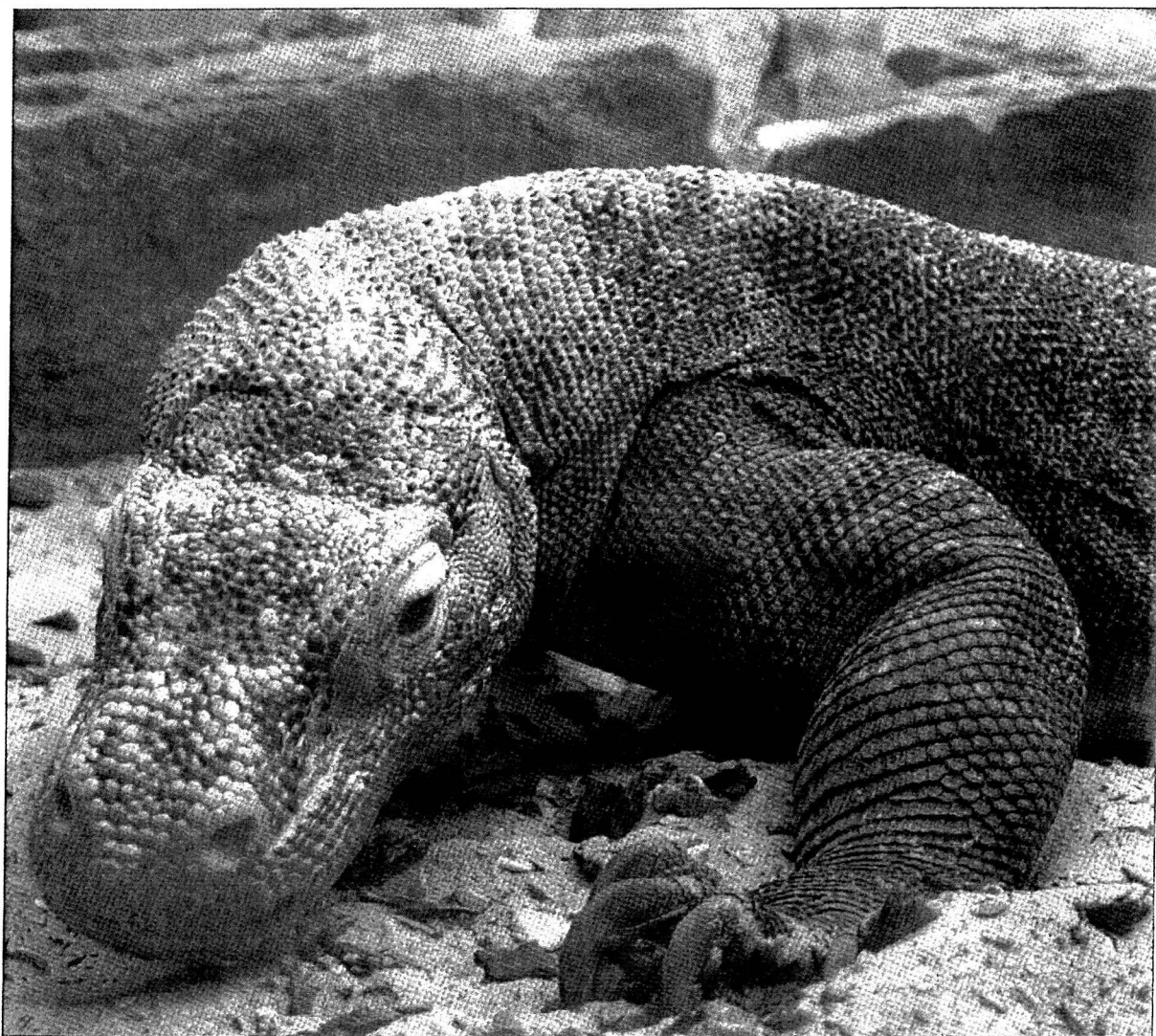


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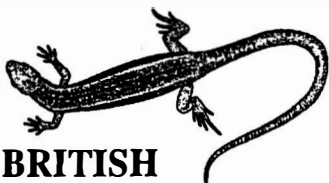
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FRONT COVER: Komodo dragon, *Varanus komodoensis* (R. Gibson)

DIETARY SHIFTS OF SYMPATRIC FRESHWATER TURTLES IN PRISTINE AND OIL-POLLUTED HABITATS OF THE NIGER DELTA, SOUTHERN NIGERIA

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The diet of sympatric freshwater turtles was studied at two study areas in the Niger Delta (southern Nigeria), to test whether oil pollution affects the ecological relationships between free-ranging turtles. Two study areas, one unpolluted and one polluted by an oil spill, were used for our comparisons. Both areas had similar environmental conditions, i.e. a main river tract with banks covered by dense gallery forest, seasonal swamps in riverine forest, and almost permanent marshes with rich aquatic vegetation. Four species of turtle (*Trionyx triunguis*, *Pelusios castaneus*, *Pelusios niger*, and *Pelomedusa subrufa*), were captured in the unpolluted area, whereas only two species (*Pelusios castaneus* and *Pelusios niger*) were captured in the polluted area. At the unpolluted area, the taxonomic composition of the diets of *Pelusios castaneus* and *Pelusios niger* was similar, whereas the diets of *Pelomedusa subrufa* and *Trionyx triunguis* were very different from the other two species and one another. In the polluted area, the taxonomic composition of the diet of *Pelusios castaneus* was significantly different from that of conspecifics in the unpolluted area, and consisted mainly of plant matter, annelids (earthworms and leeches), and gastropods. The taxonomic composition of the diet of *Pelusios niger* was also significantly different from that of conspecifics at the unpolluted area, and consisted mainly of annelids and gastropods, and secondarily of plant matter. Amphibian prey (eggs, tadpoles, and adults), which were one of the main food types for all turtles in the unpolluted area, practically disappeared from the diet of turtles at the polluted area. It was evident from this study that the two species that survived the oil spill event shifted considerably in their dietary preferences. In particular, in both species there was an obvious trend towards a reduction in the breadth of the trophic niche, with many fewer food categories eaten at the polluted area compared to the unpolluted area. It is suggested that such reduction in trophic niche breadth may depend directly on the reduced availability of most food sources (particularly amphibians, fish, and environmentally-sensitive invertebrates) in the polluted area, despite over 10 years having elapsed since the spill, and restoration operations at the site. It is likely that the above-mentioned reduction in trophic niche breadth also depended on the shifts in habitat use by the surviving turtles, which tended to concentrate into single habitat types in the polluted area, compared to the unpolluted area where they were more habitat generalists.

Key words: Chelonia, community ecology, feeding ecology, pollution, resource partitioning

INTRODUCTION

The territory of the Niger Delta (southern Nigeria) is one of the largest wetland areas of West Africa and the main production area of sub-Saharan Africa for oil and its derivatives (De Montclos, 1994; Carbone, 2002). This territory risks serious environmental collapse as a result of both natural habitat loss (due to deforestation for industrial reasons, and overpopulation, with several million people inhabiting an area previously almost unpopulated) and pollution. One of the main reasons of environmental pollution is the frequent occurrence of oil spills from pipelines crossing forests, swamps, and mangroves (Carbone, 2002). Several oil spills, which may have catastrophic effects on the local flora and fauna (Odu *et al.*, 1989; NDES, 1998), have been caused

mainly by malicious attacks by groups of youths who retaliate against the government and damage oil companies economically by breaking pipelines.

Freshwater turtles are omnivorous (Ernst & Barbour, 1989; Luiselli, 1998; Akani *et al.*, 2001), and their communities are often characterized by rather complex interspecific relationships (Lagler, 1943; Legler, 1976; Vogt, 1981; Toft, 1985; Jackson, 1988; Moll, 1990; Stone *et al.*, 1993; Kennett & Tory, 1996; Pritchard, 2001), and thus they are important organisms for the dynamics of freshwater ecosystems (Legler, 1976; Vogt & Guzman, 1988; Luiselli *et al.*, 2000; Akani *et al.*, 2001). Because of (1) their position in food chains (Williams & Christiansen, 1981; Vogt & Guzman, 1988; Akani *et al.*, 2001), and (2) their regional abundance and considerable specific diversity (Luiselli *et al.*, 2000), freshwater turtles are among the ideal targets for studies on the effects of oil pollution on the freshwater

ecosystems of the Niger Delta. Thus they have been used as study cases for environmental impact assessments by oil companies and other organizations operating in the study region (e.g., Politano, 1998; Luiselli & Politano, 1999; Luiselli & Akani, 2002).

By studying the turtle communities of two rainforest water bodies (one affected by an oil spill and one in good environmental condition), Luiselli & Akani (2003) previously showed that there were both direct and indirect effects of oil pollution on the complexity and habitat use of Nigerian freshwater communities of turtles. The main direct effect was a considerable reduction in turtle species diversity, with half of the species being lost after oil spillage (from four species, *Trionyx triunguis*, *Pelusios castaneus*, *Pelusios niger* and *Pelomedusa subrufa*, found in the unpolluted area, to just two in the polluted area, *P. castaneus* and *P. niger*), and with a very strong decline in the numbers of turtle specimens also for those species which were able to survive the pollution event. There was also a shift in habitat use after the oil spill by both species of *Pelusios*, and this shift may have strong effects on the long-term persistence of the species (independent of the direct pollution effects of the oil spill) because it considerably reduced habitat niche separation between these species, which are potential competitors. Therefore, it was stressed (Luiselli & Akani, 2003) that eco-ethological modifications in populations of animals subjected to oil pollution events must be studied in order to properly understand the long-term effects of these catastrophic phenomena.

By analysing the same communities of turtles, in this paper we try to determine (1) whether there is a significant shift in the species' dietary habits at the polluted area compared to the unpolluted area; and (2) if this is the case, whether these shifts may have altered significantly the respective niche positions of the turtle species.

STUDY AREAS AND METHODS

Two study areas (one unpolluted and one polluted by an oil spill) were used for our comparisons. Both areas contained similar habitats (i.e. a main river tract with banks covered by dense gallery forest, with seasonal swamps into the riverine forest and almost permanent marshes with rich aquatic vegetation). Among the plant species found in both areas were *Pterocarpus* sp., *Raphia* sp., *Triumphetta eriophlebia*, *Mitragyna stipulosa*, *Triplichiton scleroxylon*, *Khaya* sp., *Terminalia superba*, and *Mitragyna ciliata*. The linear distance between the two areas was approximately 20 km. Both areas were of approximately the same surface area (1 km of main river tract with its forested banks). The unpolluted study area was situated along a tributary of the Sambreiro River (Rivers State), approximately 7 km north-east of Degema town (Kula, Degema Local Government Area). The polluted study area was situated in the neighbouring area of the Sakie Stream and Baki

Creek (Bayelsa State), where a well-known oil spill had occurred. On 27 January 1988 a spill of crude oil (estimated at about 1026 barrels) was detected along the Nun River delivery line of the Shell Petroleum Development Company. This was the result of a burst pipeline caused by an internal tear. The oil flowed down an area of seasonally flooded gallery swamp forest (Sakie Stream) into the Baki Creek, which links up with the Nun River to form Igbibiri Creek during the rainy season (Odu *et al.*, 1989). Four different species of freshwater turtle (*Trionyx triunguis*, *Pelusios niger*, *Pelusios castaneus* and *Pelomedusa subrufa*) were found in this river before the spill (Odu *et al.*, 1989; Akani, unpublished data), and only two (*Pelusios niger*, *Pelusios castaneus*) have survived until now (Luiselli & Akani, 2003). The spill was devastating, resulting in crude oil pollution upstream to a distance of 1 km (for total hydrocarbon content of waters at the study area, see Luiselli & Akani, 2003).

Data were gathered mainly during the years 2000–2002, but some additional observations were made in both study areas between 1996 and 1999. In total, these two study areas were surveyed for 20 field days at each locality, both in dry and wet seasons. Each field day lasted at least 12 hrs. Thus, in total there were 80 field days (40 in the dry and 40 in the wet seasons). The search for free-ranging turtles along non-linear transects was conducted along various microhabitats known to be frequented by these species (see Luiselli *et al.*, 2000). Several standard turtle-collecting techniques were used, including dip-netting and trawling (see also Gibbons *et al.*, 2001, for a similar procedure), and many additional specimens were brought by local villagers employed for this research project.

Once the turtles were captured, they were measured (midline plastron length), sexed, identified to species, and permanently individually marked by unique sequences of notches filed into the marginal scutes. The dietary study is based on both stomach analysis of a few dead specimens (offered in bush-meat markets) and faecal analysis of living specimens. No specimen was killed or injured by the researchers. Masses of filamentous algal mats were commonly found in stomachs (in over 65% of stomachs of all species in both study sites), but we assumed this material was ingested secondarily. However, it is uncertain whether mats of algae are only incidentally ingested. Many turtles forage directly on algae, and any large quantities of algae in faeces or stomach contents would possibly suggest deliberate consumption of this resource. In any case, as there were no significant differences in terms of frequency of algae consumption between species (in all cases, χ^2 test, at least $P > 0.3$) and within species from different study areas (χ^2 test, at least $P > 0.2$), to include or exclude these data from calculations appears rather irrelevant. The same was true for sand, gravel, and presumably parasitic nematodes. Faeces were collected from freshly captured free-ranging specimens.

TABLE 1. Summary of the diet data collected from turtles at the unpolluted study area in south-eastern Nigeria. Numbers represent the number of turtles that consumed each prey type. Percentages indicate the proportion of turtle specimens containing a given prey type. The total numbers of specimens examined were 14 (*Trionyx triunguis*), 217 (*Pelusios castaneus*), 113 (*Pelusios niger*), and 9 (*Pelomedusa subrufa*). Only identified items are considered for this table.

Prey type	Number of turtles containing each prey item			
	<i>Trionyx triunguis</i>	<i>Pelusios castaneus</i>	<i>Pelusios niger</i>	<i>Pelomedusa subrufa</i>
PLANTS				
Fruits	0	11 (5.1%)	8 (7.1%)	2 (22.2%)
Seeds	0	8 (3.7%)	4 (3.5%)	2 (22.2%)
Aquatic plants	0	16 (7.4%)	9 (7.9%)	3 (33.3%)
INVERTEBRATES				
Annelida	0	8 (3.7%)	12 (10.6%)	2 (22.2%)
Gastropoda	1 (7.1%)	11 (5.1%)	4 (3.5%)	0
Bivalvia	0	2 (0.9%)	0	0
Arachnida	0	6 (2.8%)	3 (2.6%)	0
Insecta	0	13 (6.0%)	1 (0.9%)	0
Odonata (larvae)	0	6	1	0
Coleoptera (larvae)	0	1	0	0
<i>Nepa</i> sp.	0	2	0	0
Hemiptera unidentified	0	1	0	0
Ephemeroptera	0	1	0	0
Larvae (unidentified)	0	2	0	0
Crustacea	1 (7.1%)	41 (18.9%)	27 (23.9%)	3 (33.3%)
VERTEBRATES				
Fish	11 (78.5%)	114 (52.5%)	79 (69.9%)	6 (66.7%)
Anurans (adults)	5 (35.7%)	8 (3.7%)	14 (12.4%)	0
Anuran eggs	0	20 (9.2%)	17 (15.0%)	2 (22.2%)
Anuran tadpoles	10 (71.4%)	49 (22.6%)	33 (29.2%)	4 (44.4%)
Indeterminate	2 (14.3%)	1 (0.4%)	1 (0.9%)	0

To avoid statistical problems due to pseudoreplication of observations (Mathur & Silver, 1980; Hurlbert, 1984), diet data were recorded only once from individual turtles, i.e. the recaptured turtles were not used again for data recording and analyses. For uniformity, data relative to the first time a given specimen was encountered were recorded. To avoid biases in data resulting from dissection of stomachs and analysis of faecal pellets, we did not analyse the total number of food items, but simply recorded the presence of the various items in each individual turtle. This procedure was necessary because it is difficult to count exactly the total number of items of a given food type found in the faeces of the turtles, whereas the same operation is much easier when dissecting turtle stomachs.

All data were statistically analysed using STATISTICA (version 5.0, for Windows) PC+ package (Statsoft Inc., 1996), with all tests being two-tailed and alpha set at 5%. To partially remove the sample size problem in between-site comparisons (for instance, 217 *P. castaneus* were found at the unpolluted site compared to only 21 at the polluted site; likewise 113 versus 39 *P. niger*; see below), χ^2 tests were conducted category by category: i.e. to compare fruit in unpolluted and polluted sites. When $df=1$, Yates' correction was applied to the χ^2 test. However, due to the difficulty of identifying the ingested plant material, we assumed that a single type of plant was eaten by a single individual, although it may

well be possible that the same individual may have ingested several plant categories.

RESULTS

DIET OF TURTLES IN THE UNPOLLUTED AREA

A total of 510 turtles (*Trionyx triunguis*, $n=23$; *Pelusios castaneus*, $n=314$; *Pelusios niger*, $n=160$; and *Pelomedusa subrufa*, $n=13$) was captured in the unpolluted area (Luiselli & Akani, 2003). Identifiable food items were obtained from stomachs and/or faecal pellets of 14 *Trionyx triunguis*, 217 *Pelusios castaneus*, 113 *Pelusios niger* and 9 *Pelomedusa subrufa* (Table 1). Contingency table analysis revealed that males and females did not differ significantly in terms of taxonomic diet composition in either *Pelusios* species (at least $P>0.27$), whereas the same analysis was not performed on the other two species due to small sample sizes.

Based on the proportion of animals containing a given prey type, the data show that: (1) the diet of *Trionyx triunguis* consisted mainly of aquatic vertebrates, i.e. tadpoles and fish (each of them found in > 70% of individuals) and ranid frogs (> 35% of individuals); (2) the diet of *Pelusios castaneus* was very diverse, with small fish being the most common food source (found in > 50% of individuals); (3) the diet of *Pelusios niger* was also very diverse, but the main prey were clearly small fish (found in about 70% of individuals) followed by tadpoles (found in about 30% of individu-

TABLE 2. Summary of the diet data collected from turtles at the polluted study area in south-eastern Nigeria. Numbers represent the number of turtles that consumed each prey type. Percentages indicate the proportion of turtle specimens containing a given prey type. The total numbers of specimens examined were 21 (*Pelusios castaneus*) and 39 (*Pelusios niger*). Only identified items are considered for this table.

Prey type	Numbers of turtles containing each prey item	
	<i>Pelusios castaneus</i>	<i>Pelusios niger</i>
PLANTS		
Fruits	4 (19%)	3 (7.7%)
Seeds	16 (76.2%)	12 (30.8%)
Aquatic plants	14 (66.7%)	13 (33.3%)
INVERTEBRATES		
Annelida	9 (42.9%)	24 (61.5%)
Gastropoda	12 (57.1%)	27 (69.2%)
VERTEBRATES		
Anuran tadpoles	2 (9.5%)	4 (10.2%)
Anurans (adults)	1 (4.8%)	4 (10.2%)
Fish	3 (14.3%)	5 (12.8%)

als); (4) the diet of *Pelomedusa subrufa* consisted also of many small fish (found in over 65% of specimens), but plant matter accounted for a higher percentage of food than in the other three species; (5) amongst invertebrates, crustaceans were commonly eaten by all species.

DIET OF TURTLES IN THE POLLUTED AREA AND COMPARISONS BETWEEN SITES

A total of 88 turtles (*Pelusios castaneus*, $n=31$; *Pelusios niger*, $n=57$) was captured in the polluted area (Luiselli & Akani, 2003). The presence of the other two turtle species (*Trionyx triunguis* and *Pelomedusa subrufa*) was documented prior to the oil spill (Odu et al., 1989; Luiselli & Akani, 2002), but today they appear to be completely extirpated (Luiselli & Akani, 2002, 2003). Identifiable food items were obtained from stomachs and/or faecal pellets of 21 *Pelusios castaneus* and 39 *Pelusios niger* (Table 2). Contingency table analysis revealed that males and females did not differ significantly in terms of diet composition in either species of *Pelusios* ($P>0.46$ for both).

Based on the proportions of turtles containing a given prey type, the data show that: (1) the taxonomic composition of the diet of *Pelusios castaneus* was very different from that of conspecifics at the unpolluted area, and consisted mainly of plant matter (seeds and aquatic plants, each of them found in > 65% of the individuals), and of annelids (earthworms and leeches) and gastropods (found in 42-57% of individuals). Moreover, there were significant differences between the sites in terms of frequency of occurrence in faeces of fruits

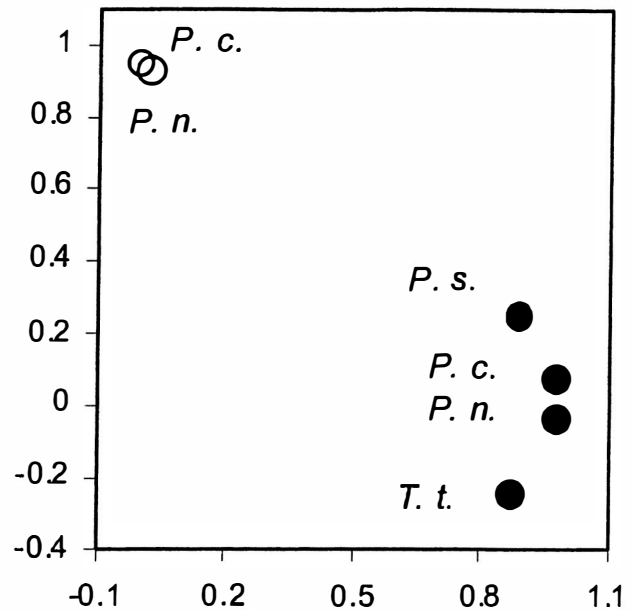


FIG. 1. Factorial plan of a Principal Component Analysis (PCA) on the diet similarities across turtle species (VARIMAX standardized rotated model), based on the proportion of specimens containing each food type. Solid circles indicate the unpolluted area, hollow circles the polluted area. Abbreviations: *P.c.*, *Pelusios castaneus*; *P.n.*, *P. niger*; *T.t.*, *Trionyx triunguis*; *P.s.*, *Pelomedusa subrufa*.

($\chi^2=30.16$, $df=1$, $P<0.0001$), seeds ($\chi^2=450.92$, $df=1$, $P<0.0001$), aquatic plants ($\chi^2=100.02$, $df=1$, $P<0.0001$), annelids ($\chi^2=164.80$, $df=1$, $P<0.0001$), gastropods ($\chi^2=184.28$, $df=1$, $P<0.0001$), anuran tadpoles ($\chi^2=40.69$, $df=1$, $P<0.0001$) and fish ($\chi^2=227.68$, $df=1$, $P<0.0001$); (2) the taxonomic composition of the diet of *Pelusios niger* was also very different from that of conspecifics in the unpolluted area, and consisted mainly of annelids and gastropods (found in 61-69% of the individuals) and secondary plant matter (found in > 30% of the individuals). Moreover, there were significant differences between sites in terms of frequency of occurrence in faeces of seeds ($\chi^2=110.12$, $df=1$, $P<0.0001$), aquatic plants ($\chi^2=53.71$, $df=1$, $P<0.0001$), annelids ($\chi^2=143.03$, $df=1$, $P<0.0001$), gastropods ($\chi^2=551.83$, $df=1$, $P<0.0001$), anuran tadpoles ($\chi^2=44.80$, $df=1$, $P<0.0001$), and fish ($\chi^2=306.13$, $df=1$, $P<0.0001$); (3) amphibian prey (eggs, tadpoles, and adults), which was one of the main food types for all turtles in the unpolluted area, practically disappeared from the diet of turtles in the polluted area, and the same was true for fish, insects and crustaceans.

The ordination of the various turtle species in a PCA factorial plan (with a standardized VARIMAX rotated model) is presented in Fig. 1. In this PCA factorial plan (det. corr. matrix = -3.499; eigenvalues = 3.482 with 58.04% of total variance explained, and 1.906 with 31.8% of total variance explained), based on the similarities between species in terms of food types which were eaten, it appeared that: both *Pelusios niger* and *P. castaneus* in the polluted area were differentiated from

TABLE 3. Summary of the diet data collected from turtles at the unpolluted study area in south-eastern Nigeria, according to season (dry season: October to April; wet season: May to September). Numbers represent the number of turtles that consumed each prey type. Percentages indicate the proportion of turtle specimens containing a given prey type. The total numbers of specimens examined were 7 (dry season) and 7 (wet season) for *Trionyx triunguis*, 105 and 112 for *Pelusios castaneus*, and 60 and 53 for *Pelusios niger*. Data for *Pelomedusa subrufa* are not presented in this table because only one specimen with identifiable food was collected in the dry season. Only identified items are considered for this table.

Prey type	<i>Trionyx triunguis</i> Dry	<i>Trionyx triunguis</i> Wet	<i>Pelusios castaneus</i> Dry	<i>Pelusios castaneus</i> Wet	<i>Pelusios niger</i> Dry	<i>Pelusios niger</i> Wet
PLANTS						
Fruits	0	0	6 (5.7%)	5 (4.5%)	8 (13.3%)	0
Seeds	0	0	5 (4.8%)	3 (2.7%)	1 (1.7%)	3 (5.7%)
Aquatic plants	0	0	6 (5.7%)	10 (8.9%)	5 (8.3%)	4 (7.6%)
INVERTEBRATES						
Annelida	0	0	3 (2.8%)	5 (4.5%)	7 (11.7%)	5 (9.4%)
Gastropoda	0	1 (14.3%)	3 (2.8%)	8 (7.1%)	1 (1.7%)	3 (5.7%)
Bivalvia	0	0	2 (1.9%)	0	0	0
Arachnida	0	0	6 (5.7%)	0	3 (5%)	0
Insecta	0	0	5 (4.8%)	8 (7.1%)	0	1 (1.9%)
Odonata (larvae)	0	0	3	3	0	1
Coleoptera (larvae)	0	0	1	0	0	0
<i>Nepa</i> sp.	0	0	0	2	0	0
Hemiptera unid.	0	0	1	0	0	0
Ephemeroptera	0	0	0	1	0	0
Larvae (unidentified)	0	0	0	2	0	0
Crustacea	0	1 (14.2%)	18 (17.1%)	23 (20.5%)	17 (28.3%)	10 (18.9%)
VERTEBRATES						
Fish	6 (85.7%)	5 (71.4%)	51 (48.6%)	63 (56.2)	38 (63.3%)	41 (77.3%)
Anurans (adults)	2 (28.6%)	3 (42.8%)	2 (1.9%)	6 (5.3%)	9 (15%)	5 (9.4%)
Anuran eggs	0	0	2 (1.9%)	18 (16.1%)	3 (5%)	14 (26.4%)
Anuran tadpoles	4 (57.1%)	6 (85.7%)	23 (21.9%)	26 (23.2%)	11 (18.3%)	22 (41.5%)
Indeterminate	2 (28.6%)	0	1 (0.9%)	0	1 (1.7%)	0

TABLE 4. Summary of the diet data collected from turtles at the polluted study area in south-eastern Nigeria, divided by season (dry season: October to April; wet season: May to September). Numbers represent the number of turtles that consumed each prey type. Percentages indicate the proportion of turtle specimens containing a given prey type. The total numbers of specimens examined were 10 (dry season) and 11 (wet season) for *Pelusios castaneus* and 17 and 22 for *Pelusios niger*. Only identified items are considered for this table.

Prey type	<i>Pelusios castaneus</i> Dry	<i>Pelusios castaneus</i> Wet	<i>Pelusios niger</i> Dry	<i>Pelusios niger</i> Wet
PLANTS				
Fruits	2 (20%)	2 (18.2%)	1 (5.9%)	2 (9.1%)
Seeds	9 (90%)	7 (63.6%)	7 (41.2%)	5 (22.7%)
Aquatic plants	6 (60%)	8 (72.7%)	6 (35.3%)	7 (31.8%)
INVERTEBRATES				
Annelida	8 (80%)	1 (9.1%)	15 (88.2%)	9 (40.9%)
Gastropoda	2 (20%)	10 (90.9%)	12 (70.6%)	19 (86.4%)
VERTEBRATES				
Anuran tadpoles	0	2 (18.2%)	0	4 (18.2%)
Anurans (adults)	0	1 (9.1%)	0	4 (18.2%)
Fish	1 (10%)	2 (18.2%)	2 (11.8%)	3 (13.6%)

all the other turtle species (including conspecifics) in the unpolluted area. In this analysis, the four turtle species in the unpolluted area correlated significantly with Factor 1 (high positive scores correlated with fish, amphibians of all ages, and crustaceans), whereas the two *Pelusios* species in the polluted area were arranged in completely separate positions and correlated with Factor 2 (high positive scores correlated with annelids and gastropods).

SEASONAL DIETARY CHANGES IN THE TWO STUDY AREAS

Seasonal variations in turtle diets at both the study areas is presented in Table 3 (unpolluted area) and Table 4 (polluted area). Seasonal variation in the diet of *Pelomedusa subrufa* at the unpolluted area was not studied because only one specimen with identifiable food was collected in the dry season. After pooling sexes of all species because of their non-significant differences in prey composition (see above), diet composition was apparently similar between seasons in *Trionyx triunguis*, but the sample size was not large enough to allow any robust statistical test. On the other hand, diet composition was varied seasonally in both *Pelusios castaneus* and *Pelusios niger*. For *Pelusios castaneus*, there were significant differences between seasons in the frequency of consumption of gastropods ($\chi^2=10.21$, $df=1$, $P<0.0014$) – which were consumed more in the wet season, and amphibian eggs ($\chi^2=131.52$, $df=1$, $P<0.0001$) – which were also consumed more in the wet season. For *Pelusios niger*, the significant differences between seasons were found in the frequency of consumption of fruits ($\chi^2=7.05$, $df=1$, $P=0.0078$) and crustaceans ($\chi^2=4.49$, $df=1$, $P=0.034$) – which were consumed more in the dry season, and amphibian eggs ($\chi^2=59.02$, $df=1$, $P<0.0001$) and tadpoles ($\chi^2=23.36$, $df=1$, $P<0.0001$) – which were consumed more in the wet season.

Diet composition was also very different between seasons in both *Pelusios castaneus* and *Pelusios niger* in the polluted study area. For *Pelusios castaneus*, the significant differences were found in the frequency of consumption of annelids ($\chi^2=62.15$, $df=1$, $P<0.0001$) – which were consumed more in the dry season, and gastropods ($\chi^2=37.53$, $df=1$, $P<0.0001$) – which were consumed more in the wet season. For *Pelusios niger*, the significant differences were found only in the frequency of consumption of annelids ($\chi^2=14.89$, $df=1$, $P=0.0001$) – which were consumed more in the dry season, although gastropods, amphibian adults and tadpoles were consumed more in the wet season but not at a statistically significant level. The interseasonal differences in the frequency of consumption of annelids in either species were mainly due to the preponderance of leeches in the water of the polluted area during the dry season. These animals were often observed while sucking the blood of the turtles, and so it may be hypothesized that *Pelusios* turtles, which live in small groups, may easily forage on these annelids by ingest-

ing leeches sucking blood from themselves or their conspecifics.

DISCUSSION

Before any discussion of the present data, the theoretical limitations of our study procedure must be noted. As we did not compare the feeding habits of the turtles in the same study plot before and after the oil spill, we could not directly test whether the environmental pollution had any direct effect on the dietary changes of the species, but we can indirectly test this hypothesis by assuming that the feeding habits of the various species were the same in the two study areas, given the close geographic position (just 20 km linear distance) and the similar habitat characteristics.

There is very little literature available on the feeding ecology of the four turtle species studied here (e.g. Ernst & Barbour, 1989), and the only detailed data relate to Nigerian populations of *Pelusios castaneus* (Luiselli, 1998) and *Trionyx triunguis* (Akani *et al.*, 2001). At least with regard to diets of these two species, our data from the unpolluted study area are consistent with those available in the literature, and indicate that *Trionyx triunguis* is more carnivorous than the three sympatric pelomedusids (Ernst & Barbour, 1989; Luiselli, 1998; Akani *et al.*, 2001).

The examination of the data available on diet similarity (this study) and habitat use (see Luiselli *et al.*, 2000; Luiselli & Akani, 2002) of the three pelomedusids suggests that *Pelusios niger* and *Pelusios castaneus* are potentially strong competitors, although they exhibit clear-cut differences in microhabitats – one species is linked to seasonal and ephemeral water bodies and the other to permanent water bodies – whereas *Pelomedusa subrufa* is distinctly ecologically different from the other two species (Luiselli *et al.*, 2000). Unfortunately, no such diet and ecological comparison can be done with regard to the turtles from the polluted area, because, to the best of our knowledge, there is no similar study available in the literature.

Our data on the evident shifts in diet composition of the two species of the genus *Pelusios* are likely attributable to the effects of oil pollution, which has probably changed the food resource availability for turtles considerably. This would have produced the observed dietary shifts, chiefly towards an increase in the consumption of vegetation, annelids, and gastropods, and a reduction in the consumption of the vertebrate prey, by the two *Pelusios* species. In addition, a logical interpretation of our multivariate analysis is that these oil-induced changes in food resource availability may have forced the two surviving turtle species to exploit nearly the same trophic resources, which are possibly the only remaining abundant resources in the polluted environment. As a consequence, these two potential competitors, which were situated in more distant positions of the multivariate space in the unpolluted area, were very close to one another in the polluted area. In particular, in both species there was an obvious trend to-

wards a reduction in the breadth of the trophic niche, with many fewer food categories eaten at the polluted area compared to the unpolluted area. Such a reduction in the trophic niche breadth may depend directly on the reduced availability of most food sources (particularly amphibians, fish, and environmentally-fragile invertebrates) in the polluted area, despite over 10 yrs having elapsed since the spill, with restoration operations taking place in the interim. Insects and Crustacea are absent food categories at the polluted site, where fish and tadpole consumption was also considerably reduced, suggesting a drastic impoverishment of aquatic life. Though clearly apparent in the PCA analysis, this pattern needs further investigation because - due to the fact that our samples are small - we can confidently say what these species eat, but we are not sure of the significance of the absence of some food categories in the faeces.

It is likely that the reduction in trophic niche breadth depended also on the shifts in habitat use by the surviving turtles, which tended to concentrate into single habitat types in the polluted area, whereas they were more habitat generalists in the unpolluted area (Luiselli & Akani, 2002, 2003). However, different species may ingest the same general prey category with the same frequency while differing considerably in the species (or genera or orders) that they feed on. Thus, it is possible that the interspecific dietary relationships are more complex than those described in this study.

It is also obvious from the present study that the ecological effects of oil spills are catastrophic for the wildlife of tropical water bodies, not only immediately after the event, but also many years after the event, due to a complex sequence of ecological modifications in the environment, and to new types of ecological relationships emerging between species. Further studies must be conducted to investigate in detail these long-term ecological effects.

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A MORPHOMETRIC ANALYSIS OF *TRIMERESURUS VOGELI* (DAVID, VIDAL AND PAUWELS, 2001), WITH NEW DATA ON DIAGNOSTIC CHARACTERISTICS, DISTRIBUTION AND NATURAL HISTORY

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Morphological similarity has created considerable taxonomic uncertainty among the Asian green pitvipers. A new species of green pitviper, *Trimeresurus vogeli*, was recently described from Thailand. *T. vogeli* represents a distinct phylogenetic clade within the *Trimeresurus stejnegeri* group and is morphologically different from other clades of the *T. stejnegeri* group in several respects. However, the only obvious consistent difference between *T. vogeli* and other clades of *T. stejnegeri* is its lack of a red tail. Here, we perform a morphometric analysis to compare *T. vogeli* to other species with which it may be confused. Our data on *T. vogeli* differs in many respects to those presented in the species description, including characters considered diagnostic. In the past, *T. vogeli* has frequently been mistakenly identified as *Trimeresurus popeiorum*, from which it can be distinguished by the hemipenis structure in males. The tail colour characteristic is not reliable in distinguishing *T. vogeli* from all populations of *T. popeiorum*, and we review the morphological differences between these and *T. vogeli* females. We report a range extension to Cambodia, Laos and Vietnam, and provide habitat data for the species. The range of *T. vogeli* does not overlap with that of *T. popeiorum* or other members of the *T. stejnegeri* group.

Key words: green pitviper, SE Asia, taxonomy, Viperidae

INTRODUCTION

The green pitvipers or bamboo vipers form a distinctive part of the Asian venomous snake fauna, because of their striking appearance and because they are often the most common venomous snakes in their range. However, their morphological similarity has created substantial taxonomic uncertainty, which has not been satisfactorily resolved despite almost a century of effort (Stejneger, 1927; Pope & Pope, 1933; Regenass & Kramer, 1981). Recently, molecular work has promised to resolve certain particularly vexing taxonomic issues. Malhotra & Thorpe (2000) presented a phylogeny of 21 species based on cytochrome *b* sequences, and evaluated the taxonomic value of certain morphological characteristics against it. They defined four species groups within *Trimeresurus sensu stricto* (*s.s.*), which are diagnosed by a combination of the condition of the first upper labial and nasal scale (fused or separate) and the hemipenial structure. *T. stejnegeri* formed a distinct species group under these criteria. While monophyletic, not enough sequences were included to fully evaluate the presence of cryptic species, as was possible for the *T. albolabris* species group in Malhotra & Thorpe (2000). Recently, increased access to remote and politically restricted areas has yielded a significant number of

new specimens of green pitvipers for analysis. This has provided the opportunity to make a significant advance in the systematics of the green pitvipers in general, and *T. stejnegeri* in particular.

We have extensively reanalysed the relationships among populations of *T. stejnegeri*, based on phylogenetic analysis of DNA sequences (mitochondrial cytochrome *b* gene) and multivariate morphometrics (external and internal characters), from existing museum and newly collected material from across the known range of *T. stejnegeri* (Malhotra & Thorpe, in press). *T. stejnegeri sensu lato* (*s.l.*) was found to consist of at least three reciprocally monophyletic and morphologically distinct clades. The first occurs in Vietnam (north of latitude 20° N) and China and corresponds to the nominate form of *T. stejnegeri* (Schmidt, 1925), referred to here as *T. stejnegeri s.s.* A proposed subspecies of *T. stejnegeri*, *T. s. chenbihui* (Zhao, 1995) was indistinguishable from the nominate form. The second clade occurs in north-eastern Thailand, the Annamite Mountains on the border of Laos and Vietnam, and in southern Yunnan province, China. The north-eastern Thailand population has been recently described as *T. gumprechtii* (David *et al.*, 2002). The third clade occurs in Thailand, Cambodia, Laos and Vietnam. David *et al.* (2001) have recently described the population from Thailand as *T. vogeli*. In this paper, we present the results of a morphometric analysis of the three clades of *T. stejnegeri s.l.* Our data for this species are inconsistent

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with the published description in a number of points (e.g. in 12 out of 14 characters that are stated to separate the new species from other populations of the *T. stejnegeri* complex). Consequently, we evaluate and supplement the data on *T. vogeli* presented by David *et al.* (2001), and extend its known range.

T. stejnegeri group species can be separated from all other species groups (*sensu* Malhotra & Thorpe [2000]) by the structure of the hemipenis. The long, thin hemipenes of the *albolabris* group and the *popeiorum* group are easily distinguished from the short, stout hemipenes of *T. stejnegeri* (at least in adults) by an external examination of the shape of the tail (in *T. stejnegeri*, there is an abrupt reduction in tail thickness between subcaudals 20 and 25, whereas the tail tapers gradually to the tip in the *T. albolabris* and *T. popeiorum* group). Eversion of the hemipenis is necessary to distinguish the similarly short, stout hemipenes of the "Indian subcontinent" group (Malhotra & Thorpe, 2000), which however, differ considerably in the number, shape and distribution of the spines. Nevertheless, this character is not relevant for females, and there is no consistent, easily applied character that is capable of distinguishing female *T. vogeli* from females of the *T. popeiorum* group. Contrary to David *et al.* (2001), *T. vogeli* is not the only species of green pitviper which lacks obvious red coloration on the tail, this condition also being found in populations of *T. popeiorum* from southern Thailand and Sumatra, and *T. gramineus* from India. These species also may have 21 scale rows at mid-body (the Sumatran population of *T. popeiorum* does not invariably have 19 scale rows at mid-body as stated in Regenass & Kramer [1981]). All female *T. gramineus* seen by the senior author have some degree of dark cross-banding and a dark post-ocular streak, which is never seen in females of the *T. stejnegeri* group (although Smith [1943] states that this may be absent in *T. gramineus*). Thus, the females of *T. vogeli* may most easily be confused with *T. popeiorum*. We therefore also consider features that serve to distinguish females of *T. vogeli* and populations of *T. popeiorum* from southern Thailand and Sumatra.

MATERIALS AND METHODS

In 1999–2000, specimens were collected in Laos and Cambodia (BLS) and preserved in 10% buffered formalin after liver samples were fixed in 95% ethanol for later genetic analyses. These are deposited in the Field Museum, Chicago (FMNH), and specimens were transferred to 70% ethanol upon arrival, several months after preservation. A further specimen was found in the Dongraek Mountains of Thailand in 1999 by the senior author. A blood sample was taken from the caudal vein and preserved in buffer (5% EDTA, 100 mM Tris, 3% SDS), for later genetic analysis. Morphometric measurements and macro photographs were taken while the specimen was anaesthetized, and it was subsequently released. We also examined material in the holdings of

a number of museums. Data were also obtained from specimens collected in the field in Thailand and Vietnam (AM and RST) and trade sources. All specimens used are listed in Appendix 2.

Phylogenetic analysis of cytochrome *b* sequences identified the presence of three distinct, reciprocally monophyletic clades (these data will be published separately). A multivariate analysis of morphological data (canonical variate analysis) was performed using only those populations represented in the phylogenetic analysis, grouped into clades. Specimens from populations not represented by DNA sequences were then mapped onto the resulting axes in order to establish their affinities. Specimens that were not clearly assignable to one of the three clades using this procedure were excluded from subsequent analysis. Canonical variate analysis (CVA) was then carried out to identify characters that distinguish the clades morphologically. Sexes were treated separately as considerable sexual dimorphism is present. A list of characters used can be found in Appendix 1. Sample sizes are given in Table 1. Certain characters (particularly colour-pattern characters) showed a degree of heteroscedascity, which may perturb the analysis. Its presence should be detectable in the results, as the heteroscedastic characters would dominate the axes. The presence of potential perturbation due to heteroscedascity was also checked by carrying out a principal component analysis (PCA). This has much less discriminatory power, but is less affected by departures from the assumptions of the model of homoscedascity (Thorpe, 1983). Since PCA does not take between-character correlations into account, all size-related characters were first adjusted to a common size using the pooled within-group slope, with either snout-vent length (SVL) or head length (LHEAD) as the covariate. If the same characters were found to be important in discrimination between groups using both methods, then CVA results were used in preference.

Adding internal characters improved the resolution of the clades. However, internal characters are not particularly useful for identification in many situations and also substantially reduce the sample size, as internal data were not available for many specimens. Therefore, two sets of analyses were carried out, the first including external characters only and the second including all characters. In order to find the characters most useful at distinguishing *T. vogeli*, a discriminant function analysis was also carried out between *T. vogeli* and each clade separately. This process was repeated to compare females of *T. vogeli* with *T. popeiorum* populations from southern Thailand and Sumatra. However, because of the smaller sample size (Table 1), it was necessary to screen the characters beforehand by one-way analysis of variance (ANOVA) or covariance (ANCOVA), as appropriate, so that non-significant characters could be removed from the analysis.

The 33 specimens used to describe *T. vogeli* were all from Nakhon Ratchasima Province in Thailand (David

TABLE 1. Sample sizes in the multivariate analyses. *Ts1*, *T. stejnegeri* (s.s.); *Tg*, *T. gumprechtii*; *Tv*, *T. vogeli*; *Tp1*, *T. popeiorum* (southern Thailand); *Tp2*, *T. popeiorum* (Sumatra).

Analysis	<i>Ts1</i>		<i>Tg</i>		<i>Tv</i>		<i>Tp1</i>	<i>Tp2</i>
	M	F	M	F	M	F	F	F
All characters	18	23	7	10	14	14	-	-
External characters	41	34	10	15	25	23	4	7

et al., 2001). David *et al.* (2001) suggested that the species occupies a wider range. It is therefore likely to show a wider range of character variation than provided in the description, and we evaluate the distinguishing characters described in David *et al.* (2001), using ANOVA and ANCOVA. The assumption of homogeneity of variance was checked using Levene's test, and the Brown-Forsythe variant of the ANOVA, which relaxes this assumption, was used where it was violated (Brown & Forsythe, 1974). Where a significant result was found, post-hoc tests were used to examine which groups the difference lay between. Since this involves multiple tests (in this case, *t*-tests), the critical probabilities for rejection of the null hypothesis of no difference were adjusted using a Bonferroni correction (Grafen & Hails, 2002). All analyses were carried out using the BMDP software package.

RESULTS

MULTIVARIATE MORPHOMETRICS

PCA and CVA results were similar, with no apparent perturbation from heteroscedascity in the CVA. The CVA successfully discriminated between the three groups with 100% success. Inclusion of internal characters substantially improved the discrimination of the groups, particularly for females (Fig. 1), as was also found to be the case in distinguishing subspecies of the ringed snake, *Natrix natrix*, by Thorpe (1979, 1989). Table 2 lists characters that contribute to the discrimination of *T. vogeli*, their mean value, and range. The difference in any single character is subtle, with largely overlapping ranges (Table 2).

T. vogeli is distinguished from *T. stejnegeri* s.s. in both sexes by a relatively larger head (LHEAD, WHEAD), narrower internasal scales (WINTNAS), and more sublabial scales (SUBLAB). In males of *T. vogeli*, the scale reductions from 19 to 17 rows (VS19TO17) and 21 to 19 rows (VS21TO19) occur closer to the head, the scale reduction from 8 to 6 rows on the tail (SC8TO6) occurs closer the vent, and a postocular streak is less common (OCTSRIPE) than in *T. stejnegeri* (Table 2A). The right testis (RTANT, RTPOST) of male *T. vogeli* is more proximal in position, as is the anterior edge of the liver (LVANT) and posterior edge of the left testis (LTPOST), than in *T. stejnegeri*. In females, the reduction from 17 to 15 rows (VS17TO15) most clearly distinguishes the two species (Table 2B), again occurring closer to the head in *T. vogeli* (Table 2B), as does the liver (LVANT, LVPOST) and the anterior edge of

the right kidney (RKANT). *T. vogeli* females also tend to have more scales between the supraocular scales (BTWSUPOC1 and 2), more ventral scales (VSC), more pterygoid teeth (PTERY), and fewer subcaudals (SCS) than *T. stejnegeri* females.

Male *T. vogeli* can be distinguished from *T. gumprechtii* by the position of the scale reductions from 17 to 15 (VS17TO15) and 19 to 17 (VS19TO17) rows (Table 2C), which occur closer to the head in *T. vogeli*. Male *T. vogeli* also have more subcaudal scales, less keeled temporal scales (KTEMP), and narrower internasal scales (WINTNAS), than male *T. gumprechtii*. Again, the relative position of the testes (RTANT, RTPOST, LTANT, LTPOST) allows *T. vogeli* males to be distinguished from *T. gumprechtii* males, this time occurring closer to the vent in *T. vogeli* (Table 2C). Female *T. vogeli* can chiefly be distinguished by the fact that they have a longer head (LHEAD), smaller eye (DEYE), narrower internasal scales (WINTNAS), and a

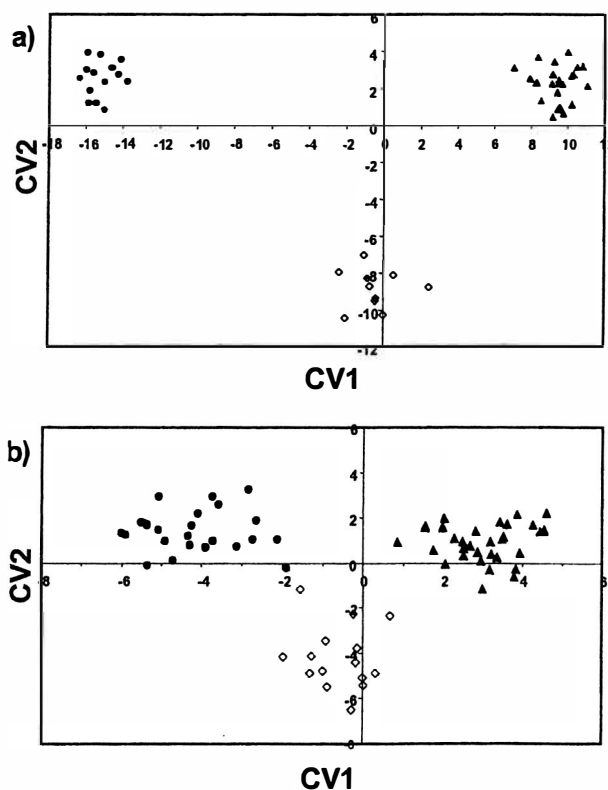


FIG. 1. Plot of first two canonical variates for females only, showing the increase in resolution gained by using internal as well as external characters. The difference is not as dramatic for males. (a) external and internal characters; (b) external characters only. Grey circles: *T. vogeli*; open diamonds: *T. gumprechtii*; black triangles *T. stejnegeri* (s.s.).

TABLE 2. Mean values and range (in parentheses) of morphological characters important in multivariate discrimination between *T. vogeli* and other *stejnegeri* group clades (see text). To maximize sample size, the results of the analysis of external characters are used in preference. However, internal characters that are important in the discrimination when all characters are used are also listed. Data are for the maximum number of specimens available for that character. Size-related characters are adjusted to the grand mean size of SVL and LHEAD (54.15 cm, 30.53 mm for females; 54.38, 27.59 for males respectively). A, *T. vogeli* and *T. stejnegeri* (s.s.) males; B, *T. vogeli* and *T. stejnegeri* (s.s.) females; C, *T. vogeli* and *T. gumprechtii* males; D, *T. vogeli* and *T. gumprechtii* females. Characters are listed in order of magnitude of their contribution to the discriminant function, and their abbreviations are explained in Appendix 1.

A. MALES	<i>T. vogeli</i>	<i>T. stejnegeri</i> (s.s.)	B. FEMALES	<i>T. vogeli</i>	<i>T. stejnegeri</i> (s.s.)
LHEAD	29.1 (25.8–40.3)	27.0 (24.2–30.6)	VS17TO15	70.1 (66.8–73.2)	76.1 (70.5–93.2)
WHEAD	13.5 (12.1–17.3)	2.7 (10.3–14.9)	LHEAD	32.9 (26.8–56.6)	28.8 (13.6–33.0)
VS19TO17	65.1 (51.2–69.6)	68.7 (61.7–77.4)	BTWSUPOC1	11 (9–13)	10.7 (8–14)
SC10TO8	6.3 (3.1–10.7)	7.9 (3.0–15.9)	DEYE	3.9 (2.7–5.5)	4.1 (3. –5.3)
WINTNAS	2.0 (1.4–2.6)	2.2 (1.7–2.6)	DV17TO15	4.6 (3–7)	3.9 (3–5)
SUBLAB	12.4 (11–14)	11.8 (10–13)	SUBLAB	13.2 (11–14)	12.5 (11–15)
OCSTRIPE	0.16 (0–1)	1.1 (0–2)	KTEMP	0.02 (0–0.5)	0.3 (0–0.5)
INTNAS	1.6 (1–4)	1.8 (1–4)	WINTNAS	1.9 (1.5–2.4)	2.1 (1.4 –2.7)
VS21TO19	60.1 (9.6–65.8)	64.1 (53.1–73.6)	BTWSUPOC2	16.5 (14–19)	15.7 (12–20)
SC8TO6	14.6 (7.0–27.4)	19.2 (7.5–29.7)	DV10TO8	3.0 (1–4)	3.4 (1–4)
RTPOST	73.1 (70–79)	75.0 (72.6–78.1)	VS25TO23	7.4 (5.5–12.9)	8.2 (5.7–13.9)
RTANT	70.4 (66.5–76.5)	71.6 (67.9–75.6)	VSC	165.5 (157–173.5)	161.6 (152–171)
LKPOST	93.1 (91.3–94.3)	94.4 (93.1–98.8)	LVANT	38.3 (35.9–40.6)	39.5 (37.0–42.9)
LVANT	40.1 (38.1–42.1)	41.2 (38.9–45.8)	LVPOST	56.4 (53.2–61.1)	58.3 (55.4–63.6)
LTPOST	77.7 (75.3–80.1)	79.5 (77.4–87.7)	PTERY	13.5 (12–16)	13.0 (11–15)
			RKANT	78.3 (74.3–82.1)	79.7 (75.9–83.8)
C. MALES	<i>T. vogeli</i>	<i>T. gumprechtii</i>	D. FEMALES	<i>T. vogeli</i>	<i>T. gumprechtii</i>
SC10TO8	6.3 (3.1–10.7)	8.6 (5.5–12.7)	LHEAD	32.9 (26.8–56.6)	31.8 (29.2–36.0)
VS17TO15	69.2 (62.0–78.4)	73.8 (69.8–77.7)	DEYE	3.9 (2.7–5.5)	4.1 (3.3–5.1)
DV23TO21	4.3 (3–5)	4.2 (3–5)	VS23TO21	9.1 (5.3–12.6)	12.1 (7.9–17.2)
VS19TO17	65.1 (51.2–69.6)	67.0 (64.7–69.9)	WINTNAS	1.9 (1.5–2.4)	2.0 (1.5–2.6)
SCS	66.7 (61–72)	64.8 (59–74)	DV27TO25	5.6 (4–10)	7.1 (4–13)
SC8TO6	14.6 (7.0–27.4)	18.7 (14.2–21.2)	VS27TO25	5.7 (4.1–9.2)	6.9 (4.4–9.3)
KTEMP	0.2 (0–0.5)	0.3 (0–0.5)	STRIPE	2.0 (2–2)	1.5 (0–2)
WINTNAS	2.0 (1.4–2.6)	2.2 (1.8–3.1)	SC8TO6	11.2 (6.5–15.3)	15.9 (12.1–22.1)
DV12TO10	2.5 (1–5)	2 (1–5)	VENTEDGE	8.9 (7–10)	8.3 (8–10)
RTPOST	73.1 (70.0–79.0)	71.6 (70.2–73.4)	PREOC	3 (2–3)	2.4 (2–4)
RTANT	70.4 (66.5–76.5)	68.5 (66.7–70.4)	INTNAS	2.0 (1–3)	1.3 (1–2)
LTPOST	77.7 (75.3–80.1)	76.2 (72.0–78.2)	VS17TO15	70.1 (66.8–73.2)	77.0 (69.0–87.2)
LTANT	75.1 (72.4–77.0)	73.4 (70.1–75.2)	HTANT	34.8 (32.4–37.7)	33.6 (30.3–36.8)

much more pronounced lateral stripe (STRIPE) than female *T. gumprechtii*. The scale reduction from 23 to 21 rows (VS23TO21) also occurs closer to the head in female *T. vogeli* than in female *T. gumprechtii* (Table 2D), as does the scale reduction from 27 to 25 rows (VS27TO25) and the reduction from 17 to 15 rows (VS17TO15). Female *T. vogeli* have a larger number of scales between the internasals (INTNAS) and between the last sublabial and ventral scales (VENTEDGE) than female *T. gumprechtii*. There is not much difference between females of these clades in position of internal organs, although the anterior edge of the heart (HTANT) tends to be more distal in *T. vogeli*.

Table 3 gives similar data for *T. vogeli* compared to *T. popeiorum* (females only), although only exter-

nal characters were used because of very limited internal data for *T. popeiorum*. The most useful character distinguishing between *T. vogeli* and *T. popeiorum* from southern Thailand and Sumatra is the extent of the lateral stripe (STRIPE), which is much more prominent in *T. vogeli*. In southern Thailand *T. popeiorum* in particular, the lateral stripe is almost non-existent, being barely present on the first scale row (SCR1) and rarely encroaching upon the second scale row (SCRSTR). The pit is also closer to the eye (PIT2EYE) and there are more scales bordering the supraoculars (BORSUPOC) in *T. vogeli* than in either of the *T. popeiorum* populations. The internasal scales (WINTNAS) are much wider, the scale reduction from 17 to 15 rows on the body (DV17TO15) is more likely to involve lower scale rows, and the scale reduction from 6 to 4 rows on the tail (SC6TO4) occurs closer to the vent in

TABLE 3. Mean values and range of morphological characters important in multivariate discrimination between females of *T. vogeli* and populations of *T. popeiorum* with which it might be confused (see text). Data are for the maximum number of specimens available for that character. Size-related characters are adjusted to the grand mean size of SVL (50.91 cm) and LHEAD (30.55 mm). A, *T. vogeli* and *T. popeiorum* from Sumatra; B, *T. vogeli* and *T. popeiorum*, southern Thailand. Characters are listed in order of magnitude of their contribution to the discriminant function, and their abbreviations are explained in Appendix 1.

Character	Taxa	
	<i>T. vogeli</i>	<i>T. popeiorum</i> (Sumatra)
A.		
SUBLAB	13.2 (11–14)	11.9 (10–13)
PIT2EYE	1.5 (1.1–1.8)	1.6 (1.3–1.8)
WINTNAS	1.9 (1.6–2.4)	2.5 (2.3–2.9)
STRIPE	2.0 (2–2)	0.3 (0–1)
SC6TO4	26.8 (16.4–42.5)	21.6 (15.5–32.0)
POSTOC	2.6 (2–4)	2.1 (2–3)
BORSUPOC	7.7 (6.5–9)	6.6 (6–8)
DV17TO15	4.6 (3–7)	3.8 (3–5)
VSC	165.5 (157–175.5)	147.9 (144–152)
DV10TO8	3.0 (1–4)	2.4 (1–3)
NASPIT	1.5 (0–2.5)	0.6 (0–2)
B.		
	<i>T. vogeli</i>	<i>T. popeiorum</i> (south Thailand)
EYE2NOS	6.5 (6.1–7.0)	6.9 (6.7–7.1)
PIT2EYE	1.5 (1.1–1.8)	1.8 (1.7–1.9)
STRIPE	2.0 (2–2)	0.25 (0–1)
KHEADSC	0.03 (0–0.5)	0.25 (0–0.5)
SCRSTR	1.1 (1–2)	0.25 (0–1)
BORSUPOC	7.7 (–9)	6.9 (6–8)
BTWSUPOC1	11.0 (9–13)	10.3 (10–11)
SCR1	0.31 (0.1–0.7)	0.03 (0–0.1)
VS19TO17	66.1 (63.8–69.1)	67.6 (66.0–69.9)
ROST	0.36 (0.23–0.50)	0.28 (0.22–0.34)

Sumatran *T. popeiorum* than *T. vogeli*. Sumatran *T. popeiorum* also tend to have fewer postocular scales (POSTOC) and ventral scales (VSC), and fewer small scales between the nasal scale and the scute forming the anterior border of the pit (NASPIT). Southern Thailand *T. popeiorum* tend to have a greater distance between the eye and the nostril (EYE2NOS), more keeled scales on the rear of the head (KHEADSC), fewer scales between supraoculars (BTWSUPOC1), a more distal scale reduction from 19 to 17 rows (VS19TO17), and a more pointed apex to the rostral scale (ROST) than *T. vogeli*.

EVALUATION OF DIAGNOSTIC CHARACTERS PRESENTED IN THE SPECIES DESCRIPTION.

David *et al.* (2001) presented a combination of six characters that distinguish *T. vogeli* from all other green pitvipers (listed as 1–6 below), four characters that dis-

tinguish *T. vogeli* from particular species of green pitvipers (of which two are discussed in 7–8 below), and 14 characters that separate *T. vogeli* from other populations of the *T. stejnegeri* complex (9–22 below). Our findings are inconsistent with many of these characters; this is expanded upon below. Phrases in italics are taken directly from David *et al.* (2001).

1. *Short, spinose hemipenis.* In contradiction to David *et al.* (2001), this description is insufficient to distinguish *T. vogeli* from many other *Trimeresurus* species. For example, *T. gramineus* also has a short spinose hemipenis, and the shape, number and distribution of spines is also important to distinguish *T. vogeli* from this species (as described above).

2. *First supralabial is separated from the nasal.* This will only distinguish *T. vogeli* from members of the *T. albolabris* group.

3. *Ventrolateral stripe nearly always white, whitish blue, or whitish yellow when present, very seldom red in females.* While the red stripe may be narrow, it was never absent altogether in the males examined, and it may, rarely, be present in females. Females always have a lateral stripe, and although not many live individuals have been seen, it was always yellow in those examined.

4. *White vertebral spots are always present in males, always absent in females.* White vertebral spots or flecks were not always present in males of *T. vogeli* examined. This may be an artefact of preservation. However, in a series from Dongraek, Thailand, which were all preserved at around the same time and are in a similar state of preservation and not excessively darkened, six out of nine males lacked vertebral spots. On the other hand, they were always found to be present in males from Dong Hua Sao National Biodiversity Conservation Area (NBCA), Laos. White vertebral spots are also present in males of *T. popeiorum* from southern Thailand, and juvenile male *T. gumprehti*. The difference in the mean number of spots between the *T. stejnegeri* group clades was found to be significantly different in an ANOVA ($P=0.001$), but this difference was largely due to the difference between *T. vogeli* (mean=14.9, range=0–58), and *T. stejnegeri* (s.s.) (mean=1.1, range=0–17), with the difference between *T. vogeli* and *T. gumprehti* not being significant. This character was also not important in the multivariate discrimination of *T. vogeli* from other clades of *T. stejnegeri*.

5. *Less than 174 ventrals.* This is confirmed, but does not serve to distinguish *T. vogeli* from many species. *T. popeiorum* from southern Thailand, for example, also have a similar number of ventral scales (range in females, $n=4$, is 166–173).

6. *No more than about 25% of its tail is rusty red.* This character is not reliable in specimens that have darkened in preservative. In live specimens that we have examined, the tail tip varies from grey to dark brown mottled, almost appearing banded. However, *T.*

gramineus, and some populations of *T. popeiorum*, also share this condition.

Thus a combination of these six characters will not distinguish female *T. vogeli* from *T. popeiorum* from southern Thailand, and possibly also from Sumatra. The next two characters were used by David *et al.* (2001) to distinguish *T. vogeli* from *T. popeiorum*.

7. *Thicker head.* Head depth was not measured in our study so cannot be evaluated.

8. *Lower number of subcaudals.* There is no significant difference between the mean number of subcaudals in *T. vogeli* females and southern Thailand and Sumatran populations of *T. popeiorum* ($P < 0.05$).

Thus at least one of the cited characters does not serve to diagnose female *T. vogeli*. The following 14 characters are those stated by David *et al.* (2001) to separate *T. vogeli* from other *T. stejnegeri* populations.

9. *A greater maximal size, especially in female specimens.* The maximum sizes we have recorded for the species (720 mm, 990 mm SVL for males and females respectively) are in accord with data in David *et al.* (2001). However, this is not significantly different ($P > 0.25$) from the maximum sizes recorded for *T. gumprechtii* in north-eastern Thailand (745 mm, 876 mm SVL for males and females, respectively), contradicting the statement in David *et al.* (2001) that they are distinctly smaller than *T. vogeli*. This statement was also contradicted later by David *et al.* (2002), who gave large size as a diagnostic characteristic of *T. gumprechtii*.

10. *Males of T. vogeli are dark green with faint black fasciatures, and females are bright grass green, whereas both males and females of other populations are bright, grass or deep green.* The difference between male and female dorsal coloration is not very obvious in close-up photographs of the Dong Hua Sao NBCA population, where both males and females are dark-green in colour. In a captive-born pair acquired from the trade, which DNA analysis indicates most likely come from the Dongraek Mountains of Thailand, the male and female are very different in dorsal coloration, with the male being blue-green and the female grass-green. The fasciatures mentioned are not obvious in the male specimens from Laos.

11. *The white or yellow ventrolateral stripes are only rarely bordered below by a red line in subadult and adult males of T. vogeli.* In later discussion, it is also stated by David *et al.* (2001) that juvenile male *T. vogeli* are more likely to possess a red stripe, implying that they lose it as they grow. This is unusual, but not unknown: in most *Trimeresurus* that possess a red stripe, it is present throughout life. However, as stated above, the rarity of the red stripe in *T. vogeli* is not supported by our data. Although in some preserved specimens which have darkened considerably, the stripe may be difficult to distinguish, in others it is perfectly clear as a darker region bordering the white stripe, clearly distinct from the lighter general dorsal hue. In two extensive and well preserved series of this species in the Field Museum, Chicago, from Sakaerat Experimental Station in Thai-

land (where many of the paratypes of the species originated), and Dong Hua Sao NBCA in Laos, 100% of males had this red stripe ($n = 9$ and 4 respectively). Unusually, one female from Sakaerat also possessed a red lateral stripe. As stated by David *et al.* (2001), in several populations of *T. stejnegeri* (*s.s.*), females also have a red stripe (notably in parts of China and north Vietnam), but this is clearly a rare condition in *T. vogeli* (one out of 23 specimens examined).

12. *A white or yellowish streak is present, although thin and faint in males, but always absent in females.* Postocular stripes were seen in two out of nine males examined from the Dongraek region and two out of eleven males examined in the central Vietnam population. It was absent altogether in the four males examined from Laos. Thus, it would seem that the occurrence of a postocular streak in male *T. vogeli* is at best a rare condition. Conversely, it is always present in male *T. gumprechtii* and frequently present in *T. stejnegeri s.s.* (the difference between clades is highly significant, $P = 0.0001$). This character is especially useful for distinguishing male *T. vogeli* from *T. gumprechtii*, as the presence of the streak in *T. gumprechtii* can easily be discerned in preserved specimens even if the constituent colour(s) cannot. A postocular stripe is never present in female *T. vogeli*, but the difference between clades in the presence of a postocular streak is not significant ($P = 0.13$). The postocular stripe is also consistently absent in both sexes in other populations, such as *T. stejnegeri s.s.* from northern Vietnam.

13. *In T. vogeli the eye is yellow or yellowish green, and never red... whereas in T. stejnegeri the eye is red, orange or amber in males and females.* This statement overlooks sexual dimorphism in eye colour in *T. stejnegeri s.l.* In most populations, females have yellow eyes, as indeed is stated in Table 3 of David *et al.* (2001). Moreover, ontogenetic variation is present in males (senior author, pers. obs.). In Taiwan and north-east Thailand, where an extensive series of live animals has been examined, males are born with yellow eyes, and the degree of red pigmentation increases with age until they are bright or brick red in colour in large males. Thus, the discriminatory power of this character is weak for females and subadult males.

14. *The coloration of the tail is rather different from other green pitvipers of the mainland.* This is true for all *T. stejnegeri* populations, but not for all species of the mainland as indicated above. Here, the authors state that the rusty coloration may extend up to 50% of the tail on the upper side, rather than the maximum of 25% stated in point 6. We did not measure the extent of coloration on the tail, except in the three live specimens examined (where it is in accord with the lower figure). However, if the rusty coloration does extend to 50% of the tail, it would further decrease the contrast between *T. vogeli* and southern Thailand *T. popeiorum*.

15. *T. vogeli has a lower value for the ratio tail length: total length, especially in females.* The use of ratios is inappropriate where the relationships between

the component measurements is allometric (Thorpe, 1983), as they will be biased if the total length of the populations being compared is different, such being the case here. A better procedure would be to adjust tail length by regression (SVL rather than total length was used as a covariate) and then compare the groups. The difference between *T. vogeli* and other *T. stejnegeri* group populations is then not significant in females ($P>0.5$). However, in both sexes the assumption of equal within-group slopes is violated, due to a significantly lower slope in *T. vogeli*. This suggests that, although tail size of small individuals of *T. vogeli* may not be very different, the tail will grow less in this species than the others, and thus the tail may be considerably shorter in large animals: this makes the statistical significance of this difference impossible to assess between animals of different sizes.

16. *T. vogeli* has a higher number of ventral scales than in all populations of *T. stejnegeri*, except for those from Hainan island. The difference between clades is significant for both males and females ($P=0.01$) but this is mainly due to the difference between *T. vogeli* and *T. stejnegeri* (s.s.) (including Hainan island). *T. vogeli* and *T. gumprechtii* are not significantly different in ventral scale number. This result did not differ when Hainan specimens were excluded from *T. stejnegeri* s.s., although the significance of the difference with *T. vogeli* increased ($P=0.003$ in both sexes). However, VSC did not contribute to the multivariate discriminant analysis of male *T. vogeli* and *T. stejnegeri* s.s. (Table 2).

17. There is a lower number of subcaudal scales in *T. vogeli*... although this character is barely significant. In our data, there is a significant difference in the number of subcaudals between clades of *T. stejnegeri* ($P=0.03$, 0.0001 for males and females respectively). However, the difference is mainly between *T. vogeli* (mean=66.7, 60.9 in males and females respectively) and *T. gumprechtii* (mean=64.8, 58.1 in males and females respectively), so this character is less useful in distinguishing *T. vogeli* and *T. stejnegeri* s.s. This character contributes to the discriminant analysis of *T. vogeli* and *T. gumprechtii* males only (Table 2).

18. In *T. vogeli*, the number of cephalic scales in males is slightly higher than in males of *T. stejnegeri*, except for specimens from Hainan island. The definition of this character appears to be similar to BTWSUPOCI. However, we found no significant differences between clades for this character, whether Hainan island specimens were included or excluded ($P=0.385$, 0.300 respectively) from *T. stejnegeri* s.s. However, this character did contribute to the discriminant analysis of females of the two species (with Hainan island included in *T. stejnegeri* s.s.).

19. The total number of supralabials is higher in *T. vogeli* than in *T. stejnegeri*, except for Hainan island specimens. Although this character was measured in this study as the average of right and left sides rather than the total number, this character was only found to differ significantly between clades in females ($P=0.12$, 0.02 in

males and females respectively). Again, this was solely due to the difference between *T. vogeli* (mean=10.7, range=10–12) and *T. stejnegeri* s.s. (mean=10.1, range=9–14), and will not serve to distinguish *T. vogeli* from *T. gumprechtii*. This character also did not contribute to the discriminant analysis of *T. vogeli* and *T. stejnegeri* s.s.

20. The third supralabials are much less frequently in contact with the subocular in males of *T. vogeli*. This character was only found to differ significantly between clades in females ($P=0.94$, 0.01 for males and females respectively). However, post-hoc tests showed that the difference was mainly between *T. stejnegeri* s.s. and *T. gumprechtii*. *T. vogeli* was not significantly different from *T. gumprechtii* ($P>0.1$), and only just significantly different from *T. stejnegeri* s.s. ($P=0.04$).

21. The fourth supralabials are more frequently separated by at least two scales (from the subocular) in males of *T. vogeli*. This character was not found to differ significantly between clades in our study ($P=0.08$, 0.64 for males, females).

22. The microdermatoglyphic pattern is different. The patterns of *T. vogeli* from Thailand are described as being identical to those of *T. popeiorum* (locality not specified), while being different from that of Chinese *T. stejnegeri*. We cannot add to this observation. However, the systematic value of these patterns has been questioned, as the relationships inferred from these patterns is often in conflict with those inferred from genetic data (Estos, 1981; Beyerlein, 1998). Thus the diagnostic value of this character needs to be further investigated in additional populations of *T. vogeli* and other species of the *T. stejnegeri* group.

A few additional points are cited as being characteristic of *T. vogeli* in other parts of David *et al.* (2001), which are not covered in the list above.

23. Twenty-one scale rows at mid-body, strongly keeled. Twenty-one scale rows at mid-body is characteristic of many species of green pitviper, including most of the *T. stejnegeri* group. Strong keeling of the scales at mid-body is only significantly different between female *T. vogeli* and *T. stejnegeri* s.s. ($P<0.003$), with no significant difference between *T. vogeli* and *T. gumprechtii* ($P>0.9$). However, it is *T. stejnegeri* s.s. that is the more heavily keeled and this character does not contribute to the multivariate discrimination of the two clades.

24. An elongated snout covered with rather small scales. We did not measure this character directly and so cannot evaluate it statistically.

25. Internasals always separated by 1 or 2 (rarely 3) scales. The maximum number of internasals recorded is four. The mean is significantly different between clades in both sexes ($P=0.05$, 0.0004 in males and females respectively), but this is mainly due to a significantly higher mean in *T. vogeli* (mean=1.6, 2.0, range=1–4, 1–3 in males and females respectively) than in *T. gumprechtii* (mean=1.2, 1.3, range=0–2, 1–2 in males and females respectively). This is reflected in INTNAS and/or WINTNAS being important in discriminating both sexes of *T. gumprechtii* (Table 2).

26. *Large, irregular supraoculars, as wide as internasals.* The ratio of the length to the width of the supraoculars is given as 2.4–2.8. Our data (2.1–4.2) shows upper limit of the range is much higher. There is no significant difference between clades in either sex ($P=1.0$, 0.15 in males and females respectively).

DISCUSSION

The lack of agreement of our data with the distinguishing characteristics presented in the species description may be due to the limited geographic sampling of *T. vogeli* in David *et al.* (2001). We therefore present a detailed description of variation in the specimens of *T. vogeli* examined for this study from Thailand, Laos, Vietnam and Cambodia.

REDESCRIPTION OF VARIATION WITHIN *T. VOGELI*

Colour in preservative. The lateral stripe is always well developed in males and was seen, unusually, in one female from Sakaerat, Thailand. A white stripe is present on the upper half of the first scale row, extending onto the second row, and a darker (originally red) stripe is present on the lower half of the first scale row. Specimens from Dong Hua Sao NBCA, examined shortly after preservation when the background colour was bright blue, had very clear red stripes. Although they have since darkened to uniform steely grey blue, the red pigmentation on the first scale row is still visible. The ventral surface is lighter than the dorsal, and the tail is entirely uniform in colour, although traces of the lateral stripe continue onto the subcaudal scales to about the tenth pair. Upper lip coloration is not distinct from the rest of the head. About 30 small light vertebral flecks are present in males of all sizes. Postocular stripes are only occasionally present in males as indistinct pale streaks.

Colour in life. This description is based on photographs of male and female specimens from Dong Hua Sao NBCA, Laos, and a female from Khao Yai National Park, Thailand. Dorsal surface is dark to grass green, contrasting with the ventral surface, which is yellowish green. The lateral stripe, on the first two scale rows of the body, is red below and white above. The upper lip is slightly more yellow than the rest of the dorsal surface of the head, although this is not discernible in preserved specimens. The bright blue interstitial skin may be very obvious towards the posterior of the body. The last 20 or so subcaudals are darker (but not red), although there are occasional rows of lighter scales interspersed with this to give a banded appearance. The pale vertebral flecks, although small, are very obvious towards the posterior of the body. Eye colour is light orange. In females, the red and white lateral stripe is replaced by a narrow yellow stripe, and the contrast between dorsal and ventral colour is less marked. Eye colour appears to be the same in both sexes.

MORPHOMETRIC AND MERISTIC CHARACTERS.

Females have relatively shorter tails than males, fewer subcaudals (ranging in females from 52–70, com-

pared to 61–72 in males), relatively larger heads, and reach an overall larger size (maximum recorded 99.0 cm SVL compared to 70.0 cm for males). The number of ventral scales varies between 157 and 173 in both sexes. Body scales range from having no keeling to fairly strong keeling, while temporal and rear head scales are never strongly keeled, and often unkeeled. The ratio of the upper and lower edges of the rostral scale varies between 0.2 and 0.5 (note that this character is not noticeably allometric as it is not correlated with any linear measurement on the head or body). Supralabials vary from 8–12 and sublabials from 10–14. The minimum number of scales between supraoculars varies from 9–13 and there are 13–18 scales between the posterior edges of the supraoculars. The number of scales between the nasals and shield bordering the anterior of the pit varies from 0–3, and there may be 1–4 internasal scales. There may be 0–1 scales between the third supralabial and the subocular, and 1–2 scales between the fourth and fifth supralabials and the subocular scale. Some of these scalation patterns are illustrated in Fig. 2.

DISTRIBUTION

Based on the presence of verifiable records, *T. vogeli* is presently known from the western Dongraek Mountains (Khao Yai National Park), the western edge of the Khorat Plateau (Sakaerat Experimental Station), and small isolated south-eastern mountains (Khao Sai Dao Wildlife Sanctuary) in Thailand, the Cardamom Mountains in Cambodia (Bokor National Park), the Bolovens Plateau (Dong Hua Sao NBCA) in Laos, and the Kontum Plateau of central Vietnam (Fig. 3). David *et al.* (2001) mention literature records which apparently refer to this species from Trat and Prachin Buri provinces in south-eastern Thailand, and Krabi Province in southern Thailand (Jintakune & Chanhme, 1995). A male from Krabi (pictured in Figs. 185 and 186 in Jintakune & Chanhme [1995], while a female from Trat is depicted in Figs. 187 and 188, not as stated in David *et al.* [2001]) has been examined by the senior author, and is confirmed as a member of the *T. stejnegeri* group. However, the specimen was obtained from a dealer and must be regarded as a provisional record until further specimens of known provenance are obtained.

NATURAL HISTORY

T. vogeli occupies hill areas from about 200 m (Sakaerat, Thailand) upwards to at least 1200 m (Dong Hua Sao NBCA, Laos) throughout the southern end of the Indochinese peninsula. It is primarily found in evergreen forest, occasionally in sparsely vegetated grasslands on high elevation plateaus (e.g. at Bokor National Park in the Cardamom Mountains and on the Bolovens Plateau in Laos) and semi-evergreen or dry evergreen forest at lower elevations (e.g. at the Sakaerat Experimental Station, Nakhon Ratchasima Province, Thailand). *T. vogeli* is often found near water, and most specimens were found within a couple of metres of the ground (Table 4). Frogs were the most frequent food

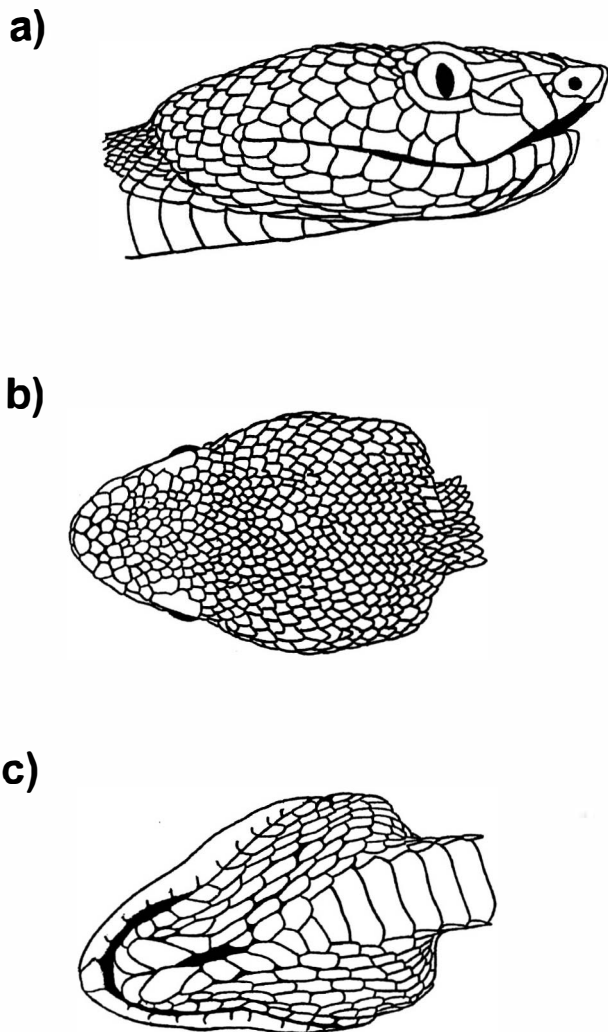


FIG. 2. Line drawing of the scalation on the head of a male specimen of *Trimeresurus vogeli* (FMNH 258946) from the Dong Hua Sao NBCA, Laos. a) lateral, b) dorsal, c) ventral.

items identified in the guts of the specimens examined (ROM 30782, 30785, 30786, FMNH 252076, 252099, 256419, 258946, RNHM 16716:1), followed by mammalian prey (FMNH 180258, 180273, 258944, ROM 34561). A skink was found in one adult female specimen (BMNH 2000.71) and insect remains in one juvenile specimen (FMNH 180277).

COMPARISONS

T. vogeli is presently known to share its geographic range with only two other green pitvipers, *T. albolabris* and *T. macrops*, both of which belong to the *T. albolabris* group (*sensu* Malhotra & Thorpe, 2000) and can be distinguished from the *T. vogeli* group by the partial to complete fusion of the first upper labial scale and nasal scale.

Trimeresurus vogeli is most similar to other members of *T. stejnegeri* s.l., but can be distinguished from them by the lack of red on the tail. The extreme tip of the tail may be grey or brown, sometimes with a few bands, but

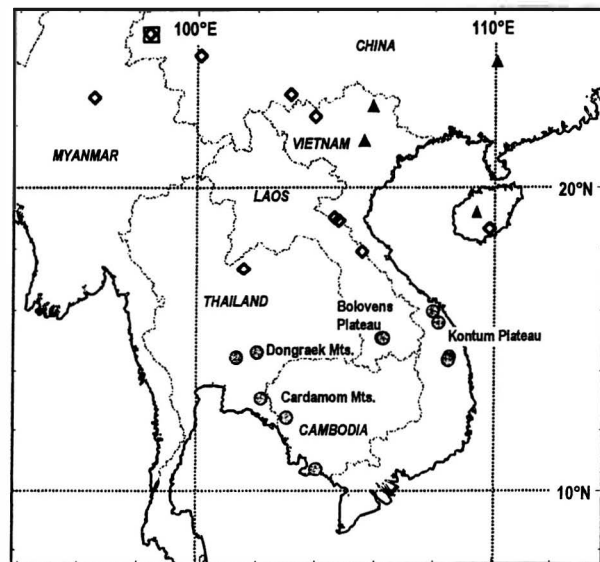


FIG. 3. Map of South-east Asia, showing the known distribution of *T. vogeli*. The occurrence of other members of the *T. stejnegeri* group in close proximity is also shown. Grey circles: *T. vogeli*; open diamonds: *T. gumprechtii*; black triangles: *T. stejnegeri* (s.s.); black square: type locality of *T. yunnanensis*.

this is confined to the extreme distal portion of the tail. However, this character is not easy to distinguish in preserved specimens. *T. vogeli* is also morphologically distinguishable from other *T. stejnegeri* group species using multivariate analysis of characters. The values of the characters that contribute most to distinguishing the new species from both clades of *T. stejnegeri* are given in Table 2. *T. vogeli* can also be differentiated from all other species of the *T. stejnegeri* group by fixed molecular differences (14 fixed differences in a 737 bp stretch of the mitochondrial cytochrome *b* gene in the dataset used in Malhotra & Thorpe (in press) and available from GenBank, accession numbers AF277677-81, AF277709-11, AY059573, AY059575-6 for *T. stejnegeri* and *T. gumprechtii* and AY059574, AY059577-81, AF171898 for *T. vogeli*). *T. vogeli* is also distinguished from all other green *Trimeresurus* species, except for *T. gramineus* and *T. popeiorum* from southern Thailand and Sumatra, by the lack of red on the tail. Male *T. vogeli* can be distinguished from *T. gramineus* and *T. popeiorum* by the presence of a hemipenis bearing 10-20 stout spines of varying size, largest near the base, with the tips being calyculate (identical to the hemipenis of *T. stejnegeri*, illustrated in Mao, Yin & Guo [1984]). Female *T. vogeli* can be distinguished from female *T. popeiorum* from populations which have similar tail coloration by the characteristics listed in Table 3. Diagnosis of this species will be more problematic for preserved specimens in which tail coloration cannot be reliably discerned, and which lack locality details. The characters given in Tables 2 and 3 can be used in combination to assist a diagnosis, but no single character will achieve this unequivocally.

TABLE 4. Natural history data for *T. vogeli*.

Museum number	Elevation (m)	Vegetation type	Distance from ground (m)	Proximity to water
FMNH 252070	700–750	bamboo thicket	-	River bank
FMNH 252076	700–750	wet evergreen	-	Near waterfall
FMNH 252097	700–750	wet evergreen	-	Near waterfall
FMNH 252099	700–750	wet evergreen	-	Near waterfall
FMNH 258940	1000	wet evergreen	0.5	Overhanging stream
FMNH 258941	1000	wet evergreen	1	3 m from stream
FMNH 258942	1000	wet evergreen	0.5	3 m from stream
FMNH 258943	1000	wet evergreen	1.5	Overhanging stream
FMNH 258944	1200	pine/grassland	0.5	None
FMNH 258945	1200	wet evergreen	1	3 m from large river
FMNH 258946	1200	wet evergreen	1	2 m from large river
FMNH 258952	1000	wet evergreen	0.4	8 m from stream
FMNH 258953	1000	wet evergreen	1.5	None
FMNH 259187	800–900	hill evergreen	2	5 m from stream
FMNH 259188	1000	heath forest	1.5	2 m from small pond
FMNH 180242	~ 200	dry evergreen	0.8	None
FMNH 180243	~ 200	dry evergreen	0	None
FMNH 180244	~ 200	dry evergreen	0.25	None
FMNH 180247	~ 200	dry evergreen	0	None
FMNH 180256	~ 200	dry evergreen	0.5	1 m from stream
FMNH 180257	~ 200	dry evergreen	0	None
FMNH 180258	~ 200	dry evergreen	2.5	None
FMNH 180259	~ 200	dry evergreen	1.5	None
FMNH 180260	~ 200	gallery	0	1 m from stream
FMNH 180261	~ 200	dry evergreen	1.2	None
FMNH 180263	~ 200	dry evergreen	0	None
FMNH 180265	~ 200	dry evergreen	0	None
FMNH 180269	~ 200	dry evergreen	0.3	3.5 m from stream
FMNH 180272	~ 200	dry evergreen	2.75	10 m from stream
FMNH 180273	~ 200	dry evergreen	2.5	None
FMNH 180274	~ 200	dry evergreen	0.6	None
FMNH 180277	~ 200	dry evergreen	< 1	None

Note added in proof. Since this paper was accepted changes to the taxonomy of the species discussed within have been made. The new generic names can be found in Malhotra & Thorpe (2004).

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APPENDIX 1

MORPHOLOGICAL CHARACTERS USED IN THE CANONICAL VARIATE ANALYSIS (CVA), AND THEIR ABBREVIATIONS.

(A) SCALATION

- VSC: the number of ventral scales (VS), not including anal scale, recorded by the Dowling (1951) method (i.e. the first VS is that which contacts the first dorsal scale row on both sides).
- SCS: the number of pairs of subcaudal scales. Any unpaired scales are treated as a pair.
- SUPLAB: the average number of supralabials on the left and right hand side.
- SUBLAB: the average number of sublabials on the left and right hand side.
- POSTOC: number of postocular scales.
- PREOC: number of preocular scales.
- BORSUPOC: the number of scales bordering the supraocular scales (average of right and left), not counting pre- or post-oculars.
- BTWSUPOC1: the minimum number of scales between the supraoculars.
- BTWSUPOC2: the number of scales between the posterior edge of the supraoculars.
- INTNAS: the number of scales separating the internasal scales.
- LAB3: minimum number of scales separating 3rd supralabial and subocular.
- ROST: the ratio of the anterior margin of the rostral scale to the posterior margin.
- KTEMP: the keeling of the temporal scales.
- KHEADSC: the keeling of the scales on the back of the head.
- VENTEDGE: the number of scales between the edge of the mouth and the ventral scales, starting at and including the last sublabial.

(B) SCALE REDUCTION FORMULA

Recorded as a series of characters, each referring to a specific reduction. Each position will have two characters, the dorso-ventral (DV) position of the reduction (the lowest of the two merging scale rows), and the ventral scale (VS) position (counted from the head), which is the ventral scale to which the scale reduction traces diagonally. Before analysis, the VS position was transformed into the percentage of the total number of ventral scales (%VS), to control for variation.

- VS31TO29: ventral scale position of the reduction from 31 to 29 scale rows.
- DV31TO29: dorso-ventral position of reduction from 31 to 29 scale rows.
- VS29TO27: ventral scale position of the reduction from 29 to 27 scale rows.
- DV29TO27: dorsoventral position of reduction from 29 to 27 scale rows.
- VS27TO25: ventral scale position of the reduction from 27 to 25 scale rows.

- DV27TO25: dorsoventral position of reduction from 27 to 25 scale rows.
- VS25TO23: ventral scale position of the reduction from 25 to 23 scale rows.
- DV25TO23: dorsoventral position of reduction from 25 to 23 scale rows.
- VS23TO21: ventral scale position of the reduction from 23 to 21 scale rows.
- DV23TO21: dorsoventral position of reduction from 23 to 21 scale rows.
- VS21TO19: ventral scale position of the reduction from 21 to 19 scale rows.
- DV21TO19: dorsoventral position of reduction from 21 to 19 scale rows.
- VS19TO17: ventral scale position of the reduction from 19 to 17 scale rows.
- DV19TO17: dorsoventral position of reduction from 19 to 17 scale rows.
- VS17TO15: ventral position of the reduction from 17 to 15 scale rows.
- DV17TO15: dorsoventral position of reduction from 17 to 15 scale rows.
- SC12TO10: subcaudal scale position of the reduction from 12 to 10 scale rows.
- DV12TO10: dorsoventral position of reduction from 12 to 10 scale rows.
- SC10TO8: subcaudal scale position of the reduction from 10 to 8 scale rows.
- DV10TO8: dorsoventral position of reduction from 10 to 8 scale rows.
- SC8TO6: subcaudal scale position of the reduction from 8 to 6 scale rows.
- SC6TO4: subcaudal scale position of the reduction from 6 to 4 scale rows.

(C) BODY DIMENSIONS

All measurements are made on the right side of the head only unless this was damaged, in which case they were done on the left.

- SVL: distance between the tip of the snout and the cloaca.
- TAIL: distance between the anterior edge of the first subcaudal scale and the tip of the tail.
- WHEAD: width of the head measured between the outer edges of the supraoculars.
- LHEAD: length of the head measured between the tip of the snout to the posterior edge of the lower jawbone.
- DEYE: diameter of the eye measured between the edges of the scales surrounding it.
- EYE2NOS: distance between the eye and the nostril, measured between the suture between the second and third preocular (from the bottom) and the inner edge of the nostril.
- NOS2PIT: distance between the pit and the nostril, measured between the outer edges.
- WSUPOC: the width of the supraoculars measured in mm, at the widest part.
- LSUPOC: the length of the supraoculars measured in mm.

WINTNAS: the width of the internasals (in mm).

(D) INTERNAL CHARACTERS

VS positions are transformed to % VS before analysis (see scale reductions).

PTERY: the number of pterygoid teeth.

DENT: the number of dentary teeth.

HTANT: VS position of the thyroid gland.

LVANT: VS position of the anterior tip of the liver.

RKANT: VS position of the anterior tip of the right kidney.

RKPOST: VS position of the posterior tip of the right kidney.

LKANT: VS position of the anterior tip of the left kidney.

LKPOST: VS position of the posterior tip of the left kidney.

RETRACT: SC position of the insertion of the hemipenis retractor muscle (males only).

(E) COLOUR PATTERN

STRIPE: presence of a lateral stripe (0, absent; 1, indistinct; 2, distinct).

SCRSTR: number of scale rows involved in stripe.

OCSTRIPE: presence of postocular stripe (0, absent; 1, indistinct; 2, distinct).

SCROC: number of scale rows involved in postocular stripe.

DORSPOT: the number of spots on the dorsal surface.

SPOTSIZE: the mean number of scales covered by the three largest dorsal spots.

SCR1: the proportion of the first scale row covered by the light area.

APPENDIX 2

SPECIMENS EXAMINED

Specimens not used in the canonical variate analysis (CVA) are indicated in italics. Abbreviations are as follows: American Museum of Natural History, New York (AMNH); the Natural History Museum, London (BMNH); California Academy of Sciences, San Francisco (CAS); Field Museum, Chicago (FMNH); Museum of Comparative Zoology, Harvard (MCZ); National Museum of Natural Science, Taiwan (NMNS); Naturhistorisches Museum Wien (NMW); Phu Luang Wildlife Research Station, Thailand (PLWRS); Royal Ontario Museum, Toronto (ROM); Shanghai Natural History Museum (SNHM); United States National Museum of Natural History, Smithsonian Institute; Washington (USNM); the author's personal collection (AM and RTV).

T. STEJNEGERI (S.S.)

Northern China: SNHM 729159, MCZ 163259, AMNH 33222-9, BMNH 99.4.24.61, BMNH

54.2.10.18, FMNH 25196-204, FMNH 170642, USNM 73140, NMNS 3651: 12347, 12349, 12351, 12354, NMW 23913:1, CAS 71957, USNM 64022-23;

Taiwan: FMNH 96807-11, FMNH 96816, FMNH 120772-5, NMNS 01882-7, NMNS 01889, NMNS 01334:1-3, NMNS 01549, NMNS 01584, NMNS 01434, NMNS 01479, NMNS 01722, NMNS 01841, NMNS 01845;

Southern China: SNHM 720068, SNHM 112-3;

Northern Vietnam: NMW 23913:3, ROM 35312-15, ROM 35318, ROM 35320-22, ROM 31066, ROM 31068, ROM 31072, AM99.15, AM99.17-18;

Hainan, China: SNHM 500128-9, SNHM 720065, SNHM 720069-72;

T. GUMPRECHTI

Annamite Mountains (Laos and Vietnam): FMNH 255579-80, FMNH 256419;

North-eastern Thailand: PLWRS 3-5, PLWRS 920503, AM94.1, AM94.3-18, AM94.20;

T. VOGELI

Central Vietnam: NMW 23913:2 (locality listed as Annam, Tonkin; both names refer to parts of what is now Vietnam, and is referred to this species on the basis of morphological analysis), ROM 30781, 30782, 30785, 30786, 30788, 30791, 25403 (Tram Lap District, Gia Lai Province, Vietnam, 14° 26' N, 108 33' E), ROM 34559-61, 34565 (Krong Pa District, Gia Lai Province, Vietnam, 14° 20' N, 108° 28' E), FMNH 252076, 252097, 252099 (Buon Luoi, 20 km north-west of Kannack, Ankhe District, Gia Lai Province, Vietnam, 14° 20' N, 108° 36' E), USNM 163967 (0.1 mile south, 1 mile west of Mt Sontra, Quang Nam, Vietnam), FMNH 1153 (Bana, Vietnam, 15° 59' N, 107° 59' E);

Bolovens Plateau, Laos: FMNH 258940-6, *FMNH 258952-53* (from the Dong Hua Sao National Biodiversity Conservation Area (NBCA), Pakxong District, Champasak Province, Laos, 15 03' 55" N, 106 13' 03" E);

Cardamom Mountains, Cambodia and south-eastern Thailand: BMNH 2000.71 (Tumpor Mt, Mt Samkos Wildlife Sanctuary, Pursat Province, Cambodia, 12° 26' N, 103° 02' E), RNHM 16716:1-2 (Khao Soi Dao Wildlife Sanctuary, Chantaburi Province, Thailand); *FMNH 259187-88* (Bokor National Park, Kampot Province, Kampot District, south-eastern Cardamom Mountains, Cambodia, 10° 38' 33" N, 104° 1' 33" E);

Dongraek Mountains and edge of Khorat Plateau, Thailand: RTV9-10 (trade), AM99.5, FMNH 180272 (Khao Yai National Park, Nakhon Ratchasima Province), FMNH 180242-44, 180247, 180256-61, 180263-65, 180269, 180273-74, 180277 (Sakaerat Experimental Station, Amphoe Pak Thong Chai, Nakhon Ratchasima Province, 14° 36' N, 102° 2' E).

THERMAL EFFECTS ON THE ANTIPREDATOR BEHAVIOUR OF SNAKES: A REVIEW AND PROPOSED TERMINOLOGY

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The effects of temperature on the antipredator responses of snakes have been extensively studied during the last two decades. Several contradictory results have accumulated concerning the effects of temperature on the propensity of snakes to perform various behaviour patterns. We review this literature and discuss four possible factors related to these apparently contradictory results: (1) inconsistency in terms used to characterize antipredator behaviour; (2) erroneous citations; (3) interspecific differences; and (4) variable experimental designs. The last two factors reflect biologically important phenomena, whereas the first two are artificial “noise” that causes confusion and hinders scientific interpretation. To resolve inconsistency in wording, we propose a consistent terminology for the antipredator responses of snakes. Antipredator responses were characterized from three dimensions: (1) categorization from the viewpoint of whether prey animals move towards or away from predators (response is considered as either “approach”, “neutral”, or “withdrawal”); (2) categorization from the viewpoint of how much movement is involved in the behaviour (response is considered either “locomotive”, “active-in-place”, or “static”); and (3) categorization in terms of the apparent function (response is characterized as either “threatening”, “cryptic”, or “escape”). Antipredator responses of snakes, not only in relation to temperature but also in any situation, can be well characterized from these three perspectives using the proposed terminology.

Key words: defences, predator-prey interaction, reptile, temperature effect

INTRODUCTION

Various factors influence the antipredator responses that animals use when confronted with a predator. Although the behavioural repertoire and past experiences of the individual animal are important, much intraspecific variation is due to contextual factors such as the presence of conspecifics, the nature and number of the predators, the structure of the habitat, and climatic parameters such as light, humidity, and, especially for ectotherms, temperature (e.g. Burghardt & Schwartz, 1999; Magurran, 1999).

During the last two decades, more than a dozen experimental studies have explored the effects of temperature on the antipredator responses of snakes. Because performance capabilities of ectothermic animals are temperature-dependent (Stevenson *et al.*, 1985), antipredator responses that vary with temperature are usually considered adaptations for coping with physiological constraints. For instance, some snakes simply flee at high body temperature and exhibit less locomotive antipredator responses at low body temperature, because physiological mechanisms do not allow them to crawl fast enough to avoid predation (e.g. Hailey & Davies, 1986; Mori & Burghardt, 2001). However, in the past decade, contradictory results

concerning the effects of temperature on the performance of antipredator responses (e.g. striking) have appeared in the literature, even among closely related species (see below). Such variable results among the studies could be attributable to differences in terminology, responses measured, subject species, and experimental design. In the present paper we review and synthesize previous studies on temperature-dependent antipredator responses in snakes. In addition, we suggest a consistent terminology for characterizing antipredator responses of snakes to eliminate this confusion. This will aid communication between different researchers studying different species in varying ways and will help clarify the biologically significant sources of differences in antipredator responses among snakes.

REVIEW OF PREVIOUS PAPERS

We located twenty-four papers that mentioned or systematically examined thermal dependency of antipredator responses of snakes (Table 1). Most studies dealt with North American snakes: exceptions are *Natrix* in Europe, *Rhabdophis* in Japan, *Gloydius* in China, and *Pseudonaja* in Australia. Taxonomically, the subjects include colubrids – especially natricines – a few crotalines and one elapid. Except for a few earlier studies, the results are based on well-designed experiments conducted either in the field or in the laboratory.

The most overt discrepancy among the studies was the inclination of the snakes to exhibit strikes and/or

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bites. Several studies found that snakes are more apt to strike at low temperature (Arnold & Bennett, 1984; Fitch, 1965; Goode & Duvall, 1989 [but only in pregnant females]; Heckrotte, 1967; Shine *et al.*, 2000), whereas others showed that snakes tend to strike at high temperature (Keogh & DeSerto, 1994; May *et al.*, 1996; Schieffelin & de Queiroz, 1991; Shine *et al.*, 2002). In addition, some studies failed to find any temperature effects on the tendency to strike, bite, or bluff (Gibbons & Dorcas, 2002; Goode & Duvall, 1989 (in males and non-pregnant females); Mori & Burghardt, 2001; Mori *et al.*, 1996; Scribner & Weatherhead, 1995; Whitaker *et al.*, 2000). These apparently contradictory results and associated confusion can be attributed to the following four factors.

(1) INCONSISTENCY OF WORDING CONCERNING THE CHARACTERIZATION OF ANTIPREDATOR RESPONSES

Many adjectives have been used to express the propensity to perform antipredator responses by snakes: "aggressive", "offensive", "defensive", "passive", "threatening", "static", "active", "retaliatory" and so on. Heckrotte (1967) used the term, "defensive" behaviour, apparently to indicate biting, and Goode & Duvall (1989) regarded the snakes that more rapidly escalated to striking as being more "defensive." On the other hand, Arnold & Bennett (1984) applied the term "defensive" to responses such as head-hide and body-ball. The term "defensive" behaviour has also been used as a synonym of antipredator behaviour, or even used for any kind of behaviour that protects an animal from conspecifics as well as predators (Edmunds, 1974; Immelmann & Beer, 1989).

Another example of confusion is found in the term "active". Arnold & Bennett (1984) used "active" defence for head-hide and body-ball, whereas Hailey & Davies (1986) used "active" defence for escape response and called balling a "static" defence. Kissner *et al.* (1997) labeled rattling by rattlesnakes as "active" defence in contrast to crypsis. Prior & Weatherhead (1994) considered biting an "active" defence.

(2) ERRONEOUS OR EQUIVOCAL CITATIONS

Keogh & DeSerto (1994) mentioned that the study by Arnold & Bennett (1984) showed an increased flight response of *Thamnophis radix* at higher temperature. In fact, Arnold & Bennett (1984) did not include a flight response in their variables; their experimental protocol did not allow them to record any kind of flight response (see below). Passek & Gillingham (1997) mentioned that their results are inconsistent with the findings of Schieffelin & de Queiroz (1991). However, both studies showed that energetically costly responses involving much movement are more frequently exhibited as temperature increases, and thus, their "inconsistency" is equivocal. As has already been pointed out by Schieffelin & de Queiroz (1991), a cursory examination of previous studies may lead to erroneous conclusions

and create a potential source of confusion in subsequent studies.

(3) INTERSPECIFIC DIFFERENCES IN RESPONSE TO TEMPERATURE

It is not surprising that different species may respond differently to changes in temperature (Shine *et al.*, 2000). Snakes have adapted to various ecological niches with tremendous physiological, morphological, and behavioural specialization (Greene, 1997), and show varied antipredator responses even among closely related species (Bowers *et al.*, 1993; Herzog & Burghardt, 1986) or among populations of the same species (Burghardt & Schwartz, 1999; Mori & Burghardt, 2000). Thus, it is likely that closely related species have evolved different adaptive responses to changes of temperature. The absence of temperature effects may simply reflect the low tendency in performing the focused responses (e.g. strike in *Rhabdophis tigrinus*: Mori & Burghardt, 2001). In addition, when interspecific comparisons are made, we should keep in mind the fact that snake species have different preferred body temperatures (Lillywhite 1987; Mori *et al.*, 2002, and the references therein), and thus, "low" body temperature for a given species may not be necessarily "low" for another species. In some species (e.g. *T. ordinoides* and *R. tigrinus*) consistent individual differences in response to temperature can also occur (Brodie & Russell, 1999; Mori & Burghardt, 2001).

(4) DIFFERENCES IN EXPERIMENTAL DESIGN

The most important problem underlying inconsistent results may arise from differences in experimental design. This is not a minor problem, because it underlies an important issue in understanding the behavioural mechanisms of animals. In most studies, flight responses are observed or enhanced at higher temperatures (Table 1). Among the eight studies using *Thamnophis*, however, this trend was observed only in five (Brodie & Russell, 1999; Fitch, 1965; Heckrotte, 1967; Passek & Gillingham, 1997; Shine *et al.*, 2000). This does not necessarily imply that the remaining three studies (Arnold & Bennett, 1984; Schieffelin & de Queiroz, 1991; Scribner & Weatherhead, 1995) showed the absence of an increased flight response at higher temperature. Rather, this difference in results is clearly related to differences in experimental protocols. In the latter studies they had no opportunity to show flight responses because the snakes were continuously followed by the stimulus (human hand) (Scribner & Weatherhead, 1995) or were scored after they became exhausted (Arnold & Bennett, 1984) or motionless (Schieffelin & de Queiroz, 1991). These authors did not include "flight" in the available options of behavioural variables.

Another potentially confounding factor is the effect of test order of stimulus and thermal condition (Burghardt & Schwartz, 1999). As pointed out by various authors (Arnold & Bennett, 1984; Schieffelin & de Queiroz,

1991), the temperature effects observed by Arnold & Bennett (1984) may have been confounded with order effects, which resulted in thermal effects different from those obtained by Schieffelin & de Queiroz (1991). Balancing testing order of different conditions is typically the most effective means of dealing with the test order problem (but see Burghardt & Schwartz, 1999, for problems that might still exist even with balanced test orders, such as differential habituation effects).

The inconsistencies in results noted above may also reflect differences in the internal conditions of the animals. Snakes often shift antipredator responses sequentially (Bowers *et al.*, 1993; Duvall *et al.*, 1985; Schieffelin & de Queiroz, 1991). This behavioural sequence may reflect motivational and/or physiological changes of snakes throughout the interaction between the prey and the predator. The snakes tested by Arnold & Bennett (1984) were undoubtedly in the final stage of the sequence because behaviours were recorded when the snakes were exhausted after being chased down a track, whereas the snakes tested by Schieffelin & de Queiroz (1991) were in earlier stages of the sequence. Passek & Gillingham (1997) quickly uncovered common garter snakes in retreats, and the flight response they observed represented the initial stage of the antipredator behavioural sequence. It is also possible that captive-induced motivational and/or physiological modification, such as recent feeding (Ford & Shuttlesworth, 1986; Herzog & Bailey, 1987) and other unintentional treatments, could affect the responses of snakes (Shine *et al.*, 2000).

PROPOSED TERMINOLOGY

The above four factors can be divided into two categories. Differences in results due to interspecific differences and differences in experimental design potentially reflect biologically significant phenomena, whereas inconsistency of wording and erroneous citations represent artificial “noise” that can create confusion and hinder understanding. To remove confusion caused by semantic differences attached to words used to characterize the responses we have attempted to integrate the terminology and provide new definitions applicable to antipredator responses of snakes. Defining behaviour patterns from multiple viewpoints would be useful to understand the nature of those behaviours (Drummond, 1981). We begin by showing that antipredator responses can be characterized in at least three dimensions.

First, they can be viewed from changes in the distance between predators and prey. If a behaviour involves prey movement that reduces this distance, it can be called an “approach” response. Conversely, if a behaviour involves prey movement that increases this distance, it can be called a “withdrawal” response. All responses that do not involve active movement by the prey that decreases or lengthens the distance between the prey and the predator we term “neutral” responses.

In this perspective, strike and neck-butting are considered approach responses, body-flatten, tail-vibration, and immobilization are categorized as neutral responses, and flight is considered a withdrawal response.

Second, antipredator responses can be categorized from the viewpoint of how much movement is involved in the behaviour. From this viewpoint, the flight response is considered the most “locomotive” reaction, whereas immobilization or freezing is characterized as the most “static” response. Several common responses such as strike and tail-vibration would be considered “active-in-place” responses because they involve movement of body parts without any locomotion. This categorization partially reflects the amount of energy required for performing various antipredator responses. This strictly behavioural typology in terms of movement does not rule out the possibility that different responses have varying energetic consequences for different snakes. We envision that phylogenetic analyses of antipredator repertoires and their contextual deployment could be useful adjuncts to studies of metabolism, muscle physiology, and foraging mode.

Third, antipredator responses can be viewed in terms of their apparent function. If a response involves any behavioural element apparently designed to deter the intruding predator from attempting predation, the response can be called “threatening”. Representative threatening responses are strike, bluff, hissing, rattling, and body-flatten. In this system, antipredator responses such as immobilization and head-hide are considered “cryptic” because these behaviours rely on reducing the probability that the predator will recognize the animal as prey. Snakes that are aposematically coloured or marked may be immobile, as are cryptic prey, but may engage in some behaviour to enhance the antipredator display (e.g. Greene, 1973; Mori & Hikida 1991). Functional interpretations are more difficult to confirm than the mere description used in the other two perspectives but are also a key aspect of biological inquiry. Flight is considered a protective response labeled as “escape”: although the snake may reveal its presence, it acts to reduce the probability of capture not by actual deterrence, but by removing itself from the situation. Other examples of “escape” responses are evasive movements such as reversal of direction during flight (e.g. Brodie, 1993). We do not use the word “defensive” as the antonym of “threatening” in order to avoid confusion (see above).

APPLICATION

It is useful to characterize antipredator responses from all three perspectives. As an example, we did this for the antipredator behaviours of *R. tigrinus* recorded in Mori & Burghardt (2000, 2001). One of the most characteristic behaviours is the neck arch, in which the snake raises the head slightly and strongly bends the anterior part of the neck region ventrally so that the snout is directed to, and makes contact with, the substrate. We would label this a neutral, static, threatening response

Table 1 continued...

<i>Sistrurus catenatus</i>	adult (?)	negative, no reaction remain stationary	positive, rattle rattle while flee	field	step closely	Prior & Weatherhead (1994)
<i>N. sipedon</i> ^c	various	more refuge-seeking more predator-disorienting	n.a.	laboratory	chase while swimming in water	Scribner & Weatherhead (1995)
<i>T. sirtalis</i> ^c	ditto	more predator-disorienting	n.a.	ditto	ditto	ditto
<i>T. sauritus</i> ^c	ditto	ditto	n.a.	ditto	ditto	ditto
<i>S. miliarius</i> ^d	various	n.a.	strike	field	approach or tap on head	May <i>et al.</i> (1996)
<i>Rhabdophis tigrinus</i>	adult & neonate	body-flatten, neck-flatten neck-arch, immobilize	flee	laboratory	pin by hook or tap by hand	Mori <i>et al.</i> (1996)
<i>Crotalus v. viridis</i> ^a	adult	closer distance before rattling	longer distance before rattling	field	approach	Kissner <i>et al.</i> (1997)
<i>T. sirtalis</i> ^c	adult (?)	body-flatten	flee, bite (?) ^f	field	approach or grab by hand	Passek & Gillingham (1997)
<i>T. ordinoides</i>	neonate	fewer reversals crawled short distance	more reversals crawled long distance	laboratory	tap by hand	Brodie & Russell (1999)
<i>Pseudonaja textilis</i>	various	shorter flight distance remain stationary	longer flight distance flee	field	approach	Whitaker & Shine (1999)
<i>T. sirtalis</i>	adult	remain still, strike body flatten	flee	field	peck by finger	Shine <i>et al.</i> (2000)
<i>P. textilis</i> ^{a, b}	adult	n.a.	n.a.	laboratory	wave or touch with stimuli	Whitaker <i>et al.</i> (2000)
<i>R. tigrinus</i>	adult	body-flatten, neck-flatten neck-arch, immobilize dorsal facing posture	flee	laboratory	pin by hook	Mori & Burghardt (2001)
<i>Gloydius shedaoensis</i>	adult & juvenile	no overt response	flee, strike, tail-twitching	field	approach and tap by stick	Shine <i>et al.</i> (2002)
<i>Agkistrodon piscivorus</i> ⁱ	various	n.a.	n.a.	field	stand beside, step on, and pick up	Gibbons & Dorcas (2002)

TABLE 2. Characterization of antipredator responses of *Rhabdophis tigrinus tigrinus* (after Mori & Burghardt, 2001) and other common antipredator responses of snakes from three independent viewpoints. Definitions of terminology are presented in text.

BEHAVIOUR	CHANGE OF DISTANCE:		AMOUNT OF MOVEMENT:		APPARENT FUNCTION:	
	Withdrawal (W)	Neutral (N)	Static (S)	Active-in-place (Ac)	Escape (E)	Cryptic (C)
	Approach (Ap)		Locomotive (L)		Threatening (T)	
Strike		Ap		Ac		T
Neck-flatten		N		S		T
Body-flatten		N		S		T
Neck-arch		N		S		T
Neck-butting		Ap		Ac		T
Jerk		N		Ac		T
Immobile		N		S		C
Flee		W		L		E
Reversals		N/W		L		E
Head hide		N		S		C
Tail vibration		N		Ac		T
Rattling		N		Ac		T
Feign death		N		S		C
Hissing		N		S		T
Cloacal discharge		N		S		T
Body thrash		N		L		T

TABLE 3. Characterization of antipredator responses of snakes observed in temperature-effect studies listed in Table 1. Responses in parentheses indicate the increased tendency of the responses at the temperature. Ac, active-in-place; Ap, approach; C, cryptic; E, escape; High, higher temperature; L, locomotive; Low, lower temperature; N, neutral; S, static; T, threatening; W, withdrawal. Definitions of terminology are presented in text. *Only in pregnant females.

Authority	CHANGE OF DISTANCE		AMOUNT OF MOVEMENT		APPARENT FUNCTION	
	Low	High	Low	High	Low	High
Fukada (1961)	N	W	S	L	T	E
Fitch (1965)	N, Ap	W	S, Ac	L	T	E
Heckrotte (1967)	Ap	W	Ac	L	T	E
Mutoh (1983)	N	—	S	—	C	—
Arnold & Bennett (1984)	N, Ap	N	S, Ac	S	T	C
Layne & Ford (1984)	—	(W)	—	(L)	—	—
Hailey & Davies (1986)	N	W	S	L	C	E
Goode & Duvall (1989) ^a	Ap	W	Ac	L	T	E
Schieffelin & de Queiroz (1991)	N	N, Ap	S	Ac	C	T
Weatherhead & Robertson (1992)	—	—	—	—	—	—
Keogh & DeSerto (1994)	N	Ap	S	Ac	C	T
Prior & Weatherhead (1994)	N	N, W	S	Ac, L	C	T, E
Scribner & Weatherhead (1995)	—	—	—	—	—	—
May <i>et al.</i> (1996)	—	Ap	—	Ac	—	T
Mori <i>et al.</i> (1996)	N	W	S	L	T, C	E
Kissner <i>et al.</i> (1997) ^a	—	—	—	—	(C)	(T)
Passek & Gillingham (1997)	N	W	S	L	T	E
Brodie & Russell (1999)	—	(W)	—	(L)	—	—
Whitaker & Shine (1999)	N	W	S	L	C	E
Shine <i>et al.</i> (2000)	N, Ap	W	S, Ac	L	T, C	E
Whitaker <i>et al.</i> (2000)	—	—	—	—	—	—
Mori & Burghardt (2001)	N	W	S	L	T, C	E
Shine <i>et al.</i> (2002)	N	Ap, N, W	S	Ac, L	C	T, E
Gibbons & Dorcas (2002)	—	—	—	—	—	—

(Table 2). Although neck-arch may not deter predation by itself, it may attract the attention of the predator to the nuchal glands, and the secretions from the glands may act as a predator deterrent (Mori *et al.*, 1996; Mori & Burghardt, 2000, 2001). Thus, functionally, neck-arch can be regarded as a threatening response. Another characteristic behaviour of *R. tigrinus* is neck butting, in which the snake swings its head backwards with erratic movements so that the dorsal part of the neck region is butted against the stimulus object. This behaviour is labeled as an approach, active-in-place, threatening response. These three perspectives also help characterize the nature of components revealed by principal components analysis of behaviour at different temperatures (see Mori & Burghardt, 2001).

Using this terminology, some of the antipredator responses listed in Table 1 are characterized as follows. Head hide: neutral, static, cryptic response; tail vibration: neutral, active-in-place, threatening response; rattling: neutral, active-in-place, threatening response (Table 2). Death feigning is one of the most dramatic and complex antipredator responses in snakes. Because such immobility may induce predators to divert their attention from the dead prey or make them not recognize it as "food" (Burghardt & Greene, 1988), this behaviour is considered neutral, static, and cryptic. Other common antipredator responses in snakes (Greene, 1988) can be effectively characterized (Table 2).

As an overview of the temperature effects on antipredator responses of snakes, all the antipredator responses listed in Table 1 are characterized from the three viewpoints and summarized in Table 3. General tendencies, as well as the similarities and discrepancies, in antipredator responses among the previous studies are easily understood using this table. In the change of distance dimension, withdrawal is a predominant response at higher temperature and never observed at lower temperatures. Obviously, all studies except for one (Arnold & Bennett, 1984), which did not include flight as a response variable, show the same tendency in the amount of movement: as temperature increases, snakes change their responses from static to locomotive ones. In the apparent function dimension, escape is a predominant response at higher temperature followed by threatening response. No studies show escape response at lower temperatures. Different results among the studies revealed in Table 3 are not due to the artifact caused by confusing terminology but, in most cases, attributable to biologically significant factors described above. The similarities and discrepancies in the three dimensions among the studies are important sources of information that would help interpret and understand adaptive and functional significances of temperature-dependent antipredator tactics in snakes.

CONCLUSION

The use of varying experimental designs is needed to uncover novel aspects of a phenomenon. However, there

needs to be more recognition and careful consideration of the various factors that can affect behavioural responses, especially when the animal has several behavioural options that change sequentially. These factors can include changes in internal factors such as motivation and physiological condition (stress level, recent feeding, reproductive state, ecdysis). Most behavioural responses are the results of an interaction between external and internal factors (Mook, 1996). Although it may not be possible to control all the internal factors during an experiment, such internal factors should be considered when comparing studies. As with any complex behaviour that varies within and across species, it is important to eliminate any artificial confusion and precisely focus our attention on the real sources of differences. The aim of the present paper is not only to review the literature on the thermal effects on antipredator responses in snakes, but also to call researchers' attention to the existing confusion of terminology and propose a resolution. We have to admit that our proposed terminological categorization partially relies on a subjective judgment of the adaptive function of the snake's behaviour (e.g. threat, escape) and thereby infer the animal's "intention". Such judgments are actually at the heart of much behavioural research, but such testable inferences can be usefully derived through a judicious application of critical anthropomorphism (Rivas & Burghardt, 2002). We hope that our attempt to remove terminological confusion will help to clarify biologically relevant mechanisms that cause different behavioural responses of snakes under different thermal conditions, and in other contexts as well.

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THE ABUNDANCE OF PREMETAMORPHIC NEWTS (*TRITURUS CRISTATUS*, *T. MARMORATUS*) AS A FUNCTION OF HABITAT DETERMINANTS: AN *A PRIORI* MODEL SELECTION APPROACH

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Despite the key role of premetamorphic amphibians in experimental ecology, the factors affecting their abundance has received relatively little attention in natural settings. We applied a model selection approach with AIC (Akaike's Information Criterion) to predict the abundance of embryos and larvae of crested and marbled newts (*Triturus cristatus* and *T. marmoratus*) at 32 breeding sites in western France, based on 15 variables describing the aquatic habitat, and 10 variables describing the terrestrial habitat within a 100 m radius around the pond. The best model for embryos included the variables shade and floating vegetation (highest embryo abundance in intermediate ponds), and pond size (negative correlation). Larval abundance was best explained by shade (negative correlation), and the interaction between phosphate and nitrate. Pond variables were not fully comparable to terrestrial parameters, but produced better predictive models for both embryos and larvae. Due to the high explanatory value of ecological parameters the results suggest that in a metapopulation context, deterministic population processes driven by pond succession may be more important than stochastic extinctions and recolonizations of otherwise suitable habitat patches.

Key words: AIC, ecological determinants, habitat selection, Urodela

INTRODUCTION

Understanding the factors that govern the distribution and abundance of species is a major goal of ecological research (Andrewartha & Birch, 1954). The distribution of pond-breeding amphibians is likely to be influenced by features of both the aquatic and the surrounding terrestrial habitat (Semlitsch, 2000, 2002). This is likely because populations of pond-breeding amphibians with aquatic eggs and larvae – and primarily terrestrial adults – can be regulated in the aquatic larval, terrestrial juvenile and terrestrial adult stage (Wilbur, 1980; Hellriegel, 2000; but see Biek *et al.*, 2002). Even though the ecology of aquatic larvae has a long and successful history of experimental research (Smith, 1983; Wilbur, 1987, 1997), only a handful of studies has addressed the factors that affect their distribution and abundance in the field (e.g., Azevedo-Ramos & Magnusson, 1999; Gascon, 1991; Snodgrass *et al.*, 2000). In contrast, the ecological determinants that affect the distribution and abundance of adults have been documented intensively in descriptive studies (e.g., Skelly *et al.*, 1999; Pope *et al.*, 2000; Joly *et al.*, 2001). To our knowledge no studies so far simultaneously examined the factors that may

affect the abundance of the aquatic juvenile and the terrestrial adult stage.

As a part of our long-term research program on the ecological and evolutionary interactions among *Triturus* newts – primarily between *T. cristatus* and *T. marmoratus* and their hybrids (e.g. Arntzen & Hedlund, 1990; Arntzen & Wallis, 1991; Jehle & Arntzen, 2000) – we studied the environmental factors that may govern the abundance of these species in both the aquatic larval and terrestrial adult stages. Newts of the genus *Triturus* have a prolonged breeding period during which females usually wrap their eggs singly into leaves of aquatic vegetation (several hundreds per year). A full range of life stages (embryos, larvae, and adults) may hence be present in a pond at one time, with subadults and adults spending the majority of the year on land (Bell & Lawton, 1975; Griffiths, 1996). In the present paper we focused on determinants of the abundance of eggs and larvae. The abundance of eggs should largely reflect the adult population size (either the number of adults or their fecundity; embryo abundance *per se* is unlikely to affect adult abundance; Vonesh & De la Cruz, 2002), and we therefore assumed that embryo abundance is determined by features of the pond and the surrounding landscape, whereas the abundance of larvae should be affected by the presence of embryos and pond-specific factors that affect their growth and survival.

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TABLE 1. Environmental variables recorded for 32 study ponds in the Département Mayenne, western France.

Variable	Code	Specifier
AQUATIC		
Average slope of bank	BANK	<20, 21-40, 41-60, 61-80, >80% (1-5)
Decomposing leaves	LEAV	Absent, present (0,1)
Maximum pond depth	DEPTH	cm
Pond size	SIZE	m ²
Shade (canopy cover)	SHADE	0.1-20, 21-40, 41-60, >60% (1-4)
Turbidity of water	TURBID	Transparent, clear, moderate, opaque (1-4)
Floating vegetation	FLVEG	0-10, 11-20, 21-50, >50% (1-4)
Macrofauna	FAUNA	Sparse, moderate, abundant (1-3)
Marginal vegetation	MAVEG	0-10, 11-20, 21-50, >50% (1-4)
Submerged vegetation	SUVEG	0-10, 11-20, 21-50, >50% (1-4)
Predators	PRED	Sparse, moderate, abundant (1-3)
Nitrate (NO ₃)	NIT	1, 3, 10, 30, 100 mg/l
Oxygen saturation	OXY	<30, 30-90, >90% (1-3)
pH	PH	
Phosphate (PO ₄)	PHO	0.1, 0.2, 0.5, 1.0, 5.0 mg/l
TERRESTRIAL (100 M RANGE)		
Ditch	DITCH	Absent, present (0,1)
Arable fields	ARAB	Absent, present (0,1)
Hedges	HEDGE	Absent, present (0,1)
Marsh	MARSH	Absent, present (0,1)
Pasture	PAST	Absent, present (0,1)
Ponds	POND	Absent, present (0,1)
Relief	RELI	Flat, sloping, undulating (1-3)
Roads	ROAD	Absent, present (0,1)
Scrubs	SCRU	Absent, present (0,1)
Woodland	WOOD	Absent, present (0,1)

There is a large body of experimental and observational research on determinants of growth, survival, abundance, and distribution of amphibians. We used this knowledge to formulate hypotheses that reflected the results of these studies and our knowledge from many years of field work, and used information-theoretic model selection tools to assess whether these *a priori* hypotheses were supported by the data that we collected (Burnham & Anderson, 1998). Our analysis was therefore primarily confirmatory and did not suffer from the well known problems that are inherent in the exploratory and null hypothesis-based analysis of large observational data sets (Johnson, 1999; Burnham & Anderson, 1998; Anderson *et al.*, 2000; Olden & Jackson, 2000; Anderson *et al.*, 2001).

METHODS

STUDY AREA

Thirty-two ponds were studied, located in an area of ca. 12 × 33 km in the Département Mayenne, western France. Hilly and wooded areas in the north of the

Département are occupied mostly by *T. marmoratus*, whereas flat and open areas in the south are occupied mostly by *T. cristatus*. The central study area is intermediate in its characteristics, including both terrestrial habitat types, and breeding ponds are regularly shared by both species. The landscape is gently undulating, comprising pasture for cattle breeding, with a relatively high density of hedgerows and small woodlands. Most ponds are man made. For a more detailed description of the study ponds and study area see Schoorl & Zuiderwijk (1981) and Arntzen & Wallis (1991).

ENVIRONMENTAL DATA

For each site, we collected 15 habitat variables characterizing the pond and 10 variables characterizing the terrestrial habitat within a 100 m radius (Table 1; scored as in Scribner *et al.*, 2001), encompassing 95% of terrestrial refuges of radio-tracked individuals (Jehle, 2000). Oxygen saturation was measured with a WTW Microprocessor Oximeter OXI 196 at a depth of 20 cm. As daily fluctuations reduced the power of single oxy-

TABLE 2. *A priori* models considered to relate the effects of aquatic and terrestrial habitat parameters to *Triturus cristatus* and *T. marmoratus* embryo abundance. (+) positive effects (-) negative effects; intercept refers to the value on the *y*-axis where the line defined by the regression equation crosses the axis (if the complete absence of predictor variables has meaning, then the intercept represents that amount). * This model includes the parameters best describing the abundance of larvae and it therefore stands for the hypothesis that embryo abundance and linked population size is influenced by the same parameters as larval abundance, and further that juvenile recruitment regulates population size and therefore number of eggs.

Model	Variables	Hypothesis	References
1	INTERCEPT	Random distribution	
2	POND	High abundance when number of adjacent ponds is small (-)	Scribner <i>et al.</i> (2001)
3	PRED	Newts avoid predator rich ponds (-)	Kats & Sih (1992)
4	SIZE, DEPTH	Large habitat patches support large populations (+)	Flather & Bevers (2002)
5	HEDGE, WOOD, ROAD	Important as terrestrial habitat, dispersal corridor (+), roads (-)	Findlay & Houlahan (1997), Jehle & Arntzen (2000), Joly <i>et al.</i> (2001)
6	FLVEG	Important as oviposition site (+)	Miaud (1995), Joly <i>et al.</i> (2001)
7	SHADE, SIZE, DEPTH	Canopy cover (-) and hydroperiod (+)	Skelly <i>et al.</i> (1999)
8	FLVEG, SIZE, HEDGE, SHADE	Aquatic and terrestrial habitat features are important, all (+) except Shade (-)	Joly <i>et al.</i> (2001), Miaud (1995), Skelly <i>et al.</i> (1999, 2002)
9	FLVEG, SIZE, SHADE	As 8, without hedge	
10 *	SHADE, NIT*PHO	Juvenile recruitment regulates population size, Shade (-), Nit*Pho (+)	Berven (1990)

gen measurements, ponds were classified by the maximum oxygen saturation reached in the early afternoon (13:00–15:00 hrs) on a sunny day, in the categories below 30%, from 30 to 90%, and 90% or above (1–3 respectively). Acidity was measured with an Amarell Electronic Pocket pH-Meter. Nitrate and phosphate concentration was measured with Dupla aquarium tests (1, 3, 10, 30 and 100 mg NO₃/l and 0.1, 0.2, 0.5, 1.0, and 5.0 mg PO₄/l). Environmental variables were recorded at the first visit at each pond from 30 April to 24 May 1999, during the main egg laying period. Water parameters were measured in the pond area where most eggs were detected. The abundance of predators (fish, dragonfly larvae, dytiscid beetles and their larvae) and macrofauna were recorded during dipnetting for larval newts between 20–29 June 1999. Abundance was classified according to the percentage of dipnet sweeps containing at least one individual as low (0–30%), moderate (31–60%), or high (>60%). All ecological and abundance data were collected by the same person (MS).

ABUNDANCE OF *T. CRISTATUS* AND *T. MARMORATUS* EMBRYOS AND LARVAE

We estimated the abundance of embryos by visual egg counts, classified into four size classes by the maximum number possible to obtain by one person in one hour, as low (<200 eggs), moderate (200<500 eggs), high (500<1000 eggs) or very high (>1000 eggs). All parts of each study pond containing vegetation appropriate as

substrate for newt eggs were surveyed. Larval abundance was estimated by a standardized number of dipnet sweeps per pond, with 50, 100, 150 and 200 sweeps for small (<50 m²), medium (<100 m²), large (<300 m²), and very large ponds (>300 m²), respectively. Each dipnet sweeps was about 2.5 m wide, inserting the net at the most distant point and pulling it towards the body. All accessible sections of the pond were covered. We used the number of larvae per dipnet sweep as an index of the size of the larval population (Nichols, 1992; Anderson, 2001). The number of larvae per dipnet sweep was log (*n* + 1) transformed for statistical analysis (Zar, 1999). Embryos and small to medium-sized larvae of *T. cristatus* and *T. marmoratus* are not distinguishable in the field and occupy indiscernible spatial and habitat niches within ponds (Jehle *et al.*, 2000). Therefore, records for both species were pooled.

MODEL SELECTION

We used an information-theoretic model selection approach for the statistical analysis of the data (Burnham & Anderson, 1998; Anderson & Burnham, 2002). First, we used the published literature and our own knowledge from years of field work to build candidate statistical models that reflect biological hypotheses. The models are *a priori* because they were formulated before the data analysis. Tables 2 and 3 list the candidate models and state the biological hypoth-

eses, the factors included in the model, whether their effect was expected to be positive or negative, and the references from which the model was derived. To predict the abundance of embryos we chose models that included both aquatic and terrestrial variables. Models for larval abundance were set up using pond-related variables only and always included the variable "abundance of embryos" (EGG), as differences in embryo abundance between ponds would otherwise have made effects of ecological parameters undetectable. Given that the sample size was only 32, we (1) kept the number of models small; and (2) kept models simple, i.e. with a small to moderate number of factors and no interactions (except the nitrate by phosphate concentration interaction which reflects productivity) or quadratic terms. As a second step, we used the small-sample Akaike's Information Criterion AIC_c to rank models. AIC_c is defined as:

$$AIC_c = (\ln L) + 2K + \frac{2K(K+1)}{n-K-1}$$

where $(\ln L)$ is the natural logarithm of the likelihood function, K is the number of estimable parameters from that model, and n is the sample size (Burnham & Anderson, 1998). Model selection based on information theory does not require predictor variables to be uncorrelated (D. R. Anderson, pers. comm.). AIC_c estimates the support that a model receives from the data. The model with the lowest AIC_c value is the best supported by the data. The absolute value of AIC_c is not relevant; it is the difference in AIC_c between models i and the model with the lowest AIC_c value ($AIC_{c_{min}}$) ($\Delta AIC_{c_i} = AIC_{c_i} - AIC_{c_{min}}$) that gives information whether a model is relatively well or poorly supported. We also calculated the Akaike weights w_i for all models. Akaike weights are defined as:

$$w_i = \frac{\exp\left[-\left(\frac{\Delta AIC_{c_i}}{2}\right)\right]}{\sum \exp\left[-\left(\frac{\Delta AIC_{c_i}}{2}\right)\right]}$$

TABLE 3. *A priori* models considered to relate the effects of aquatic and terrestrial habitat parameters to *Triturus cristatus* and *T. marmoratus* larval abundance. (+) positive effects, (-) negative effects, EGG (= abundance of embryos) is included in all models. Intercept refers to the value on the Y axis where the line defined by the regression equation crosses the axis (if the complete absence of predictor variables has meaning, then the intercept represents that amount).

Model	Variables	Hypothesis	References
1	intercept only	Distribution not different from random	
2	EGG	No effects of ecological variables on larval abundance, EGG (+)	
3	OXY, SUVEG, FLVEG, LEAV, PRED, EGG	OXY (+) for embryo development, SUVEG, FLVEG, LEAV (+) as egg substrate, shelter, PRED (-)	Seymour & Bradford (1995), Wilbur (1997)
4	NIT*PHO, PRED, EGG	Reduced food level increases predation risk, NIT*PHO (+), PRED (-)	Anholt & Werner (1995), Thurnheer & Reyer (2001)
5	NIT*PHO, FLVEG, EGG	Higher productivity (+) and more floating vegetation (+) means more food	Braz & Joly (1994)
6	PH, OXY, EGG	Low pH (-) and oxygen (-) for embryo development	Seymour & Bradford (1995), Griffiths & de Wijer (1994)
7	PH, OXY, PRED, EGG	Low pH (-) and high oxygen (-) for predation risk	Kutka (1994), McIntyre & McCollum (2000)
8	DEPTH, SIZE, EGG	Pond size (-) for larval development	Pearman (1993; 1995)
9	DEPTH, SIZE, PRED, EGG	Greater incidence of predators with increased pond size (-)	Pearman (1993)
10	SHADE, EGG	Canopy cover (-)	Skelly <i>et al.</i> (1999; 2002)
11	SHADE, NIT*PHO, EGG	Canopy cover (-), productivity (+)	Skelly <i>et al.</i> (1999), Werner & Glennemeier (1999), Thurnheer & Reyer (2001)

TABLE 4. Ranking of *a priori* models relating embryo abundance of *Triturus cristatus* and *T. marmoratus* to aquatic and terrestrial habitat parameters. Ranking is based on smallest AIC_c value; lnL = log likelihood, K = number of parameters in the model, w_i = Akaike's weight.

Model	lnL	K	AIC _c	ΔAIC _c	w _i
9	-27.82	5	67.939	0.000	0.733
8	-27.32	6	70.008	2.069	0.261
10	-34.04	4	77.556	9.617	0.006
6	-38.10	3	83.067	15.128	0.000
7	-37.78	5	87.874	19.935	0.000
4	-39.59	4	88.671	20.732	0.000
1	-41.67	2	91.875	23.936	0.000
3	-43.73	3	92.631	24.692	0.000
5	-42.89	4	94.044	26.105	0.000
2	-42.28	3	94.227	26.288	0.000

TABLE 5. Ranking of *a priori* models relating larval abundance of *Triturus cristatus* and *T. marmoratus* to aquatic habitat parameters. Ranking is based on lowest AIC_c value; lnL = log likelihood, K = number of parameters in the model; w_i = Akaike weight.

Model	lnL	K	AIC _c	ΔAIC _c	w _i
11	40.55	5	-68.789	0.000	0.516
4	40.31	6	-68.307	0.482	0.406
5	38.63	6	-64.956	3.833	0.076
3	39.60	8	-56.941	11.847	0.001
10	31.05	4	-52.628	16.160	0.000
6	31.86	5	-51.413	17.375	0.000
2	28.81	3	-50.767	18.021	0.000
7	32.81	6	-50.253	18.536	0.000
8	30.29	5	-48.276	20.513	0.000
9	30.52	6	-45.681	23.108	0.000
1	13.03	2	-21.640	47.149	0.000

Akaike weights are data-dependent, posterior model probabilities (Burnham & Anderson, 1998). They can be used to calculate evidence ratios w_i/w_j that can be used to judge how much better a model is (a ratio of 3/1 would suggest that one model is three times better supported by the data than the other model; Burnham & Anderson, 1998).

We used regression procedure GENMOD in SAS (SAS Institute, 2001) to fit the models to the data and to obtain the log-likelihoods of the models that were needed for the calculation of AIC_c. The abundance of eggs was a variable with four classes. We therefore assumed a multinomial distribution and used the 'cumlogit' link function for modelling. For the abundance of larvae, we assumed a normal distribution and therefore used the 'identity' link function for modelling.

RESULTS

Eggs were observed in all ponds. Larvae were observed in 23 (72%) out of the 32 study ponds. In all ponds where embryo abundance was classified as very high, larvae were caught in 16% to 100% of the dipnet sweeps. Larvae were not observed in nine ponds categorised low to high in embryo abundance.

Model 9, representing the abundance of floating vegetation, pond size, and shade is the model that best explains variation in the abundance of embryos (i.e. lowest AIC_c value, highest Akaike weight; Table 4). This model explained 59.9% of the total variance. The highest abundance of embryos occurred in ponds intermediate in floating vegetation and shade (Fig. 1). Pond size was negatively correlated to embryo abundance ($\beta = -0.005$, $SE = 0.002$). Model 8, including the additional variable presence of hedgerows, ranked second, but was about three times less plausible (the ratio of the Akaike weights was 0.733/0.261). Model 10, including the variables best explaining the abundance of the larvae, was ranked third, but had less than 1% of the plausibility of Model 9. All other models had little or no support from the data. Thus, the abundance of embryos

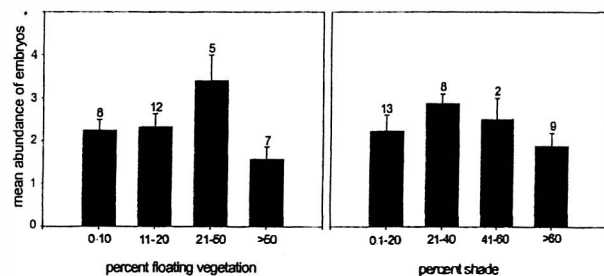


FIG. 1. Mean abundance of *Triturus cristatus* and *T. marmoratus* embryos (1 = low, 2 = moderate, 3 = high, 4 = very high) in response to extent of floating vegetation and extent of shade; error bars show S.E.; numbers above bars show sample size.

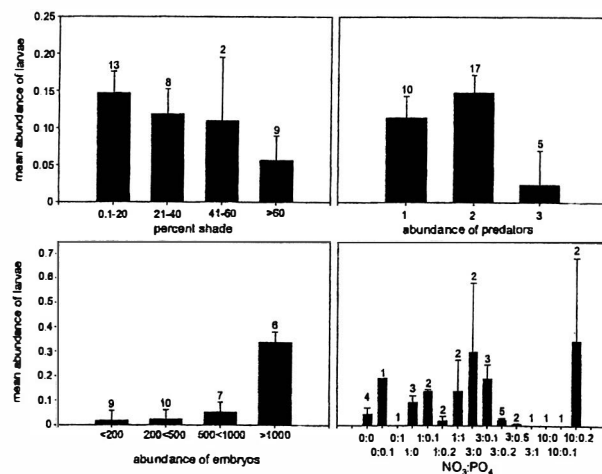


FIG. 2. Response of the abundance of *T. cristatus* and *T. marmoratus* larvae (measured in larvae per dipnet sweep) to extent of shade, abundance of predators, (1 = low, 2 = moderate, 3 = high), abundance of embryos and NO₃ × PO₄ interaction; error bars show S.E.; numbers above bars show sample size.

was best explained by characteristics of the pond rather than the surrounding landscape.

The models suggest that environmental factors were important in regulating larval abundance. The abundance of embryos explained a large fraction of the variance in larval abundance ($R^2=0.62$), but the corresponding model (no. 2) was ranked only seventh (Table 5). The best model for larval abundance was model 11, containing shade and $\text{NO}_3 \times \text{PO}_4$, with shade being negatively – and abundance of embryos being positively – correlated with larval abundance (Fig. 2). Model 11 explained 82.1% of the total variance. It was followed by Model 4 which was 21% less plausible and included the variable predators instead of shade. The highest larval abundance was observed in ponds with moderate predator abundance (Fig. 2). All other candidate models did not exceed 1% of the maximum (Table 5).

DISCUSSION

The model selection analysis indicates that the abundance of eggs and larvae of the newts *Triturus cristatus* and *T. marmoratus* is influenced by environmental factors at the scale of the pond rather than at the scale of the surrounding landscape.

METHODOLOGY

The results must be viewed under the limitations of the semiquantitative data collection procedure of the abundance data (i.e. indices of abundance rather than estimates of abundance; Nichols, 1992; Anderson, 2001), particularly with regard to comparing ponds of different shapes and sizes. Temporal fluctuations in water parameters (NO_3 , PO_4 , pH, and oxygen), and changes ponds may have undergone during the study period remained undetected. A pond's size and maximum depth might be an insufficient approximation for hydroperiod. Embryos and larvae may have been over-proportionately spread in relation to pond perimeter in large ponds and hence more difficult to find, and the standardized dip netting might have been less efficient, for example, in more overgrown ponds than in ponds that were lacking underwater structures. However, dip netting does allow a large number of sites to be compared within a reasonable amount of time, and the catchability is equal across species (Arntzen, 2002) and we must assume that capture probabilities did not vary strongly across ponds. Eggs can be quantified more efficiently than adults which are more difficult to detect (Griffiths *et al.*, 1996). However, different numbers of eggs laid by the two study species can bias the reflection of the adult population size (Arntzen & Hedlund, 1990). Another important aspect to be considered in the current study is the pooling of larvae from species that differ in landscape preference (Schoorl & Zuiderwijk, 1981). Previous studies failed to demonstrate clear ecological differences in and around syntopic ponds, and suggest that ecological niche segregation acts at the between-pond rather than at the within-pond scale (Jehle & Arntzen,

2000; Jehle *et al.*, 2000). Moreover, the advantage of pooling two species with similar but not identical morphology and ecology lies in a more generalised signal in the data analysis. Finally, the binomial terrestrial variables might have been less suitable to detect potential effects than the more accurately measured aquatic parameters, as for example multinomial variables can not always be sufficiently quantified by binomial predictors.

Model selection based on information-theoretic methods offers a strong alternative to the more traditional null hypothesis testing approach and is simpler to implement than Bayesian methods (Johnson, 1999; Anderson *et al.*, 2000; Olden & Jackson, 2000). Rather than asking whether the effect of an environmental factor is exactly zero (which is unlikely anyway), model selection methods ask which factors are necessary to adequately describe the data without over-parameterizing the statistical model (Burnham & Anderson, 1998). Analyses of similar data sets using multiple stepwise regression methods risk uncovering spurious patterns. In contrast, the candidate models were formulated before the analysis and are therefore not affected by random patterns in the data set (Burnham & Anderson, 1998; Anderson *et al.*, 2001). Given that the ecology of amphibians in general and *Triturus* newts in particular is rather well understood (Griffiths, 1996; Wilbur, 1997), it seems preferable to use the existing knowledge to build candidate models. These models represent alternative biological hypotheses, to assess which one(s) of the hypotheses is or are best supported by the data, and to compare the relative support of alternative hypotheses, including those which are not nested (in a statistical sense; Burnham & Anderson, 1998; Anderson *et al.*, 2001). Not all recorded variables listed in Table 1 were included in the analysis but served to extract the candidate models. We have studied only a small number of ponds and we therefore decided to use only simple candidate models (i.e. no interactions, except $\text{NO}_3 \times \text{PO}_4$, no quadratic terms, etc.). The distribution and abundance of newts is likely to be determined by a more complex interplay of ecological factors than we used in the candidate models; nevertheless, our best model was at least three times better than the other models. An analysis that attempts to uncover complex interactions between environmental factors and the distribution and abundance of newt larvae would probably have to be restricted to presence/absence data (see MacKenzie *et al.* (2002) for relevant methodology).

ABUNDANCE OF EMBRYOS

Surprisingly, embryo abundance was not related to terrestrial variables because embryo abundance is expected to reflect adult population size, which is most likely to be influenced by the terrestrial environment. The abundance of embryos was best explained by a combination of the amount of floating vegetation, pond size, and shading (canopy cover). The extent of aquatic vegetation has been shown previously to be a good indi-

cator for predicting site occupancy and abundance of newts (Cooke & Frazer, 1976; Oldham *et al.*, 2000; Joly *et al.*, 2001), and is in accordance with our assumption that embryo abundance largely reflects adult population size. Aquatic vegetation provides a food source for prey organisms, cover from predators, and a substrate for egg laying. *Glyceria fluitans* was particularly important as an egg substrate, as already shown by other studies (Vallée, 1959; Miaud, 1995). However, beyond a certain plant density indicating an advanced stage of succession, ponds become unsuitable for newts as aquatic space gets restricted and drying probability increases (Oldham *et al.*, 2000). The negative relationship of embryo abundance and pond size in the model opposes our hypothesis that large habitat patches may support large populations (e.g. Flather & Bevers, 2002), but agrees with Joly *et al.* (2001), who detected a negative relationship between pond area and abundance of newts. Pond area has also been shown to adversely affect survival, growth rate, and mass at metamorphosis of anuran tadpoles (Pearman, 1993).

Closed canopy cover has been shown to be negatively associated with the occurrence and performance of larval amphibians (Skelly *et al.*, 1999; 2002). An increase in aquatic and marginal terrestrial vegetation indicates an advanced stage of succession (Werner & Glennemeier, 1999), and as both study species are long-lived (Francillon-Vieillot *et al.*, 1990), high embryo abundance might be the result of high recruitment in the past. Radio-telemetry has shown that more than 50% of adult *T. cristatus* and *T. marmoratus* utilized refuges within 15 m of a pond (Jehle, 2000), and the high embryo abundance might be caused by habitat preferences of the adults for areas with canopy cover. Indeed, more distant habitat features known to be important (hedgerows and woodland; Jehle, 2000; Jehle & Arntzen, 2000; Joly *et al.*, 2001) were not included in the best model. The terrestrial buffer width necessarily incorporates a gradual decline in relative use with distance from the pond, making a clear delineation difficult. Moreover, the binomial terrestrial parameters probably were less powerful to assess their impact on embryo abundance than the measured aquatic parameters.

ABUNDANCE OF LARVAE

Two models for larval abundance were almost equally well supported by the data (evidence ratio $w_1/w_4 = 1.27$). Both models included productivity (the nitrogen-by-phosphorus interaction) and embryo abundance. They differed in the other variables, which was shade in the best model and predator abundance in the second-best model.

Productivity of breeding sites has been shown to affect the survival of anuran larvae (Thurnheer & Reyer, 2001). Canopy cover and shading of breeding ponds negatively affect productivity and hence are important parameters for larval performance (Werner & Glennemeier, 1999; Skelly *et al.*, 1999; 2002). Open

canopy ponds often exhibit supersaturated oxygen levels after midday, whereas no diel increase in dissolved oxygen can be observed in closed canopy ponds (Werner & Glennemeier, 1999; personal observations). Differences in oxygen concentrations also indicate differences in primary production for which both nitrogen and phosphorus are key nutrients. High concentrations of nitrates resulting from agricultural fertilizer run off and urban drainage can have lethal effects on amphibian larvae (Hecnar, 1995; Watt & Jarvis, 1997). However, the positive correlation of NO_3 and PO_4 with larval abundance implies that prime nutrients tend to become limiting factors in the extensively used landscape of the study area. Closed canopy ponds also usually contain few macrophytes and small plankton populations, reducing food availability (Braz & Joly, 1994; Werner & Glennemeier, 1999). Predator presence was included in the second best explanatory model. Abundance of predators and amphibian larvae have been shown to correlate positively as both are likely to be related in a similar way to pond productivity (Thurnheer & Reyer, 2000). In contrast to other newt species, larvae of *T. cristatus* show no plasticity in morphology and an increase in activity in the presence of predators and should hence be more vulnerable to predators than other species (Schmidt & Van Buskirk, 2001). This might explain the low abundance of newt larvae in predator rich ponds. The lowest predator abundances occur in small, non-permanent ponds, which however are also associated with high risks of pond desiccation prior to metamorphosis (Griffiths, 1997; Pearman, 1995).

CONCLUSION

The abundance of embryonic and larval *Triturus* newts can be well described using parameters of the aquatic habitats. An important feature for both embryos and larvae was shading, suggesting that the successional stage of the pond or its surroundings are important. If the successional stage determines the abundance and possibly performance of premetamorphic newts, then this is likely to also affect population persistence (Skelly *et al.*, 1999; 2002). This in turn suggests that under natural conditions population persistence and local extinction are influenced by deterministic factors and stochastic factors play a minor role (Skelly & Meir, 1997). However, in cultivated landscapes, stochastic events due to human activities (e.g. ditching, filling in) may still have severe impact on amphibian populations on a longer timescale.

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DISTRIBUTION AND CONSERVATION OF THE KOMODO MONITOR (*VARANUS KOMODOENSIS*)

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Information on population size and distribution of the Komodo monitor (*Varanus komodoensis*) has so far been restricted to early reports or to surveys conducted on only part of the species' range. We carried out a study based on transects through sampling plots and single-catch trapping events to assess the extent to which the distribution of *V. komodoensis* has changed since the last comprehensive survey was conducted, in 1971. We also report on the status of the habitat and identify conservation priorities. Resident Komodo monitor populations are now found on only four islands in Komodo National Park and on the island of Flores in south-east Indonesia. Average population density estimates recorded on Flores were more than 60% lower than those reported for Komodo National Park. Habitat fragmentation and poaching of prey species currently represent the main threats to the Komodo monitor, and protection of monsoon forest in west and north Flores is crucial for the long-term conservation of the species.

Key words: geographical distribution, lizard conservation, population density estimates, Varanid

INTRODUCTION

The Komodo monitor (*Varanus komodoensis*) has long captured the interest of ecologists and evolutionary biologists for having one of the narrowest naturally occurring ranges of all large terrestrial predators. Since its first description (Ouwens, 1912), this species of monitor lizard has been reported from six islands in the Lesser Sunda region, Indonesia (Auffenberg, 1981), and no fossil records have been found so far that can provide evidence of a larger distribution in the past.

After a number of preliminary surveys conducted on a few islands (e.g. Horst, 1926; Burden, 1928; De Jong, 1937; Pfeffer, 1959), between 1969 and 1972 Auffenberg (1981) provided the first detailed – although not comprehensive – account on the extent of the species' range. The Komodo monitor was recorded on the islands of Komodo, Rinca, Padar, Gili Motang, Gili Dasami and Flores (Fig. 1). However, Auffenberg did not report estimates of population size nor conduct an exhaustive search throughout the island of Flores.

In 1980, five islands (not including Flores) became part of Komodo National Park, while later legislation established two nature reserves within the Komodo monitor range on Flores: the Wae Wuul reserve on the west coast and the Wolo Tado reserve on the north coast. According to estimates conducted in 2001 by the Indonesian Department of Forest Protection and Nature Conservation (Perlingdungan Hutan dan Konservasi Alam – PHKA) the islands of Komodo (340 km²) and Rinca (210 km²) contain populations of approximately 1,150 and 1,110 Komodo monitors, respectively. PHKA obtained these estimates by counting animals observed

in a number of baited areas of known size and then extrapolating the counts to the size of each island. Surveys conducted in 1991 by PHKA on Gili Motang counted 106 individuals. This figure, however, was based on an overestimate of the island size. Gili Motang is about 10 km² (Pet & Yeager, 2000) and since four animals were counted during that survey over an area of 125 ha (PHKA, personal communication), the actual estimate would give a population of 32 lizards. Using the same method, 66 animals were estimated in 1991 by PHKA in the Wae Wuul reserve (about 30 km²). Estimates of population size are not available for Gili Dasami and Padar, and the distribution of the species on Flores has never been monitored since Auffenberg last visited this island in 1971.

In this study, we conducted a survey on Padar, Gili Dasami and Flores, compared our data to previous information given by Auffenberg (1981), and assessed the extent to which the Komodo monitor distribution has changed in the last three decades. We carried out transects and set up baiting stations on sampling plots to assess the presence or absence of monitor lizards, and provided an example of how preliminary information on reptile population densities can be obtained when only data based on single-catch trapping events are available (Lancia *et al.*, 1996). We also report on the status of the habitat within the former and present range of the species on Flores, and identify conservation priorities.

MATERIALS AND METHODS

NATURAL HISTORY

Varanus komodoensis occurs principally from sea level up to 800 m in altitude, mainly in tropical dry and moist deciduous monsoon forest and savannah. It is a carnivorous lizard which both actively seeks or am-

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bushes its prey, and eats carrion. Information on the life history of the species is provided in Auffenberg (1981) and Murphy *et al.* (2002). The Komodo monitor has faced some major human-related pressures in the past 20 years; it is now listed in Appendix I of CITES and considered "vulnerable" according to the red list of threatened animals of IUCN.

STUDY AREA

The study was conducted during three two-month sessions in 1997, 1998 and 2000 on the islands of Padar, Gili Dasami and Flores. On Flores, we surveyed about 110 km of coast, in the western and northern part of the island (Fig. 1), covering the range of *V. komodoensis* formerly described by Auffenberg (1981).

Padar is about 20 km². Savannah is the dominant biome. Narrow strips of dry deciduous monsoon forest occur along a few seasonal water streams and on the south-west and north-east coast, on flat terrain by the seashore. There are no human settlements. The island of Gili Dasami covers an area of about 10 km² and has a

round elongated shape roughly centred on a hill of about 350 m of altitude. It is mainly covered by dry deciduous monsoon forest. Gili Dasami is also uninhabited. Flores has an area of 13 540 km² and harbours a population of about 1.5 million inhabitants. Main habitat types in the study area, from the south-western to the northern coast of the island are savanna, small patches of thorn forest, and dry and moist deciduous monsoon forest, with different degrees of occurrence depending on the location, distance from the seashore, altitude and degree of human disturbance. The study sites included the nature reserves of Wae Wuul and Wolo Tado.

SURVEY TECHNIQUES

We carried out linear transects and transects on rectangular plots of different sizes, and set up baited box traps (300 × 50 × 50 cm) with vertically-sliding doors (see Ciofi [1999] for further details) to assess for presence of Komodo monitors on the island of Padar. Transects were conducted on two plots of approximately 500 × 2000 m and 500 × 1500 m, respectively,

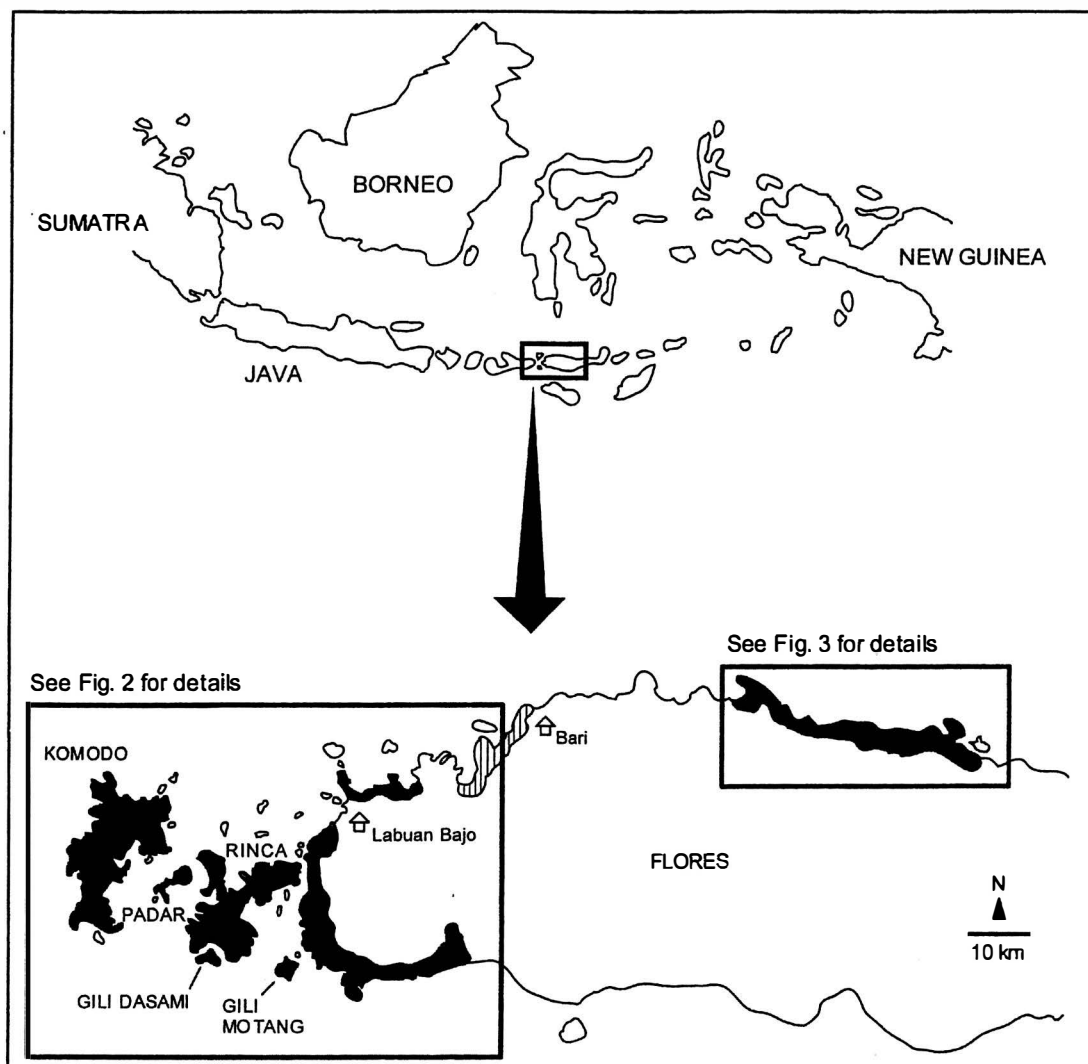


FIG. 1. Known distribution of the Komodo monitor *Varanus komodoensis*. Grey areas show current range. Black regions are sites described as part of the species' distribution by Auffenberg (1981) where no evidence of Komodo monitors was recorded during this study. Previous reports on additional sites in which Komodo monitors may be found (hatched areas) need to be substantiated.

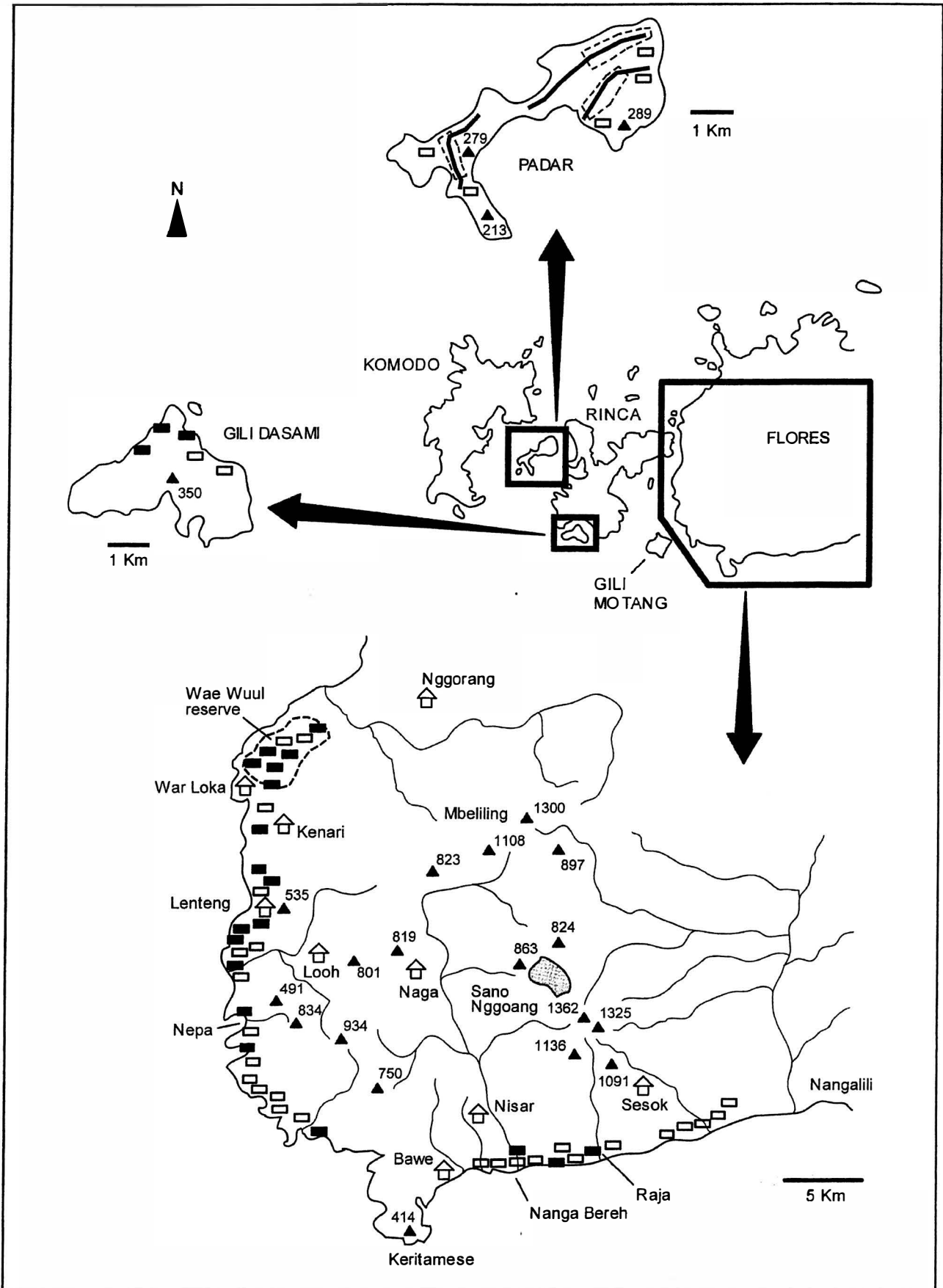


FIG. 2. Distribution of *V. komodonesis* on Padar, Gili Dasami and West Flores. Black rectangles are baited traps where at least one specimen was captured. Empty rectangles represent baiting stations where no Komodo monitors were trapped. Polygons on Padar represent transects on sample plots; heavy lines are trails used for linear transects. On Flores, heavy lines are rivers, grey areas are lakes. Elevations are reported in metres.

on the north of Padar, and on one plot of about 400×800 m in the south, covering an area of 2.07 km^2 , equal to about 10% of the total size of the island. Plots included savannah and monsoon forest. Two transects using 10 beaters and three observers were conducted for each plot at an interval of approximately 10 days. Linear transects partially overlapped with rectangular plots; they were carried out by a single observer every third day for a period of one month. A maximum observation distance can be established in linear transect. However, animals can also be counted regardless of their location with respect to the transect line (Lancia *et al.*, 1996). We adopted the latter design. The number of investigators required by each of the two methods entailed different levels of logistic difficulties and determined the different number of surveys conducted for each type of transect. Baiting stations were set on the southern and northern parts of the island (Fig. 2).

On Gili Dasami and on Flores, tree foliage and forest undergrowth interfered with the view of the study area, and rendered surveys by transects unsuitable to assess the distribution of the species. Therefore, only baited traps were used to assess the presence and population density of the Komodo monitor on these islands. We set up five baited traps on the north of Gili Dasami. On Flores, 10 traps were used in each of five approximately contiguous plots on the west coast, and in four plots on the north coast (Fig. 2 and Fig. 3). Traps were set at distance of between 600 m and 1 km from each other, depending on the terrain, in grassland, savannah and dry deciduous monsoon forest. We used meat as bait. In each plot, traps were kept open for up to six days in order to provide enough scent and sufficient time for the animal to locate the baiting station. We defined this period as a trapping session.

Baiting stations were checked once a day and positioned in shaded areas in order to avoid overheating of trapped individuals. Weight was recorded by hanging the cage, with the animal inside, from a spring balance and later subtracting the weight of the trap from the total

measure. Sliding doors were then used to restrain the lizard in the trap so that measures of snout-vent length and total length could be taken. Young individuals were handled outside of the cage. Specimens were marked with paint for short-term identification so that double counts could be avoided. This technique was used in previous field studies (e.g. Ciofi & Bruford, 1999) and no injuries due to handling procedures were recorded in any instance.

DATA ANALYSIS

Transects were designed according to standard methods based on total counts on sample plots (e.g. Lancia *et al.*, 1996). However, analysis of data was not performed as our survey found no evidence of monitor lizards on Padar (see Results).

The survey on Gili Dasami and Flores was based on single-catch trapping events. This method can often provide information on animal density when time and logistical constraints do not allow implementation of surveys, such as mark-recapture, based on data collection over multiple time periods (Lancia *et al.*, 1996). In our survey, traps were set at approximately equal distances over an area that was divided into sampling units of equal size (Fig. 4), each with a trap located at its centre. The proportion (p) of sampling units that contains at least one animal is a frequency index which can be related to abundance or density of individuals in the study area (Seber, 1982). We considered the study sites (Gili Dasami, West and North Flores) subdivided into S adjacent sampling units each of area a . According to Cochran (1963), if n sampling units from a sample of s units contain animals, then $p=n/s$ can be considered an unbiased estimate of p . If animals are randomly distributed, the number of individuals in the sampling unit follows a Poisson distribution, and the frequency index can be converted into an estimate of the absolute population density D (Seber, 1982). However, we assumed that the different ecotypes and altitudes found on coastal Flores were likely to affect both directly and indirectly

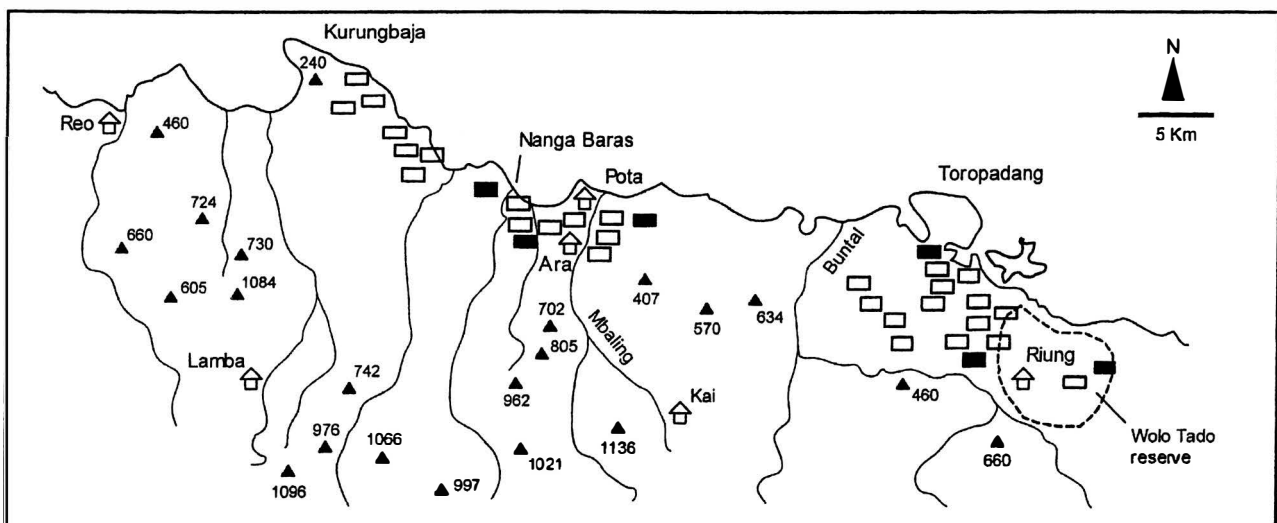


FIG. 3. Distribution of *V. komodonesis* on North Flores. Legend as in Fig. 2.

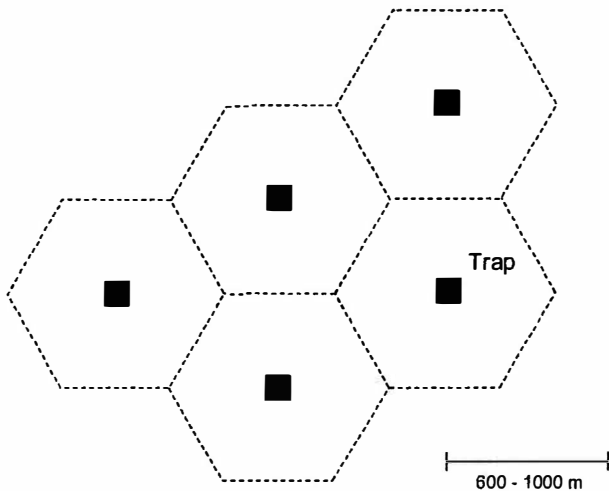


FIG. 4. Example of hexagonal sampling units used to position baited traps during the survey on Gili Dasami and Flores (see text for further details).

(for instance, through different availability of main prey species) the distribution of *V. komodoensis* in the study areas. We therefore considered a pattern of non-random distribution of the species. In this case, the size of the sampling unit should be reduced until the probability that the unit contains more than one individual is very small (Cochran, 1963). A trapping event would then correspond to the presence of roughly one individual in the sampling unit. Considering the ability of Komodo monitors to locate carcasses at distances of up to 10 km (Auffenberg, 1981), we regarded the space between baiting stations as a conservative figure for a trapping design

TABLE 1. Estimates of Komodo monitor population density for Komodo National Park and Flores. Refer to Fig. 2 and Fig. 3 for location of study sites. ^a Indonesian Department of Forest Protection and Nature Conservation. ^b Not available.

Location	Area size (ha)	Population density	Source
Komodo	34 000	1 lizard / 30 ha	PHKA ^a
Rinca	21 000	1 lizard / 19 ha	PHKA ^a
Gili Motang	1000	1 lizard / 32 ha	PHKA ^a
Gili Dasami	700	1 lizard / 52 ha	This study
West Flores Raja-Bawe	na ^b	1 lizard / 141 ha	This study
Keritamese-Nepa	na ^b	1 lizard / 141 ha	This study
Nepa-Lenteng	na ^b	1 lizard / 71 ha	This study
Wae Wuul	3000	1 lizard / 60 ha	This study
North Flores Nanga Baras-Pota	na ^b	1 lizard / 141 ha	This study
Toropadang	na ^b	1 lizard / 424 ha	This study
Wolo Tado	4000	1 lizard / 212 ha	This study

to conform to the above assumption. The unbiased estimate of the frequency index p was then calculated as $\hat{p} \approx \hat{D}a$ (Seber, 1982), and the population density by $\hat{D} = n/(sa)$. The unbiased estimate of the variance is given in Seber (1982).

RESULTS

PADAR AND GILI DASAMI

We found no evidence of *V. komodoensis* on the island of Padar along linear transects and transects on sample plots. During a third survey, carried out using baited traps, we found no monitor lizards either at the baiting stations set in the north or at those located in the south-western part of the island (Fig. 2). The results of these surveys strongly suggested either a very low Komodo monitor population density or – most probably – the absence of a resident population on Padar.

On Gili Dasami, we caught three individuals in one trapping session. Specimens had a mean body mass of 13.3 ± 4.4 kg (mean \pm SE), SVL of 90.6 ± 8.7 cm, and total length of 192.7 ± 20.8 cm. The average area for each sampling unit was 31.2 ha. Considering the presence of one animal in three out of the five sampling units set on the island, we estimated an unbiased population density of about 1 ± 0.1 individual per 52 ha.

FLORES

Population survey. On the west of Flores, 19 monitors were caught during five trapping sessions conducted from Nangalili bay to the Wae Wuul reserve (Fig. 2). Specimens had an average weight of 11.6 ± 2.7 kg, SVL of 76.6 ± 5.4 cm and total length of 168.7 ± 9.3 cm. Six Komodo monitors were trapped at baiting stations set on the north coast (Fig. 3). Specimens had a mean body mass of 13.0 ± 3.6 kg, SVL of 83.3 ± 7.9 cm and total length of 184.5 ± 16.0 cm. Population densities were assessed for each trapping session on sampling units of 42.4 ha calculated using an average distance between traps of about 700 m. No Komodo monitors were found between Nangalili and the river Raja, on the south-west coast, or at baiting stations set in the Kurungbaja peninsula, in northern Flores. Population density estimates for the other areas are reported in Table 1.

Habitat status. The south-west coast around Nangalili was covered mainly by livestock grazing grounds and crop plantations, while grassland and savannah dominated the coastal area as far as Bawe (Fig. 2). From this village to the north-west, through the Keritamese peninsula as far as the Wae Wuul reserve, dry deciduous monsoon forest was the predominant habitat. Cultivates and pastures extend inland from Wae Wuul along with small patches of dry deciduous monsoon forest. To the north-east of the reserve, new settlements have been established as part of the government transmigration program from inland Flores (PHKA, personal communication). We also observed

evidence of arson in savannah forest along the entire west coast, from the north of the Keritamese peninsula to the Wae Wuul reserve.

According to reports collected by Auffenberg (1981) from local villagers, Komodo monitors were found along part of the coastal region north-east of the town of Labuan Bajo. Settlements now extend north of Labuan Bajo where natural habitats have been cleared for cultivation or grazing grounds. On the other hand, interviews with the local community suggest that the species may still occur in dry deciduous monsoon forest along the coast near the village of Bari (Fig. 1). However, no direct evidence of this was collected during our study.

On the north coast, wide patches of dry deciduous monsoon forest have been converted to cultivated areas from the town of Reo to Pota. Slash-and-burn agricultural plots were observed east of Nanga Baras, while cultivated areas and rice fields were common around Pota and surrounding hamlets. Dry deciduous monsoon forest, savannah and grassland covered the coast eastwards as far as Wolo Tado and Riung (Fig. 3).

DISCUSSION

According to our survey, the range of *Varanus komodoensis* as described by Auffenberg (1981) in 1971 has decreased appreciably during the last three decades both in Komodo National Park and on the island of Flores. Here, we describe the extent of such reduction and compare, when possible, estimates of population size with counts reported by previous studies. We report an example of estimation of population density using frequency indexes for a case study where logistics allowed the determination of the presence or absence of animals by single-catch trapping events only (Lancia *et al.*, 1996). Our estimates represent the first data set for the Komodo monitor populations on Flores. However, because a number of factors may have affected the rigor of our analysis, we regard our results as preliminary, but at the same time as valuable information for guiding pilot conservation initiatives.

We acknowledge, for instance, that overestimates of population density could result from trapping individuals coming from a region outside of the area where the trapping session was being conducted. However,

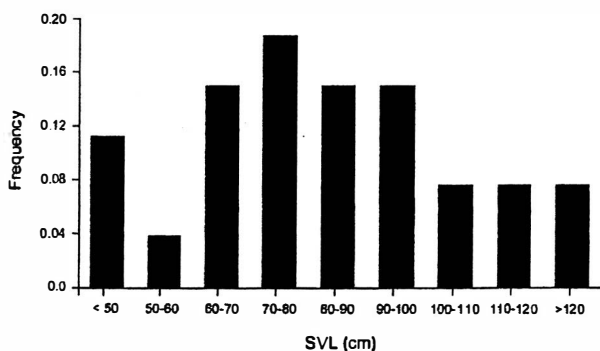


FIG. 5. Distribution of snout-vent lengths (SVL) of 28 Komodo monitors trapped during surveys on the islands of Gili Dasami and Flores.

Auffenberg (1981), describing the scavenging behaviour of the species, noticed that environmental variables affected the search pattern of lizards the greater the distance between the animal and the bait. In our study, monitor lizards were generally caught within 48 hours from the day the bait was set, suggesting that we were more probably catching monitors from nearby areas rather than animals from other regions. Underestimates of population density, on the other hand, might have resulted if more than one lizard occurred within the same sampling unit. Although the vagility of the species observed during feeding excursions (Auffenberg, 1981) suggests that an animal could easily move to a vacant trap nearby, this possibility cannot be excluded and represents a factor difficult to account for. In a few cases, we caught the same animal more than once, but success rates were limited to one lizard per trap. Also, baiting stations that did not capture any monitor lizard were found empty for the whole duration of a trapping session. Other factors, relating to the season in which our survey was carried out, could also have determined low counts. However, Auffenberg (1981) found no significant seasonal difference in the number of Komodo monitors observed per day or in habitat preference, and recorded no evidence of lizard congregation.

Trap response may have varied among individuals (Lancia *et al.*, 1996), although no reports are available of differences between individuals in the motivation of a Komodo monitor to feed (Auffenberg, 1981; PHKA, personal communication). Gender-biased trapping events cannot be ruled out, but we are not able to assess this possibility yet. Unlike other species of monitor lizards (King & Green 1999), gender of *V. komodoensis* is difficult to determine in the field and a DNA test is necessary for sex determination (Halverson & Spelman, 2002). A similar type of bias could have been introduced if animals of only a certain size were trapped. However, lizards varied from 650 g to 42 kg in weight and from 34 cm to 135 cm in snout-vent length, corresponding to the body size of a juvenile and an adult individual, respectively (Auffenberg, 1981; Walsh *et al.*, 1993). It is difficult, from our data set to identify a significant bias towards a specific body size (Fig. 5).

PADAR AND GILI DASAMI

No evidence of *V. komodoensis* was recorded on Padar. In the last two decades, fires have frequently been set on this island in connection with poaching of the deer *Cervus timorensis*. Although juvenile Komodo monitors feed primarily on insects and small vertebrates, both adult and subadult individuals rely heavily on ungulates (PHKA, unpublished data). Indeed, Auffenberg (1981) found that 51% of the prey represented in faecal pellets collected on Padar was deer, and it is possible that past depletion of deer populations due to illegal hunting contributed to a significant decrease or to the disappearance of resident Komodo monitors on this island (PHKA, personal communication).

The island of Gili Dasami, where Komodo monitor population estimates have never been reported prior to this study, appears to have a lower population density than that recorded in 1991 on Gili Motang, a slightly larger island with similar topography and habitat characteristics.

FLORES

The survey conducted by Auffenberg (1981) showed that the Komodo monitor had a continuous, narrow distribution along the south-west coast of Flores, from Nangalili to Labuan Bajo. At present, Komodo monitors are still found, although with a relatively low density, along the coastal area from the river Raja to the Wae Wuul reserve (Fig. 2). Habitat changes around Labuan Bajo and Nangalili have probably caused a decrease in the species' range. We did not extend our survey to the mountain ridges of Mbeliling and Sano Nggoang. Reports from Naga and Sesok (PHKA, personal communication) confirmed the distribution described by Auffenberg (1981) in which high altitudes and moist forest habitat types would represent a main constraint to the presence of *V. komodoensis* beyond 5-6 km from the coastline.

A habitat survey carried out by the Food and Agriculture Organization of the United Nations (unpublished report) on the north of Flores, 10 years after the study of Auffenberg (1981), described a continuous forest canopy with little open grassland habitat from the town of Reo eastwards to the village of Nanga Baras. Expansion of human settlements and forest clearance have substantially reduced Komodo monitor habitats in this region. The trapping events recorded during our survey, in fact, strongly suggest that the northern distribution of the Komodo monitor has decreased, since 1971, to approximately 45 km of coastline, between Pota and the Wolo Tado reserve. Reports obtained from the villages of Kai and Riung (PHKA, personal communication) suggest that the species' range is confined to low altitudes (see Fig. 3).

Average population density values recorded on the western and northern coasts of Flores were 68% and 88% lower, respectively, than those recorded in Komodo National Park (see Table 1). Land conversion represents the main threat to Komodo monitors on this island. Forest fragmentation reduces thermoregulatory sites, diminishes the number of arboreal species that form the diet of juvenile lizards, and depletes nests located on breeding mounds of the megapode bird *Megapodius reinwardt* (Monk *et al.*, 1997). Interspecific competition, for instance with the sympatric (on Flores only) and more versatile water monitor *V. salvator*, may also increase as the forest is converted into cultivated areas. The survey conducted in 1991 by PHKA in the Wae Wuul reserve estimated a density of about one individual per 45 ha, a value approximately 25% higher than that recorded during our study. Until 1995, Wae Wuul was managed by Komodo

National Park and was subject to frequent and regular patrolling. In 1996, the jurisdiction of the reserve changed and surveillance diminished due to lack of personnel (PHKA, personal communication). Since then, arson and deer poaching have intensified. According to PHKA (unpublished report) fires burn more than 3000 ha of savannah each year. Fires promote grass growth, thus providing fresh grazing ground, which in turn entices deer into the open glades where they can be better identified by poachers and pursued by dogs (PHKA, personal communication). In west Flores, deer comprised 46% of the diet of Komodo monitors (Auffenberg, 1981). It is conceivable, therefore, that the differences in population density recorded between 1991 and the present study may reflect the increased human-related pressure on both the Wae Wuul habitat and main prey species.

CONSERVATION IMPLICATIONS

In Komodo National Park, illegal deer hunting has been significantly reduced since 1996, when local authorities gained logistical and financial support from international NGOs (J. Pet personal communication). However, poaching still represents an indirect anthropogenic threat to the four island populations of *V. komodoensis*. Other factors likely to affect Komodo monitor populations within the park boundary include genetic and demographic stochasticity, particularly in small populations (Lande, 1988, 1993; Frankham, 1998). Reduced genetic variation and a low degree of gene flow to and from the other islands was recorded, for instance, on Gili Motang by Ciofi & Bruford (1999). Regional regulations are now enforced to limit illegal hunting of ungulates in Komodo National Park (PHKA, personal communication) and annual surveys of population demography, genetics and reproductive physiology are being conducted to monitor the viability of the species (Jessop *et al.* 2004; Ciofi *et al.*, unpublished data).

The results of the survey on Padar may raise questions as to whether a reintroduction (or augmentation) plan would help the conservation of the species as a whole. A higher number of island populations may, in fact, reduce extinction probabilities in the face of environmental changes by augmenting intraspecific genetic variation (e.g. Lande, 1993; Ballou *et al.*, 1995). Population genetic studies have already described different gene pools within Komodo National Park and identified possible source populations for reintroduction (Ciofi *et al.*, 1999). Several other parameters would need to be considered, however, prior to the implementation of a potential reintroduction on Padar (Dodd & Seigel, 1991; Denton *et al.*, 1997; Genet & Burrows, 1999). Forest coverage is crucial for hatchling survival and for thermoregulation, while soil characteristics are important to assess the presence of potential nesting grounds. These data can be integrated with information on thermoregulatory behaviour and physiology (Green *et al.*, 1991; Wikramanayake *et al.*, 1999) to identify suitable habitat

types. Preliminary information on carrying capacity has been obtained for Padar by a recent survey on ungulate population density (C. Ciofi unpublished data), but data on smaller prey species that form the diet of juvenile Komodo monitors are not yet available. A number of demographic parameters also need attention for creating models to predict probability of population persistence (e.g. Saenz *et al.*, 2002). This would include information on reproductive cycles, recruitment and survival rates, age and size structure, sex ratio (e.g. Sarrazin & Legendre, 2000), dispersal, home range and activity patterns (Ciofi *et al.*, unpublished data). The collection of such data sets – which conform to the IUCN Species Survival Commission guidelines for reintroduction – should be part of a regular monitoring program which would assess, after translocation, whether a viable, self-sustaining population has been established.

Despite habitat encroachment, relatively wide patches of tropical dry deciduous monsoon forest are still present both on the western and northern coasts of Flores. On the west coast, this habitat represents a good candidate for a potential buffer zone to Komodo National Park, or for an extension of currently protected land. Monitoring and protection measures implemented on the northern range of the species would also allow for further representation of Komodo monitor habitat in the Indonesian network of protected areas (Trainor & Lesmana, 2000), and would significantly help the protection of extant, genetically distinct (Ciofi *et al.*, 1999) Komodo monitor populations. Monitoring programs should include regular estimates of population distribution and abundance conducted over consecutive years and different areas to infer average direction and magnitude of change of populations over time and habitat types. Although indices of population density obtained at one point in space and time can provide preliminary information on the general status of a species, other methods, based for instance on capture and recapture of marked individuals, would give more accurate estimates of animal abundance and also allow collection of demographic data. Information should also be obtained on the distribution and level of threats to the Komodo monitor in the north-west and particularly in the east of Flores. Reports from the local community suggest, in fact, that one or more small populations may still be present on the north-east coast, in the district of Maumere. A comprehensive survey of the species' distribution on Flores may provide new information that can help PHKA in setting forestry planning and conservation priorities to protect the Komodo monitor throughout its range.

Finally, the preliminary data reported in this study may serve as a base to consider a potential reevaluation of the most appropriate category to describe the level of threat to *V. komodoensis*. Although it is difficult to determine the proportional reduction in the number of individuals with respect to past total population size (the first criteria defined for all three main IUCN red list cat-

egories), the total range of the Komodo monitor is most likely to be lower than 5000 km², extant populations are fragmented, and decline in the extent of occurrence, area of occupancy, and natural habitats has been observed. This would comply with criteria B1 of the "endangered" category (IUCN, 2001).

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SHORT NOTE

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**ECOLOGICAL OBSERVATIONS ON
MABUYA DORSIVITTATA
(SQUAMATA; SCINCIDAE) FROM A
HIGH ALTITUDE HABITAT IN
SOUTH-EASTERN BRAZIL**

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We present new data on the ecology of a high-altitude population of *M. dorsivittata*, at the Itatiaia National Park in south-eastern Brazil, based on 16 lizards collected in February 2000. Litter size for five mature females was 3-4. Body temperatures of eight lizards averaged 29.1 ± 3.4 °C and was positively correlated with air and substrate temperatures. *M. dorsivittata* consumed a range of arthropods, with no clear dominance of any one prey category.

Key words: diet, reproduction, skink, thermoregulation

The ecology of Neotropical skinks of the genus *Mabuya* was, until recently, very poorly known. Most ecological studies on these lizards were published after 1990 (Vitt, 1991, 1995; Vitt & Blackburn, 1991; Stevaux, 1993; Vrcibradic & Rocha 1995, 1996, 1998a,b, 2002a,b; Rocha & Vrcibradic, 1996, 1999; Vitt *et al.*, 1997; Vitt & Zani, 1998; Mesquita *et al.*, 2000; Rocha *et al.*, 2002a,b). These studies include information on about half of the fifteen currently recognized mainland South American members of the genus (see Mijares-Urrutia & Arends, 1997; Rodrigues, 2000), including the widespread species *M. frenata* and *M. nigropunctata*. *Mabuya dorsivittata* also has a relatively wide distribution in South America (Peters & Donoso-Barros, 1970; Cei, 1993), but ecological data available for this species are presently restricted to some observations on habitat use and general habits and behaviour (Vanzolini, 1948; Gallardo, 1968; Gudynas, 1980). Quantitative data on food habits, thermal ecology and reproduction of *M. dorsivittata* are presently lacking in the literature. In this study, we present data on the ecology of a high-altitude population of *M. dorsivittata*, including information about microhabitat

use, body and environmental temperatures, reproduction and diet.

Sixteen lizards were collected between 0830-1500 hr during 6-7 February 2000 at a site (22° 23' S, 44° 40' W; altitude 2460 m) on the Prateleiras mountain, in the Itatiaia National Park, Rio de Janeiro state, Brazil. The study area is characterized by vegetation typical of the "campos de altitude" (montane fields) biome and by the presence of numerous roundish granitic boulders surrounded by tall grass (for a more detailed description of the area see Scarano *et al.*, 2001).

Lizards were captured using rubber bands and glue-traps. A piece of elastic rubber band about 40 cm long and 1 cm in diameter, with both ends knotted together, was used in collections. Whenever a lizard was sighted, the band was stretched and released so that the knot would hit the animal and immobilize it (whereupon it was captured). Glue-traps consisted of rectangular pieces of cardboard with one adherent surface. Glue-traps were set randomly on top of rocks and checked every 15 min for lizards. Captured lizards were released from the traps by using an ether-soaked ball of cotton wool (ether will readily dissolve the glue), and then immediately euthanased by being placed in a plastic bag with an ether-soaked ball of cotton wool. We believe the removal of 16 specimens of *M. dorsivittata* from the study area is unlikely to have a significant effect on that population, as the species appears to be quite abundant locally.

For lizards collected with rubber bands, cloacal temperatures and temperatures of the substrate and air (1 cm above the point where the lizard was sighted) were taken with fast-reading cloacal thermometers, microhabitat type was recorded and perch height was taken with a measuring tape. Lizards were measured and weighed in the field after being humanely euthanized. Snout-vent length (SVL) was taken with a digital calliper (to the nearest 0.1 mm) and body mass was taken with Pesola spring balances. All lizards were fixed with 10% formalin and later transferred to 70% ethanol. In the laboratory, all animals were opened for examination of gonads and excision of stomachs. Prey items found in stomachs were identified to the level of order and had their longer and shorter axes measured with a digital calliper. Volume of each prey item was estimated using the

TABLE 1. Sizes of juvenile and adult *Mabuya dorsivittata* from Itatiaia, Brazil. For each variable, we give sample size (*n*), mean value \pm SD, and range.

Stage	<i>n</i>	Mean	Range
JUVENILES			
SVL	4	44.3 \pm 2.9 mm	40.0-46.3 mm
Mass	4	1.6 \pm 0.5 g	0.8-1.9g
ADULTS			
SVL	12	64.9 \pm 3.5 mm	58.8-74.3 mm
Mass	12	4.9 \pm 0.9g	3.5-7.0g

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formula for an ellipsoid (see Vitt, 1991). Basic statistics given throughout the text refer to arithmetic means plus one standard deviation.

Four of the lizards (one male, three females) were immature, judging by the state of their gonads, whereas the remaining twelve (seven males, five females) were adult (Table 1). Of the five adult females (64.0-74.3 mm SVL), four had oviductal ova 2.5-3.5 mm in diameter (three in three females, four in one female) and one had three near-term embryos. This indicates that brood size for this population (mean=3.2±0.45; n=5) is equivalent to that of lowland coastal populations of *M. agilis* (Rocha *et al.*, 2002b), and relatively small compared to most Neotropical congeners studied so far (Rocha & Vrcibradic, 1999; Mesquita *et al.*, 2000). Unfortunately, we know of no published data on brood size of other *M. dorsivittata* populations, thus we cannot say if the small brood size observed is a characteristic of that particular population or of the species as a whole. It is also worth noting that 80% of the collected adult females had implanted ova in an early stage of development (stage 3 of Rocha & Vrcibradic, 1999), whereas a single female had well-developed fetuses (stage 6 of Rocha & Vrcibradic, 1999). This suggests that the month of February may represent the end of the parturition period for the present population of *M. dorsivittata*, as in a few other studied populations of Brazilian congeners (see Rocha & Vrcibradic, 1999).

All animals collected with rubber bands were first sighted while basking on granitic boulders, at a height above the ground ranging from 15-55 cm (mean 33.0±11.0 cm; n=9). Mean body temperature of *M. dorsivittata* was 29.1±3.4 °C (range 24.4-35.6 °C; n=8), whereas mean air temperature was 25.0±3.8 °C (range 20.0-29.4 °C; n=7) and mean substrate (rock) temperature was 26.3±2.6 °C (range 23.0-30.6 °C; n=8). These values are somewhat lower than those reported for other Neotropical congeners from lowland and mid-elevation habitats (Brooks, 1968; Fitch, 1968; Vitt & Blackburn,

TABLE 2. Absolute values and proportions for volume (Vol., in mm³), number (n) and frequency of occurrence (Freq.) of each prey category in the diet of *Mabuya dorsivittata* in Itatiaia, Brazil (n=16). Category "Miscellaneous" refer to unidentifiable fragments of arthropods.

Items	Vol.	%Vol.	N	%N	Freq.	%Freq.
Araneae	153.7	7.6	10	17.5	8	50.0
Blattaria	15.1	0.7	1	1.8	1	6.3
Coleoptera	478.3	23.6	11	19.3	7	43.8
Diptera	471.0	23.3	12	21.1	8	50.0
Hemiptera	7.6	0.4	1	1.8	1	6.3
Homoptera	58.5	2.9	15	26.3	7	43.8
Hymenoptera	0.1	0.01	1	1.8	1	6.3
Lepidoptera	639.9	31.6	6	10.5	4	25.0
Miscellaneous	198.6	9.8	-	-	-	-
Total	2022.8		57			

1991; Vitt, 1995; Rocha & Vrcibradic, 1996; Vitt *et al.*, 1997; Vrcibradic & Rocha, 1998a, 2002a,b), but body temperatures of *M. dorsivittata* were always higher than environmental temperatures and averaged 4.5±2.4 °C above air temperature (range 0.4-6.2 °C; n=7) and 2.9±1.4 °C above substrate temperature (range 0.6-5.0 °C; n=8). Such difference values are comparable to those reported for other *Mabuya* species in the Neotropics (Brooks, 1968; Fitch, 1968) and in south-east Asia (Inger, 1959), even though mean body and environmental temperatures were higher in the latter cases. This indicates an active thermoregulatory behaviour for *M. dorsivittata* and may suggest possible limitations for thermoregulation in high-altitude areas due to the lower environmental temperatures (see Mathies & Andrews, 1995), although more data would be needed to assess this point. Body temperatures of *M. dorsivittata* were positively and significantly correlated with both air ($r^2=0.63$; $P<0.05$; n=7) and substrate ($r^2=0.86$; $P=0.001$; n=8) temperatures.

All sixteen lizards contained food in their stomachs, indicating that the population must be in positive energy balance (see Huey *et al.*, 2001). Mean number of prey items per stomach was 3.8±2.2 (range 1-8; n=16). Diet of *M. dorsivittata* comprised a diverse array of arthropod types (mainly insects), with no clear dominance of any one prey category (Table 2). The consumption of a great diversity of food items seems to be the rule among the New World *Mabuya* (Vitt & Blackburn, 1991; Vitt, 1995; Vrcibradic & Rocha, 1996, 2002b; Vitt *et al.*, 1997; Pinto, 1999; Mesquita *et al.*, 2000; Rocha *et al.*, 2002a), with few exceptions (Vrcibradic & Rocha 1995, 1998a). Even taking the small sample size into account, the absence of termites in the diet of this population is notable, considering that such insects are important items in the diet of some populations of other Brazilian congeners (Vitt, 1995; Vrcibradic & Rocha, 1995, 1996; 1998a; 2002b; Vitt & Zani, 1998; Pinto, 1999). The absence of termites in the diet of *M. dorsivittata* from Itatiaia may be due to a low density of such insects in the area or to the particular food preferences of that species.

In summary, our data on the ecology of *M. dorsivittata* in the montane habitat of Itatiaia point to a population with relatively low body temperatures and small broods (compared to most Neotropical congeners) and with a varied diet, based on arthropods (as in most Neotropical congeners). Also, *M. dorsivittata* from Itatiaia seems to have saxicolous habits, but these skinks may actually use the rocks mostly for basking and probably forage among the surrounding vegetation, as appears to be the case for a population of *M. frenata* previously studied by us (Vrcibradic & Rocha 1998a).

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