African Journal of Herpetology, 2009 58(2): 131-136.

Short Communication

Predation on chameleons in Madagascar: a review

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Abstract.—We reviewed the diet of nocturnal and diurnal chameleon predators on Madagascar from the available literature and identified 28 species. Diurnal raptors were the main predators of chameleons, although the literature was biased towards birds and probably underestimated predation by other animals, notably snakes. *Eutriorchis astur* (Accipitridae) and *Falco zoniventris* (Falconidae) are the principal avian predators of *Furcifer* spp. and *Calumma* spp. and the *Brachypteracias leptosomus* (Brachypteraciidae) of *Brookesia* spp.

Key words.—Chamaeleonidae, Madagascar, avifauna, predators.

Of the ten chameleon genera, three occur exclusively in Madagascar (Glaw & Vences 2007). *Calumma* and *Furcifer* species are mostly arboreal and forage and roost in trees, although a few taxa of the latter genus also use low herbaceous vegetation (Raxworthy 1988). *Brookesia* species roost in low vegetation at night and are active on the ground during the day (Raselimanana & Rakotomalala 2003; Randrianantoandro *et al*. 2007). *Brookesia* and *Calumma* are mostly associated with relatively intact forest whilst *Furcifer* species occur in a wide variety of habitats including grassland, farmland, urban areas, spiny and deciduous forest.

Birds and snakes are the main predators of chameleons and are likely to exert strong selection on chameleon anti-predator responses (Branch 1998; Stuart-Fox *et al*. 2006). Because observational studies on the behaviour of wild chameleons are time consuming and difficult to undertake there are few published studies on predation of these lizards. There are a few studies however on anti-predator behaviour in African chameleons (Raxworthy 1991; Stuart-Fox *et al*. 2006). These found that chameleons use a variety of anti-predator strategies, such as changing skin colour in the South African genus, *Bradypodion*, and spine-thrusting in *Brookesia*. All chameleons also roost off the ground at night and this is thought to be a strategy against nocturnal predators (Raxworthy 1991; Stuart-Fox *et al*. 2006).

Herein, we summarize the available literature regarding predation of Malagasy chameleons and identify the main predators that have been recorded. We collated results from studies that used stomach contents or pellet analysis, and classified them according to the frequency of occurrence of chameleons in the diet. Observations and/or descriptions of predators feeding on chameleons were also included in our assessment.

We reviewed 34 publications on feeding habits covering 32 potential predators of chameleons in Madagascar. These studies consisted of 26 quantitative assessments of diet from detailed

Table 1. Summary of quantitative avian dietary studies using pellet analyses of nest observations, in descending order of contribution made by Malagasy chameleons to the diet. Percentage of dietary items for different taxa is given as a proportion of the total sample (unidentified prey items not shown). The percentage dietary contribution of chameleons is given, and these data contribute to the total for all reptiles in the diet. For some species that consumed reptiles, the original study did not provide further taxonomic precision and this is indicated by '-' under chameleons. Species are classed as diurnal (D) or nocturnal (N) foragers.

Family	Species	Activity	N	Chameleons	Reptile	Frog	Bird	Mammal	Fish	Inverts.	Source
Falconidae	*Falco zoniventris*	D	188	47.3	47.3	0.5	1.6	0.0	0.0	30.9	Réne de Roland et al. 2005
Accipitridae	*Eutriorchis astur*	D	155	43.0	72.8	14.0	0.0	0.0	0.0	0.0	Thorstrom & Réne de Roland 2000
Accipitridae	*Buteo brachypterus*	D	318	11.0	37.4	4.4	23.3	2.2	0.0	2.8	Berkelman 1997
Vangidae	*Vanga curvirostris*	D	506	10.1	28.1	2.4	0.6	0.0	0.0	8.9	Rakotomanana et al. 2001
Brachypteraciidae	*Brachypteracias leptosomus*	D	318	7.2	8.8	0.0	0.0	0.0	0.0	63.2	Thorstrom & Lind 1999
Falconidae	*Falco zoniventris*	D	30	6.7	26.3	0.0	0.0	0.0	0.0	0.0	Thorstrom 1999
Accipitridae	*Circus macrosceles*	D	50	6.0	20.0	0.0	44.0	12.0	0.0	24.0	Réne de Roland et al. 2004
Accipitridae	*Polyboroides radiatus*	D	63	1.6	11.5	0.0	24.0	32.0	0.0	31.7	Karpanty & Goodman 1999
Vangidae	*Euryceros prevostii*	D	106	0.9	5.6	0.9	0.0	0.0	0.0	69.2	La Marca & Thorstrom 2000
Strigidae	*Tyto alba*	N	1,358	< 0.1	2.1	39.2	2.9	55.7	0.0	0.0	Goodman et al. 1993a
Vangidae	*Oriolia bernieri*	D	109	0.0	6.8	0.0	0.0	0.0	0.0	68.5	Thorstrom & Réne de Roland 2001
Falconidae	Falco peregrinus	D	383	0.0	0.0	0.0	92.8	0.0	0.0	0.0	Razafimanjato et al. 2007
Accipitridae	*Polyboroides radiatus*	D	167	0.0	23.8	31.3	26.9	17.5	0.0	0.0	Thorstrom & La Marca 2000
Strigidae	*Asio madagascariensis*	N	28	0.0	7.1	7.1	7.1	67.9	0.0	10.7	Goodman et al. 1991
Strigidae	*Tyto alba*	N	3,025	0.0	0.0	20.6	4.5	67.2	0.0	7.4	Rasoma & Goodman 2007
Strigidae	*Tyto soumagnei*	N	111	0.0	0.9	0.0	0.0	99.1	0.0	0.0	Thorstrom et al. 1997
Accipitridae	*Haliaeetus vociferoides*	D	99	0.0	0.0	0.0	0.0	0.0	100.0	0.0	Berkelman et al. 1999
Brachypteraciidae	*Geobiastes squamiger*	D	269	0.0	1.4	7.0	0.0	1.0	0.0	90.6	Rakotoarisoa & Be 2004
Falconidae	*Falco newtoni*	D	370	0.0	93.8	2.4	1.2	0.0	0.0	2.6	Réne de Roland et al. 2005
Strigidae	*Asio madagascariensis*	N	59	0.0	0.0	0.0	0.0	100.0	0.0	0.0	Langrand & Goodman 1996
Strigidae	*Asio madagascariensis*	N	33	0.0	0.0	0.0	3.0	97.0	0.0	0.0	Rasoloarison et al. 1995
Strigidae	*Tyto soumagnei*	N	24	0.0	0.0	0.0	0.0	100.0	0.0	0.0	Goodman & Thorstrom 1998
Strigidae	*Tyto soumagnei*	N	45	0.0	27.9	5.2	0.0	60.5	0.0	0.0	Cardiff & Goodman 2008
Strigidae	*Tyto alba*	N	1,416	-	2.3	37.6	5.6	54.4	0.0	0.0	Goodman & Langrand 1993
Strigidae	*Asio madagascariensis*	N	133	-	8.3	3.8	4.5	83.5	0.0	0.0	Goodman et al. 1993b
Accipitridae	*Accipiter francesii*	D	305	-	42.0	1.0	14.8	1.5	0.0	6.9	Réne de Roland 2000

Table 2. A list summarizing the results of other non-quantitative studies on the predation of Malagasy chameleons. Species are classed as diurnal (D), nocturnal (N) or cathemeral (C) foragers.

Class	Family		Species	Note/observation	Source
Amphibia	Mantellidae	N	*Mantidactylus femoralis*	Hatching Calumma or Furcifer	Vences *et al*. 1999
Amphibia	Ptychadenidae	C	*Ptychadena madagascariensis*	Juvenile F. lateralis	D'Cruze & Sabel 2005
Aves	Accipitridae	D	*Eutriorchis astur*	Chameleon in 1 stomach	Rand 1936
Aves	Accipitridae	D	*Buteo brachypterus*	Chameleons in 4/21 stomachs	Rand 1936
Aves	Accipitridae	D	*Accipiter francesii*	Chameleon in 1/32 stomachs	Rand 1936
Aves	Brachypteraciidae	D	*Brachypteracias leptosomus*	Chameleons in 2/8 stomachs	Rand 1936
Aves	Cuculidae	D	*Coua caerulea*	Chameleons in 1/19 stomachs	Rand 1936
Aves	Falconidae	D	*Falco zoniventris*	Chameleons in 3/7 stomachs	Rand 1936
Aves	Falconidae	D	*Aviceda madagascariensis*	Chameleons in 11/15 stomachs	Rand 1936
Aves	Leptosomatidae	D	*Leptosomus discolor*	Chameleons in 5/23 stomachs	Rand 1936
Aves	Strigidae	N	*Ninox superciliaris*	Chameleon in 1/11 stomachs	Rand 1936
Aves	Vangidae	D	*Vanga curvirostris*	Chameleons in 18/65 stomachs	Rand 1936
Aves	Vangidae	D	*Leptopterus viridis*	Chameleons in 2/25 stomachs	Rand 1936
Mammalia	Viverridae	C	*Cryptoprocta ferox*	Chamaeleonidae found in scats	Hawkins & Racey 2008

observations of foraging birds or the analysis of prey remains at bird nests and perches (Table 1). Studies that described the stomach contents of birds and amphibians, as well as scat analysis of a carnivore species were also included (Table 2). In addition, twelve descriptions of other feeding behaviour or diet by birds, reptiles and primates were reported (Table 3). Our assessment therefore was heavily biased toward avian species, due to the disproportionate number of existing studies on avian diet.

Twenty-eight taxa were recorded feeding on chameleons. Birds were the most frequently recorded predator of chameleons (n = 19 species), followed by snakes (n = 5), anurans (n = 2), carnivores (n = 1) and primates (n = 1). Chameleons were recorded in the diet of ten species during quantitative assessments of avian feeding biology (Table 1). The highest percentage contribution of chameleon prey was in the diet of Eutriorchis astur and Falco zoniventris. These results were supported by stomach content analysis (Table 2). Analyses of the stomach contents of two other species, *Aviceda madagascariensis* and *Leptosomus discolor*, found chameleons in 73% and 22% of stomachs (Table 2). *Buteo brachypterus*, *Circus macrosceles*, *Brachypteracias leptosomus* and *Vanga curvirostris* also fed on chameleons (Tables 1 & 2). There were reports of predation on *Brookesia* chameleons by *Atelornis pittoides*, *Brachypteracias leptosomus* and *V. curvirostris* but in all other predator species the predated chameleons were either *Calumma* or *Furcifer* species.

Quantitative studies on the diet of three nocturnal bird species (*Tyto alba*, *Asio madagascariensis* and *Tyto soumagnei*) revealed that they rarely predate chameleons. Chameleons were however found in the diet of two other nocturnal bird predators (*Otus rutilus* and *Ninox superciliaris*) but quantitative assessments for these species are lacking.

Eutriorchis astur and *F. zoniventris* were the main chameleon predators, based on the studies that we reviewed. The former species is associated with intact humid forest in the east and is considered to be a specialist predator of herpetofauna (Thorstrom & René de Roland 2000). Its talon morphology is more suited to capturing lizards than snakes, and chameleons and *Uroplatus* geckos are important prey items (Table 1). Thorstrom & René de Roland (2000) reported that *E. astur* was rarely observed greater than 50 m from humid forest and that it probably foraged in the canopy and on the ground near streams. It is likely that *E. astur* takes *Furcifer* from exposed vegetation (i.e.

Table 2. Allometric trends in *P. biseriatus* and *P. p. trivirgatus*. Differences across sex were first evaluated by testing for homogeneity of slopes and then by single-factor ANCOVAs. Sex was used as the factor in all analyses.

Class	Family	Species	Note/observation	Source
Aves	Accipitridae	*Buteo brachypterus*	Preying on *Calumma* or *Furcifer*	Goodman *et al*. 1997
Aves	Alcedinidae	*Corythornis madagascariensis*	Preying on *Calumma nasutum*	Goodman *et al*. 1997
Aves	Brachypteraciidae	*Atelornis pittoides*	Preying on *Brookesia* spp.	Thorstrom & Lind 1999
Aves	Cuculidae	*Coua caerulea*	Preying on *Calumma nasutum*	Goodman *et al*. 1997
Aves	Rallidae	*Dryolimnas cuvieri*	Preying on *Calumma gastrotaenia*	Jenkins 2001
Aves	Strigidae	*Otus rutilus*	Preying on *Calumma nasutum*	Goodman *et al*. 1997
Mammalia	Lemuridae	*Lemur catta*		Oda 1996
Reptilia	Colubridae	*Mimophis mahafaliensis*	Preying on *Furcifer labordi*	Andriamandimbiarisoa 2007
Reptilia	Colubridae	*Madagascarophis meriodionalis*	Preying on Furcifer labordi	Andriamandimbiarisoa 2007
Reptilia	Colubridae	*Stenophis betsileanus*	Preys on *Furcifer balteatus* & *Furcifier willsii*	Glaw and Vences 2007
Reptilia	Colubridae	*Ithycyphus perineti*	Preying on *Calumma brevicorne*	Glaw and Vences 2007
Reptilia	Colubridae	*Ithycyphus oursi*	Preying on *Furcifer oustaleti*	Glaw and Vences 2007

forest edge and canopy top) and *Calumma* from vegetated tree branches underneath the canopy. The presence of *Calumma* species in the diet of the *F. zoniventris* indicates that this raptor forages in close proximity to relatively intact forest, even though it nests in human-modified landscapes (René de Roland *et al*. 2005). As this species has a broad distribution in different biomes on Madagascar, the diet recorded from the north-eastern humid forest may not be representative across its complete range. *Buteo brachypterus* is a generalist that also preys on birds and small mammals, whilst *Circus macrosceles* feeds mainly on insects, birds and mammals (Berkelman 1997; René de Roland *et al*. 2004). Both these raptor species therefore consume a wide spectrum of prey types and although chameleons were frequently eaten, they are probably preyed on in an opportunistic manner. Another generalist, *Accipiter francesii*, preyed on mostly lizards but information on the specific composition of the lizard component of its diet is lacking (René de Roland *et al*. 2005). *Brachypteracias leptosomus* was the only chameleon predator that preyed on *Brookesia* rather than *Calumma* and *Furcifer*. Although 70% of the diet of *B. leptosomus* consisted of invertebrates, chameleons represented a notable proportion of the prey biomass (Thorstrom & Lind 1999).

The extent to which a predator feeds on chameleons may vary according to the season, geographical region, habitat or the breeding cycle. Thus, our assessment of just a limited number of studies does not take into account any seasonal affects. For example, Thorstrom (1999) did not record chameleons in the diet of *F. zoniventris* during nest watches between October and December, but a second study of this species at the same location, between August and January, found evidence for high predation on chameleons (René de Roland *et al*. 2005). In another study, Thorstrom & La Marca (2000) found no evidence of chameleons as prey in the diet of *Polyboroides radiatus* in the east, but Karpanty & Goodman (1999) observed predation on *Furcifer lateralis* from sites in southern Madagascar.

In addition, due to the lack of seasonal data, most quantitative assessments of diet that were reviewed were based on small samples sizes, such as observations at a few nests or analysis of a few stomachs. It is perhaps therefore not surprising that there were certain discrepancies, such as the absence of chameleons in the diet of *Accipiter francesii* reported by René de Roland (2000) but their presence in stomachs of this species analysed by Rand (1936). Our assessment is a first pass at summarising the available data, and we have identified gaps in the avail-

able knowledge, highlighting the need for additional studies into the diet of avian (and other) predators with respect to the importance of chameleons as a dietary item. For example, we were not able to account for seasonal variation for all predators, nor were we able to assess the importance of nocturnal predators (for example, snakes).

In terms of conservation, dietary studies can indicate the importance of certain habitats for predators. In the case of Malagasy birds, a high proportion of *Calumma* or *Brookesia* chameleons in the diet of given predator is indicative of an animal that forages inside relatively intact forest and suggests that these avian predators would suffer should the forest become disturbed.

Chameleons employ crypsis during the day and roost in the vegetation at night. These are presumed to be related to reducing predation and imply that chameleon predators are active in the day and night. Other anti-predator behaviour, such as dropping off perches, freezing and vibrating may deter both diurnal and nocturnal predators. Nocturnal predation, especially by snakes is likely to be more prevalent than the results of our literature review suggest.

ACKNOWLEDGEMENTS

We would like to thank Russell Thorstrom for sending us copies of his published work, Marianne Carter of the Conservation Leadership Programme provided copies of some literature that was difficult for us to access from Madagascar. S. M. Goodman and K. Tolley greatly improved earlier versions of the manuscript.

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Received: 27 May 2009 *Final acceptance: 18 August 2009*