Consequence of inter class competition and predation on the adaptive radiation of lizards and birds in the dry forest of western Madagascar

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**ORNITHOLOGICAL
SCIENCE**

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Abstract   Species interactions among phylogenetically distant but ecologically related vertebrates were studied in a dry forest of western Madagascar to evaluate whether competition and predation between lizards and birds have reciprocally affected adaptive radiation in Madagascar. Of 49 terrestrial and diurnal birds regularly seen in the study forest, we identified six guilds as carnivore (5 spp.), omnivore (2 spp.), carnivore/insectivore (7 spp.), strict insectivore (15 spp.), insectivore/nectarivore (6 spp.), and frugivore (5 spp.). Twelve lizards species were classified as omnivore (1 sp.), strict insectivore (9 spp.), and insectivore with occasional frugivory and nectarivory (2 spp.). The most dominant guilds of the vertebrates in terms of biomass were folivorous/frugivorous parrots, doves, and lemurs (6.7 kg/ha), followed by insectivorous lizards (1.7 kg/ha) and insectivorous birds (0.8 kg/ha) in the Ampijoroa dry forest. Despite their lower biomass, insectivorous birds appeared to be competitively more advantageous than the lizards in terms of prey consumption speed (230 prey/ha/hr by birds vs. 35 prey/ha/hr by lizards). Insectivorous and carnivorous birds may have kept insectivorous lizards from radiating in various niches in Madagascar, and may have promoted a reclusive lifestyle in lizards.

Key words   Adaptive radiation, Birds, Competition, Lizards, Predation

Adaptive radiation is one of the most important processes bridging ecology and evolution, because the process gives rise to ecological diversity and attendant adaptations in different species within a lineage. The study of adaptive radiation, therefore, requires integration of phylogeny, adaptation, ecology, biogeography, and almost all biological sciences (Givnish 1997). Although there are many examples of adaptive radiation among the different lineages of organisms, studies conducted in remote oceanic islands such as the Galapagos and Hawaii Islands are the most classical and well-known. This is because environmental conditions on these islands allow for release from competition with other lineages, thus promoting ecological radiation within a lineage (Futuyma 1997; Grant & Grant 2008).

Adaptive radiation of vertebrate species on Madagascar Island is another classical example (Eguchi 1995). Recent studies on the birds of the family Vangidae demonstrated a wide range of radiation in beak morphology, prey hunting methods, microhabitat utilization, and social system within a lineage (Yamagishi & Eguchi 1996; Yamagishi et al. 2001). However, not all vertebrates on Madagascar Island have exhibited similar extent of radiation. Among the mammalian species, there is a sharp contrast between

the greater species diversity in the lemurs and that in the carnivores (Garbutt 2007). Similarly, among the reptiles, radiation within the Chameleonidae lizard family (Raxworthy et al. 2002) is far greater than that within the Opluridae family (Glaw & Vences 2007). The different degrees of radiations and species diversity among different lineages of the Madagascar vertebrates suggest that we should consider that competitive interactions not only among the closely related species within lineages but also among the distantly related species have potential roles in controlling the extent and speed of adaptive radiations.

In discussing phylogenetic perspectives on community ecology, Losos (1996) clearly stated that the most important criterion in ecological studies is that the taxa included be those likely to interact. Losos also stated that the exclusive use of Linnean taxonomy was the worst solution in deciding which taxa to include in community studies. Therefore, we have explored species interactions among phylogenetically distant but ecologically related groups of vertebrates inhabiting a particular forest in western Madagascar.

Our aim of this study is threefold. The first aim is to describe the guild structure of the vertebrates in a particular forest in western Madagascar. The second is to obtain evidence that the birds and lizards on Madagascar Island have interacted intensively by competing for insectivorous niches or by predating upon each other. The third aim is to discuss the evolutionary consequences of competition and predation on resource segregations both among and within the birds and lizards species, in order to evaluate whether competition and predation between lizards and birds reciprocally affect adaptive radiation in Madagascar Island.

MATERIALS AND METHODS

1) Study site

The study was conducted at the Jardin Botanique A (JBA) and its surrounding forest, located in the Ampijoroa Forest Station of the Ankarafantsika Nature Reserve (16°15′S, 46°48′E, ca. 200 m above sea level), which is approximately 110 km southeast of Mahajanga. The vertebrate fauna of this nature reserve consists of 89 species of birds, 47 species of reptiles, 9 species of amphibians and 19 species of mammals (Mizuta 2005; Mori et al. 2006).

The trail system and vegetation profile of JBA are described by Mizuta (2005). Briefly, the forest is classified as western Malagasy deciduous dry forest (Langrand 1990), and is dominated by 3 species of Strichnos trees that are generally 9–12 m in height. Undergrowth consists of scattered evergreen grasses and low shrubs with rich leaf litter. The climate alternates between the hot, dry season from May to October and the warm, wet season from November to April (Mizuta 2005).

2) Field observation

Observations on the birds' and lizards' foraging behavior, foraging microhabitat, and diet were undertaken from November 8, 2000 to January 20, 2001. To obtain the bird data, we regularly and repeatedly traversed the path and trail daily from just before sunrise (0400) till noon. When a foraging bird was encountered, we followed it for as long as it could be kept in sight. We recorded every movement directed at searching for and capturing prey, location (height above ground, position in tree, tree species as and when possible), capture success, and the kinds of prey obtained. For each foraging sequence by birds, we recorded the number of hops, flights, and prey-attacking maneuvers (glean, hover, and hawk). Diet data was also supplied by recording prey returned to the nest by the parent birds. The nests of several birds that were detected and were subject to the study of social systems, as conducted by Nakamura, Mizuta, Rakotomanana and Asai, were observed directly with binoculars (*Vanga curvirostris*, *Schetba rufa*, *Artamella viridis*, *Leptopterus chabert*, and *Neomixis tenella*) or indirectly using a video recorder (*Terpsiphone mutata* and *Phyllastrephus madagascariensis*).

Foraging maneuvers of the lizards were observed in a similar but slightly different manner. When sunshine fell on the forest floor, usually after 0730, we made censuses on small paths or trails repeatedly over JBA and its vicinity. For every lizard encountered, the location in JBA, the lizards' microhabitats (height above ground; position in tree as trunk, branch, twig and leaf; and tree species as and when possible) and behavior (bask in sun spot, move continuously to search for prey) were recorded. Focal observation was made for quantifying the foraging behavior. We attempted to follow the lizards (*Oplurus cuvieri*, *Mabuya elegans*, and *Zonosaurus laticuadatus*) for at least 10 min and the chameleons (*Frucifer oustaleti* and *F. rhinoceratus*) for 30 min. Durations of foraging movement and basking, distance moved while foraging to the nearest 1 m, prey capture, and the kinds of prey obtained were recorded for the respective focal individuals.

3) Prey category

Prey taken by the vertebrates at JBA was recorded as the lowest possible taxon, and we arbitrarily classified prey items into 45 operational taxonomic units (Table 1). Casual observation for the diel activity pattern, behavior, and microhabitat of the potential prey species was made if time allowed. On the basis of these observations, we further grouped prey items based on their taxonomic position and microhabitats (Table 1).

4) Density and biomass estimates

Densities of 20 regularly seen birds and 3 species of diurnal lemurs (*Eulemur fulvus*, *E. mongoz*, and *Propithecus coquereli*) were measured by spot mapping. We walked the trails of JBA slowly (<2 km/hr) from sunrise till late morning. Exact or approximate locations of singing birds were plotted in relation to the locations of counter-singing birds. Highly vocal interaction among the groups of *E. fulvus* enabled us to adopt a spot mapping method. The density of *E. mongoz* was not determined because of few sightings within JBA. Relatively slow movement by the group of *P. v. coquereli* enabled us to count the groups by systematic and rapid walking on the major trail system of JBA. Densities of territorial birds and group-living lemurs were then estimated by multiplying the number of territories or groups by the mean group size. Except for the bird species known to have helpers (i.e. *Schetba rufa*; Yamagishi et al. 1995) or the species apparently living in groups (*Phyllastrephus madagascariensis*), the mean group size was always assumed to be two.

Density of the lizard (*Oprulus cuvieri*) has already been determined by Randriamahazo and Mori (1999) at the study site (16.6 ha) within JBA. Densities of the other common lizards were estimated in two ways. For *Zonosaurus laticaudatus*, a visual survey was conducted several times in mid-December. Sections of JBA (ca. 1 ha) were carefully surveyed by walking through the fine trails, which subdivided the sections into 5 m×5 m subplots. The total area covered for the survey was 7.5 ha. Although we did not capture or mark the lizards, natural markings such as throat color, length of regenerated tails and scars enabled us to count individual lizards without confusion. The densities of the two arboreal chameleons (*Frucifer oustaleti* and *F. rhinoceratus*) were estimated by direct counts and registration. These chameleons were studied in conjunction with this study by the capture, mark and release method to ex-

Table 1. List of prey items recorded during the field study. Microhabitat of prey are classified as flying (fly), arboreal (arb), terrestrial (ter), hidden in soil or under bark (hid) and fossorial (fos). Three prey taxa are distinguished as invertebrate (inv), vertebrate (ver) and Plant (plt).

Prey item	Habits and microhabitat	taxa
Fly	fly	inv
Dragonfly	fly	inv
Wasp/bee	fly	inv
Butterfly/moth	fly/arb	inv
Cicada	arb	inv
Katidid grasshopper	arb	inv
Aphid	arb	inv
Insect trapped in spider web	arb	inv
Ant lion adult	arb	inv
Walking stick	arb	inv
Leaf hopper	arb	inv
Lepidopteran larvae (hairless)	arb/ter	inv
Lepidopteran larvae (hairy)	arb/ter	inv
Coleoptara adult	arb/ter	inv
Coleopteran larvae	arb/ter	inv
Spider	arb/ter	inv
Mantis	arb/ter	inv
Termite	arb/ter	inv
Spider egg sac	arb/ter	inv
Grasshopper	ter/arb	inv
Ant	ter/arb	inv
Criket/arboreal criket	ter/arb	inv
Pupae/cocoon	hidden	inv
Centipede	ter	inv
Cockroach	ter	inv
Insect carried by ants	ter	inv
Millipede	ter	inv
Land snail	ter	inv
unidentified insect		inv
unidentified small insect (<5 mm)		inv
Frog	ter/arb	ver
Chamereon (*Frucifer* spp.)	arb	ver
Gecko (grey small)	arb	ver
Gecko (grey large)	arb	ver
Day gecko (*Phersuma*)	arb	ver
Lizard (*Amphiglossus*)	fos	ver
Bird egg	arb	ver
Bird nestling	arb	ver
Bird fledgling	arb	ver
Lemur	arb	ver
Leaf(old)	arb	plt
Leaf(new)	arb	plt
Flower nectar	arb	plt
Fruit	arb/ter	plt
Seed	ter	plt

Table 2. Diet overlap among the vertebrate species belonging to six different guild at Ampijoroa forest statation, western Madagascar. Numerals at the respective cells of the table are the number of diet records, and n is sample size. Species in each guild are ordered according to their body mass, and their taxonomic position are distinguished by lettering. Mammals are indicated by bold, reptiles by bold and italic and birds by italic letters.

Species	Body mass	Arthropod						Vertebrate						Plant				N
		Fy	Ab	A/T	Tr	Hd	Un	Fg	Cm	Gk	Sk	Lr	Bd	Lf	Nt	Ft	Sd	
Canivore																		
Accipiter henstii	1050											3						3
Haliaeetus vociferoides	780																	
Polyboroides radiatus	537											2						2
Omnivore																		
Eulemur fulvus	2600		1	2									2	21		17		43
Lophotibis cristata	265																	
Coua ruficeps	182			6	3		1				1					2		13
Zonosaurus laticaudataus	170			5	3			1								2		11
Insectivore/carnivore																		
Leptosomus discolor	255																	
Coua coquereli	180	1	2	4				1										8
Coua cristata	146.9	1	4	12			2			1	1							21
Accipiter francesii	117		1							1		1		1				4
Falculea palliata	111		2	25	5	4				2	1							39
Vanga curvirostris	70	1	3	4				2	24	7								41
Schetba rufa	37	7	2	35	7		15		1									67
Insectivore																		
Frucifer oustleti	282	3		6			17											26
Centropus toulou	161		1	1	1	1												4
Eurystomus glaucurus	148.6		2	5			1											8
Frucifer rhinoceratus	80			1			3											4
Upupa epops	77			1														1
Xenopirostris damii	52			1														1
Artamella viridis	50	1	3	8			1											13
Coracina cinerea	40	2	1	7														10
Merops superciliosus	40	9					9											18
Dicrurus forficatus	37	3	5	10	1		5											24
Phyllastrephus madagascariensis	29	5	13	17			2											37
Copsychus albospecularis	23	1	4	26	2		9											42
Leptopterus chabert	21	27	5	1														33
Cyanolanius madagascarinus	21		2															2
Terpsiphone mutata	13	40	9	4			4											57
Newtonia brunneicauda	10		1	10			10											21
Mabuya elegans	7																	
Amphiglossus intermedius	4																	
Voeltzkowia mira	3																	
Brookesia brygooi	3																	
Phersuma mutabilis	2																	
Lygodactylus tolampyae	1																	
Brookesia sp.	0.4																	
Insectivore/frugivore/nectarivore																		
Oprulus cuvieri	165	1	2	13	2		1									8		27
Mesitornis variegata	89																	
Hypsipetes madagascariensis	43	1	4	7			6									13		31
Phersuma madagascariensis	33																	

Table 2. Continued.

Species	Body mass	Arthropod						Vertebrate						Plant				N
		Fy	Ab	A/T	Tr	Hd	Un	Fg	Cm	Gk	Sk	Lr	Bd	Lf	Nt	Ft	Sd	
Insectivore/frugivore/nectarivore																		
Ploceus sakalava	23			1										1	3	2		7
Zosterops maderaspatana	11		5	1												2		8
Nectarinia souimanga	7	4	3	30			8								45			90
Neomixis tenella	6	3	3	36		3	3									1		49
Folivore/frugivore																		
Propithecus verreauxi	3760													**35**	**8**			43
Eulemur mongoz	2000													**11**	**8**			19
Coracopsis vasa	525													6	2			8
Coracopsis nigra	246														7			7
Treon australis	235														4			4
Streptopelia picturata	182																	
Agapornis cana	31														15			15
Foudia madagascariensis	19														5		2	7

amine life history and demographic characteristics. Intensive daytime and night surveys were conducted to capture and mark out the resident chameleons in a small section of JBA (ca. 1 ha). We assumed the total number of chameleons registered at the site as the minimum number alive within the study plot.

In order to evaluate the relative contribution of each vertebrate group to the biomass of the whole vertebrate community, we estimated the biomass of the respective species at JBA by multiplying the estimated density by the mean body mass. Body mass data were supplied from several sources, including measurement of the individual birds and lizards captured during the study, literatures for birds (Rakotomanana 1998; Ravokatra et al. 2003) and lemurs (Albiganc 1981; Ganzhorn 1988; Mittermeier et al. 1989), a body size database that compiled past measurement data by S. Asai, and estimation from an allometric equation between body length and mass.

RESULTS

1) Guild structure

Of 89 species of birds recorded at the Ampijoroa forest station from 1994–2000 (Mizuta 2005), 49 terrestrial and diurnal species were regularly encountered at JBA during our survey from November 2000 to January 2001. Our own observation of their diet compositions (Table 2), supplemented by the natural history accounts by Langland (1990) and Wilme & Goodmann (2003), identified the guild composition as carnivores (5 spp.), omnivores (2 spp.), carnivore/insectivores (7 spp.), strict insectivores(15 spp.), insectivore/nectarivores (6 spp.), and frugivores (5 spp.).

The mammal fauna at the Ampijoroa forest (Ito et al. unpublished data) consisted of 19 species belonging to Primates (8 spp.), Insectivora (5 spp.), Carnivore (1 sp.), Artiodactyla (1 sp.), and Rodentia (3 spp.). Of these, the most diurnally active and commonly seen species were 3 species of lemurs (*Eulemur fulvus*, *E. mongoz*, and *Propithecus verreauxi*). These largely herbivorous mammals have been studied in detail for their diets and food resource partitioning at Ampijoroa (Ganzhorn 1988; Mittermeier et al. 1994), and we obtained essentially the same result as the preceding studies (Table 2). However, we found that *E. fulvus* is more omnivorous than previously shown because Mizuta (2002) and Nakamura (2004) recorded predation by *E. fulvus* on the eggs and nestlings of *Terpsiphone mutata* and *Plocea sakalava*.

Twelve species of the diurnal lizards at JBA (Mori et al. 2006) were classified according to the diet data (Table 2) into 1 omnivore, 9 strict insectivores, and 2 insectivores with occasional frugivory and nectarivory. The chameleon *Frucifer oustaleti* was assigned as an insectivore in this study, although a re-

cent dietary study showed that this large chameleon occasionally feeds on plant fruits (Takahashi 2008). Diet data for the smaller species of skinks, diurnal geckos, and ground chameleons of genus *Brookesia* were not available, and we simply assumed that they are insectivorous. *Phersuma madagascariensis* was often observed licking tree liquid on the bark (Ikeuchi et al. 2005); hence, we regarded it as an insectivore with occasional nectarivory.

Body mass distributions of the species belonging to the six guilds were compared between the birds and lizards that are active during daytime (Table 2). Two thirds of the 15 strictly insectivorous birds were 10–49 g in body mass, while the same proportion of 9 insectivorous lizards were less than 5 g. The three largest lizards (ca. 150–300 g), each belonging to the families Zonosauridae, Opluridae, and Chameleonidae, were basically insectivorous, with varying degree of carnivory and frugivory (Table 2). Body size classes of 5–50 g were less represented by the insectivorous lizards than by the insectivorous birds.

2) Foraging microhabitat

Mean foraging height and substrate use of the three classes belonging to six guilds are summarized in Table 4, and it appears that the pattern of habitat use was different among the guilds. Two avian carnivores (*Accipiter henstii* and *A. madagascariensis*) mainly used branches at the middle layer of vegetation to scan prey, but we did not observe position of prey capture in a vegetation profile. Three of the 4 omnivorous vertebrates were ground foragers, widely searching for prey in leaf litters and on the leaf litter of fallen fruits. Seven insectivorous birds with occasional carnivory foraged and scanned prey, mainly on the branch at varying heights. Focal observation of these birds suggested that *L. discolor*, *A. francii*, *V. curvirostris*, and *S. rufa* were slow-moving and scanning hunters and that *F. palliata*, *C. cristata*, and *C. coquereli* were continuously moving searchers. Although prey scanning positions were similar among the four hunters, their exact prey capture positions were different. A few direct observations suggested that *L. discolor* and *V. curvirostris* hunted prey on the vegetation high above the ground, while *S. rufa* mostly descended to capture prey on the ground (Yamagishi et al. 1996).

Strict insectivores used a variety of microhabitat for prey scanning and searching (Table 3). Five of 9 insectivorous lizards used ground surface as foraging sites, while among the 14 insectivorous birds, only Upupa epops mainly used the ground as a foraging site. However, as in the case with prey scanning hunters like *S. rufa*, two slow-moving and scanning birds (*E. glaucurus* and *D. forficatus*) often captured prey on the ground surface.

Avian insectivores with occasional frugivory and nectarivory used twigs for prey searching in much greater proportion than the birds belonging to the other guilds (Table 3). As was the case with the exclusively folivorous and frugivorous vertebrates, the species foraging on fruits harvested fresh fruits on the vegetation or picked the fallen ones on the ground surface. Proportional use of twigs and ground thereby became greater in the species showing frugivory than in species belonging to the other guilds.

3) Potential competitive pair between birds and lizards

Based largely on the impressions gained during the field work, we attempted to identify possible competitive species pairs between birds and lizards. Of the six guilds identified in this study, we assumed there was no competitive pair between birds and lizards in carnivores and the folivore/frugivore guild (Table 2). Of the species in the remaining four guilds, the most likely candidates are the two pairs of lizards and birds (*Zonosaurus laticaudatus* and *Coua ruficeps*, and *Oprulus cuvieri* and *Schetba rufa*).

Apart from gross similarities in diet compositions (Table 2), both pairs shared similar foraging microhabitat with similar prey searching modes (Table 3). The lizard *Z. laticuadatus* and the bird *C. ruficeps* actively searched for prey in the leaf litter (Table 3), and both the lizard *O. cuvieri* and the bird *S. rufa* perched on branch or tree trunk and scanned prey moving on the ground (Table 3).

4) Density and biomass

For density and biomass estimation, the vertebrates found at JBA were crudely grouped either into insectivore or folivore/frugivore. Thereafter, we measured densities and biomasses for 20 insectivorous birds (Table 4), 4 folivorous/frugivorous birds and lemurs (Table 5), and 4 insectivorous lizards (Table 6).

The most dominant groups of the vertebrates in terms of biomass were the folivorous/frugivorous parrots, doves, and lemurs (6.7 kg/ha), followed by the insectivorous lizards (1.7 kg/ha) and insectivorous birds (0.8 kg/ha). Although the biomass of insectivorous lizards was two times greater than the birds, the

Table 3. Perch height and perch site selected by the vertebrates at Ampijoroa Forest Station. Abbrebiation used for microhabiat catogory are Gr/Lg as ground and fallen log, TT as tree trunk, Br as alive and dead branch, Vn as vine or liana stem, Tw/Lf as twig with leaf, and Ar as in the air. A: aves; M: mammalia; R: reptilia

Species	Taxa	Perch height	Microhabitat Category						N
			Gr/Lg	TT	Br	Vn	Tw/Lf	Ar	
Carnivore									
Accipiter henstii	A	4.0	0.33		**0.67**				3
Accipiter madagascariensis	A	4.0			**1.00**				2
Omnivore									
Eulemur fulvus	M	5.9		0.02	**0.78**		0.20		46
Zonosaurus laticaudataus	R	0.4	**0.88**	0.12					25
Lophotibis cristata	A	0.0	**1.00**						6
Coua ruficeps	A	0.0	**0.98**		0.03				40
Insectivore/carnivore									
Leptosomus discolor	A	10.6			**1.00**				16
Falculea palliata	A	7.7		0.22	**0.78**				27
Accipiter francesii	A	5.8			**1.00**				10
Coua cristata	A	5.7			**0.80**	0.09	0.11		45
Vanga curvirostris	A	4.0			**0.60**		0.40		5
Schetba rufa	A	3.6		0.02	**0.84**	0.07	0.07		44
Coua coquereli	A	1.4	**0.39**		**0.39**	0.13	0.09		23
Insectivore									
Merops superciliosus	A	31.4			**0.38**		0.25	**0.38**	8
Eurystomus glaucurus	A	9.1			**0.93**	0.07			14
Dicrurus forficatus	A	8.3			**0.88**	0.03	0.09		34
Leptopterus viridis	A	7.8			**0.92**		0.08		12
Coranina cinerea	A	7.7			**0.91**		0.09		11
Leptopterus chabert	A	7.0	0.20		**0.40**		**0.40**		5
Cuculus rochii	A	5.7			**0.67**		0.33		3
Xenopirostris damii	A	5.5			**1.00**				4
Centropus toulou	A	4.0			**0.50**	0.25	0.25		4
Newtonia brunneicauda	A	3.8			0.26		**0.74**		31
Terpsiphone mutata	A	3.0	0.03		**0.64**	0.06	0.27		33
Phyllastrephus madagascariensis	A	2.4			**0.54**	0.18	0.28		39
Phersuma mutabilis	R	2.0		**1.00**					4
Frucifer oustaleti	R	1.7	**0.30**	0.15	**0.32**	0.13	0.11		47
Copsychus albospecularis	A	1.2	**0.31**		**0.49**	0.05	0.15		39
Lygodactylus tolampyae	R	1.1	0.13	**0.50**	0.38				8
Upupa epops	A	1.0	**0.78**		0.17	0.06			18
Frucifer rhinoceratus	R	0.8	**0.29**		**0.29**	0.24	0.18		17
Mabuya elegans	R	0.0	**0.96**	0.04					23
Brookesia cf. minima	R	0.0	**1.00**						2
Brookesia ebenaui	R	0.0	**1.00**						2
Amphiglossus intermedius	R	0.0	**1.00**						5
Voeltzkowia mira	R	0.0	**1.00**						1
Insectivore/frugivore/nectarivore									
Hypsipetes madagascariensis	A	5.3	0.03		**0.73**	0.03	0.22		37
Neomixis tenella	A	4.4			0.00		**1.00**		8
Ploceus sakalava	A	4.0			0.25		**0.75**		4
Nectarinia souimanga	A	4.0			0.16	0.03	**0.81**		32
Zosterops maderaspatana	A	3.8			0.20		**0.80**		5
Phersuma madagascariensis	R	1.5		**0.80**		0.20			10
Oprulus cuvieri	R	1.0	**0.50**	**0.45**	0.04	0.01			140
Mesitornis variegata	A	0.0	**1.00**						13

Table 3. Continued.

Species	Taxa	Perch height	Gr/Lg	TT	Br	Vn	Tw/Lf	Ar	N
			Microhabitat Category						
Insectivore/frugivore/nectarivore									
Turnix nigricollis	A	0.0	**1.00**						5
Folivore/frugivore									
Coracopsis vasa	A	16.1			**0.75**	0.25			8
Treon australis	A	10.0			**1.00**				1
Coracopsis nigra	A	8.7			0.33		**0.67**		15
Eulemur mongoz	M	7.3		0.04	**0.79**		0.17		24
Agapornis cana	A	7.0			**1.00**				16
Propithecus verreauxi	M	5.9		**0.48**	0.50	0.02	0.00		54
Streptopelia picturata	A	0.9	**0.83**			0.17			18
Lonchura nana	A	0.3					**1.00**		1
Oena capensis	A	0.0	**1.00**						2

Table 4. Density and biomass estimates for the insectivorous birds at Ampijoroa forest statation, western Madagascar during the peak breeding season in December 2000.

Species	Density #/ha	Biomass g/ha	# pairs/ groups	mean groups size	Survey area (ha)
Leptosomus discolor	0.20	53.5	2.5	2	24.75
Lophotibis cristata	0.12	32.1	1.5	2	24.75
Coua ruficeps	0.32	58.2	4	2	24.75
Coua coquereli	0.40	72.7	5	2	24.75
Coua cristata	1.45	231.3	18	2	24.75
Accipiter francesii	0.16	18.9	2	2	24.75
Eurystomus glaucurus	0.24	23.1	3	2	24.75
Mesiornis variegata	0.65	57.3	8	2	24.75
Vanga curvirostoris	0.04	2.8	2	2	100
Xenopirostris damii	0.10	5.2	5*	2	100
Coranina cinerea	0.73	29.4	9	2	24.75
Dicrurus forficatus	0.65	24.2	8	2	24.75
Hypsipetes madagascariensis	0.97	36.3	12	2	24.75
Schetba rufa	1.16	42.8	11**	2.6	24.75
Phyllastrephus madagascariensis	1.17	30.1	10	2.9	24.75
Copsychus albospecularis	1.13	26.0	14	2	24.75
Terpsiphone mutata	0.81	10.3	10	2	24.75
Newtonia brunneicauda	3.36	31.9	34	2	20.25
Nectarinia souimanga	4.74	32.2	48	2	20.25
Neomixis tenella	1.13	6.7	14	2	24.75
Total	19.5	825.1			

* Mizuta et al. (2001), **Yamagishi et al. (1995)

higher metabolic cost of endothermic birds would consume a far greater amount of insect prey than the lizards.

Focal observations yielded prey capture rates for the 24 insectivorous birds and 4 lizard species (Fig. 1). Smaller bird species generally captured prey more frequently than the larger species (Fig. 1), as their feeding rates were negatively correlated with body mass (r=−0.508, P<0.05). Individual birds with a body mass of 50–180 g captured 0.24 prey/min

Table 5. Density and biomass estimates for the frugivorous birds and lemurs at Ampijoroa forest statation, western Madagascar during the peak breeding season in December 2000.

Species	Density #/ha	Biomass g/ha	# pairs/ groups	mean groups size	Survey area (ha)
Coracopsis nigra	0.48	119.4	6	2	24.75
Streptopeila picturata	0.32	58.9	4	2	24.75
Eulemur fulvus	1.03	2678.8	3	8.5	24.75
Propithecus verreauxi coquereli	1.05	3886.9	4	6.5	24.75
Total	2.89	6743.9			

Table 6. Density and biomass estimates for the four common insectivorous lizards at the Ampijoroa forest station, western Madagascar. See text for the procedure of estimation.

Species	Density #/ha	Biomass g/ha	# pairs/ groups	mean groups size	Survey area (ha)
*Oprulus cuvieri**	3.5	402.5	58.6	1	16.6
*Zonosaurus laticaudatus***	0.7	113.9	5	1	7.5
*Frucifer oustaleti****	4.0	736.0	4	1	1
*Frucifer rhinoceratus****	21.0	483.0	21	1	1
Total	29.2	1735.4			

* Randriamahazo and Mori (1999); ** data from visual census; *** number registered within survey area.
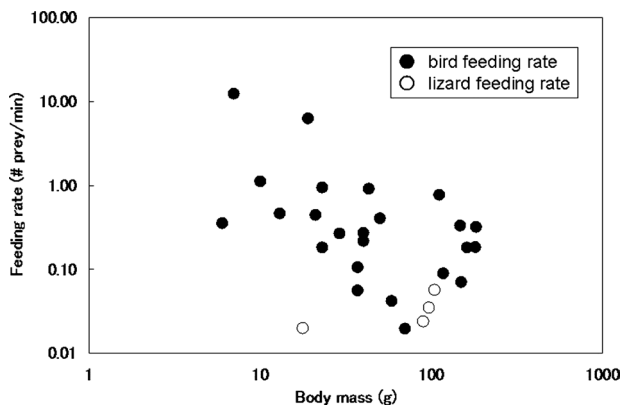
Fig. 1. Prey capture rate of the diurnal insectivorous birds and lizards in relation to body mass in a dry forest of western Madagascar. Prey capture rates are the number of successful prey capture per minute of focal observation. Closed and open circles represent bird and lizard data, respectively.

(0.02–0.77, N=10), approximately 10 times more prey than the lizards (ca. 0.03 prey/min, range=0.02–0.06, N=4) of similar body mass (20–200 g). Approximate prey consumption rates were calculated using the above data. It appeared that the insectivorous birds consumed 230 prey/ha/hr, roughly 7 times more than the insectivorous lizards (35 prey/ha/hr).

These figures suggested that if competition between the insectivorous birds and lizards was exploitative, the birds were competitively more advantageous than the lizards in terms of prey consumption speed.

DISCUSSION

Competitive relationships between birds and lizards, and their ecological consequences on the distribution and abundance of both taxa have received considerable attention from particular regions of the world. In the West Indies (Greater and Lesser Antilles), anolis lizards are diverse and conspicuous elements of the ecological communities, but the insectivorous birds are depauperated. In contrast, on the Central and South American mainland, anolis lizards are much less abundant, and birds are far more diverse on the mainland (Roughgarden 1995). On Madagascar Island, no lizard genus is comparably diverse as anolis lizards of the West Indies. At most, two lizard species belonging to the same genus could be sympatric to the particular kind of forest. Lizard density summed over the four common species (29.2/ha; Table 6) is merely 0.3% of the anolis densities measured in the West Indies (Schoener &

Schoener 1980).

Studies focused on birds-lizards interactions in the West Indies have attempted to explain the biogeographic pattern of birds and lizards abundances by proposing several hypotheses (Terborgh & Faaborg 1980; Wright 1981; Waide & Reagan 1983; McLaughlin & Roughgarden 1989). One is a competition hypothesis, and the other is a predation hypothesis. We will examine these hypotheses to ascertain which one is superior to explain the situation in Madagascar, and then discuss evolutionary consequences on the adaptive radiations by the Madagascar birds and lizards.

1) Competition and predation hypotheses

Wright (1981) proposed that competition occurs between insectivorous birds and anolis lizards, and his proposal was based on three lines of evidence. (1) Extensive diet overlap between the two taxa, (2) food limitation in anolis lizards and (3) Reciprocal changes in the abundances of anoles and insectivorous birds. Wright (1981) explained that the higher density of anolis lizards on small islands is a result of competitive release from the birds, which can no longer sustain themselves on such small islands. Thus, the phenomenon was termed an extinction-mediated competitive release.

Waide & Reagan (1983) rejected Wright's hypothesis, and they proposed that release from predation by birds allows for increased abundances of anolis lizards on small islands. They similarly thought that reduced diversity and abundance of insectivorous birds on small islands was due to the higher extinction rates of birds than lizards. Reciprocal changes in the abundances of anoles and insectivorous birds could be evidence of both the competition and predation hypotheses. Therefore, the difference between the two hypotheses is just in terms of the factor allowing the lizards to increase their density in the absence of birds.

Our study at the dry forest of western Madagascar can provide some evidence supporting the competition hypothesis. First, we noticed that *Oplurus* and *Zonosaurus* lizards were more abundant around the camp site where their possible competitors (*Schetba rufa* and *Coua ruficeps*) were absent (Masami Hasegawa unpublished data). Adults of both lizards became heavier than these birds; hence, it was unlikely that the lizards became abundant due to release from predation by these primarily insectivorous birds. Until the present, we have not identified avian preda-

tors upon *Oplurus* and *Zonosaurus*. Evidence supporting the predation hypothesis was, therefore, very weak for these lizards.

There is indirect evidence supporting high dietary overlap, prey foraging methods and microhabitats between birds and lizards at Ampijoroa (Tables 3, 4). Prey consumption rates by the insectivorous birds were estimated to be 7 times greater than the insectivorous lizards, although lizard biomass is two times larger than the birds. Therefore, we assumed that at least *Oplurus* and *Zonosaurus* lizards are affected by the competitive pressure from insectivorous birds.

2) Predation on small lizards by insectivorous birds

Adults and well-grown individuals of large lizards such as *Frucifer oustaleti*, *Oplurus cuvieri*, and *Zonosaurus laticaudatus* would be immune to any vertebrate predators at JBA. However, juveniles and eggs of larger species and adults of smaller species seemed to be intensively predated by the snakes (Mori et al. 2006) and birds (Table 2). Among the potential avian predators on lizards, we identified *Vanga curvirostris*, *Falculea palliata*, *Coua cristata*, and *Schetba rufa* as the predators upon chameleons and geckos, and *Accipiter francesii* and *Coua ruficeps* as predators upon fossorial skinks.

In contrast to the immune and fearless large lizards, smaller species of geckos and skinks were very cautious to the approaching human observers. This behavioral response toward humans suggests that escape from predation is of prime importance for these geckos and skinks. Apparently, low densities of the geckos and skinks suggested that they were under high predation pressure throughout the Ampijoroa.

3) Evolutionary consequence of adaptive radiation

In the West Indies (Adolph & Roughgarden 1983), anolis lizards forage on the ground and in low vegetation, while no insectivorous bird species forage primarily in these places. The researchers suggested that the absence of the ground-feeding insectivorous birds in these islands is the result of competitive exclusion by the anolis lizards. On the tropical oceanic islands in the south-western Pacific, Hasegawa (unpublished) found that no insectivorous birds use ground or tree trunk for foraging, four skinks foraged exclusively or primarily on the ground, and one arboreal species foraged exclusively on the tree trunk. Overlap in foraging location was, therefore, essentially zero between

the birds and the skinks. In Madagascar, separation of microhabitats between insectivorous birds and lizards is not very clear (Table 3) as compared to the West Indies (Adolph & Roughgarden 1983) and the oceanic Pacific islands (Masami Hasegawa unpublished). However, microhabitat segregations in general are traditionally considered as an evolutionary outcome to reduce competition for food resources.

Higher extinction rates in the smaller Caribbean islands and the combination of high extinction rates and low immigration rates on the remote oceanic islands allow the lizards to take advantage and occupy more available microhabitat than the birds. The low endemicity of oceanic island birds suggested that the avian community has been formed by differential colonization from different sources (Diamond 1978). Subsequent evolutionary adjustments or expansion in resource use might be limited by the presence of dense lizard populations in the Pacific islands.

However, on larger islands like Madagascar, major in situ radiation in birds, for example, from small insectivores (*Newtonia brunnelicauda*) to large carnivores (*Vanga cuviestris*) and even in Vangidae (Yamagishi et al. 2001) may have kept the insectivorous lizards from radiating into various niches. The lizards' reciprocal inhibitory impact on the adaptive radiation of the insectivorous birds might be negligible in Madagascar. Even though we are not certain whether ecological radiation by birds was chronologically earlier than lizards, predation from large carnivorous birds and competition with medium- and small-sized insectivorous birds would restrict lizard ecological niches in Madagascar. This scenario might explain why major arboreal lizards of the family Opluridae and the ground lizards of Zonosauridae have been major competitors with insectivorous birds. These two lizard genera were not as diverse as chameleons, geckos, and skinks. Rather rich species diversity of inconspicuous fossorial skinks and geckos in comparison with low sympatric species diversity of *Opurulus* and *Zonozaurus* lizards (Glaw & Vences 2007) could be possible, because fossorial and nocturnal niches have rarely been exploited by the insectivorous birds (Wilme & Goodmann 2003).

In order to test whether species interactions among distantly related taxa have molded convergent patterns in community structures of vertebrates, we should conduct comparable community studies in other areas with similar climate and vegetation profiles from the perspectives of historical contingency and community phylogeography (Losos 1996; Vitt et al. 2003).

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