ResearchGate

See discussions, stats, and author profiles for this publication at: https://www.researchgate.net/publication/256605373

Abundance and roosting ecology of chameleons in the Eastern Arc Mountains of Tanzania and potential effects of harvesting

Article *in* Herpetological Conservation and Biology · December 2011

Impact Factor: 0.6

CITATIONS
6

READS
39

5 authors, including:



Philip Shirk
University of Florida
5 PUBLICATIONS **7** CITATIONS
SEE PROFILE



James R Vonesh
Virginia Commonwealth University
82 PUBLICATIONS **1,548** CITATIONS
SEE PROFILE



Elizabeth B Harper
New England College
32 PUBLICATIONS **530** CITATIONS
SEE PROFILE

Kim Howell
University of Dar es Salaam
64 PUBLICATIONS **893** CITATIONS
SEE PROFILE

Available from: James R Vonesh
Retrieved on: 15 July 2016

Herpetological Conservation and Biology 6(3):422−431.
Submitted: 11April 2011; Accepted: 27 September 2011; Published: 31 December 2011.

ABUNDANCE AND ROOSTING ECOLOGY OF CHAMELEONS IN THE EAST USAMBARA MOUNTAINS OF TANZANIA AND THE POTENTIAL EFFECTS OF HARVESTING

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

[1]*Division of Forestry, Natural Resources and Recreation, Paul Smith's College, Paul Smith's, New York 12970, USA, e-mail: dpatrick@paulsmiths.edu, eharper@paulsmiths.edu*
[2]*Department of Biology, Virginia Commonwealth University, Richmond, Virginia 23284-20123, USA, e-mail: philip.shirk@gmail.com, jrvonesh@vcu.edu*
[3]*Department of Zoology and Wildlife Conservation, PO Box 35064, University of Dar es Salaam, Dar es Salaam, Tanzania, e-mail: kimhowellkazi@gmail.com*

***Abstract.*—Harvesting of chameleons from the East Usambara Mountains of Tanzania for the exotic pet trade is of concern due to the high rates of habitat loss in this region and the fact that many of the species are endemic or near endemic to this isolated montane forest. Export of the majority of chameleons found in the East Usambaras is regulated by their listing under CITES Appendix II. To ensure harvesting is sustainable, however, greater knowledge of the ecology of species is needed. We conducted this study in and around Amani Nature Reserve in the East Usambara Mountains during August 2009. We used transects on the forest edge and interior to gather baseline data relating to the ecology of chameleons and to assess if any effects of harvesting on populations could be detected. We compared abundance of chameleons between forest edge and interior, the age/size of species, and sex-ratios between these two habitat types. We observed 108 chameleons during surveys, representing seven species. Some species were restricted to forest interior while others were only found on forest edges. When comparing age/size and sex ratios of the most valued species for the exotic pet trade, *Trioceros deremensis*, we found a strong female sex-bias in adults only, and that adult females were larger than adult males. This is in contrast to reports in published literature showing that males are capable of growing larger than females. Based on the low abundance of some species, we suggest careful consideration of future export quotas under CITES. Further investigation into the potential reasons for the size and sex-ratios of *T. deremensis* is also needed.**

Key Words.—Chamaeleo; CITES; exotic pet trade; *Kinyongia*; *Rhampholeon*; *Rieppeleon*; sex-dependent harvesting; *Trioceros*.

INTRODUCTION

Unsustainable harvesting by humans is a principal cause of species declines and extinctions worldwide (Wilcove et al. 1998; Reynolds et al. 2001). The effects of harvesting are of particular concern in biodiversity hotspots such as the East Usambara Mountains of Tanzania (part of the Afromontane biodiversity hotspot) where forest patches with high species richness and endemicity are embedded in a landscape of high human density (Hamilton 1989; Burgess et al. 2007). These isolated montane forests have seen large-scale habitat loss and fragmentation due to logging and land-conversion for tea, sisal, teak, and eucalyptus plantations. Animal populations found in remaining forest patches have experienced reductions in population size, resulting in an increased risk of extinction (Newmark 1991, 2006). These conditions make these populations particularly vulnerable to decline or extinction from harvesting.

Many people in the East Usambaras are still reliant on the forest for their livelihoods, which include collection of animals for sale. Villagers in the Usambaras have identified chameleons as the most collected vertebrates (Roe, D., T. Mulliken, S. Milledge, J. Mremi, S. Mosha, and M. Grieg-Gran. 2002. Making a killing or making a living? Wildlife trade controls and rural livelihoods. Biodiversity and Livelihoods issue number 6, International Institute for Environment and Development and TRAFFIC. Available at http://www.traffic.org/general-reports/traffic_pub_trade4.pdf). The chameleons collected by villagers are passed through a chain of intermediaries, with those that survive eventually sold wholesale on the international pet-trade market. Thousands of chameleons are exported from Tanzania annually (e.g. > 1,400 Usambara Two-horned Chameleons (*Kinyongia* spp.) per year for the last 25 years; Carpenter et al. 2004). Tanzanian chameleons, with the exception of the pygmy chameleons (genera *Rhampholeon* and *Rieppeleon*), are protected under the Convention on International Trade in Endangered

Copyright © 2011. David A. Patrick. All rights reserved.

Species of Wild Fauna and Flora (CITES) Appendix II. The Tanzanian government manages chameleon exports with the goal of ensuring non-detrimental collection levels. However, insufficient demographic data are available to assess the effects of harvesting on the viability of Tanzania's chameleon populations.

Estimates of sustainable harvest levels are hindered by a lack of knowledge of the ecology of these species including patterns of occurrence, habitat preferences, and age and sex structures. Without this information, it is impossible to separate the effects of changes in abundance and the characteristics of populations due to harvesting from the natural ecology of the species. Previous research in other regions has clearly demonstrated that chameleon communities tend to be segregated based on habitat characteristics, such as proximity to forest edge and riparian areas (Andreone et al. 2005), anthropogenic disturbance (Karsten et al. 2009), and elevation (Hofer et al. 2003). Developing a similar understanding of the drivers of patterns of occurrence in the East Usambaras is vital in understanding the likely implications of harvesting.

This lack of knowledge also includes taxonomic uncertainty. For example, the Usambara Two-Horned Chameleon, previously considered under CITES as *Bradypodion fischeri*, was recently divided into three species based on phylogenetic analyses, one occurring in the West Usambara Mountains and two in the East Usambara Mountains (Mariaux et al. 2008). The fact that previous harvesting quotas were set for a single species that was already considered endemic to a small area clearly illustrates the importance of taxonomic information in regulating harvest (the Tanzanian government is currently revising export quotas for these species). Understanding the ecology of these species is also important as the desirability, and thus collection pressure, varies by species. It is also likely that for some species, sex-dependent collection may occur. Either this can be due to sex-specific patterns of habitat use influencing vulnerability to collection, or because one sex is more charismatic than the other; examples are individuals possessing rostral protuberances or a larger body size.

The goal of this research was to gather fundamental data relating to the ecology of chameleons in the East Usambaras, and to use this information to assess if any effects of harvesting on populations could be detected. These data will then be used to aid Tanzanian management agencies, specifically the CITES Scientific Authority (Tanzania Wildlife Research Institute) and the CITES Management Authority (Wildlife Division) in setting sustainable harvest levels. Specific objectives included: (1) determining relative abundance and factors driving patterns of occurrence of chameleons; (2) assessing the age and sex structure of populations; and (3) identifying focal topics for ongoing research in this arena.

MATERIALS AND METHODS

Study species and site.—Eight species of chameleons (Fig. 1) are found in sub-montane areas of the East Usambara Mountains. These species include *Chamaeleo dilepis*, *Kinyongia matschiei*, *K. vosseleri*, *K. tenuis*, *Rhampholeon temporalis*, *Rhampholeon spinosus*, *Rieppeleon brevicaudatus*, and *Trioceros deremensis* (Fig. 1; Spawls et al. 2006; Mariaux et al. 2008). Our study was conducted in the southern part of the East Usambara Mountains of Tanzania (Fig. 2). The East Usambaras are part of the Eastern Arc Mountains, an area with extremely high species endemicity and widespread forest loss (Lovett and Wasser 1993). Forest extends from 250–1100 m in elevation in the southern part of the East Usambaras, with an average of 2000 mm of rain falling annually (Hamilton 1989). Where native forest has been removed, it has principally been replaced with tea plantations or small-scale "shamba" agriculture. We confined survey sites to the vicinity of the protected 722 ha sub-montane rainforest block surrounding the Amani Nature Reserve headquarters at Amani village. The sub-montane rainforest at this altitude is extremely diverse, with surveys finding 109 species of large trees between 1,000 and 1,200 m elevation (Lovett 1998). The forest canopy averages 20–30 m (Hamilton 1989). Although currently protected, this area has seen logging in the past, primarily during the German colonial era (Hamilton and Bensted-Smith 1989) thus, the forest is best categorized as mature second-growth. The area has also seen invasion of woody plants, particularly as a result of the botanical gardens established at Amani village during the German colonial era (Cordeiro et al. 2004). Current forest disturbance includes natural small-scale events such as wind-throws and collection of firewood by local people. We conducted surveys as part of the training for the 2009 Tropical Biology Association Course during August 2009, with the goal of developing ongoing chameleon monitoring through annual course participation.

Transect establishment and habitat measurements.—We established 11 transects along existing dirt roads and forest paths to minimize habitat disturbance. Transects ranged in length from 135 m to 1,270 m and were established either from the forest edge to interior (forest; n = 8), or immediately adjacent to forest where one side of the transect was forested (edge; n = 3). We mapped all transects using a handheld global positioning system (GPS) device. Due to the steep topography of the area, these roads and paths often had earth-side banks that lacked ground-cover. Forest transects had canopy cover. Edge transects were typically only covered by canopy



FIGURE 1. Examples of chameleon species found in sub-montane areas of the East Usambara Mountains, Tanzania. Images shown left to right by row beginning at the top include *Chamaeleo dilepis*, *Kinyongia matschiei*, *K. tenuis*, *K. vosseleri*, *Rhampholeon spinosus*, *R. temporalis*, *Rieppeleon brevicaudatus*, *Trioceros deremensis* (male) and *Trioceros deremensis* (female). (Photographed by Philip Shirk)

from one side of the road, and literally bordered the edge of the forest block. Previous research focusing on edge-effects in the region has shown that air temperature, humidity, and light intensity vary between forest edge and interior, although these relationships are temporally dynamic (Newmark 2001).

Chameleon surveys.—We conducted surveys 4–27 August 2009 at night from 1930 to 0000. We used visual surveys aided by high-powered flashlights to locate chameleons. The size of field teams ranged from one to five people due to the presence of student volunteers from the Tropical Biology Association's "Tropical Forest Ecosystems in Tanzania" field course (http://www.tropical-biology.org/). We sampled one to three transects per night in random order to minimize any bias due to temporal differences in detectability during the study period. We sampled each transect at least twice (total of 21 survey nights). We also encountered chameleons on transects during the day, although these anecdotal sighting were not used in analyses. Chameleons were either hand-captured or removed from higher branches using a stick to which they were encouraged to cling. For each chameleon encountered, we recorded species, sex (as indicated by hemipenal bulges in males or secondary sexual characteristics in some species), age class (juvenile or adult), and we measured snout-vent length (SVL), tail, and rostral appendage (horn) length (mm) using a plastic ruler. We also measured perch height (m) where we caught chameleons. We did not include a vertical height ceiling on observations as no chameleons were observed in locations from which they could not be collected. We recorded a GPS location and marked the position of the chameleon and any resightings using biodegradable flagging tape. We restricted this flagging to areas where low human traffic suggested little risk of collection as we did not want to increase collection risk by highlighting the location of animals. We used this locational information to reduce the probability of including multiple observations of the same chameleons in our analyses. Once we processed chameleons, we returned them to their capture location.

Patterns of occurrence, age, sex ratios, and perch height.—To compare occurrence between edge and

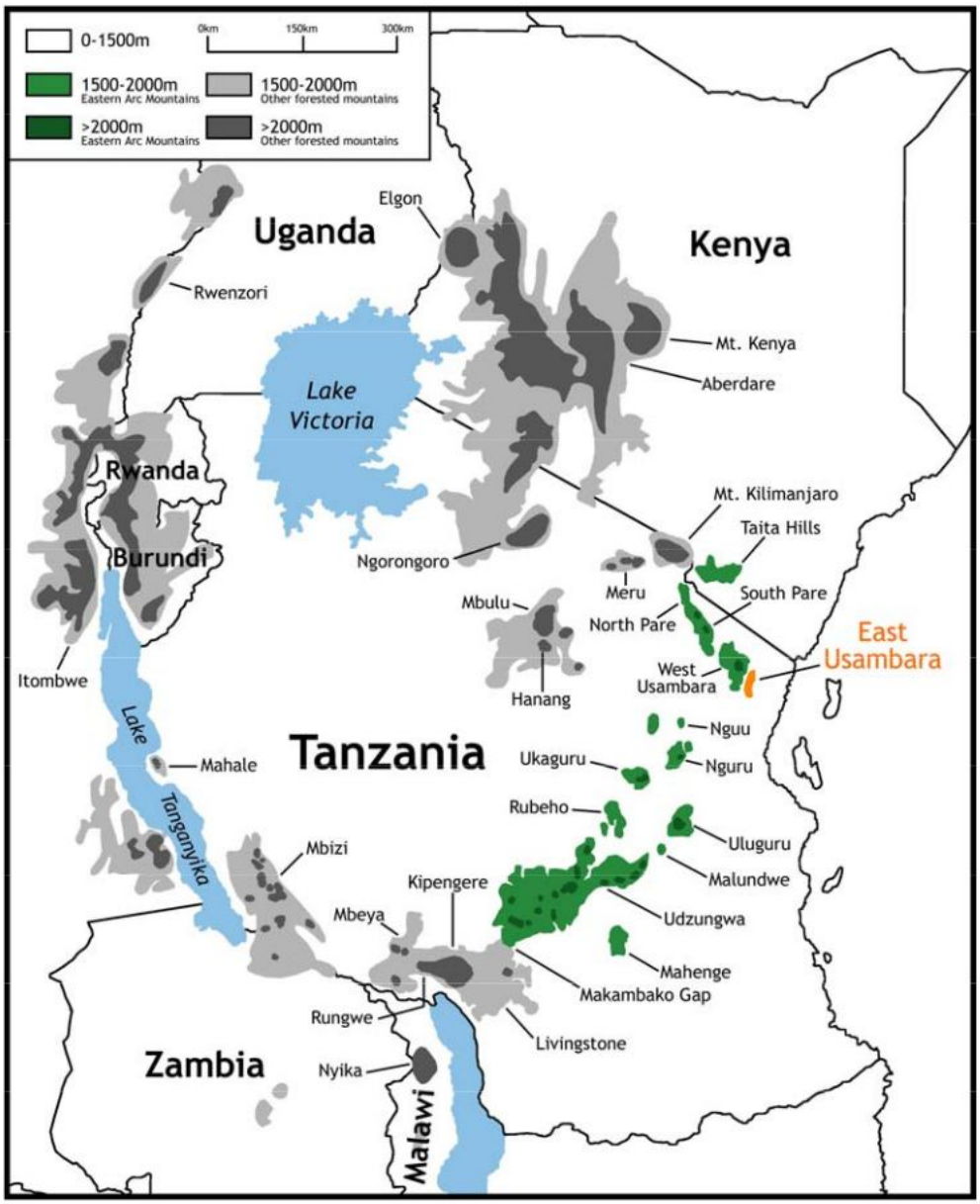


FIGURE 2. Location of the East Usambara Mountains (EUM - orange) in Tanzania. Map reproduced with permission from Rebecca Banasiak, Research Assistant, The Field Museum of Natural History, Chicago, Illinois, USA.

forest transects, we used individual transects as our unit of analysis. Initially we accounted for variation in the number of observers per survey as well as variation in transect length. Because chameleons are stationary at night, were highly visible, and there was no time limit to sampling, we suspected that the number of observers would not influence the number of observations (i.e., a single trained observer would find as many chameleons on a transect as would multiple individuals, although it would take them longer to conduct the survey). We used regression analysis to assess if there was a relationship between the number of chameleons seen per meter of transect and the number of observers. Because we found no relationship between these variables ($F_{1,28} = 0.001$, $P = 0.973$), we used the mean observations/100 m of transect as our response variable. Previous chameleon studies have employed distance sampling as a means of correcting for variation in the detectability of animals depending on habitat type (Jenkins et al. 2003). Our small sample size would not allow reliable estimation of density estimates based on distance sampling (Buckland et al. 1993); thus, we report unadjusted results from our visual encounter surveys. Qualitatively, we did not observe strong differences in habitat structure between

TABLE 1. Numbers of chameleons sighted in the vicinity of Amani Nature Reserve, Tanzania during August 2009. Males and females could be positively assigned based on secondary sexual characteristics for only two species with remaining individuals classified as unknown.

Species	Juveniles	Juv. male	Juv. female	Adults	Adult male	Adult female	Total	Annual fecundity (max)
Trioceros deremensis	22	6	4	12	1	11	34	
Chamaeleo dilepis	5	NA	NA	6	1	4	11	2–50 (65) a,b
Kinyongia tenuis	2	NA	NA	9	2	5	11	3–4 b
Kinyongia matschiei	3	NA	NA	4	NA	NA	7	
Kinyongia vosseleri	14	9	NA	9	8	NA	23	12 c
Rieppeleon brevicaudatus	0	NA	NA	2	1	1	2	
Rhampholeon temporalis	5	NA	NA	31	17	14	36	3–8 d

Sources of fecundity data: a) Spawls et al. 2006; b) Necas 1999; c) Mariaux et al. 2008; d) Jeroen van Leeuwen, pers. comm.

our edge and forest transects with both transect types having areas of relatively open and dense vegetation. To compare relative abundances of chameleons on edge versus forest transects, we used Wilcoxon rank sum tests due to non-normality of errors. We used $\alpha = 0.05$ for all statistical tests.

To compare age and sexes of chameleons, we needed to assign individuals to different classes based on these characteristics. Our ability to do so varied among species. We could readily differentiate *Trioceros deremensis* into age and sex classes based on secondary sexual characteristics including presence and size of rostral appendages, presence of hemipenal bulge, and size. For species such as *K. vosseleri and K. matschiei*, however, size dimorphism between sexes and/or a lack of clear secondary sexual characteristics made assigning ages and sexes challenging. In the case of *K. vosseleri*, we could readily identify males and assign them to an age class due to the presence of specific characteristics including presence of rostral appendages, overall size, and dorsal scale size. However there was insufficient information available on smaller females to assign them to age classes. For *K. matschiei*, both sexes possess rostral protuberances and we could not reliably separate them from one another. Once individuals had been assigned to classes (bearing in mind the aforementioned caveats), we compared age and sex ratios within species only for species with sufficient data. For these species we implemented three comparisons: (1) sex-ratio of juveniles versus adults; (2) size of males versus females; and (3) size of chameleons on edge versus forest transects (lumping sexes together).

For sex-ratios, we compared the number of males to females (where we could positively determine the sex) using Fisher's Exact Test as expected counts per sex were fewer than five. For size, we compared snout-vent lengths using t-tests. To compare perch heights between edge and forest observations, we used a t-test assuming unequal variance. We used Program R (version 2.9.1; R Foundation for Statistical Computing, Vienna, Austria) for all statistical analyses.

RESULTS

In 10,169 m of total transect sampled (4,511 m edge; 5,658 m interior), we observed 124 chameleons representing seven species (Table 1). Of these individuals, we observed 108 during formal nighttime surveys, while 16 were anecdotal sightings. Included in our samples were a number of recently hatched chameleons, including four *R. temporalis* (20–24 mm SVL), four *T. deremensis* (34–40 mm SVL), and two *K. vosseleri* (32–39 mm SVL). In total we sampled seven

TABLE 2. Mean number of chameleons of seven species observed per 100 m of transects (± SD) in the vicinity of Amani Nature Reserve, Tanzania during August 2009. Transects were classified as either edge or forest. Results are also shown for Wilcoxon rank sum tests (*P* value and test statistic, *W*) comparing ranked relative abundances in edge versus forested transects (significance at 0.05 shown using an asterisk).

Transect type	N transects	*Trioceros deremensis*	*Chamaeleo dilepis*	*Kinyongia tenuis*	*Kinyongia matschiei*	*Kinyongia vosseleri*	*Rieppeleon brevicaudatus*	*Rhampholeon temporalis*
Edge	3	0.097 ± 0.167	0.131 ± 0.227	0.171 ± 0.232	0	0.509 ± 0.815	0.026 ± 0.045	0
Forest	8	0.545 ± 0.719	0	0.056 ± 0.105	0.060 ± 0.084	0.061 ± 0.129	0	0.609 ± 0.508
Wilcoxon		0.257 (6)	0.153 (16)	0.287 (17)	0.299 (7.5)	0.287 (17)	0.153 (16)	0.037 (1.5)*

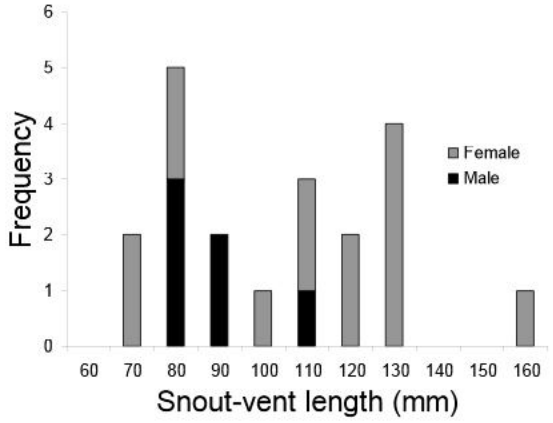


FIGURE 3. Histogram of adult and juvenile *Trioceros deremensis* females (n = 14) and males (n = 6) captured in the vicinity of Amani Nature Reserve, Tanzania.

of the eight species known from the region. We did not find any *R. spinosus*. We observed five species on each transect type (forest and edge), but species composition differed (Table 2). *Kinyongia matschiei* and *R. temporalis* were only found on forest transects while *C. dilepis* and *R. brevicaudatus* were only found on edge transects. We found *Kinyongia tenuis*, *K. vosseleri*, and *T. deremensis* in both habitat types, but *T. deremensis* was more abundant in forest transects, albeit not significantly. The only species for which a statistical difference in relative abundance between forest and edge transects was *R. temporalis*, with significantly more observations within the forest (Table 2).

The age class and size structure of chameleons varied among species. Mean SVL (± SD) of male *T. deremensis* (83 ± 14 mm) was significantly smaller than that of females (107 ± 29 mm; $t = 2.464$, df = 18, $P = 0.024$; Fig. 3). Of species commonly collected for the pet trade, we only had sufficient sightings of *K. vosseleri* to be able to compare size between edge and forest transects. For this species we found no significant difference in the mean size of individuals grouped across all ages and sexes on the two transect types (edge SVL = 75 ± 22 mm, forest = 70 ± 27 mm; $t = 0.374$, df = 6, $P = 0.361$).

TABLE 3. Mean perch heights (± SD) for seven species of chameleon observed in the vicinity of Amani Nature Reserve, Tanzania during August 2009.

Species	Mean perch height (m)
Trioceros deremensis	2.10 ± 2.24
Chamaeleo dilepis	1.63 ± 0.66
Kinyongia tenuis	4.14 ± 2.19
Kinyongia matschiei	4.21 ± 2.87
Kinyongia vosseleri	2.83 ± 2.27
Rieppeleon brevicaudatus	0.35 ± 0.07
Rhampholeon temporalis	0.60 ± 0.45

When comparing sex-ratios, we found that the proportion of male to female *T. deremensis* differed significantly between juveniles and adults (Fisher's Exact Test, $P = 0.020$), with 60% of juveniles (for which sex could be positively identified) being male, and only 9% of adults (the sex of juveniles of this species could be determined, even in quite small individuals, by the early presence of rostral appendage buds in males). We spotted the single adult male of this species outside of formal surveys at the conclusion of the study. In contrast, the sex ratio of *K. vosseleri* suggests that the population of this species was male-skewed. We found six *K. vosseleri* females (adult and juvenile combined due to lack of clear differentiation) and 17 males (nine juvenile and eight adult).

When evaluating perch height, we found that species differed in their vertical use of the forest (Table 3). Pygmy chameleons remained close to the ground, with *T. deremensis*, *C. dilepis*, and *K. vosseleri* occupying habitat averaging approximately 2 m from the ground. *Kinyongia tenuis* and K. *matschiei* were found in the highest vegetation, with the average perch height > 4 m. We found no differences in the mean perch heights on edge and forest transects for the two species that yielded sufficient sample sizes for comparison (*K. tenuis*: edge = 3.54 ± 1.89 m; forest = 4.76 ± 2.73 m; $t = -0.821$, df = 7, $P = 0.439$; *K. vosseleri*: edge = 3.42 ± 2.07 m; forest 3.00 ± 2.94 m; $t = 0.289$, df = 6, $P = 0.782$).

DISCUSSION

This study, albeit short in duration, shows some potential habitat segregation and use by different chameleons in the East Usambara Mountains as well as providing some potential population traits that raise conservation concern regarding the sustainability of existing harvesting levels. In general, our data suggests strong patterns of habitat selection for many species, with observations restricted to either edge or forest transects. However, it is important to recognize that limited sample size (number of transects) meant that statistical significance could only be shown for one species. Our results suggest that habitat fragmentation and loss is likely to benefit species favoring edge (*C. dilepis*) at the expense of species favoring forest (*R. temporalis* and *T. deremensis*). One important question is whether absence of some species on the forest edge is a result of habitat choice or because of increased harvesting. Qualitatively, we observed far higher human traffic on the edge of the forest compared with the interior. This may translate into higher rates of collection, particularly opportunistic gathering of animals. Although we cannot definitively answer this question, we found *K. vosseleri* and *K. tenuis* to be abundant along forest edges even though these species are the subject of collection pressure (David Patrick,

TABLE 4. Distribution, trade, and habitat of chameleons found in the East Usambara (EU) Mountains, Tanzania (adapted from Jenkins et al. 1999). Distribution data from Spawls et al. 2002, Mariaux et al. 2008, and Necas 1999 and export quotas from http://www.cites.org/eng/resources/species.html (accessed 4/11/2011) numbers refer to wild origin only).

Species	Distribution	Export quotas in 2010	N total observations on transects during surveys	
			Edge	Forest
Trioceros deremensis	Endemic to EU, Uluguru, and Nguru Mountains	500	2	28
Chamaeleo dilepis	Widespread	4000	10	0
Kinyongia tenuis	Endemic to Eastern Arc Mountains	0	5	4
Kinyongia matschiei	Endemic to EU	3000[a]	0	4
Kinyongia Vosseleri	Endemic to EU	3000[a]	12	5
Rieppeleon brevicaudatus	Widespread	Not listed under CITES	2	0
Rhampholeon temporalis	Endemic to EU	Not listed under CITES	0	36
Rhampholeon spinosus	Endemic to EU and West Usambara Mountains	0	0	0

[a]Figure refers to quotas set for *Bradypodion fischeri*, the single species split into *K. matschiei*, *K. vosseleri*, and *K. fischeri*.

pers. obs.), which may indicate that the observed patterns of habitat use are a result of choice rather than collection. The distinct segregation of chameleon species based on habitat characteristics is similar to that shown by previous research in other regions (Hofer et al. 2003; Andreone et al. 2005; Karsten et al. 2009). For example, Andreone et al. (2005) found that *Furcifer* species preferred riparian habitat and habitat along roads, whereas *Calumna* species preferred closed forest to more open habitat. In addition to the horizontal segregation of chameleon species in regard to edge versus forest habitat, we also observed vertical habitat segregation; with different species of chameleon occupying different places in the forest canopy. This finding also fits with that of previous research evaluating patterns of habitat use by chameleon species (Randrianantoandro et al. 2007).

In addition to the occurrence of species, the patterns of abundance we observed among different species of chameleon have clear implications for conservation and management. The second most abundant species, *T. deremensis* has the highest value in the pet-trade market (Roe et al. *op. cit.*). An export quota of 500 wild-taken individuals of this CITES Appendix II species was set by Tanzania in 2010 (Table 4). Other valued species for trade were well represented in our sample (Table 4), including *K. vosseleri* and *K. tenuis*, suggesting that at present these species are fairly abundant in the study area. Conversely *K. matschiei*, another valued species, was not particularly abundant, with only seven individuals found during the course of the study (compared with 23 of the similar *K. vosseleri*). Variation in abundance of morphologically similar species of chameleons has been reported from other regions, presumably due to niche partitioning (Jenkins et al. 1999, 2003), thus it may be that *K. matschiei* is more abundant in habitat types outside of the study region such as shamba. This seems unlikely, however, given that our only observations of the species were in the interior forest. The lower abundance of *K. matschiei* suggests that regulators may want to consider this information when setting harvest quotas. This information is particularly pertinent given the recent separation of *K. matschiei* and *K. vosseleri* into two distinct species, both endemic to the East Usambaras (Mariaux et al. 2008). We also failed to locate a single individual of one endemic species known from the area, *Rhampholeon spinosus*, even though the authors have previously found this species in the study area. This species is known to be valued for the exotic pet trade, although no legal export of wild caught specimens is currently allowed under CITES (Table 4).

Perhaps the most important findings from this research relate to the differences in the size and sex ratios we observed in *T. deremensis*. As previously stated, this large and conspicuous species is the most valued chameleon found in the East Usambaras for the pet trade (Roe et al. *op. cit.*). Thus we would expect that harvesting pressure of this species would also be high. When we conducted our surveys, however, we observed 34 individuals, which provided evidence that a relatively large population exists in the area. This in turn might suggest that current harvesting levels are not likely to be detrimental to the population. On closer examination of our data, however, we observed a significant skew towards more adult females compared to the juvenile sex ratio, and that males were on average much smaller than females. The latter observation is contrary to the published literature for this species, which documents males as the larger sex (Necas 1999; Spawls et al. 2006). Previous research has shown a female sex bias in other chameleon species (Jenkins et al. 1999; Rakotondravony 2004; Rabearivony et al. 2007), but these studies did not report age-class-specific sex ratios. Two potential hypotheses can be advanced to explain these observations. The first is that adult males of this species were missing from the sample due to differences in either behavior (for example if males occupied different habitat) or vital rates (particularly if adult males naturally had much lower survival). The second

hypothesis is that males are experiencing higher rates of apparent mortality, perhaps due to preferential collection of males, which are the only sex with cranial horns in this species (thus making them more desirable for collection). While it is important to note that we did observe recent hatchlings of this species, and the adult females typically thought to limit population growth were abundant, this highly skewed sex ratio has the potential to have effects on the long-term viability of the species, particularly if females are unable to mate; thus, reducing the effective population size (Frankham et al. 2002). There is also the potential for detrimental population effects if the largest adult males are continually removed. This could lead to a reduction in average fitness if small animals become the principal breeders (Fenberg and Roy 2007; Milner et al. 2007).

In summation, our research provides some base line data on which future studies of chameleons in the East Usambara Mountains can be based. Although our study represented a basic assessment of the ecology of chameleons in the East Usambara Mountains with limited statistical power, we were able to identify specific focal areas where further research is clearly warranted. Without these types of rapid assessments, it is challenging to pinpoint exactly where more focused research is of most value. In terms of future research, we believe that one of the most valuable studies will be separating out natural spatio-temporal variation in the ecology of chameleon species from anthropogenic effects. For example, do we see sex-dependent differences in survival under natural conditions? This line of research will necessitate the study of fecundity, longevity, and natural mortality rates, most likely by means of intra- and inter-annual mark-recapture studies. This type of information is necessary for developing the population models we need to evaluate harvesting levels. Understanding the variation in collection pressure across the East Usambara Mountains is also extremely important if we are to be able to ensure sustainable collection levels. Another important line of future research relates to pygmy chameleons; these genera are currently not protected under CITES but are collected for the pet trade. Researchers have provided a strong data-based rationale for protection of dwarf chameleon species in Madagascar under CITES (Carpenter and Robson 2005). Future research may well reveal that African pygmy chameleons are similarly vulnerable to over-collection.

In terms of specific recommendations to the Tanzanian management authorities, we suggest close monitoring of *T. deremensis* populations to ensure that populations are not declining. The inter-specific differences in ecology we observed between *K. vosseleri* and *K. matschiei* also indicate that these two species should be considered separately when setting quotas, and caution should be used in extrapolating life-history data gathered from one species to the other. While it is clear from our research that chameleons still persist in the remaining unfragmented habitat of the East Usambara Mountains despite continued collection pressure, the question remains as to how long this will be the case, and what steps managers can take to ensure that these charismatic and valuable organisms persist.

Acknowledgments.—We would like to thank the Tropical Biology Association (TBA) for all their help and support with our research. We would also like to thank the Tanzanian government for their support of the research conducted as part of the TBA course, including this study. The staff at the Amani Nature Reserve headquarters provided numerous helpful contributions to this project. Chris Anderson and Jeroen van Leeuwen provided valuable information about chameleon biology. Rebecca Banasiak at the Field Museum of Natural History kindly provided a map of the study region.

LITERATURE CITED

Andreone, F., F.M. Guarino, and J.E. Randrianirina. 2005. Life history traits, age profile, and conservation of the Panther Chameleon, *Furcifer pardalis* (Cuvier 1829), at Nosy Be, NW Madagascar. Tropical Zoology 18:209–225.

Buckland, S.T., D.R. Anderson, K.P. Burnham, and J.L. Laake. 1993. Distance Sampling: Estimating Abundance of Biological Populations. Chapman and Hall, London, UK.

Burgess, N.D., T.M. Butynski, N.J. Cordeiro, N. Doggart, J. Fjeldså, K. Howell, F. Kilahama, S.P. Loader, J.C. Lovett, B. Mbilinyi, M. Menegon, D.C. Moyer, E.A. Nashanda, A. Perkin, W.T. Stanley, and S.N. Stuart. 2007. The biological importance of the Eastern Arc Mountains of Tanzania and Kenya. Biological Conservation 134:209–231.

Carpenter, A.I., J.M. Rowcliffe, and A.R. Watkinson. 2004. The dynamics of the global trade in chameleons. Biological Conservation 120:291–301.

Carpenter, A.I., and O. Robson. 2005. A review of the endemic chameleon genus *Brookesia* from Madagascar, and the rationale for its listing under CITES Appendix II. Oryx 39:375–380.

Cordeiro, N.J., D.A. Patrick, B. Munisi, and V. Gupta. 2004. Role of dispersal in the invasion of an exotic tree in an East African sub-montane forest. Journal of Tropical Ecology 20:449–457.

Fenberg, P.B., and K. Roy. 2007. Ecological and evolutionary consequences of size-selective harvesting: How much do we know? Molecular Ecology 17:209–220.

Frankham, R., J.D. Ballou, and D.A. Briscoe. 2002. Introduction to Conservation Genetics. Cambridge University Press, New York, New York, USA.

Hamilton, A.C. 1989. The climate of the East Usambaras. Pp. 97–102 *In* Forest Conservation in the East Usamabara Mountains, Tanzania. Hamilton, A.C., and R. Bensted-Smith (Eds.). IUCN, Gland, Switzerland.

Hamilton, A.C., and R. Bensted-Smith (Eds.). 1989, Forest Conservation in the East Usamabara Mountains, Tanzania. IUCN, Gland, Switzerland.

Hofer, U., H. Baur, and L. Bersier. 2003. Ecology of three sympatric species of the genus Chamaeleo in a tropical upland forest in Cameroon. Journal of Herpetology 37:203–207.

Jenkins, R.K.B., L.D. Brady, M. Bisoa, J. Rabearivony, and R.A. Griffiths. 2003. Forest disturbance and river proximity influence chameleon abundance in Madagascar. Biological Conservation 109:407–415.

Jenkins, R.K.B., L.D. Brady, K. Huston, J.L.D. Kauffmann, J. Rabearivony, G. Raveloson, and J.M. Rowcliffe. 1999. The population status of chameleons within Ranomafana National Park, Madagascar, and recommendations for future monitoring. Oryx 33:37–45.

Karsten, K.B., L.N. Andriamandimbiarisoa, N. Laza, S.F. Fox, and C.J. Raxworthy. 2009. Population densities and conservation assessments for three species of chameleons in the Toliara region of south-western Madagascar. Amphibia-Reptilia 30:341–350.

Lovett, J.C. 1998. Continuous change in Tanzanian moist forest tree communities with elevation. Journal of Tropical Ecology 14:719–722.

Lovett, J M. and S.K. Wasser. 1993. Biogeography and Ecology of the Rain Forests of Eastern Africa. Cambridge University Press, Cambridge.

Mariaux, J., N. Lutzmann, and J. Stipala. 2008. The two-horned chameleons of East Africa. Zoological Journal of the Linnaen Society 152:367–391.

Milner, J.S., E.B. Nilsen, and H.P. Andreassen. 2007. Demographic side effects of selective hunting in ungulates and carnivores. Conservation Biology 21:36–47.

Necas, P. 1999. Chameleons: Nature's Hidden Jewels. Krieger Publishing Company, Malabar, Florida, USA.

Newmark, W.D. 1991. Tropical forest fragmentation and the local extinction of understory birds in the East Usambara Mountains, Tanzania. Conservation Biology 5:67–78.

Newmark, W.D. 2001. Tanzanian forest edge microclimate gradients: dynamic patterns. Biotropica 33:2–11.

Newmark, W.D. 2006. A 16-year study of forest disturbance and understory bird community structure and composition in Tanzania. Conservation Biology 20:122–134.

Rabearivony, J., L.D. Brady, R.K.B. Jenkins, and O.R. Ravaohangimala. 2007. Habitat use and abundance of a low-altitude chameleon assemblage in eastern Madagascar. Herpetological Journal 17:247–254.

Rakotondravony, H.A. 2004. Diversity of forest chameleons in Andasibe area (Madagascar) and pattern of their distribution in the various physiognomic forest types. Revue d'Ecologie-La Terre et La Vie 59:529–544.

Randrianantoandro, J.C., R. Randrianavelona, R.R. Andriantsimanarilafy, H.E. Fideline, D. Rakotondravony, and R.J.B. Jenkins. 2007. Roost site characteristics of sympatric dwarf chameleons (genus *Brookesia*) from western Madagascar. Amphibia-Reptilia 28:577–581.

Reynolds, J.D., G.M. Mace, K.H. Redford, and J.G. Robinson, editors. Conservation of Exploited Species. Cambridge University Press, Cambridge, UK.

Spawls, S., K.M. Howell, and R.C. Drewes. 2006. Pocket Guide to Reptiles and Amphibians of East Africa. Princeton University Press, Princeton, New Jersey, USA.

Spawls, S., K.M. Howell, R.C. Drewes, and J. Ashe. 2002. A Field Guide to the Reptiles of East Africa. Academic Press, San Diego, California, USA.

Wilcove, D.S., D. Rothstein, J. Dubow, A. Phillips, and E. Losos. 1998. Quantifying threats to imperiled species in the United States. Bioscience 48:607–615.



DAVID PATRICK is a Conservation Biologist whose research focuses on population biology and the effects of habitat alteration and has a particular interest in amphibian and reptiles. (Photographed by Elizabeth Harper)



PHILIP SHIRK is a masters student at Virginia Commonwealth University where he is studying chameleon population biology and habitat use. His broader research interests include herpetological ecology and conservation. (Photographed by David Patrick)



JAMES VONESH is a population and community ecologist whose research has focused in large part on tropical amphibians and reptiles, particularly those of East Africa and Central America. (Photographed by Sophia Balcomb)



ELIZABETH HARPER's research interests include using a combination of field data and ecological modeling to address conservation issues. She also studies the natural history of East African amphibians and recently co-authored a Field Guide to the Amphibians of the Eastern Arc and Coastal Mountains of Tanzania and Kenya. (Photographed by David Patrick)



KIM HOWELL has been based at the Department of Zoology & Wildlife Conservation, University of Dar es Salaam, since 1970. His research interests are broad and include small vertebrate taxonomy, distribution, ecology, and conservation. (Photographed by Tim Davenport)