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Sex-specific Habitat Use and Responses to Fragmentation in an Endemic Chameleon Fauna

Philip Shirk
Virginia Commonwealth University

The College of Humanities & Sciences
Virginia Commonwealth University

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James Vonesh, Ph. D., Professor, Department of Biology, College of Humanities and Sciences

Leslie Bulluck, Ph. D., Assistant Professor, Department of Biology, College of Humanities and Sciences

David Patrick, Ph. D., Assistant Professor, Division of Forestry, Natural Resources, and Recreation, Paul Smith's College, Paul Smiths, NY

Bryan Watts, Ph. D., Research Professor, Department of Biology, The College of William & Mary, Williamsburg, VA

Donald R. Young, Ph. D., Chair of the Department of Biology, College of Humanities and Sciences

Jim Coleman, Ph. D., Dean of the College of Humanities and Sciences

F. Douglas Boudinot, Ph. D., Dean of the Graduate School

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SEX-SPECIFIC HABITAT USE AND RESPONSES TO FRAGMENTATION IN AN ENDEMIC CHAMELEON FAUNA

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science at Virginia Commonwealth University.

by

PHILIP L SHIRK
Bachelor of Arts
B.A., Eastern Mennonite University, 2007

Major Professor:
JAMES VONESH, PH.D.
Professor, Department of Biology

Virginia Commonwealth University
Richmond, Virginia
July, 2012

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Abstract

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By Philip Shirk, B.A.

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science in Biology at Virginia Commonwealth University.

Virginia Commonwealth University, 2010

Director: James Vonesh, Ph.D., Professor, Department of Biology

Chameleons are an understudied taxon facing many threats, including collection for the international pet trade and habitat loss and fragmentation. A recent field study reports a highly female-biased sex ratio in the Eastern Arc Endemic Usambara three horned chameleon, *Trioceros deremensis*, a large, sexually dimorphic species. This species is collected for the pet trade, and local collectors report males bring a higher price because only this sex has horns. Thus, sex ratios may vary due to differential rates of survival or harvesting. Alternatively, they may simply appear to be skewed if differences in habitat use biases detection of the sexes. Another threat facing chameleons is that of habitat loss and fragmentation. Despite enormous amounts of research, the factors of fragmentation that different species respond to is still under debate. Understanding these responses is important for current mitigation efforts as well as predicting how species will respond to future habitat alteration and climate change. My study suggests that differences in survival and detection may explain much of the observed seasonal sex skew in adult *T. deremensis*. Within fragmented habitat chameleons consistently responded more to edge effects and vegetative characteristics associated with fragmentation than to area or isolation effects. This may bode poorly for chameleon populations in the coming decades as climate change further alters vegetative communities and exacerbates edge effects.

Chapter 1:

Female-biased sex ratios in the Usambara three-horned chameleon, real or apparent?

PHILIP L. SHIRK[1,*], DAVID A. PATRICK[2], KIM M. HOWELL[3], ELIZABETH A. HARPER[2], JAMES R. VONESH[1]

[1] Department of Biology, Virginia Commonwealth University, Richmond, Va

[2] Division of Forestry, Natural Resources, and Recreation, Paul Smith's College, Paul Smith's, Ny

[3] Department of Zoology and Wildlife Conservation, University of Dar es Salaam, Dar es Salaam, Tanzania

* Corresponding author at: Department of Biology, Virginia Commonwealth University, 1000 W. Cary St., Rm 126, Richmond, Va 23284, USA. Tel.: (804) 482-1804. E-mail address: philip.shirk@gmail.com

ABSTRACT

Differential harvesting of sexes can accelerate population declines by reducing both numbers as well as the ability of the population to rebound through new recruitment. A recent field study reports a highly female-biased sex ratio in the Eastern-Arc Endemic Usambara three horned chameleon, *Trioceros deremensis*, a large, sexually dimorphic species. This species is collected for the pet trade, and local collectors report males bring a higher price because only this sex has horns. Thus, sex ratios may vary due to differential rates of survival and harvesting. Alternatively, they may simply appear to be skewed if differences in habitat use biases detection of the sexes. For example, if females prefer edge habitat, where the previous survey was conducted, or if males spend more time high in the forest canopy, an apparent sex skew could result. We examine a variety of factors that may have contributed to the apparent skew in adult sex ratio. Consistent with earlier studies, we find that the bias in sex ratio is strongest from Aug. through Oct. along forest trails. However, sex ratios did not differ from the null expectation of a 1:1 ratio in other seasons. Differences in both detectability and survival may contribute to this observation. Females are seasonally more abundant along trails, and males may seasonally spend more time in the canopy than females, making them more difficult to observe close to the time of year when sex skew has been observed. Estimated mean annual survival of males is 15% lower than females, although confidence intervals on survival estimates for the sexes overlap considerably. We used population projection models to estimate the contribution of differential survival to observed sex ratios and

compare this to the effect of detection bias on observed sex ratios. This analysis suggests that differences in survival and detection may explain much of the observed seasonal sex skew.

INTRODUCTION

Skewed sex ratios may result from a variety of causes, including natural (Hamilton, 1967; Schoener and Amy Shoener, 1980) and anthropogenic reasons (Ginsberg and Milner-Gulland, 1994; Milner-Gulland et al., 2003). Skewed sex ratios may result naturally from differential survival rates , which can vary for many reasons; including lethal male-male combat (Wakano, 2005), differential movement rates (Costantini et al., 2007; Kwiatkowski et al., 2008), differences in reproductive burden (Laurie and Brown, 1990), differences in home range size / access to resources (Civantos, 2000), or differential habitat use (Schoener and Schoener, 1982; Pulliam and Danielson, 1991; Knapp et al., 2010).   Anthropogenic causes include selective harvesting (Ginsberg and Milner-Gulland, 1994; Milner et al., 2007), habitat alterations that affect sexes differently (Aresco, 2005; Grüebler et al., 2008), and potentially climate change (Hawkes et al., 2007). Sex-biased over-exploitation of wild populations can even cause population collapse (Milner et al., 2007). Alternatively, apparent skews in sex ratio may be an artifact of survey methodology. If sexes prefer different habitats, have different spatial or temporal movement patterns, or vary in visibility (body size, color, auditory cues), a search is likely to yield more of one sex than the other, which distorts estimates of natural populations (Phillips 1995).

The Usambara three-horned chameleon, *Trioceros deremensis,* is a large, sexually dimorphic lizard endemic to the montane forests of the Eastern Arc Mountains of Tanzania. The species has been historically collected for the pet trade, and local collectors report having been paid 25% more for males, which have three large horns, than for hornless females (P. Shirk, anecdotal information). Recent surveys along forest trails and roads in and around the Amani Nature Reserve (ANR) in the East Usambaras revealed an extremely female-biased sex ratio (Patrick et al., 2011). This does not appear to be the case historically, as Barbour and Loveridge (1928) found males, including a very large individual, during limited sampling in 1926. This evidence points to the possibility that sex-biased harvesting may underlie the observed skew, with potentially important implications for conservation and management of this CITES Appendix II species. However, there may be other explanations. Sex ratios may be skewed by differential survival of the sexes that is unrelated to collecting, or the sex skew may result from differences in detectability. For example, if differences in habitat use between the sexes results in higher detectability for one sex than the other, the apparent skew in sex ratio may be misleading. With surveys limited to a single habitat type in a small geographical area over a short period of time, earlier surveys were largely unable to address differences in detectability of the sexes. In particular, earlier surveys were conducted only along forest trails and roads bordering forest; if males avoid these edge habitats, surveys may record a female bias even if sex ratios are even. Furthermore, differences in horizontal or vertical movement patterns could make males more difficult to observe. The objective of this study is to revisit the ANR and conduct a more thorough study of *T. deremensis* population biology and movement ecology to see if we continue to see a female bias in sex ratios and to provide insight into whether this sex ratio is real or apparent.

Patrick et al. (2011) observed a 1:11 male:female adult sex ratio during their August 2009 surveys and questioned whether this bias might be driven in part by heavier harvesting of males. However, these surveys were conducted in a single season, only along trails and forest roads, and had limited ability to address differential habitat use between the sexes that might lead to differential observation of males and females. Here we sought to answer the three questions. First, is skewed adult sex ratio wide-spread geographically and temporally? To answer this we used a combination of surveys across habitats and seasons and radio-tracking to investigate the skewed sex ratio. We calculate sex ratios along trails and in the forest interior from the surveys. Second, do differences in detectability between the sexes contribute to any observed skewed sex ratio? Detectability has several components: we use program Distance 6.0 (Thomas et al., 2009) (survey data) to estimate the horizontal detectability and comparisons of roost height (survey and radio-tracking data) and the proportion of time spent above 7 m (radio-tracking data) to address vertical detectability. Third, do differences in survival contribute to any observed skewed sex ratio? We compare survival using life tables (survey data) and known-fate survival models (radio-tracking data). We also compare home range sizes and movement, which may cause a disparity in survival via differential access to resources or exposure to predators.

METHODS

Study site. The East Usambara Mountains are part of the Eastern Arc Mountain biodiversity hotspot (Myers et al., 2000). Within the Eastern Arc Mountain range, the East Usambara, Uluguru, Mkungwe, Nguru, Udzungwa, and possibly West Usambara mountains (if present, very rare) comprise the entire range of *T. deremensis*, the Usambara three-horned chameleon. Collectively, these mountain blocks contain approximately 2500 km^2 of forest (Hall et al., 2009). Research was conducted in and around the ANR, at the southern end of the East Usambara Mountains. Although this forest is now protected, much of it was logged in the past, and is therefore best categorized as mature second growth forest (Hamilton and Bensted-Smith, 1989). There are four distinct seasons in this area, the cool dry season (Austral winder from June – November), the mini-rainy season (a few weeks in late November or early December), the warm dry season (Austral summer from December – March) and the rainy season (mid-March - May).

Distance-based density surveys. Surveys in ANR were conducted in Sept.-Oct., 2010 and again in March-April, 2011 along a combination of randomly-placed, 200m-long transects (n = 27 in dry season, n= 31 in rainy season) and transects along random, 200 m-long segments of forest trails (n=16 in both seasons, with 5 of the 16 repeated in each season). An additional 117 randomly-placed, 100 m-long transects in forest fragments near the nature reserve were surveyed either in Feb.-Mar., 2011 or May, 2011. All transects were placed using Hawth's Tools 3.1 (Beyer, 2004) in ArcGIS 9.3 (ESRI, 2011). Sightings above 7 m in height were excluded from density estimates to ensure the assumption of perfect detection on the transect line, but were included in estimates of sex ratio and roost height where sex and height could be positively determined. Densities and horizontal detection probabilities were estimated using the program Distance. For all density estimates, we first ran the default model (Half-Normal + Cosine expansion) in program distance, truncated the data to include only sightings with at least a 15% probability of detection (Buckland et al. 2001), and then ran four candidate models (Half Normal + Cosine, Half Normal + Hermite polynomial, Uniform + Cosine, Hazard-Rate + Simple Polynomial) and used AIC to select the best model. Densities of both sexes were increased by a factor of 1.35 to account for the average proportion of time chameleons spend above 7 m, as estimated from the radio-tracked individuals. Detectability has several components; the program Distance estimates the horizontal detectability, but fails to address vertical detectability. Therefore, we address horizontal and vertical detectability separately. Roost heights were compared using one-tailed t-tests (because we suspected that males were higher) in R 2.15.0 (R Development Core Team, 2012).

Radio-tracking. Chameleons for radio-tracking were located haphazardly near trails surrounding the ANR headquarters beginning on 9 Oct. 2010. Radio-transmitters were a combination of ATS R1680 (3.6g), Holohil BD-2 (0.9g), and Holohil BD-2N (0.51g), all of which were V-shaped, allowing them to be placed over the dorsal ridge of the chameleon and super-glued in place (Figure 1.1). To allow for variation in chameleon size, the transmitters' V-shape was wider than any chameleons' dorsal ridge. The extra space was filled with a small piece of sponge, which hardened and provided contoured support as the super glue dried. All radio-transmitters were <10% of chameleon body weight, which in a slow-moving, non-volant species is unlikely to cause harm (Napp and Abarca, 2009). Chameleons that shed their skin and lost their transmitters were replaced with new chameleons, leading to different chameleons being tracked over different time periods. At any given point in time, between 3 and 14 chameleons were being tracked. Radio-tracking continued through 1 July, 2011. In total 29 individual chameleons were radio-tagged.

To ensure the independence of consecutive relocations, we used an autocorrelation analysis (Schoener, 1981) of three individuals and determined that chameleons should be relocated no more than once per day. Whenever a chameleon was located, we recorded the horizontal distance and direction moved from the last location point, the perch (daytime) or roost (night) height, vegetation characteristics in a 1 m2 area under the chameleon as well as a randomly located 1 m^2 area within 5 m of the chameleon, and took a GPS (Garmin GPSMAP 76CSx) point of the chameleon's location. All heights and distances were measured with tape measures. Vegetation characteristics included ground-level (0 to 0.5 m), low (0.5 m to 2 m), and medium (2 m to 5 m) vegetation cover; four measurements of leaf litter depth; four measurements of canopy cover using a spherical densiometer; the number of trees in the plot; the proportional coverage of ferns, vines, and two particular plant species – *Dracaena spp.* and *Maesopsis eminii* – intended to represent various unmeasured micro-climactic variables.

Due to limited GPS accuracy relative to chameleon movement distances, we used the initial GPS location and calculated each new location based off of the measurements of distance and direction moved. Of 1238 total relocations, 1133 (91.5%) included visual sightings. Points without visuals were only excluded if the chameleon was not subsequently observed alive. For each chameleon, auxiliary data (e.g. habitat characteristics, movement distance, roost height) were averaged across all relocations so that each data point for subsequent analyses corresponded to an individual chameleon rather than a relocation event. Chameleons with fewer than 10 relocations for any particular analysis were excluded from analyses. We used t-tests in R 2.15.0 (R Development Core Team, 2012) for all 2-way comparisons between sexes, seasons, and age classes and ANOVA for 3-way comparisons. When comparing habits of the same individual (e.g. perch vs. roost height), we used paired t-tests and included individuals with fewer than 10 relocations.

Home range. While some meta-analysis authors support the use of minimum convex polygon (MCP) (e.g. Perry & Garland, 2002), others point out its many limitations (Laver and Kelly, 2008). In the absence of known home ranges, it may be impossible to know which estimation technique is best (Perry and Garland, 2002); currently it appears as though the best methods may vary from case to case (Robertson et al., 1998). We chose two commonly-used techniques, the MCP and 95% isopleths of kernel density estimates (KDE) (estimated using the PLUGIN bandwidth estimator (Jones et al., 1996), cell size of 1 m, and a Gaussian kernel). MCP's and isopleths of KDE's were calculated using Geospatial Modeling Environment (Beyer, 2012).

Although the area of MCP's often increases continually with an increasing number of relocations (Gautestad and Mysterud, 1995), the home range area will often begin to asymptote, suggesting that the sample size is adequate (Laver and Kelly, 2008). Using an area-observation plot of MCP home range areas, we determined that many individuals' home range areas begin to asymptote fairly quickly; therefore home ranges will be calculated for all individuals with at least 10 relocations. For seasonal home ranges, home range was calculated for all individuals with at least 10 relocations in a given season. The dates of specific seasons were determined using actual rainfall data for the months in question, and included the small rainy season (10 Oct – 22 Nov), the Austral summer (23 Nov. – 12 Mar), and the rainy season (13 Mar – 1 Jul).

Survival. Survival was estimated using two independent methods. First, we employed a life table approach using survey data on the seasonal abundance of difference sizes classes over a 6 month period. Individuals were assigned to cohorts according to natural breaks in a histogram of chameleon sizes (Figure 1.2), and survival was calculated between the survey in ANR in Oct. and the survey of the same area in April We also estimated survival using radio-tracked individuals and the known-fate nest survival model in program MARK (White and Burnham, 1999). For known-fate models, all individuals must be assigned a fate. Chameleons that lost their transmitters (n=6) when they shed were assumed to be alive, as were chameleons that disappeared after the transmitter had noticeable battery weakening (n=5). Chameleons that are strongly suspected to have been eaten (n=2) or collected by humans (n=3) were assumed to have died. Chameleons that disappeared unexpectedly (without any hint of battery problems or where they went) (n=5) were assumed to be alive. This may still overestimate survival. Additionally, 2 chameleons were observed dead, and 5 chameleons lived to the end of the study.

Comparing the relative contributions of survival and detectability to sex ratio skew. The influences of survival and detectability on adult sex ratios are not readily comparable because they they are in different units.   In order to determine the extent to which differential survival alone would alter the stable adult sex ratio, we constructed a deterministic population projection matrix using fecundity values from Spawls et al. (2002), hatchling and juvenile survival estimates from our life table, and sex-specific estimates of adult survival rates from our known-fate models of radio-tracked individuals. Because reproduction is believed to occur once annually, all survival estimates were extrapolated over the course of a full year. Extrapolating the population projection matrix over many generations/years shows the stable adult sex ratio that will result from differences in survival. Horizontal and vertical detection probabilities can be easily combined using multiplication. Furthermore, they can be combined with the effects of differential survival by multiplying them by the projected population structure. The resulting sex ratio is what one would expect to observe given our estimates of survival and detectability. If this sex ratio is similar to our observed sex ratio, then survival and detectability may be sufficient to explain our observed sex ratio. If the ratios are different, then other factors are likely contributing to the sex ratio skew.

RESULTS

Sex ratios. Consistent with Patrick et al. (2011), we observed that adult sex ratios were strongly female-biased during the Austral spring along forest trails (male:female – Patrick et al. (2011) 1:11; this study 2:12 (Table 1.1)). However, this sex skew was habitat- and season- dependent. Pooling across all habitats and seasons, the sex ratio of adult *T. deremensis* was not statistically different from the null expectation of 0.50 (Table 1.1). The sex ratio also varied by body size, with the female bias becoming stronger as animals became larger (Figure 1.3).

Detectability - Horizontal detectability. If males are more cryptic – either because they are smaller or have different behaviors – an apparent female sex bias could arise due to differences in observer detection of the sexes, even if the sex ratio is even or male biased. Despite considerable overlap in 95% confidence intervals, the estimated horizontal detection probability for adult males (0.560, 95% CI = 0.45 to 0.70) may be slightly lower than that for adult females (0.655, 95% CI = 0.54 to 0.80). An indicator of horizontal detectability is the average distance from the transect that each sex was observed, but there is no effect of sex (t = -0.11, df = 42.7, p = 0.456) on this distance.

Detectability - Vertical habitat use. Adult males roost 1.20 m higher, on average, than adult females (3.46 m vs. 2.26 m, respectively; t = -1.97, df = 38.4, p = 0.028), and all chameleons roost higher in April than in October (3.68 m vs. 1.79 m, respectively; t = -2.83, df = 207.0, p = 0.005). The difference in roost heights between the sexes is not significant if considering only the Oct. surveys or only the April surveys, although both surveys show a trend of males roosting higher (Figure 1.4). The difference in roost heights between the sexes is not present in juveniles (t = -0.58, df = 89.3, p = 0.280), although juveniles and hatchlings each roost 1.55 m higher than adults (4.31 m, 4.31 m, and 2.76 m, respectively; F = 9.035, df = 2, p < 0.001). While not statistically significant, radio-tracked individuals tended to show a similar trend to roost heights from the survey data; for both roost height and the proportion of time spent over 7 m, adult males were slightly higher than adult females, with a larger difference between males and female before the onset of the rainy season in March (Figure 1.4). Overall, adult males spend 31.0% of their time above 7 m, while adult females spend 22.8% of their time above 7 m. Although perch height (daytime) is less directly related to observers' ability to detect animals during nighttime surveys, it can provide further evidence in differences in vertical habitat use between the sexes. Patterns observed are consistent with trends in roosting: adult males perch 1.6 m higher than females (males = 4.86 m, females = 3.24 m; t = -2.24, df = 8.5, p = 0.027). Interestingly, females may roost lower than they perch (3.23 m vs. 4.34 m, respectively; t = 1.946, df = 11, p = 0.078), suggesting diel vertical migration in the canopy.

Detectability - Vegetation preferences. Radio-tracked adult males and adult females lived in very similar micro-habitats; the only measured difference was that males lived in areas with 6% more *Dracaena spp.* cover (t = -2.63, df = 6.08, p = 0.039), a difference that was most prevalent during the rainy season. All radio-tracked chameleons were in areas with more cover than random locations, averaging 6% more low-level (0.5 m – 2 m) cover, 7% more medium-level (2 m – 5 m) cover, and 4% more vine cover (all p-values < 0.007). They also roosted in areas with 2% more canopy cover than where they perched during the day (t = 2.30, df = 16, p = 0.035).

Densities. Estimated total population densities were very similar between survey types (along trails or randomly placed) but not between survey times (Table 1.2). One reason for the difference in densities is seasonal reproduction, which results in an influx of hatchlings during the Austral spring (Sept - Nov). Sample sizes of adults prohibited estimating the density of each sex in each of the four time/habitat combinations. Rather, we estimated detection functions for adult males and adult females using all surveys combined, which assumes that detection probabilities vary only by sex, not by habitat type or season. When accounting for differences in horizontal detection probabilities by sex, adult females are ~4.0 times as dense as adult males along forest trails in the ANR, but only 0.9 times as dense as adult males in the forest interior (Table 1.2). Over all surveys, the density of females is ~1.7 times that of males.

Survival. According to basic life-table estimates, approximately 21% of adult females survived the 6 months from the first survey to the second. Estimates of adult male survival were not possible because the few adult males that were seen in Oct. were of an intermediate size between two cohorts and could not be reliably assigned to a cohort (all between 100 and 110 SVL, see Figure 1.2 for population size distribution and cohort classes). If these were large 1-year-olds (typically 60 to 100 mm), then we observed no adult males of at least two years of age in the Oct surveys and cannot estimate survival. If they were small 2-year-olds (typically 115 to 135 mm), then the life-table estimate of adult male survival would be ~33%. Unexpectedly, hatchling survival was higher than juvenile survival (Table 1.3). Survival estimates of radio-tracked adults were considerably higher than estimates from life tables; when daily survival rates were extrapolated over an equivalent six-month time period, adult females had an estimated survival of 56.2% and adult males had an estimated survival of 52.9% (Table 1.3). Although a comparison between the sexes in adult survival was not possible for life table estimates, radio-tracked females may have slightly higher survival than adult males.

Survival - Movement rates and home ranges. Overall, adults' home range areas averaged 0.32 ha for MCP and 0.44 ha for the 95% isopleths of the KDE. Although home range areas of both the MCP and 95% isopleths of the KDE were at least 2.5 times larger for adult males than adult females, these differences were marginally significant (MCP: $t = -1.23$, $df = 8.9$, $p = 0.125$; KDE: $t = -1.61$, $df = 7.8$, p-value = 0.073). Differences in mean home range area were largest during the Austral summer (MCP: 0.5 ha male vs. 0.2 ha female, $t = -1.25$, $df = 5.8$, p-value = 0.130; KDE: 1.2 ha male vs. 0.4 ha female, $t = -1.98$, $df = 3.7$, p-value = 0.062). By the rainy season, point estimates of home range area for both adult sexes varied by only 3% (MCP) and 10% (KDE) (all p-values $\gg 0.05$). During the rainy season (the only time when both adults and juveniles were tracked concurrently), adults had home ranges approximately 7 times larger than juveniles (MCP: 0.12 ha vs. 0.02 ha, $t = 4.55$, $df = 9.4$, $p = 0.001$; KDE: 0.08 ha vs. 0.01 ha, $t = 4.74$, $df = 10.0$, $p < 0.001$).

Comparisons of mean distances moved between relocations are nearly identical to home range comparisons: estimates for adult males are larger, especially during the Austral summer, but none of the differences are significant (all p-values > 0.18). When comparing median distance moved rather than mean distance moved, males and females are extremely similar in all seasons (all p-values $\gg 0.05$). For both mean and median distance moved, adults move further than juveniles (mean: $t = 5.46$, $df = 13.6$, $p < 0.001$; median: $t = 3.87$, $df = 12.4$, $p = 0.002$).

Comparing the relative contributions of survival and detectability to sex ratio skew. Extrapolating a population projection matrix (Table 1.4) with differing adult survival rates reveals a stable population structure with 1.29 adult females per adult male. This is very similar to the apparent sex skew that would result only from differences in detectability. Using our estimates of the proportion of time that males (31.0%) and females (22.8%) spend in the canopy (above 7 m), a population with an even adult sex ratio would appear to have 1.12 adult females per adult male. In the Austral summer, when there was a larger difference in the proportion of time that males and females spent above 7 m, surveys would reveal 1.19 adult females per adult male. Similarly, a failure to account for horizontal detectability would mean that there would appear to be 1.17 adult females per adult male. Combining the effects of horizontal and vertical detectability, a population with an even adult sex ratio would appear to have 1.31 adult females per adult male – a very similar effect to differences in adult survival. Finally, if the differences in detectability are combined with the difference in adult survival rates, a population that actually has 1.29 adult females per adult male would appear to have 1.68 adult females per adult male. Using the estimates of vertical detectability from the Austral summer, the time period closest to the extreme sex ratios, there would appear to be 1.79 adult females per adult male.

DISCUSSION

One year after Patrick et al. (2011) observed a highly skewed adult sex ratio along rain forest trails, we observed a similarly skewed adult sex ratio during the same season and along trails in the same area as Patrick et al.'s surveys. Also similar to Patrick et al. (2011), the sex skew was only observed in adults, not in juveniles (Table 1.1). However, the skewed sex ratios did not extend to the randomly-placed transects or to the rainy season in April. Male chameleons were not radio-tracked until late November, a month after the skewed sex ratio was observed. They were also located near the trails where the skewed sex ratios were initially observed. Between late October and mid-March (the Austral summer), there was a trend for adult males to be higher than adult females. The three comparisons of height use (roost heights from the surveys, roost heights from the radio-tracked individuals, and the proportion of time that chameleons spent above 7 m in height) collectively suggest that males seasonally are higher in the canopy (Figure 1.4). Similarly, our estimate of adult survival was slightly lower for adult males than for adult females. The combination of differences in survival and detectability suggest that one would expect to see 1.7 times as many females as males, which is precisely what we observed in ANR (Table 1.1: 26 females / 15 males = 1.7 females per male). A more extreme sex ratio was observed (4 females per male along trails in August through October), but radio-tracking did not cover this time period, so we would not expect the estimates of survival or vertical detectability to fully account for this skewed sex ratio. Although collection of this species for the international pet trade does occur, and was observed in the protected ANR, the apparent seasonal skew in adult sex ratio initially reported by Patrick et al. (2011) is likely more a result of differential habitat use than strongly sex-biased collection.

Sex-based differences in habitat use may be wide-spread among chameleons, as surveys have often turn up skewed sex ratios in chameleons, especially in the Malagasy genus *Calumma* (Jenkins et al., 1999; Rakotondravony, 2004; Lutzman, 2006; Rabearivony et al., 2007), and pygmy chameleons (Hall, 1970; Lutzman, 2006). However, the skewed sex ratios do not appear to be constant over time (Hall, 1970;

Lutzman, 2006), and may result from a combination of differential habitat use, small sample sizes, or sampling methodology. Habitat partitioning may help to alleviate competition between the sexes. In an arid portion of Kenya, *Chamaeleo dilepis* partition available habitat among the sexes in the dry season when resources are scarce (Hebrard & Madsen 1984). The Austral summer of 2010-2011 was unusually dry in the Amani area, with a drought that locals reported to be the worst in at least 10 years. However, with limited overlap in home range, vertical partitioning of habitat makes little sense.

Natural history of *T. deremensis*. A likely reason for the similarity in movement rates during the summer months is that mating occurs in early summer following the mini-rainy season. While mating, males appear to mate guard females, a behavior which has been previously reported in the common chameleon (Cuadrado, 2001). Mate guarding entails closely following a female for several days, followed by fast, relatively long-distance movements to find another female. These long-distance movements by males often crossed large forest trails (old logging roads), which many chameleons showed great reluctance to cross. The result is that male movement is similar to females', but with a slightly higher average. Few other studies have reported movement rates for both sexes of chameleons, but Butler (2005) reports that *Bradypodion pumilum* males also tend to be slightly more active than females. In terms of net daily movement, *T. deremensis*' rate of 3.7 m/day is similar to the Malagasy chameleons *Calumma nasutum* (~2 m/day) and *Furcifer pardalis* (from 1-20 m/day), although sample sizes for these chameleons were very small (Lutzman, 2006).

It is worth noting that many reptiles have environmental sex determination or are parthenogenic – both of which can cause drastic sex skews. We did not consider these potential causes because only anecdotal accounts of temperature-dependent sex determination exist for chameleons, and these are likely incorrect (Andrews, 2005). Similarly, parthenogenesis has been suggested in chameleons on the basis of a heavily female-biased sex ratio (Hall, 1970), but no account of parthenogenesis in chameleons is known, despite thousands being kept as solitary pets, so parthenogenesis is considered highly unlikely (Necas, 2004). Finally, a nearly even juvenile sex ratio, as was observed in both Patrick et al.'s surveys and in this study, is inconsistent with either of these phenomena.

The life-cycle of *T. deremensis* appears to be closely tied to the rainy season. Mating activities begin during or immediately after the short rainy season in late Nov. or early Dec. Egg development occurs over the warmest time of the year, when chameleons are the most active. During the main rainy season from mid-March through April, females lay their eggs. One radio-tracked female traveled ~ 100 m (a considerable distance for a chameleon) over a ridge to lay her eggs. It was the only time in the 7 months she was tracked that she ventured over the ridge. Young hatch around Sept. as the Southern hemisphere begins to warm and reach maturity in just over a year. Survival seems to vary considerably with age/body size, and much less so between the sexes. This is similar to survival estimates for *Bradypodion pumilum* (Tolley et al., 2010), which vary with body size but not sex, despite sex-dependent movement rates.

Conclusion. Upon close examination, the observed skew in adult sex ratio can be accounted for by seasonal fluctuations in habitat use among the sexes. Given the possibility of seasonal differences in detection probabilities among the adult sexes and oscillations in overall population density, proper accounting for seasonal fluctuations will be important for future studies. While strongly sex-biased harvesting for the pet trade is unlikely to have caused the observed skew in adult sex ratio, collection of *T. deremensis* and *Rieppeleon brevicaudatus* was observed within the protected Amani Nature Reserve over the course of the study. Collection from protected areas, combined with high mortality rates of captive individuals (which results in more individuals being collected than are exported), makes collection for the international pet trade an ongoing concern.

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Table 1.1. Observed adult and juvenile *T. deremensis* sex ratios of surveys. ‘Survey’ refers to the time of year in which the survey was conducted. ‘Area’ refers to the area where the survey was conducted: either in forest fragments, randomly placed transects in the Amani Nature Reserve, or along trails in the Amani Nature Reserve. ‘Ratio’ is the number of females per males. ‘Chi^2’ values are from chi-squared tests of observed sex ratios with the null expectation of a 1:1 sex ratio. Significant p-values ($p < alpha = 0.05$) are in bold.

Survey	Area	Age	# female	# male	Ratio	Chi^2	P-value
All	All	Adult	62	57	1.1	1.72	0.189
All	All	Juvenile	47	52	0.9	0.25	0.615
All	Fragments	Adult	8	9	0.9	0.06	0.808
All	Fragments	Juvenile	9	7	1.3	0.25	0.617
All	Random	Adult	13	10	1.3	0.39	0.532
All	Random	Juvenile	19	26	0.7	1.09	0.297
All	Trail	Adult	13	5	2.6	3.55	0.059
All	Trail	Juvenile	19	19	1.0	0.00	1.000
Oct	Random	Adult	3	4	0.8	0.14	0.706
Oct	Random	Juvenile	9	13	0.7	0.73	0.390
Oct	Trail	Adult	12	2	6.0	7.14	**0.008**
Oct	Trail	Juvenile	12	7	1.7	1.32	0.251
Rainy	Random	Adult	10	6	1.7	1.00	0.317
Rainy	Random	Juvenile	10	13	0.8	0.39	0.532
Rainy	Trail	Adult	1	3	0.3	1.00	0.317
Rainy	Trail	Juvenile	7	12	0.6	1.32	0.251
Patrick et al. (2011)	Trail	Adult	11	1	11.0	8.23	**0.004**
Patrick et al. (2011)	Trail	Juvenile	4	6	0.7	0.40	0.527

Table 1.2. Density estimates for *T. deremensis*. “Trans” = total number of transects sampled. “Effort” = total distance (m) of transects sampled. “N” = total number of *T. deremensis* included in the analysis. “P” = detection probability. “P LCL” and “P UCL” = 95% confidence interval on detection probability estimate. “D” = density. “D CV” = Coefficient of variation on the density estimate. “D LCL” and “D UCL” = 95% confidence limit on density estimate. Ratio is the number of females per male.

	Time	Type	Trans	Effort	N	P	P LCL	P UCL	D	D CV	D LCL	D UCL
All chameleons	Oct	Rdm	27	5400	86	0.612	0.505	0.741	17.33	0.33	9.07	33.12
	Oct	Trail	16	4200	63	0.586	0.477	0.720	17.3	0.25	10.41	28.76
	Apr	Rdm	31	6105	41	0.514	0.449	0.589	6.19	0.32	3.29	11.64
	Apr	Trail	16	4200	24	0.632	0.428	0.931	6.48	0.39	2.98	14.08

	Sex	Type	Trans	Effort	N	P	P LCL	P UCL	D	D CV	D LCL	D UCL	Ratio
Adults Only	Male	Rdm	58	19435	9	0.560	0.446	0.703	0.40	0.42	0.18	0.91	0.89
	Female	Rdm	58	19435	8	0.655	0.539	0.795	0.36	0.49	0.14	0.91	
	Male	Trail	32	16800	3	0.560	0.446	0.703	0.16	0.59	0.05	0.47	4.02
	Female	Trail	32	16800	12	0.655	0.539	0.795	0.62	0.43	0.27	1.43	
	Male	Total	223	50889	19	0.56	0.446	0.703	0.288	0.36	0.14	0.58	1.67
	Female	Total	223	50889	27	0.655	0.539	0.795	0.483	0.33	0.25	0.92	

Table 1.3. Six-month survival estimates for different size/age classes of *T. deremensis* calculated from life tables (surveys) and from known-fate mark-release-recapture models (radio-tracked individuals). Life-table survival rates were calculated by assigning individuals from two sets of surveys – the initial set in October and the second set in April – to cohorts. After accounting for differences in distances surveyed and detectability between the surveys, the number observed in the second set of surveys divided by the number observed in the first set of surveys represents the rate of survival over the 6-month time period. In order to estimate hatchling to juvenile survival for each sex, hatchlings are assumed to have a 1:1 sex ratio, as they could not be sexed by external features. Survival of adult males could not be estimated from life tables because insufficient adult males were observed in the initial survey, and those that were observed were of intermediate size between cohorts and could not be accurately assigned to a cohort.

	Hatchling to juvenile	Juvenile to adult	Small adult	Large adult	Adults - Life Table	Adults - Known-fate model
Overall	33.3%	15.0%	52.1%	0.0%	34.7%	55.6%
Female	27.0%	20.8%	31.3%	0.0%	20.8%	56.2%
Male	39.7%	8.3%	-	-	-	52.9%

Table 1.4. Matrix for population projection model. Sources for fecundity and survival estimates include: [a] (Spawls et al., 2002), [b] life tables (Table 1.3) estimates extrapolated to a full year, [c] known-fate survival model, extrapolated to a full year.

	Hatchling - Male	Hatchling - Female	Juvenile - Male	Juvenile - Female	Adult - Male	Adult - Female
Hatchling - Male	0	0	0	0	0	10[a]
Hatchling - Female	0	0	0	0	0	10[a]
Juvenile - Male	0.1089[b]	0	0	0	0	0
Juvenile - Female	0	0.1089[b]	0	0	0	0
Adult - Male	0	0	0.0225[b]	0	0.279841[c]	0
Adult - Female	0	0	0	0.0225[b]	0	0.315844[c]

Figure Captions:

Figure 1.1. A radio-transmitter attached to an adult female *T. deremensis*. Radio-transmitters were attached using super-glue and a small piece of sponge to fill the gap between the V-shaped transmitter and the chameleon's body. Transmitters fell off when chameleons shed their skin.

Figure 1.2. Histograms of the size distribution of a *T. deremensis* population at different times of year. Life table age classes for the October surveys were defined as: Year 0 ≤ 50 mm; Year 1 = 65 to 100 mm; Year 2 = 115 to 135 mm; Year 3 = 140+ mm. Age classes for the April surveys were defined as: Year 0.5 = 60 to 100 mm; Year 1.5 = 110 to 125 mm; Year 2.5 = 130 to 150 mm. Cohorts are color-coded.

Figure 1.3. Histogram of size-dependent sex ratios *T. deremensis*. Data are from the combination of both October and April surveys where sex could be determined (n = 146). Numbers in base of bars represent sample sizes of females and males, respectively and p-values of chi-squared tests vs. the null distribution of 1:1 sex ratio. Proportion varied by size class (chi-squared = 11.01, df = 4, p = 0.027).

Figure 1.4. Comparison of vertical height use of adult *T. deremensis*. Measures of vertical height use include nighttime roost heights from surveys (both October and April/Rainy season surveys), nighttime roost heights from radio-tracked

individuals (both Austral summer and rainy season), and the proportion of time individuals spent above 7 m (both Austral summer and rainy season. Above 7m chameleons became very difficult to spot and were assumed to be unavailable in the forest canopy.). Numbers at bottom of bars are sample sizes. P-values are from a one-tailed t-test. Error bars represent 95% confidence intervals (+/- 1.96 SE) of the mean.

Figure 1.1.

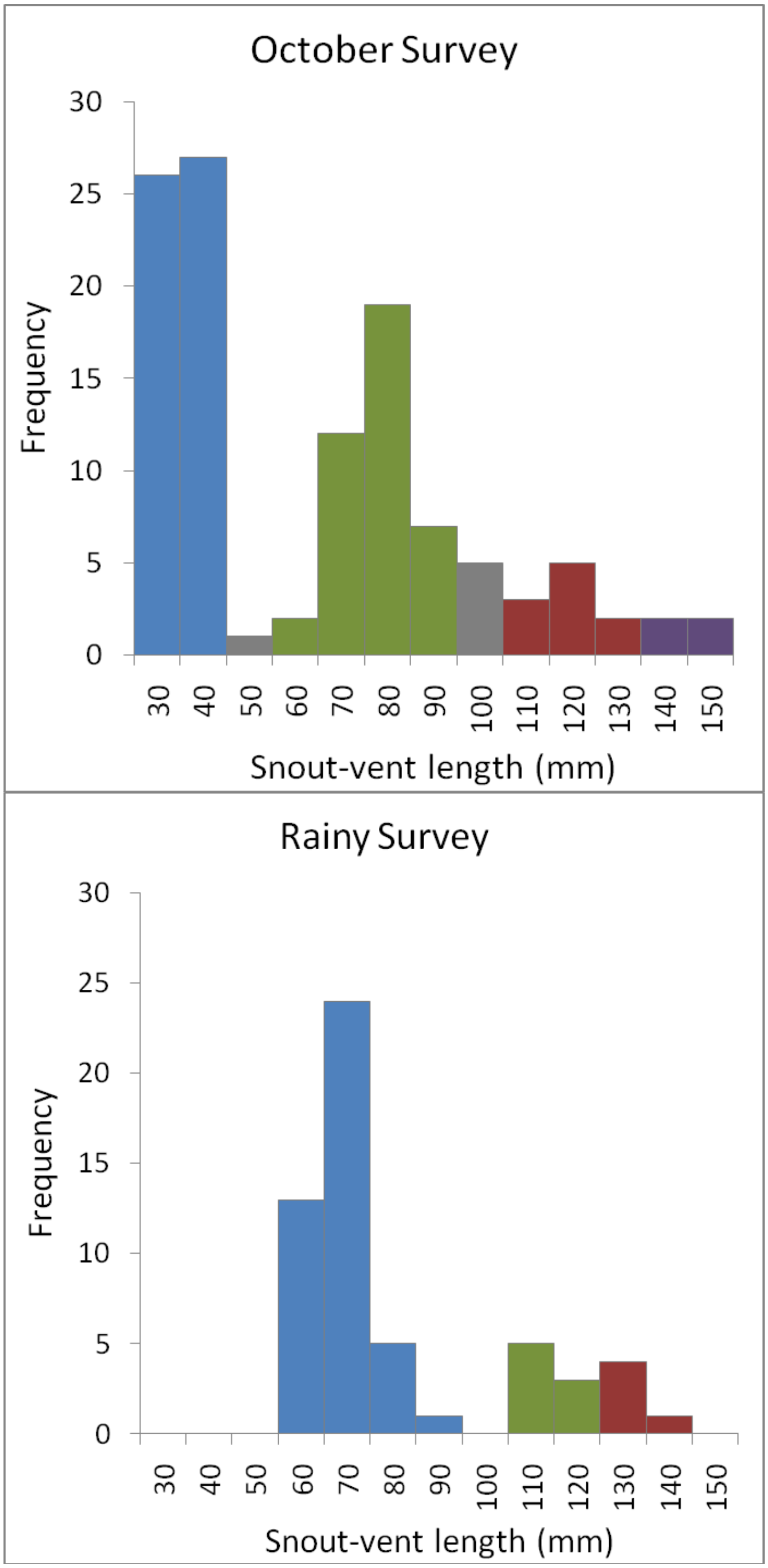
October Survey
Frequency
0
5
10
15
20
25
30
30
40
50
60
70
80
90
100
110
120
130
140
150
Snout-vent length (mm)
Rainy Survey
Frequency
0
5
10
15
20
25
30
30
40
50
60
70
80
90
100
110
120
130
140
150
Snout-vent length (mm)

Figure 1.2.

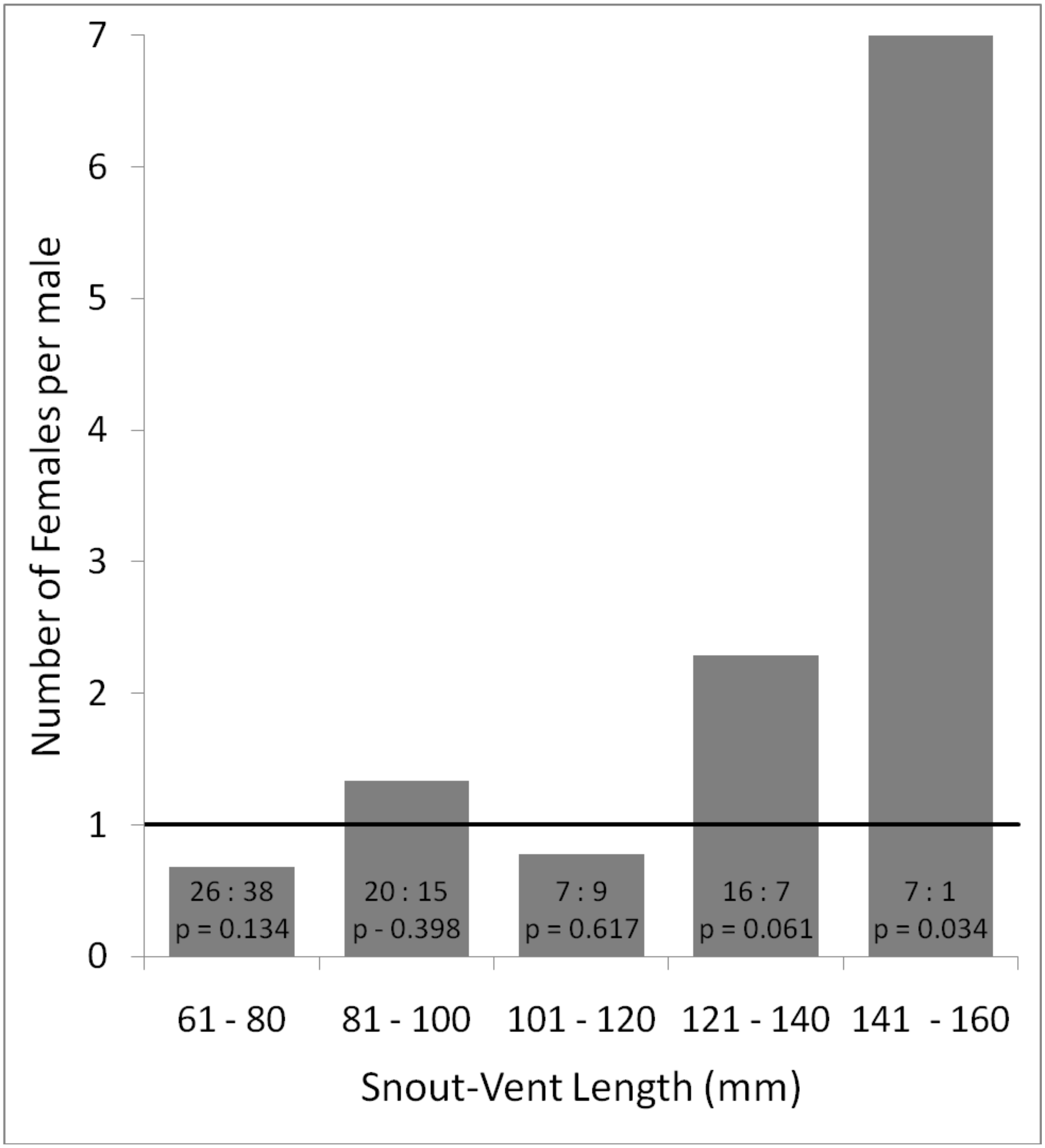
Number of Females per male
7
6
5
4
3
2
1
0
26 : 38
p = 0.134
20 : 15
p - 0.398
7 : 9
p = 0.617
16 : 7
p = 0.061
7 : 1
p = 0.034
61 - 80
81 - 100
101 - 120
121 - 140
141 - 160
Snout-Vent Length (mm)

Figure 1.3.

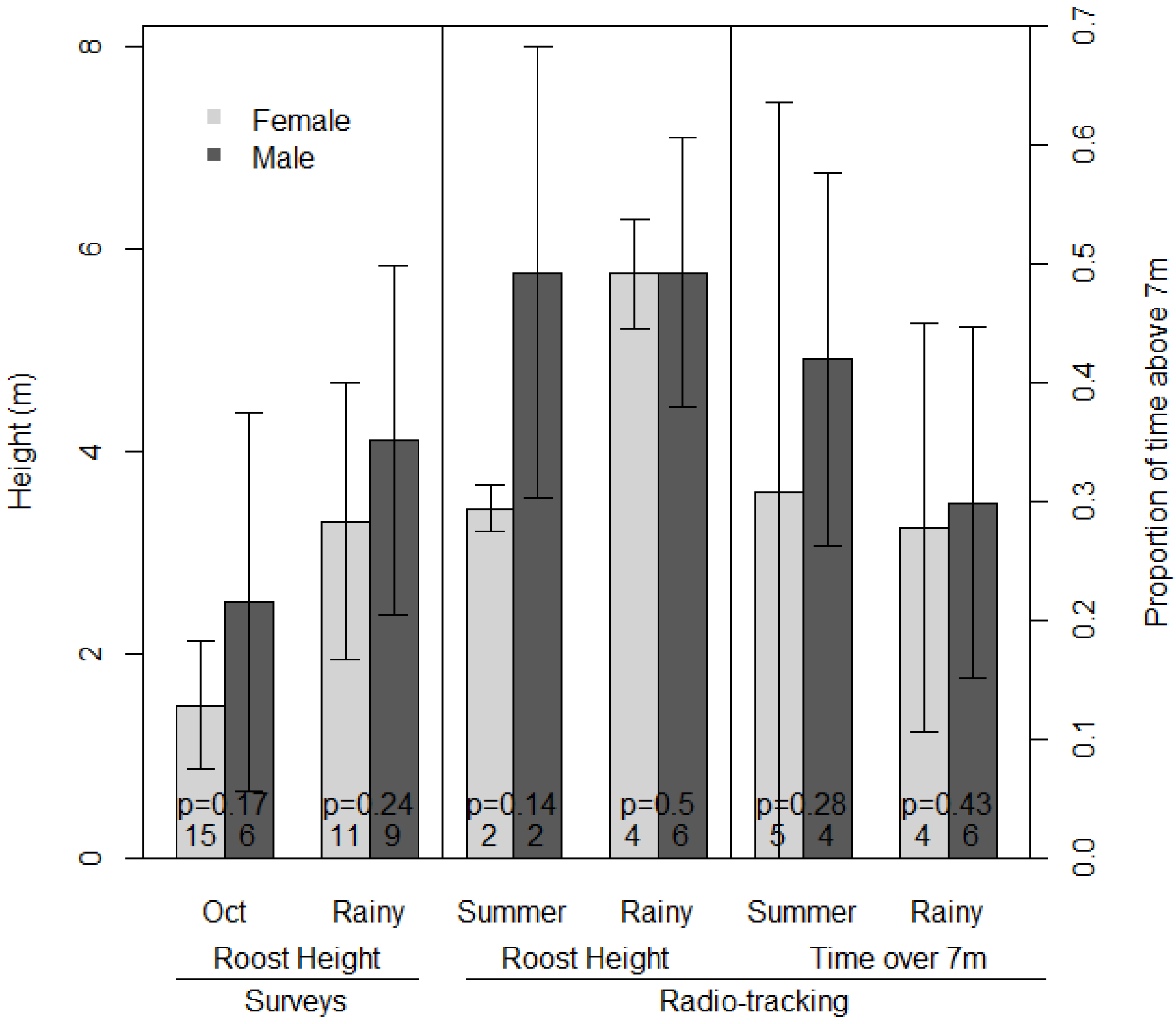
Female
Male
Height (m)
0
2
4
6
8
Proportion of time above 7m
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
p=0.17
15
6
p=0.24
11
9
p=0.14
2
2
p=0.5
4
6
p=0.28
5
4
p=0.43
4
6
Oct
Rainy
Summer
Rainy
Summer
Rainy
Roost Height
Roost Height
Time over 7m
Surveys
Radio-tracking

Figure 1.4.

Chapter 2

Chameleon community and population responses to habitat fragmentation in a tropical biodiversity hotspot

PHILIP L. SHIRK[1,]*, DAVID A. PATRICK[2], KIM M. HOWELL[3], ELIZABETH A. HARPER[2], JAMES R. VONESH[1]

[1] Department of Biology, Virginia Commonwealth University, Richmond, Va

[2] Division of Forestry, Natural Resources, and Recreation, Paul Smith's College, Paul Smith's, Ny

[3] Department of Zoology and Wildlife Conservation, University of Dar es Salaam, Dar es Salaam, Tanzania

* Corresponding author at: Department of Biology, Virginia Commonwealth University, 1000 W. Cary St., Rm 126, Richmond, Va 23284, USA. Tel.: (804) 482-1804. E-mail address: philip.shirk@gmail.com

ABSTRACT

Despite enormous amounts of research, the factors of fragmentation that different species respond to is still under debate. Understanding these responses is important for current mitigation efforts as well as predicting how species will respond to future habitat alteration and climate change. Several issues with current studies limit their predictive power, including a failure to account for detectability and narrow geographic and taxonomic focus. We used methods that account for detectability to estimate the effects of habitat fragmentation and loss on chameleon populations, richness, and composition in fragmented African rain forest. The traditional fragmentation predictors – fragment area and isolation – were poor predictors of chameleon populations and communities. No measure of chameleon populations or community responded to fragment isolation, and only one species group responded to patch area. Rather, chameleons consistently responded to edge effects and vegetative characteristics associated with fragmentation. Two species groups, overall richness, and community composition all responded to edge effects, while all population and community measures responded to vegetative characteristics associated with fragmentation. This may bode poorly for chameleon populations in the coming decades as climate change further alters vegetative communities and exacerbates edge effects.

Keywords: fragmentation; edge effects; SAR; DAR; Chamaeleonidae; reptile

INTRODUCTION

Anthropogenic habitat alteration, including habitat loss and fragmentation, is the greatest threat facing natural ecosystems (Vitousek, 1997). As a result, it has been the focus of considerable research (Fahrig, 1996, 2003; Fazey et al., 2005), and forty-five years after its introduction, fragmentation research continues to grow (e.g. Ewers et al. 2011). However, despite its ubiquity, fragmentation research has suffered from taxonomic and geographic concentration. Studies have overwhelmingly focused on a few taxa, especially birds, mammals, and insects (Mcgarigal and Cushman, 2002; Henle et al., 2004; Ewers and Didham, 2006). Data are particularly lacking for reptiles (Gardner et al., 2007), although they serve important ecological roles (Pough et al., 2004) and even alter bird populations (Weatherhead and Blouin-Demers, 2004). One recent review of 552 species' responses to fragmentation included 65% birds and only 1% reptiles (Vetter et al., 2011). Furthermore, studies of reptiles tend to be focus on terrestrial species, rather than arboreal species (Kays and Allison, 2001). Of the 21 studies of reptile responses to fragmentation that we reviewed (see literature cited for a complete list), 10 of them considered only leaf litter fauna. The current geographical concentration of studies is problematic because fragmentation is a landscape-level response and is occurring worldwide; the landscape context (matrix type/quality, size & position of fragments, etc) is important to fragmentation responses (Donovan et al., 1997; Ewers and Didham, 2006; Watling and Donnelly, 2007; Vetter et al., 2011), yet many studies are done on the same landscapes in the new world (e.g. Laurance et al. 2002). Meta-analyses would benefit from including a wider variety of landscapes, particularly in understudied portions of the world. For example, little research has focused on tropical African forests, despite their extraordinary biodiversity and the apparent trend that species in dense tropical forest are more sensitive to habitat alteration than those in other habitats (Anjos et al., 2011).

Many studies of animal responses to fragmentation assume that detection rates are similar across all areas sampled. This assumption may be especially problematic for visual encounter surveys of cryptic species, where surveyors can vary in their ability to spot the animal of interest, but is also unlikely to hold for sampling methods that do not include variation in human skill, such as pit fall traps (Mazerolle et al., 2007). Sampling and analysis methods that account for detectability are readily available whether one is estimating occupancy (Bailey et al., 2007), richness (Dorazio et al., 2011), or density (Thomas et al., 2010). Failure to account for detectability is widespread in herpetological studies (Mazerolle et al., 2007), and fragmentation studies are no exception. Of the 21 studies of reptile responses to fragmentation that we reviewed, two studies (Sarre, 1998; Hokit and Branch, 2003) of single lizard species explicitly accounted for detectability in density/abundance estimates. Other studies (Bell and Donnelly, 2006; Watling and Donnelly, 2007, 2008; Watling et al., 2009) account for detectability in species richness estimates by using species richness estimators (see Watling and Donnelly, 2008 for details), but ignored detectability in estimates of density/abundance. The only other study to mention detectability (Driscoll, 2004) cites a former study (Schlesinger, 1999) on similar species that shows that varying vegetation densities do not impact capture rates. The other 67% of studies make no mention of detectability. Since the actual number of animals in an area is a function of both their abundance and their detectability, the conclusions of studies that ignore detectability are cast in doubt. An alternative that cannot be rejected is that fragmentation affected only detection probability, not abundance (Mazerolle et al., 2007; Vonesh et al., 2009).

The effects of habitat loss and fragmentation include altering species richness and abundances (Laurance et al., 2002), decreasing genetic diversity (Delaney et al., 2010), altering or severing mutualistic interactions (Cordeiro and Howe, 2001) and predator/prey relationships (Terborgh et al., 2001), and even altering basic nutrient cycles and hydrology (Laurance et al., 2011). Historically, fragmentation research has focused on fragment area and isolation (MacArthur and Wilson, 1967), with mixed results for explaining lizard populations. In response to an increase in fragment area, various lizard species' densities have been reported to respond negatively (Schoener, 1968; Wright, 1979, 1981), neutrally (Sarre, 1998; Cosson et al., 1999; Jellinek et al., 2004; Dixo and Metzger, 2009), positively (Cosson et al., 1999; Jellinek et al., 2004), and even hump-shaped (Buckley and Roughgarden, 2006). Consistent with this variety of responses, a meta-analysis (Prugh et al., 2008) suggests that patch area has less predictive power for reptiles than for other animal taxa, perhaps because reptiles' low metabolic rates and relatively small body size enable large populations of reptiles to persist in relatively small areas. Similar to fragment area, the importance of isolation for reptiles has mixed support, with some studies suggesting that isolation has a negative influence (Smith et al., 1996; Watling and Donnelly, 2008), as the theory of island biogeography would predict (MacArthur and Wilson, 1967), but many other studies show no effect of isolation on reptiles (Jellinek et al., 2004; Schutz and Driscoll, 2008; Dixo and Metzger, 2009;

Watling et al., 2009). Meta-analyses suggest that the effects of fragment isolation are relatively less important than the effects of fragment area (Watling and Donnelly, 2006; Prugh et al., 2008), which may be due in part to the importance of matrix composition (Watling et al., 2011).

The poor predictive power of fragment area and isolation for explaining reptiles' responses to fragmentation demonstrates the importance of considering other factors of fragmentation. In particular, edge effects (Schlaepfer and Gavin, 2001; Lehtinen et al., 2003; Driscoll, 2004; Dixo and Martins, 2008; Pardini et al., 2009), matrix effects (Driscoll, 2004; Pardini et al., 2009; Watling et al., 2011), and vegetation characteristics (Kitchener et al., 1980; Jellinek et al., 2004; Brown et al., 2011) may be important for reptiles. Edge effects include warmer temperatures and lower humidity, which may benefit reptiles because they require external sources of heat and can tolerate low water availability. In particular, generalist species may benefit the most from edge effects (Pardini et al., 2009), although the importance of edge effects can vary by season (Schlaepfer and Gavin, 2001; Lehtinen et al., 2003). The permeability of matrix habitat also influences species' responses to fragmentation (Watling et al., 2011). While some reptiles, particularly generalist species (Driscoll, 2004), can tolerate the conditions in the matrix, reptiles may be particularly susceptible to matrix effects because of their poor dispersal ability. Vegetation is an important characteristic of any habitat, and is a strong predictor of reptile occurrence (Brown et al., 2011). This is especially true for arboreal species, which live on the vegetation.

Because many species respond idiosyncratically to habitat fragmentation, many studies look for life-history characteristics that correlate with responses. Traits that have been shown to predict responses include abundance, the amount of variation in abundance, matrix use, and the geographic region (Henle et al., 2004). Other traits may be significant predictors in some cases, but these traits are likely context-dependent, with multiple traits acting in unison (Henle et al., 2004). In reptile studies, population abundance (Foufopoulos and Ives, 1999; Schutz and Driscoll, 2008; Wang et al., 2009), habitat specialization (Foufopoulos and Ives, 1999; Jellinek et al., 2004), trophic specialization (Watling and Donnelly, 2007), and edge tolerance (Lehtinen et al., 2003) have been suggested as good predictors of responses to fragmentation.

Determining which aspects of fragmentation are impacting which species is important for understanding how current landscape alterations are affecting populations and also how large drivers such as climate change may affect populations (Opdam and Wascher, 2004). For example, climate change is predicted to alter vegetation (Breshears et al., 2005) and increase the frequency of extreme weather events. Therefore, habitat specialists that respond sensitively to vegetation characteristics and avoid the microclimatic variations already present in edge habitats are more likely to respond negatively to climate change than organisms that tolerate a wider variety of vegetation and the less stable micro-climate of edge habitats.

The goal of this study is to determine which aspects of habitat fragmentation and loss impact an under-studied taxon (chameleons) in an understudied biome (African tropical forests). To do this, we used methods that account for detectability. We predicted that edge-tolerant species and those with higher abundance will be less impacted by fragmentation.

METHODS

Location. The East Usambara Mountains are part of Tanzania's Eastern Arc Mountain biodiversity hotspot (Myers et al., 2000). While the East Usambaras are believed to have been continuously forested prehistorically (Newmark, 2002; Burgess et al., 2007; Hall et al., 2009), only about 32% (263 km^2 of 714 km^2) remained forested as of 2000 (Hall et al., 2009). This remaining forest is heavily fragmented by tea plantations, eucalyptus groves, and small-scale farming, creating a landscape conducive to fragmentation research (Newmark, 2006). Within this fragmented landscape are eight species of chameleon that can be categorized as forest-dependent, edge specialists, and savannah species. Forest-dependent species include *Rhampholeon spinosus*, *Rh. temporalis*, and *Trioceros deremensis*. Edge specialists include *Kinyongia matschiei*, *K. tenuis*, and *K. vosseleri*. Savannah species include *Chamaeleo dilepis* and *Rieppeleon brevicaudatus*. All research was conducted between 850 m and 1200 m elevation in the southern East Usambara Mountains in and around the Amani Nature Reserve (ANR) (Figure 2.1). The sub-montane rainforest in this area is extremely diverse, with 109 large tree species between 1000 m and 1200 m alone (Lovett, 1998). Although this forest is now protected, much of it was logged in the past, and is therefore best categorized as mature second growth forest (Hamilton and Bensted-Smith, 1989).

Surveys. In total we surveyed chameleons along 32.4 km of transects in 11 forest fragments and the ANR over a 9-month time period. Some of these fragments were previously described by Newmark (Newmark, 1991, 2006), and range in size from 0.95 ha to 722 ha and in isolation from 10 m to 1,742 m. Fragments are believed to have been isolated for at least 80 years (Newmark, 1991). Surveys were conducted at two time periods: the first survey was conducted only in the ANR block in the dry season (September and October, 2010), and the second in ANR and all forest fragments during the rainy season (February to April, 2011). In the dry season in ANR, we surveyed 27 randomly-placed transects (totaling 5.4 km) as well as 16 transects placed at random starting points along forest trails (totaling 4.2 km). During the second round of surveys, we re-surveyed all trail transects within ANR (again totaling 4.2 km) and 20 of the 27 randomly-placed transects as well as surveying 11 new, randomly-placed transects (old and new together totaling 6.105 km). We also surveyed a total of 133 randomly-placed transects across 11 forest fragments totaling 11.422 km. All randomly-placed transects in Amani Nature Reserve were 200 m, block-S-shaped lines, while transects in forest fragments larger than 4 ha in size were straight 100 m lines and transects in fragments smaller than 4 ha were parallel lines that bisected the fragment. All transects were placed using Hawth's Tools 3.1 (Beyer, 2004) in ArcGIS 9.3 (ESRI, 2011). Surveys were conducted >24 hrs after transect placement in order to avoid disturbing chameleons away from the transect line and between the hours of 18:45 and 2:30. Chameleons were located at their roost sites using powerful LED headlamps (e.g. Princeton Tec Apex). After each chameleon was located, we measured the perpendicular distance between the transect line and the chameleon, identified the species, determined the sex, and measured its snout-vent length and tail length to the nearest mm.

Vegetation sampling. Vegetation was sampled in 5 m by 5 m plots at 25 m intervals along each transect. In each plot, we: visually estimated the proportion of vegetation cover between ground level and 0.5 m, between 0.5 m and 2m, and between 2 m and 5m; took four measurements of canopy cover using a spherical densitometer; took four measurements of leaf litter depth using a ruler; counted the number of small (<10 cm DBH) and large (≥10 cm DBH) trees; visually estimated the categorical cover (no, small, medium, or large amount) of ferns, vines, *Dracaena sp.*, and *Maesopsis eminii*. These vegetation variables were then transformed to improve assumptions of normality, standardized, and condensed using principal component analysis using the R package Vegan (Oksanen et al., 2012). The first three axes, accounting for 52% of the original variation, are used for analysis (Table 2.1). PCA component 1 reflects fewer large trees, less ground and low-level vegetation cover (0 – 2 m) and leaf litter depth, and more small trees and invasive *Maesopsis eminii*, which has been linked to altered forest dynamics (Binggeli and Hamilton, 1993). Component 2 reflects more fern, ground-level, and low-level cover (0 – 2 m) and less *Dracaena* and medium-level (2 – 5 m) cover, fewer small and large trees, and less leaf litter. Component 3 signifies less *M. eminii* and low-level (0.5 – 2 m) cover, and more large trees. Vegetation variables were further examined to see if they were correlated with aspects of fragmentation by using t-tests to compare vegetation characteristics in all fragments to the ANR and by using linear mixed effects models to see if vegetation variables were influenced by fragment area, fragment isolation, or the distance to the edge of the fragment.

Density estimation. Density estimates were calculated in program Distance 6.0 (Thomas et al., 2010). Distance-based density estimation is reliant on four key assumptions: First, all animals on the transect line must be detected. Because we walk along the transect lines and chameleons are readily visible at night under bright lights, we do not expect to have missed chameleons directly on the transect line. Chameleons can roost at high heights, however, which would limit visibility above the transect line. To account for this, we set a 7 m height ceiling and did not include sightings above 7 m in the analysis (Shirk et al., in prep.). As a result, we likely under-estimate densities of species that tend to roost higher – in particular *Rh. spinosus, T. deremensis*, and all three *Kinyongia spp.* The second assumption is that surveys do not affect animal movement. Because chameleons are sleeping at night when the surveys take place, and are very slow-moving in general, this assumption is easily met. Third, distances are measured accurately. We used a tape-measure to measure the distance between the transect line and each individual chameleon, ensuring accurate measurement. Fourth, transects must be randomly placed with respect to the organism of interest. To meet this assumption we placed most transects randomly using Hawth's Tools in ArcGIS; other transects, which were placed along trails at random starting points, were analyzed separately, and because they were very similar to those placed randomly, were included in further analyses. For all density estimates, we first ran the default model (Half-Normal + Cosine expansion) in program Distance, truncated the data to include only sightings with at least a 15% probability of detection (Buckland et al., 2001), and then ran four candidate models (Half Normal + Cosine, Half Normal + Hermite polynomial, Uniform + Cosine, Hazard-Rate + Simple Polynomial) and used AIC to select the best model. In addition to density estimates, we used program Distance to estimate the effective strip width for each density estimate and species group combination, which allowed us to calculate the effective area sampled (area sampled accounting for detectability) for each transect.

Detectability. For arboreal species such as chameleons, detectability may vary by species, horizontally, or vertically. We accounted for differences in species' detectability by grouping only very similar species together and analyzing distinctly different species separately. Densities were estimated independently for *T. deremensis,* while *K. matschiei* and *K. vosseleri* were analyzed together due to limited sample sizes of each species and their similarity (they have been considered the subspecies for much of the last hundred years (Mariaux et al., 2008)). The leaf-litter chameleons, *Rh. temporalis* and *Ri. brevicaudatus*, were also analyzed together, although *Ri. brevicaudatus* was limited to 3 sightings in one forest fragment (vs. 880 *Rh. temporalis* in 11 fragments plus ANR). For simplicity, *K. matschiei* and *K. vosseleri* will be referred to as *Kinyongia spp.*; *Rh. temporalis* and *Ri. brevicaudatus* will simply be referred to as *Rh. temporalis* as this species predominated. Three species – *C. dilepis*, *Rh. spinosus,* and *K. tenuis* – were not included in density estimates due to small sample sizes. We accounted for potential differences in horizontal detectability using the program Distance. Within the ANR block, we accounted for potential differences in detectability between seasons or transect types (randomly-placed and trail transects) by analyzing each combination of season and transect type separately. Within forest fragments (excluding the ANR block), data were insufficient to analyze each fragment independently. In the case of the *Kinyongia spp.*, detection probability was assumed to be similar across all fragments (including ANR) due to limited sample size. For the *Rh. temporalis* and *T. deremensis,* we compared analyzing all fragments together versus the Multiple-Covariates Distance Sampling engine in Distance, which allows a single detection function to vary in amplitude by fragment. The best model was selected from candidate models using AIC. To account for potential differences in vertical detectability among fragments, we compared roost heights using ANOVA, Tukey's Honestly Significant Difference, and t-tests.

Chameleon species richness estimation. Because the number of species observed in an area will consistently underestimate the true biodiversity, we used an estimate of species richness rather than the number observed. We estimated species richness using the Chao1 estimator (Chao, 1984) in BiodiversityR (Kindt and Coe, 2005). Sightings for the richness estimates were not limited to specific heights or distances from the transect as they were for the density estimation.

Density models. We modeled species' densities by using the observed counts as a response variable and the effective area sampled as an offset. This takes into account differences in both area sampled and detectability. All models used the same predictor variables: the natural log of the fragment area (this will simply be referred to as area), the natural log of the distance between the fragment containing the transect and the next nearest fragment (isolation), the natural log of the distance from the transect to the edge of the fragment (edge), a dummy variable for the season in which the transect was surveyed (season), the first three components of the vegetation PCA, an interaction between area and isolation, and an interaction between edge and season. Before modeling chameleon counts, we used scatter plots to look for potential relationships and unusual data points. Unusually high chameleon counts were removed from *Rh. temporalis* (1 of 221 observations), *T. deremensis* (2 of 221 observations), and *Kinyongia* *spp.* (3 of 221 observations) in order to improve model fit and decrease over-dispersion (Zuur et al., 2009). All models were fit in R 2.15.0 (R Development Core Team, 2012). Generalized linear mixed models with Poisson distribution and a random effect of fragment were fit using the glmer function in R package lme4 (Bates et al., 2011), which uses the Laplace approximation. Model selection was performed using backwards stepwise selection to remove all non-significant ($\alpha > 0.05$) predictors. Only the final models are presented.

Community composition. We evaluated the degree to which predictor variables influenced the chameleon community response using a permutational multivariate analysis of variance (MANOVA) function in R package Vegan. Because some transects had no chameleons and permutational MANOVA cannot be calculated without positive data values, we added a dummy species with one individual per transect. Permutational MANOVA is also sensitive to the order of predictor variables, so we used a combination of foreword and backwards selection to build the model.

RESULTS

Detection. For *Rh. temporalis* and *T. deremensis*, fragments were analyzed together using a global detection function (Table 2.2). Therefore, for each of these species, we had independent estimates of detectability along trail transects in ANR in each of two seasons, along randomly-placed transects in ANR in each of two seasons, and along transects in fragments. *Rh. temporalis* had no difference in observed roost heights among fragments ($F = 1.432$, $df = 9$, $p = 0.17$). Given that 99% of roost locations were under 1 m in height, any difference in roost height for this species is unlikely to impact detectability. *T. deremensis* roost heights varied among fragments ($F = 2.29$, $df = 7$, $p = 0.027$), but no individual pairwise comparisons were significantly different (all p-values > 0.1). Additionally, there does not appear to be any systematic bias in *T. deremensis* fragment density estimates because roost heights in all fragments combined were very similar to roost heights in ANR ($t = -0.06$, $df = 48.8$, $p = 0.949$). Kinyongia spp. roost heights also varied among fragments ($F = 6.55$, $df = 7$, $p < 0.001$), but again there does not appear to be any systematic bias among in *Kinyongia spp.* fragment density estimates because only 2 pairwise comparisons are significant (all other p-values $\gg 0.1$).

Description of fragments. All three vegetation PCA components varied significantly between fragments and the ANR (two-way t-tests, all $p < 0.002$), with components 1and 2 higher in the ANR and component 3 lower in the ANR. Furthermore, vegetation PCA component 2 is positively correlated with fragment area (mixed effects model $t = 5.62$, $df = 10$, $p \ll 0.001$) and component 3 is negatively correlated with fragment isolation (mixed effects model $t = 2.56$, $df = 10$, $p = 0.028$).

***Rhampholeon temporalis* and *Rieppeleon brevicaudatus* densities.** *Rh. temporalis* occurred in the 10 largest of the 12 fragments sampled. *Ri. brevicaudatus* was found in only one medium-sized fragment. These leaf-litter chameleons' density was influenced positively by fragment area and the distance to the edge of the fragment. Their density was negatively influenced by vegetation PCA component 3, and density was higher in the rainy season than in the dry season (Table 2.3). Of the significant predictor variables, fragment area and season were the most influential (Figure 2.2), with expected counts increasing by 7.7 from the smallest to the largest blocks and by 2.3 from the dry season surveys to the rainy season surveys.

***Trioceros deremensis* densities.** *T. deremensis* occurred in 8 of the 12 fragments, including all of the 5 largest fragments. Density was positively influenced by vegetation PCA component 2 and the distance to the edge of a fragment. Density was also higher in the rainy season than in the dry season. The interaction between season and distance to the edge shows that *T. deremensis* avoided edges more during the dry season than during the rainy season. Vegetation PCA component 3 negatively influenced *T. deremensis* density (Table 2.3). Distance to the edge of the fragment and the edge*season interaction were the most influential predictors of *T. deremensis* density (Figure 2.3), with expected counts in the dry season increasing from 0.1 to 3.1 over the observed range of edge distances.

***Kinyongia matschiei* and *K. vosseleri* densities.** *Kinyongia spp.* were observed in 8 of the 12 fragments (*K. matschiei* 4 of 12, *K. vosseleri* 5 of 12), including the 4 smallest fragments and 4 of the 5 largest fragments. Density was only weakly influenced by any of the predictors (Table 2.3). Both vegetation PCA components 1 and 2 had a weak positive influence on *Kinyongia* density (Figure 2.4), with expected counts increasing from 0.0 to 0.3 over the observed values of each of the two vegetation variables.

Chameleon richness and composition. Chameleon species richness along a transect is positively influenced by the distance to the edge of the fragment and vegetation PCA component 2, and negatively influenced by vegetation PCA component 3 (Figure 2.5). Community composition was strongly influenced by the distance to the edge of the fragment and weakly influenced by vegetation PCA component 3 and the season in which the survey was conducted.

DISCUSSION

We predicted that edge-tolerant species, such as *Kinyongia spp.*, would respond better to fragmentation than forest interior species (*Rh. temporalis* and *T. deremensis*). While *Kinyongia spp.* show little response to fragmentation, both *Rh. temporalis* and *T. deremensis* are negatively impacted by edge effects and vegetation characteristics associated with fragmentation, showing some support for our prediction. We also predicted that species with high abundance, such as *Rh. temporalis*, will be less impacted by fragmentation than rarer species, such as *Kinyongia spp.* Although *Rh. temporalis* density was negatively influenced by various components of fragmentation, species occurrence in fragments was still greater than *Kinyongia spp.* occurrence, suggesting a benefit of high population size.

For species that do respond to fragmentation and the chameleon community, we expected some components of fragmentation to be more important than others. In particular, we expected edge effects and vegetation characteristics to have a greater influence than area and isolation effects. As expected, isolation was a very poor predictor of chameleon populations and communities. This may be because observed isolation distances (10 to 1742m, mean = 376m) discourage animals with low-motility, such as chameleons, from crossing the already inhospitable matrix (tea plantation). However, the effects of isolation can be difficult to determine (Watling and Donnelly, 2006), and may simply require a larger sample size and more biologically relevant measures of isolation (Prugh, 2009). Fragment area had a very weak influence on our measures of abundance and richness. However, it is important to note that richness along a transect is not the same as the well-supported species-area relationship (SAR). Species richness along a transect could correlate with the SAR because a sample from a small fragment with few species is likely to contain fewer species than a sample from a large fragment with many species. However, it may instead be a measure of species mixing if species which normally do not cohabit are compressed into over-lapping ranges in small fragments. Only one species' density (*Rh. temporalis*) was correlated with fragment area. However, both *Rh. temporalis* and *T. deremensis* were entirely absent from the two smallest fragments sampled, suggesting that there may be a threshold effect of habitat area, something that has been widely supported theoretically, but difficult to support empirically (Fahrig, 2002; Swift and Hannon, 2010).

As predicted, edge effects had a strong influence on chameleon populations and community. Both forest interior species, *Rh. temporalis* and *T. deremensis*, responded negatively to edge effects. *T. deremensis* responded more strongly to edge effects in the dry season than during the rainy season, suggesting that abiotic conditions such as temperature and humidity are primary factors in edge avoidance. Newmark (2001) showed that near forest edges in the Usambara Mountains of Tanzania, temperature and light increase, while humidity decreases relative to the forest interior. Newmark was not explicit about the seasons in which all the measurements were taken, but acknowledges that observed gradients are temporally dynamic. Another possible component of edge effects is collection for the international pet trade. All species in this study are collected and legal to export in limited numbers, and hunting has been shown to act synergistically with fragmentation in other systems (Laurance and Cochrane, 2001; Peres, 2001; Thornton et al., 2011) as hunters get easier access to forest. Many previous studies have shown higher densities (Jenkins et al., 2003; Andreone et al., 2005; Metcalf et al., 2005) or richness (Patrick et al., 2011) for chameleons along edges. However, these studies usually consider riparian (Jenkins et al., 2003; Andreone et al., 2005) or trail (Metcalf et al., 2005) edges, rather than forest edges. *Bradypodion caeruleogula* seem to prefer tree-fall gaps over forest edges or forest interior (Reisinger et al., 2006). Although many chameleon species may prefer this intermediate level of disturbance, some species, especially *Furcifur pardalis* and many members of the genus *Kinyongia* do very well in heavily disturbed habitat (Andreone et al., 2005; Tilbury, 2010). Yet the *Kinyongia spp.* in our study showed no response to edges, and unlike Patrick et al. (2011), edges had a negative impact on species richness. It is important to note that fragment area is highly correlated with edge effects, with smaller fragments having more ubiquitous edge effects. Therefore, edge effects could create an apparent density-area relationship if edge effects are not included in models.

Chameleon species also consistently responded negatively to vegetative changes associated with fragmentation. Although vegetation characteristics are often correlated with other factors of fragmentation (component 2 with fragment area and component 3 with fragment isolation), it is vegetation characteristics and not the other factors of fragmentation that best predict chameleon density and community responses. Species consistently responded negatively to a decrease in components 1 and 2 and to an increase in component 3. As a result, species richness also responded negatively to these changes. Following transformation and principal component analysis, attempting to determine the biological significance of individual vegetation characteristics is tenuous. However, chameleons appear to be responding positively to a lack of large trees (in components 1, 2, & 3), less leaf litter depth (1 & 2), less *Dracaena* cover (1 & 2), an increase in *M. eminii* cover (1 & 3), and an increase in fern cover (2 & 3). Many other characteristics are not so clear. For example, components 2 and 3 both reflect a beneficial influence of low-level vegetation cover (0.5 – 2 m), but component 1 suggests the opposite. Similarly conflicting results are seen for ground-level vegetation cover (0 – 0.5 m) and for the number of small trees in a plot. Other predictors, such as vine cover (low levels are beneficial), canopy cover (high levels are beneficial), and medium-level vegetation cover (2 – 5 m) (low levels are beneficial) have relatively large coefficient values for only one of the three principal components.

Interestingly, the reason for a strong seasonal influence on density estimates was different for different species. In the case of *T. deremensis*, density was higher in the dry season because of hatchlings temporarily inflating the population size. *Rh. temporalis*, on the other hand, have continuous breeding and a constant population structure (Shirk, unpublished data). The strong influence of season on the density estimates for this species is likely the result of partial-population aestivation. Aestivation has been reported in other species of *Rhampholeon* (Tilbury, 2010), and is likely more prevalent at higher elevations for *Rh. temporalis*, such as in the West Usambara Mountains, where nearly all *Rh. temporalis* disappear for the colder portions of the year (Shirk, anecdotal observations).

Conclusion. Large population size and edge tolerance buffer the negative impacts of habitat fragmentation for chameleons. No species were benefited by fragmentation. Chameleons consistently responded more to edge effects and vegetative characteristics associated with fragmentation than to habitat area or isolation. This may bode poorly for chameleon populations in the coming decades as climate change further alters vegetative communities and exacerbates edge effects. While there are likely some chameleons that benefit from fragmentation effects, they are still sufficiently rare in forest fragments that sampling 32 km of transects is inadequate to demonstrate their response. Although not as damaging as habitat loss, the effects of habitat fragmentation further depress rain forest chameleon populations and communities. Therefore, the continued protection of large habitat patches such as Amani and Nilo Nature Reserves and the newly established Derema Corridor are vital for the preservation of these charismatic species.

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Table 2.1. Coefficient values for the first 3 components of a PCA of transformed vegetation characteristics that were collected along all transects. PCA was run on centered values using R package 'Vegan'. 'Transformation' is the power transformation applied to each variable. 'Shapiro-Wilk's' lists p-values of Shapiro-Wilk's tests of normality for each variable. Values above 0.05 are assumed to be normally distributed.

	Trans-formation	Shapiro-Wilk's	Component 1	Component 2	Component 3
% Variance			0.216	0.181	0.126
Veg Cov 0 - 0.5 m	^0.5	p = 0.148	-0.367	0.319	0.296
Veg Cov 0.5 - 2 m	^0.2	p = 0.381	-0.425	0.382	-0.326
Veg Cov 2 - 5 m	^0.15	p = 0.538	0.138	-0.446	0.288
Leaf litter depth	^0.001	p = 0.357	-0.321	-0.395	-0.158
Canopy cover	^10	p = 0.165	0.297	-0.26	-0.22
Small trees	^0.5	p = 0.624	0.353	-0.347	0.273
Large trees	^0.71	p < 0.001	-0.515	-0.434	0.4
Fern cover	^0.42	p < 0.001	0.138	0.506	-0.295
Vine cover	^0.22	p < 0.001	-0.297	-0.255	-0.279
Dracaena cover	^0.45	p < 0.001	-0.302	-0.458	0.268
Maesopsis cover	NA	p < 0.001	0.381	0.143	-0.419

Table 2.2. Comparison of candidate models of species' densities. Model names include detection function (HN = Half Normal, Cos = Cosine, HP = Hermite polynomial, Un = Uniform, HR = Hazard-Rate, and SP = Simple Polynomial) and whether the model was using the same detection function for all fragments (Global detection) or if the detection function varied by fragment via the Multi-Covariate Distance Sampling method in the program Distance. 'Trans' = number of transects included in estimate. 'Effort' = total distance (m) of transects. 'N' = total number of chameleons in estimate. 'P' = estimate of horizontal detection probability. 'ESW' = Effective strip width. 'D' = Density estimate for all fragments combined. 'D CV' = Coefficient of variation on density estimate. For both *T. deremensis* and *Rh. temporalis*, all models with an identical detection function for all fragments were preferred over all MCDS models, which had a detection function that varies by fragment.

	Model	Trans	Effort	N	P	ESW	D	D CV	Delta AIC
T. deremensis	HN-HP_Global_Detection	133	12499	31	0.60	6.31	3.00	0.33	0.00
	HN-Cos_Global_Detection	133	12499	31	0.60	6.31	3.00	0.33	0.00
	HR-SP_Global_Detection	133	12499	31	0.74	7.71	2.45	0.30	0.36
	Un-Cos_Global_Detection	133	12499	31	0.58	6.08	3.11	0.31	0.41
	HN-Cos_MCDS	133	12499	31	0.51	5.35	3.12	0.46	2.29
	HN-HP_MCDS	133	12499	31	0.51	5.35	3.12	0.46	2.29
	HR-SP_MCDS	133	12499	31	0.51	5.35	3.12	0.46	2.29
	Model	Trans	Effort	N	P	ESW	D	D CV	Delta AIC
Rh. temporalis	HN-HP_Global_Detection	133	12499	202	0.62	3.77	26.89	0.16	0.00
	HN-Cos_Global_Detection	133	12499	202	0.62	3.77	26.89	0.16	0.00
	HR-SP_Global_Detection	133	12499	202	0.65	3.97	25.53	0.17	0.77
	Un-Cos_Global_Detection	133	12499	202	0.61	3.71	27.30	0.15	0.87
	HN-HP_MCDS	133	12499	202	0.60	3.65	22.13	0.14	4.22
	HN-Cos_MCDS	133	12499	202	0.60	3.65	22.13	0.14	4.22
	HR-SP_MCDS	133	12499	202	0.64	3.92	20.59	0.14	9.14

Table 2.3. Summary of coefficients of significant predictors for chameleon density and richness along individual transects. We accounted for differences in detectability using the effective area sampled as an offset for each density model.

Response		Chao Richness Estimate	*Rh. temporalis* Count	*T. deremensis* Count	*Kinyongia spp.* Count
Model		Linear Mixed Model	GLMM with Poisson distribution	GLMM with Poisson distribution	GLMM with Poisson distribution
Intercept		0.29	-0.09	-1.12	0.00
Area [ln(ha)]			0.49		
Isolation [ln(m to next block)]					
Edge [ln(meters to edge)]		0.25	0.18	0.57	
Season Dummy variable			1.07	1.38	
Veg PCA	Comp.1				0.31
	Comp.2	0.15		0.22	0.28
	Comp.3	-0.13	-0.25	-0.26	
Area: Isolation Interaction					
Edge: Season Interaction				-0.32	
Offset		ln(transect length)	ln(effective area sampled)	ln(effective area sampled)	ln(effective area sampled)
Random Effect St. Dev		0.37	0.82	0.56	1.93
Over-dispersion parameter			2.90	1.84	1.27

Figure captions:

Figure 2.1. Fragmented forest in southern East Usambara Mountains in area of surveys. Northern block of Amani Nature Reserve is black; forest fragments included in study are dark gray; other forest fragments are light gray.

Figure 2.2. Observed (points) and predicted (lines) counts of *Rh. temporalis* in both the rainy and dry seasons. Predicted values come from the best model of chameleon counts, with all unplotted variables, including the offset for effective area sampled, were held constant at mean values.

Figure 2.3. Observed (points) and predicted (lines) counts of *T. deremensis* in both the rainy and dry seasons. Predicted values come from the best model of chameleon counts, with all unplotted variables, including the offset for effective area sampled, were held constant at mean values.

Figure 2.4. Observed (points) and predicted (lines) counts of *Kinyongia spp*. Season was not included as it was not a significant predictor in the model of *Kinyongia spp.* counts. Predicted values come from the best model of chameleon counts, with all unplotted variables, including the offset for effective area sampled, were held constant at mean values.

Figure 2.5. Estimated (points) and predicted (lines) chameleon richness. Season was not included as it was not a significant predictor in the model of chameleon richness.

Predicted values come from the best model of chameleon richness, with all unplotted variables, including the offset for effective area sampled, were held constant at mean values.

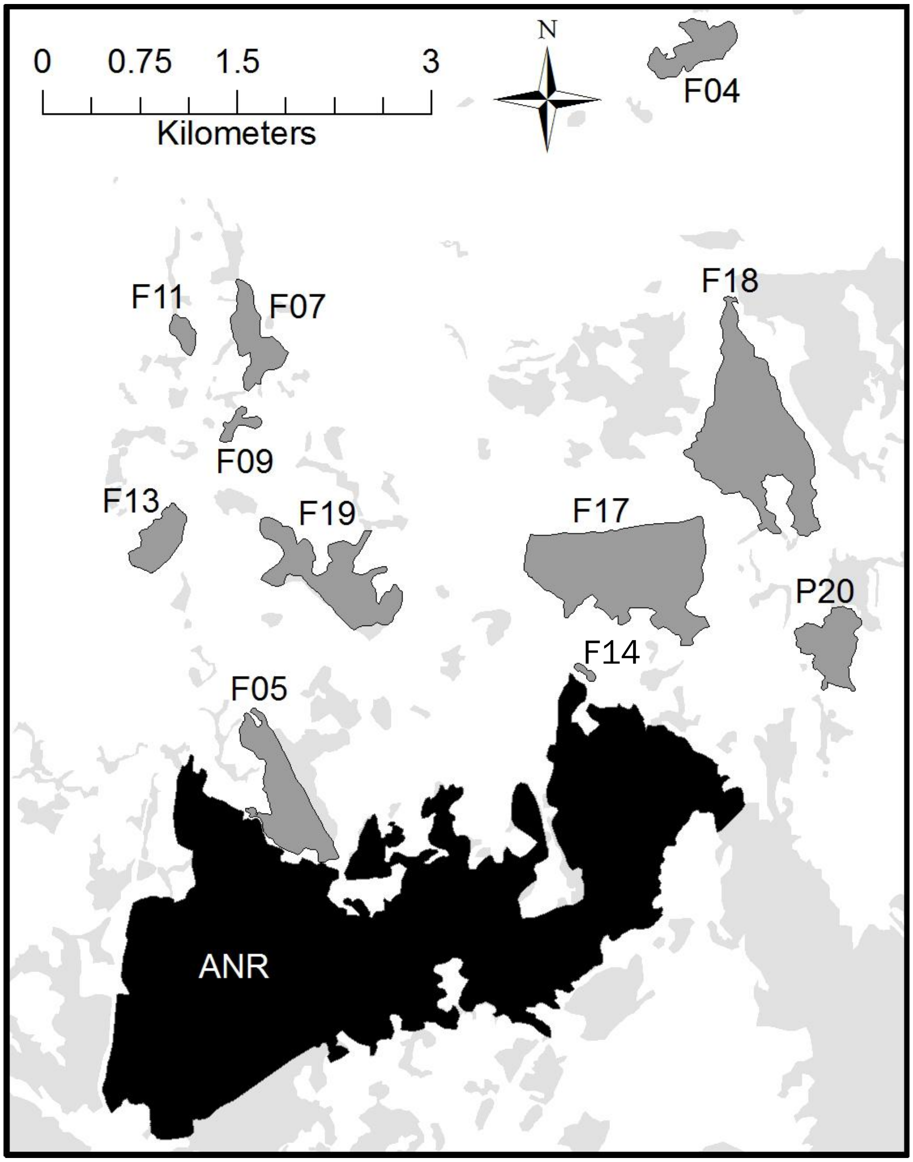
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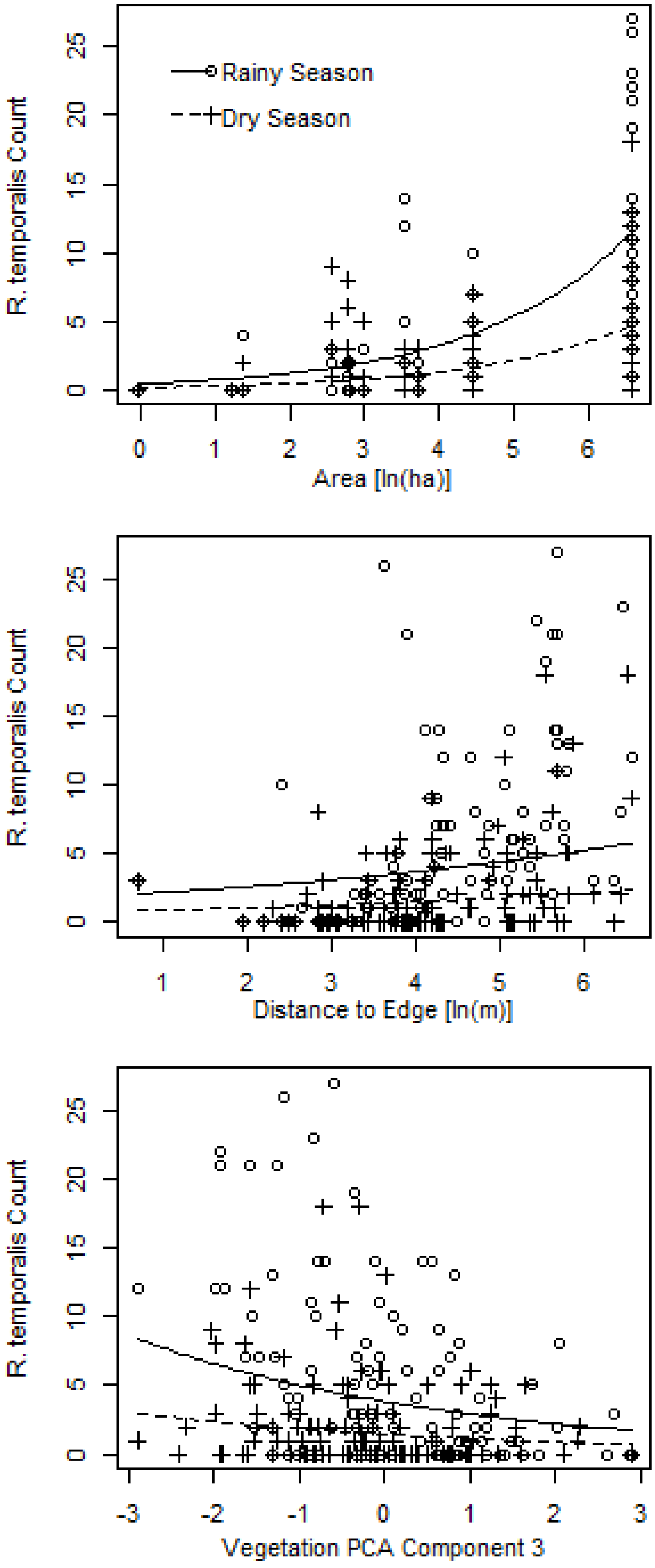
Figure 2.1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Distance to Edge [ln(m)]
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2
3
Vegetation PCA Component 3

Figure 2.2

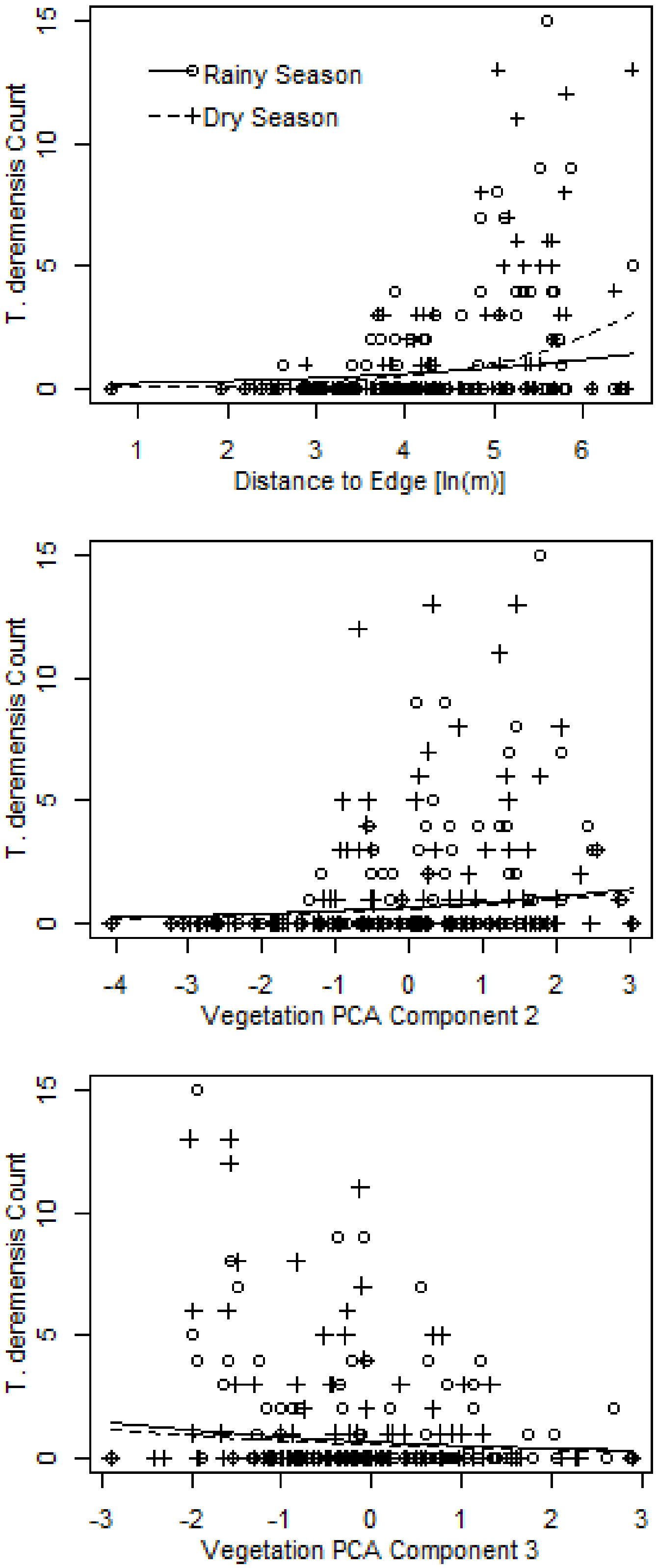
Rainy Season
Dry Season
T. deremensis Count
0
5
10
15
Distance to Edge [ln(m)]
1
2
3
4
5
6
T. deremensis Count
0
5
10
15
Vegetation PCA Component 2
-4
-3
-2
-1
0
1
2
3
T. deremensis Count
0
5
10
15
Vegetation PCA Component 3
-3
-2
-1
0
1
2
3

Figure 2.3

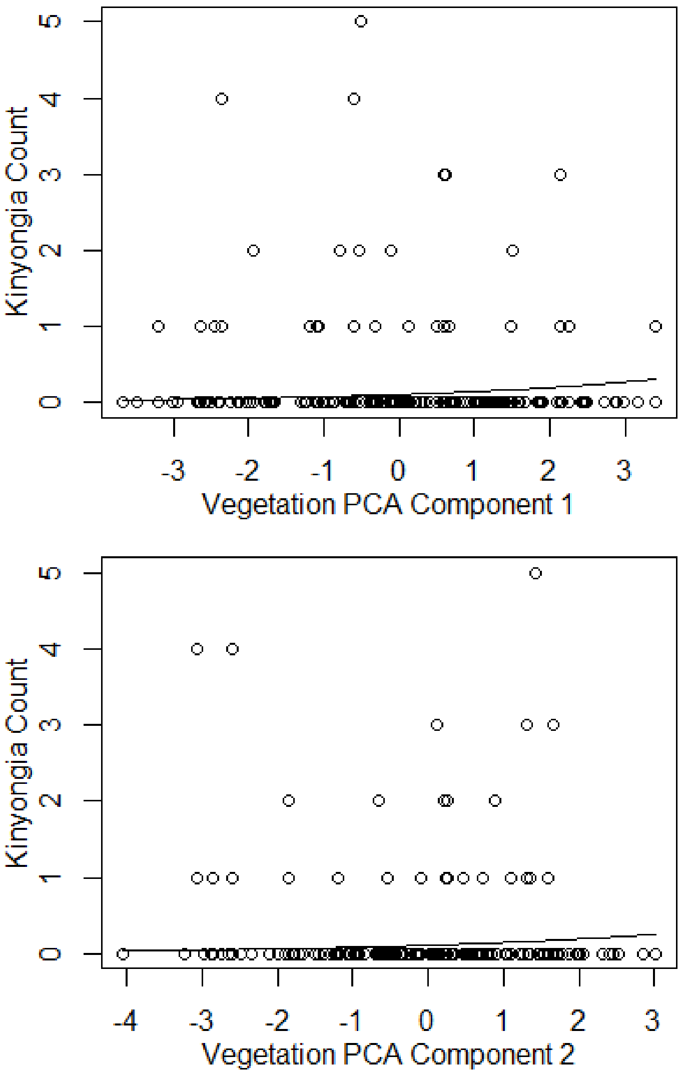
Kinyongia Count
0
1
2
3
4
5
-3
-2
-1
0
1
2
3
Vegetation PCA Component 1
Kinyongia Count
0
1
2
3
4
5
-4
-3
-2
-1
0
1
2
3
Vegetation PCA Component 2

Figure 2.4

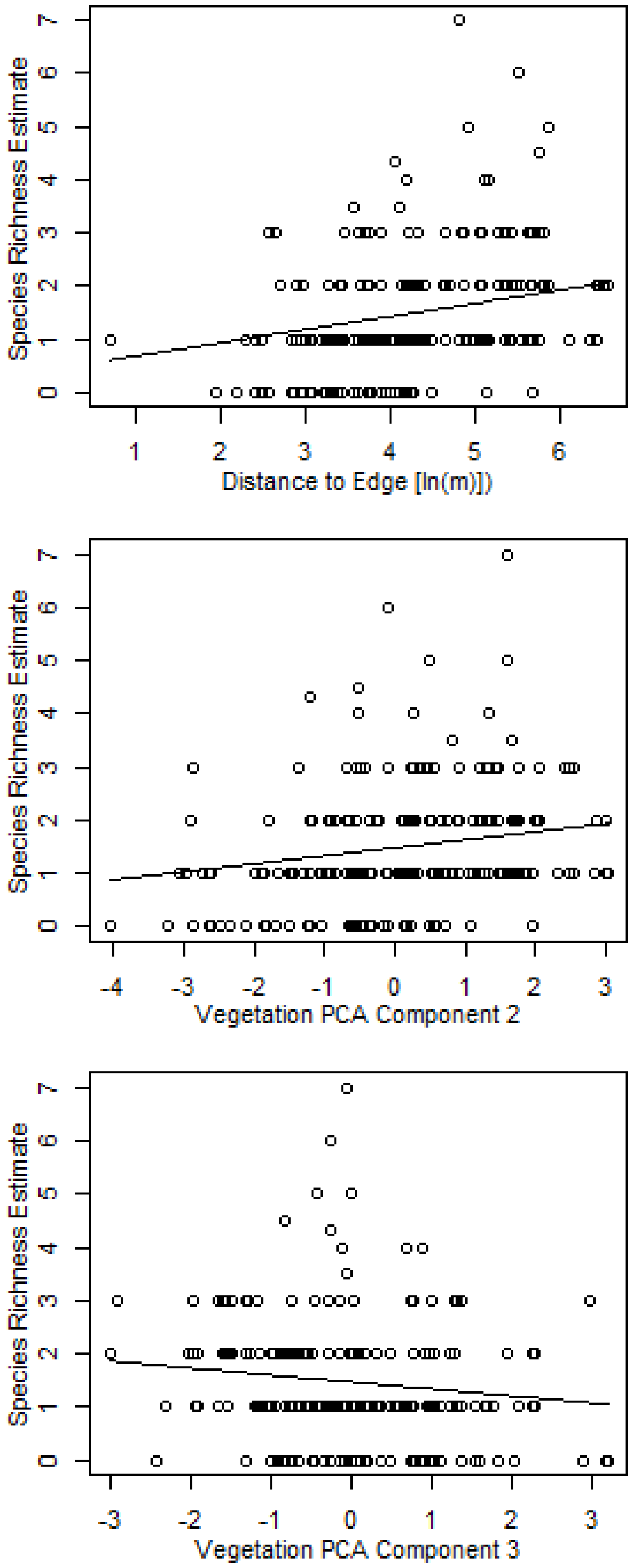
Species Richness Estimate
0
1
2
3
4
5
6
7
1
2
3
4
5
6
Distance to Edge [ln(m)])
Species Richness Estimate
0
1
2
3
4
5
6
7
-4
-3
-2
-1
0
1
2
3
Vegetation PCA Component 2
Species Richness Estimate
0
1
2
3
4
5
6
7
-3
-2
-1
0
1
2
3
Vegetation PCA Component 3

Figure 2.5

Vita

Philip L Shirk was born on 14 September, 1984 in Lancaster, Pennsylvania. After graduating Summa Cum Laude with a Bachelor of Arts in Biology and Environmental Sciences from Eastern Mennonite University in 2007, he participated in biological field studies of plants and vertebrates in Ghana, Georgia, Puerto Rico, and Dominica. While working on his Master's degree at Virginia Commonwealth University, he spent a year collecting data in Tanzania before graduating in 2012. He will next be joining the Craig Osenberg lab at the University of Florida where he will pursue his PhD.