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Isami IKEUCHI[1,2] and Akira MORI[1]*

[1]*Department of Zoology, Graduate School of Science, Kyoto University, Sakyo, Kyoto 606–8502, JAPAN*
[2]*Present address: Takinocho 2–19–3–202, Nagaokakyo, Kyoto 617–0817, JAPAN*

Abstract: **Several aspects of natural history of *Blaesodactylus ambonihazo*, a gecko distributed in a dry forest of northwestern Madagascar, were investigated in the rainy and dry seasons between 2000 and 2006. There were no significant sexual size differences in snout-vent length, and no sexual dimorphism was detected either in head width or body mass. Females ceased oogenesis during the rainy season and were recrudescent at the beginning of the dry season. They probably lay eggs in the middle of the dry season. Hatchlings were observed at the beginning of the rainy season and probably reach adult size in the subsequent dry season. At night geckos perched on tree trunks and buildings and exhibited typical sit-and-wait foraging. During the day they retreated to shelters, mainly crevices between buttress roots. The gecko was thermally passive to environmental temperatures, showing a wide range of cloacal temperatures (15–30 C), but they selected relatively higher substrate temperatures at low air temperature, possibly for thermoregulation. Because multiple individuals were observed on single trees, home ranges of the gecko were presumably overlapping each other, and no obvious territorial behavior was observed. The absence of male-biased sexual dimorphism, which suggests little male-male competition for mating, also supports the absence of territoriality of *B. ambonihazo*. Comparison with a syntopic diurnal gecko, *Phelsuma kochi*, which shows ecological characters similar to *B. ambonihazo* but has exclusive home ranges, may clarify ecological correlates associated with temporal niche partitioning.**

Key words: Gekkonidae; *Blaesodactylus ambonihazo*; Madagascar; Field observation; Ankarafantsika National Park

INTRODUCTION

Gekkota is a large monophyletic group of Squamata, which accounts for approximately one-fourth of all species of lizards (Bauer, 2013). Gekkonidae, the largest family of Gekkota, is comprised of approximately 930 species and is mainly distributed in the Old World (Bauer, 2013). Because of their high species richness, their ecology and life history are likely to be diverse. Nonetheless, information on their natural history based on quantitative field observations is lacking for the majority of the species, impeding comparative

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* Corresponding author. Tel: +81–75–753–4075;
Fax: +81–75–753–4075;
E-mail address: gappa@ethol.zool.kyoto-u.ac.jp

examinations of their ecological diversification.

Madagascar is one of the global hotspots that has a great species diversity of endemic reptiles (Myers et al., 2000; Goodman and Benstead, 2005). Gekkos are not exceptional: more than 10% of gekkonids, most of which are endemic, occur in Madagascar (Glaw and Vences, 2007). However, in spite of their tremendous diversity and high endemism, ecological and behavioral studies on wild geckos in Madagascar based on quantitative data are extremely limited (e.g., Vences et al., 2004; Ikeuchi et al., 2005, 2012). Appropriate knowledge of natural history of each species is essential to understand the patterns of their adaptive radiation. In addition, because original forests of Madagascar, which are major habitats of the geckos, currently suffer from severe fragmentation by fires, illegal logging, and deforestation for agriculture (Ganzhorn, 2001; Dufils, 2003), such knowledge is critical to evaluate the influence of deforestation on their survival and establish conservation measures and management strategies of them.

In the present study we examined several aspects of natural history of a gecko, *Blaesodactylus ambonihazo*, which is known only from a dry forest of northwestern Madagascar (Bauer et al., 2011). The taxonomic history of geckos in *Blaesodactylus* was recently reviewed by Greenbaum et al. (2007). They confirmed the sister group relationship and reciprocal monophyly of the Malagasy *Blaesodactylus* and the mainland African *Homopholis*. Greenbaum et al. (2007) also reported a specimen that is genetically highly divergent from all other recognized species of *Blaesodactylus*. Subsequently, Bauer et al. (2011) made detailed examinations of this form both morphologically and genetically and described *B. ambonihazo* as the fourth member of this genus from a dry forest in Ankarafantsika National Park. In the present study we describe its size composition, female reproductive traits, thermal characteristics, spatial usage, and foraging mode based on a long-term field study.

Materials and Methods

The study was conducted in a tropical deciduous forest at Ampijoroa, Ankarafantsika National Park (16°19'S, 46°49'E) from October 2000 to January 2001, from June to July 2003, from October 2003 to June 2004, and from November 2005 to February 2006. The dry season usually lasts from May to October, and the rainy season starts gradually in November (See Fig. 1 in Ikeuchi et al., 2012). The study area included a camping site (approximately 250×100 m), Jardin Botanique A (JBA: approximately 550×450 m), trails from the camping site to JBA (approximately 1200 m), and trails around Lake Ravelobe (approximately 5 km). The vegetation consisted of a deciduous canopy of 10–15 m high and fairly sparse understory.

We walked through the study area at least twice per week in the day (0700–1800 h) and at night (2000–0400 h), searching for geckos on trees and buildings up to ca. 4 m high. When a gecko was located, we attempted to collect it with a noose or by hand. We immediately measured its cloacal temperature (CT), air temperature at 1 m above the ground (AT), and substrate temperature at the exact spot where the gecko was perching (ST) using a quick-reading thermistor. When geckos were perching in high places (approximately more than 2 m), we measured substrate temperature at the spot as close as possible. Then we measured its snout-vent length (SVL), head width (HW), and body mass (BM). Sex was determined as male if a gecko had a swollen tail base (i.e., hemipeneal bulge). Gravidity of females was confirmed by observation and palpation of eggs in the abdomen. Individuals with SVL smaller than that of males and gravid females were considered juveniles (see Results). After measurement, the individuals were marked by toe clipping and were released at the site where they were found. We recorded habitat type (tree or building) for each gecko's perch site and whether it was exposed (exposed or in shelter). If the perch site was a tree, substrate characters (trunk, branch, crevice

between trunk, crevice between buttress roots, or hole), perch height (PH), perch diameter (PD), and diameter at the breast height (DBH; 1.2 m high) of the tree were recorded. If a marked gecko was re-sighted on a tree different from the previous one, the distance between the trees was measured.

To examine foraging mode, focal animal observations were conducted for six geckos, which were perching on trees in forest, at night (2100–0100 h) from March to June 2004 using an infrared video camera. We continuously observed their behavior at least for 17 min standing at least 5 m away from trees where they were perching. An individual was classified as either stationary or moving. Stationary included postures and actions in which the gecko remained in the same position (e.g., remaining motionless, moving its head, jaws, tongue, limbs, or tail, and turning around by 180 degrees). Moving included actions that accompany the change of location of the gecko (e.g., crawling, walking, running, jumping, and jerking forwards). When the gecko changed its behavior from stationary to moving, or vice versa, the time was recorded. To facilitate a comparison with previous studies (e.g., Cooper, 2005; Bauer, 2007; Perry, 2007), we calculated moves per minute (MPM) and percent of time spent moving (PTM) (Huey and Pianka, 1981).

An ANCOVA was used to examine sexual differences of body size (SVL as covariate) and thermal usage (CT as covariate) after tests for significance of the regression. The differences between CT and corresponding AT or ST were examined at night and in the day separately by paired t-test. Mann-Whitney U-test was used to analyze spatial usage (PH, PD, and DBH) differences between day and night. Sexual differences of SVL, diurnal and nocturnal spatial usages, and moving distance were also tested using Mann-Whitney U-test. The correlation between DBH and the number of individuals sharing the same tree and the correlation between maximum moving distance and the days from the first to last observations of an individual were analyzed using Kendall's correlation coefficient.

RESULTS

Size composition and female reproductive trait

Because the minimum SVL of males and gravid females were 66.6 mm and 85.3 mm, respectively, individuals whose SVL was less than 66.6 mm were considered juveniles. The two smallest individuals (SVL=44.0 and 44.2 mm) each had an obvious umbilicus and were considered as hatchlings. Sexual difference in SVL was not detected (Mann-Whitney U-test; U=3734.5, P=0.70; Table 1). Head width and BM were both significantly correlated with SVL (log transformed data; HW, $r^2=0.95$, P<0.0001, BM, $r^2=0.98$, P<0.0001), and there were no significant differences between sexes both in HW and BM (ANCOVA, log transformed data; HW, elevation, df=1, 170, F=0.85, P=0.36, slope, df=1, 170, F=0.90, P=0.35; BM, elevation, df=1, 170, F=0.00001, P=0.99, slope, df=1, 170, F= 0.00001, P=0.99). Small individuals (SVL<

TABLE 1. Morphological measurements of *Blaesodactylus ambonihazo*. SVL: snout-vent length, HW: head width, BM: body mass. Mean±SD are shown. Figures in parentheses are sample size and range.

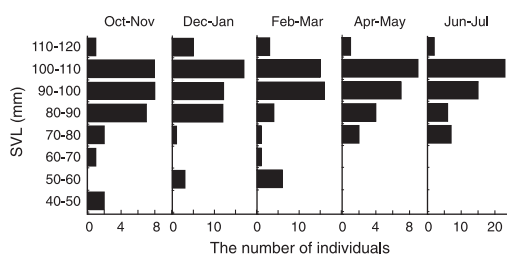| Sex	SVL (mm)	HW (mm)	BM (g)
Male	96.9±9.94	19.6±2.04	22.5±7.38
	(92, 66.6–112)	(92, 14.3–23)	(91, 6.8–40.4)
Female	97.2±10.6	19.5±2.14	23.1±7.58
	(84, 70.5–115)	(84, 14.8–23.5)	(83, 6.7–36.4)

FIG. 1. The seasonal change of the number of *Blaesodactylus ambonihazo* classified by snout-vent length. Data in 2000–2001, 2003–2004, and 2005–2006 were combined.
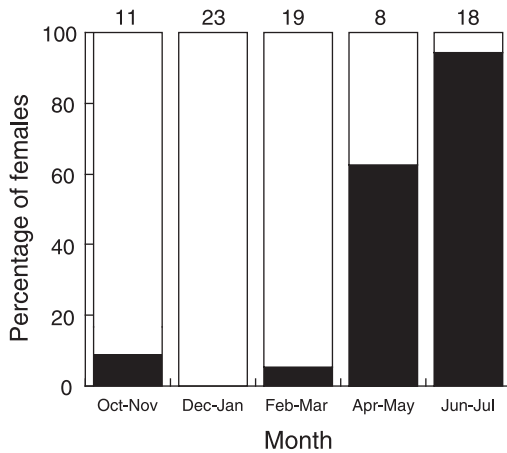
FIG. 2. The percentages of gravid (solid column) and non-gravid females (open column) of *Blaesodactylus ambonihazo* in each two-month period. The number of individuals is denoted above each column. Data in 2000–2001, 2003–2004, and 2005–2006 were combined.

50.0 mm) were observed only at the beginning of the rainy season (October to November) (Fig. 1). The cohort gradually shifted to a larger class, and no juveniles (SVL<66.6 mm) were observed at the beginning of the dry season (April and May).

The percentage of gravid individuals among mature females (SVL≥85.3 mm) was quite low during the rainy season (November-March), and it increased from the beginning of the dry season (Fig. 2). All but one mature females (95%) were gravid in June and July. Twenty-three out of 26 (88%) gravid females had two eggs in their abdomen, and the remaining three had only one egg.

Thermal usage

At night CT of geckos was significantly higher than corresponding AT and ST (paired t-test; AT, t=-12.86, P<0.0001; ST, t=-9.54, P<0.0001; Fig. 3A). However, at low ambient temperatures (less than 22 C) CT of geckos remained higher than AT, whereas CT were close to or lower than ST. During the day, CT was significantly higher than the corresponding ST, but lower than the corresponding AT (paired t-test; AT, t=4.70, P<0.0001; ST, t=-5.97, P<0.0001; Fig. 3B). Cloacal temperature was significantly correlated with AT and ST both at night and in the day (log transformed data; night, AT, $r^2=0.92$, P<0.0001, ST, $r^2=0.95$, P<0.0001; day, AT, $r^2=0.86$, P<0.0001, ST, $r^2=0.89$, P<0.0001), and there were no significant sexual differences in CT at a given AT or ST both at night and in the day (ANCOVA, log transformed data; night, AT, elevation, df=1, 45, F=2.66, P=0.11, slope, df=1, 45, F=2.5, P=0.12, ST, elevation, df=1, 45, F=0.67, P=0.42, slope, df=1, 45, F=0.72,
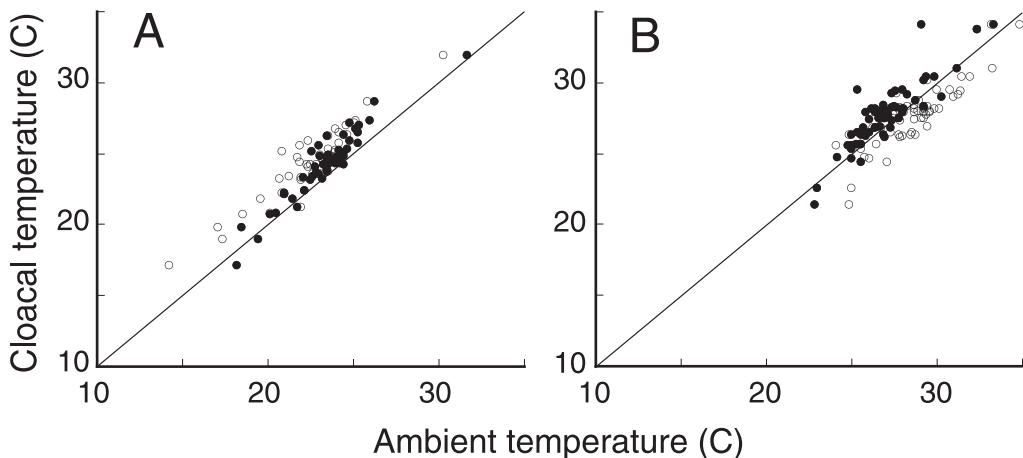

FIG. 3. Relationships between cloacal temperature of *Blaesodactylus ambonihazo* with air temperature (open circle) and substrate temperature (solid circle). The lines where cloacal temperature is equal to ambient temperature are also shown. A: night, B: day.

P=0.40; day, AT, elevation, df=1, 52, F=2.96, P=0.09, slope, df=1, 52, F=2.69, P=0.11, ST, elevation, df=1, 52, F=0.38, P=0.54, slope, df=1, 52, F=0.37, P=0.54).

Perch sites

We captured 58 and 128 geckos at night and in the day, respectively. At night all but two individuals were observed in exposed conditions, and in the day all but five geckos were in shelters (Table 2). Among geckos observed on trees, 91.4% of the individuals perched on trunks at night, and 71.0% used crevices between buttress roots in the day.

Perch height, PD, and DBH in the day were significantly larger than those at night (Mann-Whitney U-test; PH, U=1141.5, P<0.0001; PD, U=1189, P<0.005; DBH U=1184, P< 0.005; Table 3). Sexual differences in PH, PD, and DBH were not detected either at night or in the day (Mann-Whitney U-test; night, PH, U=130, P=0.83, PD, U=133.5, P=0.93, DBH, U=133, P=0.91, male, n=16, female, n=17;

TABLE 2. Perching site of *Blaesodactylus ambonihazo* at night and in the day.

Condition of gecko	Perching site	Night	Day
Exposed	Trunk	32	5
	Branch	1	0
	Building (wall, column, girder)	23	0
In shelter	Between buttress roots	1	88
	Between trunks	1	26
	Hole	0	5
	Building (under cover)	0	4

TABLE 3. Measurements of trees perched upon by *Blaesodactylus ambonihazo* at night and in the day. PH: perch height, PD: perch diameter, DBH: diameter at the breast height. Mean±SD are shown. Figures in parentheses are sample size and range.

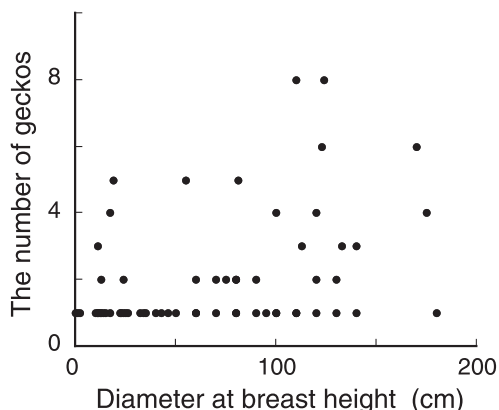| Time	PH (m)	PD (cm)	DBH (cm)
Night	1.09±0.76	49.1±48.5	48.2±48.4
	(35, 0.2–3.8)	(35, 0.2–150)	(35, 0.2–150)
Day	1.69±0.89	85.6±50.5	90.8±51.4
	(122, 0.1–4.3)	(117, 3–250)	(119, 0–210)

FIG. 4. Relationship between diameter of trees at breast height (1.2 m height) and the number of *Blaesodactylus ambonihazo* observed on the tree.

day, PH, U=1343.5, P=0.70, PD, U=1231.5, P=0.27, DBH, U=1359.5, P=0.78, male, n= 52, female, n=54).

Geckos perched on 95 different trees, and 28 of them (29.5%) were used by at least two individuals (at most eight individuals). At least two males, two females, and both sexes were collected on 12 trees (12.6%), 11 trees (11.6%), and 21 trees (22.1%), respectively. A positive correlation between DBH and the number of individuals using the same tree was detected (Kendall; t=0.32, P<0.0001; Fig. 4). On 13 trees (13.8%) two or three individuals were simultaneously perching at single observations (19 times). The compositions of the individuals using the same tree were two males (two cases), two females (one case), a male and a female (10 cases), and an adult and juveniles or unknown sex (6 cases).

Moving distance

Twenty-four individuals were sighted at least twice (maximum four times) on trees at an interval of more than a month. No correlation was found between maximum moving distance and the days from the first to last observations of an individual (46–918 days) (Kendall; t=0.15, P=0.32). Seventeen (10 males, 6 females, and a juvenile, 70.8%) of the re-sighted geckos were found on the same trees where they were first captured. Two of

seven individuals that had moved to another tree, returned to the tree they initially used. The average moving distances±SD of males and females were 7.42±14.65 m (n=13, range 0–43.3) and 7.15±10.16 m (n=10, range 0–27.3), respectively; no sexual difference was detected (Mann-Whitney U-test; U=59.0, P=0.65).

Foraging mode

Six geckos perching on tree trunks were observed for 17.0 to 50.1 min. Locomotary movement was rarely observed. Mean of MPM and PTM±SD were 0.21±0.21 (range, 0.04–0.58) and 0.86±0.96 (range, 0.07–2.27), respectively.

DISCUSSION

Although the climate of the study site has distinct dry and rainy seasons, *B. ambonihazo* seems to be active throughout the year. The seasonal changes in the frequency of gravid females and in the size distribution of the gecko suggest that females cease oogenesis during the rainy season (October to March), recrudesce at the beginning of the dry season, and probably lay eggs in the middle of the dry season (June to August). Based on the incubation period (112–126 days) of *B. sakalava* reported by Pes (2005), eggs of *B. ambonihazo* may hatch at the beginning of the subsequent rainy season, which is consistent with the occurrence of hatchlings in October-November. These reproductive traits of *B. ambonihazo* are different from those of the other syntopic lizards, whose oogenesis and oviposition occur only in the rainy season (*Oplurus cuvieri*; Randriamahazo and Mori, 2001) or continue almost annually with a higher reproductive activity in the rainy season (*Phelsuma kochi*; Ikeuchi et al., 2005), which has been also reported in a gecko in another dry forest of Madagascar (Vences et al., 2004). Hatchlings of *B. ambonihazo*, observed at the beginning of the rainy season, seem to reach adult size during the subsequent dry season. Overall, although our survey effort was not constant throughout the year,

it is obvious that this gecko does not greatly reduce its activity in the harsh, dry season, when virtually no rainfall is available (Ikeuchi et al., 2012).

We observed the gecko both during the day and at night. However, more than 95% of geckos sighted in the day were partially or entirely hiding their bodies in shelter and remained motionless. On the other hand, all but two geckos sighted at night were perching on trees or buildings while exposing their entire bodies. These observations indicate that *B. ambonihazo* is a primarily nocturnal gecko, although some diurnal activity of congeneric species as well as *B. ambonihazo* has been described or suggested (Glaw and Vences, 2007; Bauer et al., 2011). Detailed focal animal observations would clarify the biological role of the possible diurnal activity of these basically nocturnal geckos. As implied by its specific name, *ambonihazo*, which means "on tree", none out of the 186 individuals were found on the ground, confirming its tree-dwelling habit (Bauer et al., 2011).

Like other nocturnal geckos (Autumn et al., 1994, 1997), *B. ambonihazo* was active over a wide-range of environment temperatures (15–30 C) at night. This gecko is considered thermally passive to ambient temperatures but seems to select a little higher ST at low AT for thermoregulation, which is reported in some other crepuscular or nocturnal geckos (Rock et al., 2000; Vitt et al., 2007). During the day geckos retreated to narrow shelters, mainly crevices between buttress roots. Because the substrate temperatures in shelters are lower than outside air temperatures in the day, the gecko might stay in cooler sites to thermoregulate like other gecko species (Kearney and Predavec, 2000; Shah et al., 2004; Vitt et al., 2007), although we do not have any data for preferred body temperatures of *B. ambonihazo*. Otherwise, shelters might protect *B. ambonihazo* against desiccation, because they can provide suitable hydric conditions (Schwarzkopf and Alford, 1996), or the gecko may simply retreat for predator avoidance in the day.

Lizards have been categorized into a dichotomous paradigm, either sit-and-wait or widely foragers (MPM values of ≤1.5 and PTM values of <10 indicate sit-and-wait, and PTM of >10 indicates widely foraging, Huey and Pianka, 1981; Cooper, 2005; Perry, 2007), although the presence of another mode has been documented (Butler, 2005) and controversy still remains. Sit-and-wait foragers detect moving prey visually while immobile, whereas widely forager moves around to detect hidden prey using chemical cues (Cooper, 2005). Bauer (2007) suggested that a majority of gekkotan species are either sit-and-wait foragers to a large extent (Cooper et al., 1999; Werner and Chou, 2002; Ikeuchi et al., 2005; Aowphol et al., 2006), or intermediate or mixed foragers using the slow cruise foraging or serial ambushing (Werner et al., 1997, 2004). Although sample size is limited, *B. ambonihazo* is considered a typical sit-and-wait forager, spending most of the time perching on the lower part of a tree trunk.

Generally, spacing pattern of lizards is affected by the availability of resources (Fox and Shipman, 2003). The number of *B. ambonihazo* increased on old large trees, such as *Albizia* sp., *Ceiba pentandra*, and *Hura crepitans*, which would provide more spatial resources as shelters (buttress roots and holes) and foraging sites (Fitzgerald et al., 2002; Reaney and Whiting, 2003). Localized distribution of resources on large trees might result in congregative and extended occupation by this gecko of these trees. At night geckos leave their shelters for foraging sites, therefore, their home ranges presumably overlap each other although our data on home range size is insufficient. The spatial distribution of gecko home ranges hitherto reported varies among species although available information is quite limited. Some species have home ranges that overlap both intra- and inter sexually (Semenov and Borkin, 1992; Gruber and Henle, 2006; Johnston and Bouskila, 2007), whereas others are exclusive only between males (Ikeuchi et al., 2005; Hibbitts et al., 2007). *Blaesodactylus ambonihazo* may have a former type because

this gecko may share trees with other individuals, even other males. Moreover, male-biased sexual dimorphism, which is generally found in lizards in which males have exclusive home ranges as a result of sexual selection through male-male competition for mating (Ikeuchi et al., 2005; Hibbitts et al., 2007), is completely absent in *B. ambonihazo*. This also supports the possibility of overlapping home ranges between males of this gecko.

Although our data suggest the stable activity of *B. ambonihazo* throughout the year, it is likely that the above ecological and behavioral traits, such as home range size and foraging mode, may change depending on seasons. Small sample size of our study precludes confirmative seasonal comparisons of such traits. Further studies focusing on seasonal differences in ecological and behavioral features are necessary to consider appropriate conservation measures. In addition, it should be noted that *B. ambonihazo* often used artificial buildings as well as natural forest trees as perching site at night. This suggests that the gecko may be tolerant, to some extent, to artificial modification of environments by fragmentation of forest. Detailed comparisons of life history traits, such as growth and survivorship, between natural and artificial environments are important to evaluate ecological impacts of artificial modification of environments

In contrast to *B. ambonihazo*, *Phelsuma kochi*, a syntopic diurnal gecko in the Ampijoroa forest, shows exclusive home ranges within males, presumably because the dependence on visual modality in diurnal activity allows them to survey a greater distance and to defend their home ranges against other males (Ikeuchi et al., 2005). The genus *Phelsuma*, a speciose diurnal group of geckos, is inferred to be derived from nocturnal ancestors (Taniguchi et al., 1999; Han et al., 2004; Nagy et al., 2012). Comparative study of ecological and behavioral traits of *B. ambonihazo* and *P. kochi*, which have similar body size, microhabitat (tree-dwelling), and possibly diet (insectivorous) (Ikeuchi et al.,

2005, unpublished data), would help to clarify features induced by temporal niche partitioning, which allow their co-existence. Moreover, to fully understand the ecological radiation of geckos in the Ampijoroa forest, which harbors at least 12 species of geckos (Mori et al., 2006), fundamental natural history studies are essential and should be greatly encouraged. Such research would provide clues to unravel the evolutionary mechanisms of the enormous diversification in geckos on the island of Madagascar.

Literature Cited

Aowphol, A., Thirakhupt, K., Nabhitabhata, J., and Voris, H. K. 2006. Foraging ecology of the Tokay gecko, *Gekko gecko* in a residential area in Thailand. *Amphibia-Reptilia* 27: 491–503.

Autumn, K., Farley, C. T., Emshwiller, M., and Full, R. J. 1997. Low cost of locomotion in the banded gecko: a test of the nocturnality hypothesis. *Physiological Zoology* 70: 660–669.

Autumn, K., Weinstain, R. B., and Full, R. J.

1994. Low cost of locomotion increases performance at low temperature in a nocturnal lizard. *Physiological Zoology* 67: 238–262.

Bauer, A. M. 2007. The foraging biology of the Gekkota: life in the middle. p. 371–404. *In*: S. M. Reilly, L. B. McBrayer, and D. B. Miles (eds.), *Lizard Ecology*. Cambridge University Press, Cambridge.

Bauer, A. M. 2013. *Geckos. The Animal Answer Guide*. The Johns Hopkins University Press, Baltimore.

Bauer, A. M., Glaw, F., Gehring, P.-S., and Vences, M. 2011. New species of *Blaesodactylus* (Squamata: Gekkonidae) from Ankarafantsika National Park in north-western Madagascar. *Zootaxa* 2942: 57–68.

Butler, M. A. 2005. Foraging mode of the chameleon, *Bradypodion pumilum*: a challenge to the sit-and-wait versus active forager paradigm? *Biological Journal of the Linnean Society* 84: 797–808.

Cooper, Jr., W. E. 2005. The foraging mode controversy: both continuous variation and clustering of foraging movements occur. *Journal of Zoology* 267: 179–190.

Cooper, Jr., W. E., Whiting, M. J., Wyk, J. H. V., and Mouton, P. le. F. N. 1999. Movement- and attack-based indices of foraging mode and ambush foraging in some gekkonid and agamine lizards from southern Africa. *Amphibia-Reptilia* 20: 391–399.

Dufils, J. M. 2003. Remaining forest cover. p. 88–96. *In*: S. M. Goodman and J. P. Benstead (eds.), *The Natural History of Madagascar*. The University of Chicago Press, Chicago.

Fitzgerald, M., Shine, R., and Lemckert, F. 2002. Radiotelemetric study of habitat use by the arboreal snake *Hoplocephalus stephensii* (Elapidae) in eastern Australia. *Copeia* 2002: 321–332.

Fox, S. F. and Shipman, P. A. 2003. Social behavior at high and low elevations. p. 310–355. *In*: S. F. Fox, J. K. McCoy, and T. A. Baird (eds.), *Lizard Social Behavior*. The Johns Hopkins University Press, Baltimore.

Ganzhorn, J. U., Lowry II, P. P., Schatz, G. E., and Sommer, S. 2001. The biodiversity of Madagascar: one of the world's hottest hotspots

on its way out. *Oryx* 35: 346–348.

GLAW, F. AND VENCES, M. 2007. *A Field Guide to the Amphibians and Reptiles of Madagascar. 3rd Edition*. Vences & Glaw Verlag, Cologne.

GOODMAN, S. M. AND BENSTEAD, J. P. 2005. Updated estimates of biotic diversity and endemism for Madagascar. *Oryx* 39: 73–77.

GREENBAUM, E., BAUER, A. M., AND JACKMAN, T. R. 2007. *Homopholis* and *Blaesodactylus* (Squamata: Gekkonidae) revisited: new insights from a molecular phylogeny. *African Journal of Herpetology* 56: 101–114.

GRUBER, B. AND HENLE, K. 2006. The effect of movement on survival—a new method with an application in the arboreal gecko *Gehyra variegata*. p. 43–46. *In*: M. Vences, J. Köhler, T. Ziegler, and W. Böhme (eds.), *Herpetologia Bonnensis II. Proceedings of the 13th Congress of the Societas Europaea Herpetologica*. Societas Europaea Herpetologica, Bonn.

HAN, D., ZHOU, K., AND BAUER, A. M. 2004. Phylogenetic relationships among gekkotan lizards inferred from C-*mos* nuclear DNA sequences and a new classification of the Gekkota. *Biological Journal of the Linnean Society* 83: 353–368.

HIBBITTS, T. J., WHITING, M. J., AND STUART-FOX, D. M. 2007. Shouting the odds: vocalization signals status in a lizard. *Behavioral Ecology and Sociobiology* 61: 1169–1176.

HUEY, R. B. AND PIANKA, E. R. 1981. Ecological consequences of foraging mode. *Ecology* 62: 991–999.

IKEUCHI, I., HASEGAWA, M., AND MORI, A. 2012. Characteristics of sleeping sites and timing of depature from them in a Madagascan diurnal gecko, *Lygodactylus tolampyae*. *Current Herpetology* 31: 107–116.

IKEUCHI, I., MORI, A., AND HASEGAWA, M. 2005. Natural history of *Phelsuma madagascariensis kochi* from a dry forest in Madagascar. *Amphibia-Reptilia*. 26: 475–483.

JOHNSTON, G. AND BOUSKILA, A. 2007. Sexual dimorphism and ecology of the gecko, *Ptyodactylus guttatus*. *Journal of Herpetology* 41: 506–513.

KEARNEY, M. AND PREDAVEC, M. 2000. Do nocturnal ectotherms thermoregulate? A study of the temperate gecko *Christinus marmoratus*. *Ecology* 81: 2984–2996.

MORI, A., IKEUCHI, I., AND HASEGAWA, M. 2006. Herpetofauna of Ampijoroa, Ankarafantsika Strict Nature Reserve, a dry forest in northwestern Madagascar. *Herpetological Natural History* 10: 31–60.

MYERS, N., MITTERMEIER, R. A., MITTERMEIER, C. G., DA FONSECA, G. A. B., AND KENT, J. 2000. Biodiversity hotspots for conservation priorities. *Nature* 403: 853–858.

NAGY, Z. T., SONET, G., GLAW, F., AND VENCES, M. 2012. First large-scale DNA barcoding assessment of reptiles in the biodiversity hotspot of Madagascar, based on newly designed COI primers. *PLoS ONE* 7: e34506.

PERRY, G. 2007. Movement patterns in lizards: measurement, modality, and behavioral correlates. p. 13–48. *In*: S. M. Reilly, L. B. McBrayer, and D. B. Miles (eds.), *Lizard Ecology*. Cambridge University Press, Cambridge.

PES, T. 2005. Births and hatchings. Plzen Czech Republic. *EAZA News*. 52: 17.

RANDRIAMAHAZO, H. J. A. R. AND MORI, A. 2001. Egg-laying activities and reproductive traits in females of *Oplurus cuvieri cuvieri*. *Journal of Herpetology* 35: 209–217.

REANEY, L. T. AND WHITING, M. J. 2003. Picking a tree: habitat use by the tree agama, *Acanthocercus atricollis atricollis*, in South Africa. *African Zoology* 38: 273–278.

ROCK, J., ANDREWS, R. M., AND CREE, A. 2000. Effects of reproductive condition, season, and site on selected temperatures of a viviparous gecko. *Physiological and Biochemical Zoology* 73: 344–355.

SCHWARZKOPF, L. AND ALFORD, R. A. 1996. Desiccation and shelter-site use in a tropical amphibian: comparing toads with physical models. *Functional Ecology* 10: 193–200.

SEMENOV, D. V. AND BORKIN, L. J. 1992. On the ecology of Przewalsky's gecko (*Teratoscincus przewalskii*) in the Transaltai Gobi, Mongolia. *Asiatic Herpetological Research* 4: 99–112.

SHAH, B., SHINE, R., HUDSON, S., AND KEARNEY, M. 2004. Experimental analysis of retreat-site selection by thick-tailed geckos *Nephrurus milii*. *Austral Ecology* 29: 547–552.

Taniguchi, Y., Hisatomi, O., Yoshida, M., and Tokunaga, F. 1999. Evolution of visual pigments in geckos. *FEBS Letters* 445: 36–40.

Vences, M., Galán, P., Miramontes, K., and Vieites, D. R. 2004. Weak expression of reproductive seasonality in a dwarf gecko (*Lygodactylus verticillatus*) from arid southwestern Madagascar. *Journal of Arid Environment* 56: 329–338.

Vitt, L. J., Shepard, D. B., Caldwell, J. P., Vieira, G. H. C., França, F. G. R., and Colli, G. R. 2007. Living with your food: geckos in termitaria of Cantão. *Journal of Zoology* 272: 321–328.

Werner, Y. L. and Chou, L. M. 2002. Observations on the ecology of the arrhythmic equatorial gecko *Cnemaspis kendallii* in Singapore (Sauria: Gekkoninae). *Raffles Bulletin of Zoology* 50: 185–196.

Werner, Y. L., Okada, S., Ota, H., Perry, G., and Tokunaga, S. 1997. Varied and fluctuating foraging modes in nocturnal lizards of the Family Gekkonidae. *Asiatic Herpetological Research* 7: 153–165.

Werner, Y. L., Takahashi, H., Yasukawa, Y., and Ota, H. 2004. The varied foraging mode of the subtropical eublepharid gecko *Goniurosaurus kuroiwae orientalis*. *Journal of Natural History* 38: 119–134.