial bulge, requiring the use of a loupe. I frequently confirmed sexes of individuals with my chief guide, who had experience determining sex of other *Brookesia* species. I sorted individuals by size class, with adults  $\geq 13$  mm SVL and juveniles/sub-adults  $\leq 13$  mm SVL (Glaw et al. 2012). I recorded roost height by measuring the height of each roosting individual from the ground directly below with a metric ruler. I also collected microhabitat data for each *B. micra* by measuring the distance (to 1 cm) each chameleon was from the nearest tsingy outcropping (emergent from litter) and the nearest tree distance. I defined trees as the nearest shrub or tree with a woody stem or trunk; I did not consider dead twigs and herbaceous growth as trees.

While I was crawling transect lines, one to two trained guides searched for *B. micra* anywhere between the current 50 m mark and the next 50 m mark, never searching more than 10 m perpendicularly from the trail. Guides would then inform me of the location of each *B. micra* so that I could take measurements. I made all measurements to reduce recorder bias. Searches never lasted more than 40 min per each 50 m. Diurnal habitat quadrats gave a clearer picture of habitat shifts each 50 m along the trail. As opposed to transects, I selectively placed  $2 \times 2$  m ( $4 \text{ m}^2$ ) quadrats in locations I deemed most representative of the habitat between the meter marks, as transects sometimes failed to represent surrounding habitat. In each quadrat, I recorded percentage coverage of tsingy and litter.

**Analysis.**—I processed geographic information including GPS points of transects, total area of the island, and total area of potential *B. micra* habitat using Google Earth Pro v. 7.1.2.2041. I determined potential habitat using Google Earth satellite imagery, based on known habitat types surveyed. I completed statistical analysis using R (R Core Team 2016), and I used Graphpad Prism v. 7.01 (GraphPad 2016) to make graphs.

I designed the analysis comparing SVL means by sex over age class to use a one-way ANOVA. I characterized adult and juvenile classes by the SVL variable, thus necessitating the use of one-way ANOVA for each age class. I designed the analysis testing roost height against sex and SVL using a Generalized Linear Model (GLM), with sex as the discrete factor, SVL as the integer linear predictor, and roost height as the continuous response. To analyze for significant preference of *B. micra* to

proximity to either tree or tsingy features during the day and at night, I used a paired t-test. I then tested for significant differences in feature distance (Dtree – Dtsingy) between day and night by using a one-way ANOVA to retain the paired nature of the data. I set the level of statistical significance at  $\alpha = 0.05$ , and the confidence interval at 95%.

Residuals from the roost height GLM were not normally distributed (Shapiro-Wilk,  $P < 0.001$ ), so I transformed the roost height variable using natural logs and repeated the analysis (residuals Shapiro-Wilk,  $P = 0.513$ ). The difference in distance of *B. micra* from tree and tsingy (Dtree – Dtsingy) was normally distributed over both day (Shapiro-Wilk,  $P = 0.611$ ) and night (Shapiro-Wilk,  $P = 0.111$ ) time periods. I used a Welch's correction on the one-way ANOVA comparing SVL means by sex in each age class because of heteroskedastic SVL distribution (Bartlett's  $P = 0.019$ ).

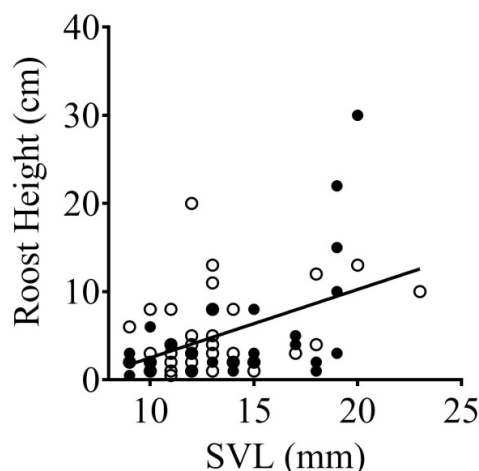
## RESULTS

**Density.**—I calculated density from both day and night transects. The density of *B. micra* on day transects gave a raw density of  $0.071 \text{ B. micra/m}^2$ , and the density on night transects gave a raw density of  $0.21 \text{ B. micra/m}^2$ . Because chameleons are more readily observed at night on their arboreal roosts, I used the nocturnal raw density for estimating the density of the population (Jenkins 1999), resulting in a density of  $2,100 \text{ B. micra/ha}$ . While I constructed transects to approach 100% detection probability of *B. micra*, I estimated a more accurate night detection rate of 70%, as detection probabilities in reptiles are almost always  $< 100\%$ , and have wide variance between species (Durso et al. 2011; McDiarmid et al. 2012). Therefore, the adjusted density gives  $3,100 \text{ B. micra/ha}$ . As of April 2015, 48.9 ha (roughly 20% of the area of the island) appears to be suitable habitat, and assuming equal *B. micra* densities throughout Nosy Hara, the total population could be between 100,000–150,000 individuals (range indicates raw and detection-rate adjusted densities).

**Sex and size classes.**—I recorded 117 *B. micra*, with 74 found at night and 43 during the day and a Catch Per Unit Effort (CPUE) of  $0.85 \text{ B. micra/h}$  along the transect path. Adult female *B. micra* tended to be larger than adult male individuals, and juvenile males tended to be larger than juvenile females (Table 1), and these differences were significant (Adults:  $F_{1,54.9} = 10.4$ ,  $P = 0.002$ ; Juveniles:  $F_{1,33.7} = 5.38$ ,  $P = 0.027$ ).

**Microhabitat and behavior.**—*Brookesia micra* use different habitat features (tsingy versus trees) differently depending on the time of day (day versus night). Variation of tree-tsingy distance was large





**FIGURE 2.** Nocturnal vertical roost heights versus body size of *Brookesia micra* from Nosy Hara, Madagascar. Open circles represent males, closed circles females. Line of best fit reflects a linear regression of all SVLs against all roost heights.

(Table 2). Chameleons were significantly more likely to be found in proximity to a tsingy outcropping during both the day ( $t = 2.79$ ,  $df = 26$ ,  $P = 0.010$ ) and at night ( $t = 8.73$ ,  $df = 73$ ,  $P < 0.001$ ). While *B. micra* were found to be significantly closer to tsingy over both time periods, there was a stronger preference for tsingy proximity at night; the tree-tsingy distance difference was significantly larger at night ( $F_{1,99} = 5.70$ ,  $P = 0.019$ ). Nocturnal transects revealed a significant positive relationship between SVL and roost height ( $F_{3,63} = 6.48$ ,  $P < 0.001$ ), but not with sex as a factor ( $F_{3,63} = 6.48$ ,  $P = 0.172$ ; Fig. 2). Mean roost height regardless of age class or sex was  $5.0 \pm (SD) 5.5$  cm.

*Brookesia micra* displayed varying defensive mechanisms, mostly in roosting individuals. Individuals found during the day tended to actively move in

**TABLE 1.** Range, mean, standard deviation (SD), and sample size (n) of snout-vent lengths (mm) of *Brookesia micra* by age class and sex on Nosy Hara, Madagascar.

Group	Range	Mean	SD	n
<b>Females</b>				
Adults	13–20	16.7	2.15	26
Juvenile	9–13	10.4	1.23	20
Total	—	13.9	3.65	46
<b>Males</b>				
Adults	13–23	14.8	2.58	30
Juvenile	9–13	11.1	.94	29
Total	—	13.0	2.68	59
<b>All</b>				
Adults	13–23	15.7	2.56	56
Juvenile	9–13	10.8	1.12	49
Total	—	13.4	3.16	105

response to litter disturbance. However, at night, I observed several defensive mechanisms, including perch release and Dead Leaf imitation behavior. Dead Leaf imitation behavior in *B. micra* constituted of rolling onto the ventral side and tucking of the limbs to imitate a small dead leaf. Three individuals, two adults and one juvenile, also displayed vibration defense, wherein I felt intercostal muscle vibration when an individual was gently held between thumb and forefinger. In addition, almost all roosting *B. micra* had the lighter gray coloration associated with roosting and sleeping and almost all displayed typical daytime brown coloration. When disturbed during the day or at night while already awake, all *B. micra* displayed typical stress coloration consisting of a darkening of the body and the presence of a light gray stripe running from the top of the head along the dorsal ridge (Fig. 3).

**Habitat classification and range.**—Including opportunistic surveys and transects, I observed 112 *B. micra* on the southern trail (Fig. 4), with a catch per unit effort of 0.85 *B. micra*/h. Most *B. micra* tended to be at marked trail length between 450 and 500 m, but other abundance peaks existed between 200 and 300 m and 600 and 650 m of the same trail. There was a noticeable decrease in abundance on the flatter sections of the trail (below 200 m; Fig. 5). The first 50 m of the trail had very little tsingy, leaf litter, and poor leaf litter quality. These two 50 m marks were on sandy soils bordering a small mangrove system and represented transition between dune and dry deciduous forest. The dry deciduous forest begins soon before the 200 m mark with an elevation increase and this marks the first peak in *B. micra* abundance. *Brookesia micra* abundance appeared to peak when percentage cover of tsingy and leaf litter were equal (about 50% each), at 200–250 m and more weakly around 450–550 m. Chameleons had a lower abundance when tsingy coverage was lower than coverage by litter. Overall, *B. micra* appeared to prefer areas with at least 20% tsingy coverage, and generally preferred rich leaf litter with dead leaves and moist hummus soil (Fig. 5), with the exception of around the 700 m mark, which was heavily dominated by tsingy with a few sticks. *Brookesia micra* found at this mark at night were actively crawling on the tsingy rock surface and in small litter pockets of tsingy.

Exploratory searches for *B. micra* revealed that they occurred at high elevation (41–43 m above sea level) on the Chauve-Souris trail. This trail climbed an isolated tsingy outcropping in the middle of the southern part of the island, and was quite far (at least 100 m horizontal and 20 m vertical) from the valley floor. I observed five *B. micra* along a dry drainage with tsingy outcroppings in a dry deciduous forest. Further explorations to the north of the island revealed no *B. micra* during quick searches, but the habitat appeared to be of good quality.



**FIGURE 3.** Representative *Brookesia micra* in nature. A. Juvenile displaying stress coloration. B. Adult female displaying daytime coloration. C. Juvenile male displaying roost coloration. (Photographed by Andrew R. Villeneuve).

### DISCUSSION

*Brookesia micra* is a unique chameleon species not only for its extreme size and small range, but also for inhabiting both leaf litter and canopy-covered tsingy outcroppings. Very little data on the habitat preference and range of *B. micra* has been recorded before this

**TABLE 2.** Paired mean distance (cm) of *Brookesia micra* from tsingy and trees during the day and at night on Nosy Hara, Madagascar.

Time of Day	Mean	SD	n
<b>Day</b>			
Tree	43.65	49.96	27
Tsingy	10.67	20.90	27
Total	27.16	41.42	27
Dtree - Dtsingy	32.98	29.06	27
<b>Night</b>			
Tree	78.03	61.32	74
Tsingy	9.74	16.96	74
Total	43.88	56.43	74
Dtree - Dtsingy	68.29	44.36	74
<b>All</b>			
Tree	68.84	60.23	101
Tsingy	9.99	17.99	101
Total	39.41	53.25	101
Dtree - Dtsingy	58.85	42.24	101

paper. Because *B. micra* were found to inhabit multiple habitat types, the range of the species could be in reality larger than described in this paper. Depending on whether *B. micra* evolved on Nosy Hara or on the mainland, the range could potentially extend beyond the island.

*Brookesia micra* had an almost exclusive preference of roost location on dead twigs, whereas past research mainly has observed *Brookesia* on live plants (Razafimahatratra et al. 2008). The preference for dead twigs despite availability of live plants in some areas could be an adaptation for a drier forest climate on Nosy Hara. The preference by these chameleons for low roost sites (< 10 cm) most likely results from the physical limitations of its extreme small size. Most twigs of an appropriately small diameter for roosting were located close to the ground and more often than not as a component of the leaf litter itself.

I estimated a preliminary density based on night transects in the southern valley. Night transects are much more reliable indicators of *Brookesia* density due to the greater ease of finding chameleons at night with a headlamp compared to sifting through leaf litter during the day. I calculated 3,100 *B. micra*/ha, which is a much higher density than previous studies of larger sized *Brookesia* species that found densities of 339.8 *B. stumpffi*/ha in Ankaz Forest, Montagne d’ Ambre (Lowin 2012), 37.8 *B. nasus*/ha in Ranomafana National Park (Jenkins et al. 1999), and 88.5 *B. thieli*/ha and 20.7 *B. minima*/ha in Andranomay Classified Forest (Jenkins et



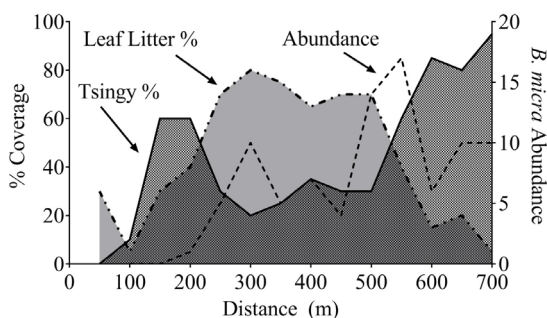
**FIGURE 4.** Locations of transects for *Brookesia micra* on the southern valley trail of Nosy Hara, Madagascar. Markers follow rough path outline. (Satellite image from Google Earth 2016).

al. 2003). Carpenter and Robson (2005) believe this to be because of census difficulties and overall low density of the *Brookesia* species. I show, however, that *B. micra* can be found in incredibly high densities. Most likely this is due to presence of good habitat all along the transect lines. Larger mainland African leaf chameleons of the genera *Rhampholeon* and *Trioceros* are less dense (densest species 0.071 *R. spinosa*/ha), probably due to larger range and body size (Shirk et al. 2014).

The extremely small size of *B. micra* could have arisen as a solution to microhabitat selection. *Brookesia micra* strongly favored proximity to tsingy, which could provide cover from predators (Malagasy Coucal, *Centropus toulou*; island guards, pers. comm.) or maintain moisture more than open areas or near tree

trunks. The rugosity of tsingy provides many holes and crevices that the *B. micra* could exploit during the heat of the day. The proximity of *B. micra* to trees during the day compared to night indicates that *B. micra* might engage in day movement to hunt for food, and that areas closer to trees could have a higher prey density than by tsingy. On days with bright sunlight, heat, or just after a rainstorm, *B. micra* were difficult to find. This tsingy also complicated obtaining density/abundance data, necessitating night transects to obtain these data from roosting chameleons.

*Brookesia micra* abundance peaks appear to be correlated with tsingy and rich leaf litter, with tsingy percentage cover being higher than litter. Abundance tended to drop with lower tsingy percentage and flatter ground. *Brookesia micra* abundance higher up on the trail (between 500–700 m) was correlated with habitats increasingly dominated by tsingy and rapidly decreasing cover of leaf litter. This was obvious at the 700 m mark, which was dominated by tsingy boulders on a steep flank with almost no litter except for on the surface of tsingy in pockets. Leaf litter cover appears not to have as much of an effect on *B. micra* abundance, despite offering moisture and other types of protection. Tsingy could offer better protection from predators, produce a moist microclimate in the dry forest, or just be the dominant habitat feature on Nosy Hara to which *B. micra* has adapted. Slope allows for water shedding, increased tsingy emergence from leaf litter, and is a more common habitat element on Nosy Hara compared to a flat valley floor. It appears, therefore,



**FIGURE 5.** Leaf litter and tsingy substrate composition and *Brookesia micra* abundance over length of trail transect on Nosy Hara, Madagascar. Abundance measurements took into account diurnal and nocturnal surveys, as well as opportunistic searching.



that *B. micra* is highly associated with tsingy presence on sloped valley sides. Exploitation by this species of this microhabitat is unique among *Brookesia* in that it does not appear to exclusively associate with leaf litter or live plants like other *Brookesia* members from tsingy forests (*B. perarmata*, *B. exarmata*, *B. brygooi*, *B. confidens*, and *B. bonisi*; Randrianantoandro et al. 2008a,b). I conclude that *B. micra* can inhabit multiple types of habitat between dense, dry, deciduous forest to extremely rugose, dry tsingy rubble falls with canopy cover and no litter. This flexibility in habitat preference could allow *B. micra* some resilience in a changing landscape, allowing it to inhabit varied forest refugia (Wilmé et al. 2006; Townsend et al. 2009).

Phylogenetic niche conservatism predicts that sister taxa of *B. micra* share similar niches (Wiens et al. 2010). *Brookesia confidens* and *B. tristis* are from dry deciduous forest habitats in Ankarana and Montagne des Français, respectively, two tsingy-dominated habitats (Glaw et al. 2012). Given the initial habitat and microhabitat descriptions presented in Glaw et al. (2012), it is difficult to determine whether the more tsingy-associated *B. micra* shares niches with these sister taxa. This question requires further study. *Brookesia exarmata* (Tsingy de Bemaraha) appears to be an example of parallel evolution with *B. minima* group A clade (dry deciduous species) in that it too has colonized dry, deciduous, tsingy habitat, but further phylogenetic and habitat studies must be undertaken to confirm this (Randrianantoandro et al. 2008a).

My study on *B. micra* has confirmed many behavioral traits unique to *Brookesia* and has established a unique habitat type for this genus. Future studies should look for this species in the north valleys of the island, other islands in the archipelago, and the adjacent mainland using more refined density methodology following Shirk et al. (2014), although accessibility could be an issue. Due to the low patchiness, high density, flexible habitat preferences, and a high estimated abundance (100,000–150,000 individuals), I agree with the IUCN rating of Near Threatened for *B. micra* (Glaw and Jenkins 2014). Future research should examine sister taxon niche preferences and evolution coupled with geological history of the Nosy Hara archipelago in the hope of better understanding the dispersal and microendemism of this genus.

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