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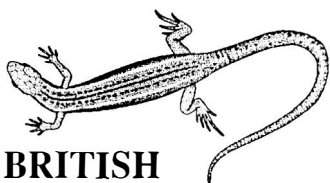
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SUMMER MICROHABITAT USE AND DIEL ACTIVITY CYCLES IN A HIGH ALTITUDE PYRENEAN POPULATION OF *RANA TEMPORARIA*

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Habitat use and activity was studied in a common frog (*Rana temporaria*) population at an altitude of 2200 m in the Circo de Piedrafita, Spain, was studied during July 1998. Adult and juvenile frogs clearly selected moist microhabitats, and avoided dry substrates such as pasture and rocks. Marshes and puddles were the preferred microhabitat of both adults and juveniles; the shore and the water body itself of a larger pond were selected by adults but much less so by juveniles. Regular surveys over seven days indicated that adults showed both diurnal and nocturnal activity, whereas juveniles were more strictly diurnal. The percentage of adults observed at night in the pond was negatively correlated with the minimum air temperature. The rather aquatic habits and diurnal activity patterns appear to differ from low-altitude populations of *R. temporaria*. They are discussed as adaptations to the lack of humid substrates (forest leaf litter) at high altitudes, and to the extreme and unpredictable climatic conditions (low nocturnal temperatures, and sudden rapid temperature decreases at night) in montane environments.

Key words: frog, Spain, Pyrenees, alpine environments, activity, microhabitat

INTRODUCTION

The ecology and biology of the common frog, *Rana temporaria*, has been well-studied in Europe. The wide array of available literature (see Grossenbacher *et al.*, 1988) permits geographical, altitudinal and temporal comparisons of common frog ecology (Miaud *et al.*, 1999). The species can thus be considered as a good model organism to survey the impact of human activities, landscape transformations and other factors on amphibian populations, especially considering the recently discussed trends of global amphibian declines (e.g. Wake, 1991; Blaustein & Wake, 1995).

Publications on common frog ecology mostly concern populations and their dynamics during the breeding season (e.g., Haapanen, 1970; Cooke, 1975; Grossenbacher, 1980; Pascual & Montori, 1981; Hintermann, 1984; Ryser, 1986; Kneitz, 1998), and phenology (Balcells, 1957; 1975; Haapanen, 1982; Bea *et al.*, 1986; Beattie, 1987). Few papers have analysed the ecology of the species in its summer habitat, and the published studies (e.g. Loman, 1978; 1980; 1984; Strijbosch, 1980; Pasanen *et al.*, 1993; Kneitz, 1998) generally refer to low-altitude populations in partly forested areas. Populations of *R. temporaria* in alpine environments, such as at the northern edge of its range or high mountain areas, have been studied in the context of shifts of their breeding season (Balcells, 1957; 1975), larval and breeding adaptations (Aebli, 1966;

Combes, 1967; Angelier & Angelier, 1968; Brand & Grossenbacher, 1979), adaptations to wintering under extremely cold conditions (Pasanen & Karhapää, 1997; Laitinen & Pasanen, 1998; Pasanen *et al.*, 1998), age structure (Ryser, 1996), and time allocation during breeding (Elmberg & Lundberg, 1991).

Many of the recently detected amphibian declines seem to affect montane populations of amphibians, such as *Rana cascadae* in North America (Blaustein & Wake, 1995) or the genus *Atelopus* in South America (Lötters, 1997). This may be partly due to increasing ultraviolet radiation, which has been demonstrated to be a contributory factor in the deaths of eggs and embryos of several species (e.g. Blaustein *et al.*, 1994; Pedraza & Lizana, 1997). Knowledge of the natural adaptations of high-mountain amphibian populations may therefore be important in developing adequate measures for the prevention of future declines. In the present paper, we analyse microhabitat choice and diel activity cycles in a population of *Rana temporaria* at an altitude of 2200 m in the Pyrenean mountain range.

MATERIALS AND METHODS

STUDY AREA

Studies were centred around the Ibón de las Ranas, a medium-sized glacial pond (water surface ca. 170 x 60 m; maximum depth 5 m), which is situated at ca. 2200 m altitude in the Circo de Piedrafita, western Pyrenees, Aragón, Spain (42°49'N, 0°17'W). All observations were carried out in July, 1998. During this period, in the pond, a large number of tadpoles were present which began to metamorphose on 29 July. *Rana temporaria*

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were common in and around the pond, and could clearly be classified into two size/age classes: juveniles (snout-vent length 15-26 mm) and adults (snout-vent length >50 mm); only very few intermediate, subadult specimens were seen (Vences *et al.*, 1999).

MICROHABITAT CHOICE

A study area of 250 m x 150 m (3.75 ha), with the pond at its centre, was divided into 60 plots of 25 m x 25 m. Four of the plots were located in the centre of the pond (100% plot surface made up by water). These plots could not be surveyed and were therefore excluded from further analysis. For each of the remaining 56 plots we estimated the percentage of surface covered by a certain microhabitat (type of substrate or vegetation). Microhabitats were classified as follows: (1) pastures on granitic stony soils (dominated by *Festuca eskia* and *Nardus stricta*, with *Trifolium alpinum*, *Conopodium majus*, *Armeria pubinervis*, *Hieracium pilosella*, *Jasione laevis* and other plants); (2) scree (smaller loose rocks and stones, covering the surface, mainly on some slopes within the study area; with scattered specimens of *Silene rupestris*, *Cardamine resedifolia*, and *Leucanthemopsis alpina* in places); (3) pond (surface of the Ibón de las Ranas); (4) rock surface (parts of the surface made up of pure rock, generally at the same level as the surrounding substrate and not in the form of loose boulders); (5) boulders (large, loose rocks, some of more than 2 m diameter, covering the surface, mainly on some of the slopes within the study area); (6) subalpine shrubs (almost exclusively low (< 1m) bushes of *Rhododendron ferrugineum*, with some specimens of *Vaccinium myrtillus*); (7) pond shore (shore of the Ibón de las Ranas, with a vegetation similar to that of the brook edges; generally, due to wind effects, the water scoured deep recesses under the shoreline which were used as refugia by amphibians and other animals); (8) dry brooks (very small brooks in which, during the study period, no water was present except after rain); (9) scattered pines (single specimens or small groups of *Pinus uncinata*); (10) rocky pond shore (the pond shore consisted of large boulders and scree in places, without any vegetation); (11) brooks (very small and shallow brooks running to and from the pond, generally of less than 1.5 m width; vegetation at the edges largely similar to that recorded for the marsh areas, except for the lower incidence of mosses); (12) marsh, including some small puddles (characterized by the presence of different mosses, e.g. *Cratoneuron commutatum*, and other plants adapted to humidity such as *Carex fusca*, *Carex frigida*, *Juncus articulatus*, *Catabrosa aquatica*, *Saxifraga stellaris*, *Leontodon pyrenaicus*, *Epilobium alsinifolium*, *Dactylorhiza maculata*).

We carried out four surveys of the entire study area on 18 July (1200-1400 hrs), 22 July (1900-2100 hrs), 27 July (2300-0100 hrs) and 28 July (0700-0900 hrs). Plots were surveyed in a random order; each plot was intensively surveyed for 5 min by two researchers (but without looking under stones or into similar refuges).

We recorded every frog encountered (distinguishing between adult and juvenile/subadult frogs) and the plot and microhabitat in which it was first observed. Observed frogs were considered as active because (1) we regularly saw feeding activity during the day and night, and (2) it is unlikely that specimens would expose themselves to the risk of predators and climatic changes if not to actively feed, thermoregulate or migrate. Due to the absence of forest and dense vegetation in the study area, visibility of frogs was similar in most microhabitat types. In fact it is likely that frogs were only overlooked in boulder habitat during the day, due to the large number of holes and crevices into which they could escape before being recorded. However, during the nocturnal surveys (when frogs were generally easier to approach) no individuals were found in amongst boulders. This suggests that the daytime numbers may not have been strongly under-recorded in this microhabitat.

The percentages of area covered by different microhabitat types in the whole study area were compared statistically to the number of individuals recorded in each microhabitat type. We calculated the expected numbers of individuals for each microhabitat type (assuming that the number of individuals should be proportionally equivalent to the surface covered by the microhabitat type under a null hypothesis of no habitat selection), and compared them with the observed numbers using Chi-square tests (e.g. Castilla & Bauwens, 1992; Galán, 1994). To determine microhabitat preference, we calculated Ivlev's electivity index (Ivlev, 1961; see also Cock, 1978; Krebs, 1989).

ACTIVITY

To record frog diel activity, we surveyed the numbers of adult and juvenile specimens along the pond shore over seven days (18, 19, 22, 23, 24, 26, 28 July) at three-hour intervals (eight surveys per day). We distinguished between frogs sitting (1) in the water, (2) on the shore (< 1 m from the water; generally frogs which needed only one jump to reach the water), and (3) frogs sitting 1-3 m from the water. Water temperature ($\pm 0.1^\circ\text{C}$) was measured at one shallow plot (water depth ca. 10 cm) of the Ibón de las Ranas at the end of each survey using a digital thermometer. Minimum and maximum air temperatures were obtained from the Respomuso meteorological station. Each 24 hr interval was completed by the same researcher or team of researchers (generally two people). Data are therefore comparable within each 24 hr period, but comparison of numbers among the seven days must be done more cautiously as different workers had different abilities to detect frogs.

RESULTS

MICROHABITAT CHOICE

In the four surveys, a total of 2537 observations were made (677 adults, 1860 juveniles). *Rana temporaria* used all microhabitats available in the study

TABLE 1. Absolute and relative (as percentages) numbers of adult (Ad.) and juvenile (Juv.) *Rana temporaria* observed during four surveys at (1) 1200-1400 hrs; (2) 1900-2100 hrs; (3) 2300-0100 hrs; and (4) 0700-0900 hrs in the study area, separately for 12 microhabitat classes as defined in Materials and Methods.

microhabitat type	% microhabitat	Ad. 1	Ad. 2	Ad. 3	Ad. 4	Ad. 1-4	Juv. 1	Juv. 2	Juv. 3	Juv. 4	Juv. 1-4	Total (Ad. + Juv.)
pasture	39.6%	16(9%)	12(8%)	19(11%)	2(1%)	49(7%)	126(13%)	13(16%)	7(11%)	6(75%)	270(15%)	319(13%)
scree	17.9%	1(<1%)	0(0%)	0(0%)	0(0%)	1(<1%)	0(0%)	0(0%)	0(0%)	0(0%)	0(0%)	1(<1%)
pond surface	15.3%	25(14%)	21(14%)	77(45%)	171(96%)	294(43%)	1(<1%)	1(<1%)	8(13%)	2(25%)	12(1%)	306(12%)
rock surface	12.0%	1(<1%)	1(1%)	0(0%)	0(0%)	2(<1%)	0(0%)	4(1%)	0(0%)	0(0%)	4(<1%)	6(<1%)
boulders	5.0%	0(0%)	2(1%)	0(0%)	0(0%)	2(<1%)	0(0%)	0(0%)	0(0%)	0(0%)	0(0%)	2(<1%)
subalpine shrubs	4.0%	5(3%)	2(1%)	2(1%)	0(0%)	9 (1%)	0(0%)	1(<1%)	0(0%)	0(0%)	1(<1%)	10(<1%)
pond shore	2.4%	91(52%)	56(37%)	44(26%)	2(1%)	193(29%)	192(19%)	66(8%)	11(18%)	0(0%)	269(15%)	462(18%)
dry brooks	1.1%	3(2%)	1(1%)	1(1%)	1(1%)	6(1%)	104(11%)	42(5%)	1(2%)	0(0%)	147(8%)	153(6%)
scattered pines	0.8%	0(0%)	0(0%)	0(0%)	0(0%)	0(0%)	0(0%)	0(0%)	0(0%)	0(0%)	0(0%)	0(0%)
rocky pond shore	0.8%	19(11%)	31(20%)	0(0%)	0(0%)	50(7%)	8(1%)	2(<1%)	0(0%)	0(0%)	10(1%)	60(2%)
brooks	0.7%	6(3%)	4(3%)	12(7%)	2(1%)	24(4%)	331(34%)	102(13%)	7(11%)	0(0%)	440(24%)	464(18%)
marsh/puddles	0.4%	9(5%)	22(15%)	16(9%)	0(0%)	47(7%)	22(23%)	456(57%)	27(44%)	0(0%)	707(38%)	754(30%)
Total	100%	176	152	171	178	677	986	805	61	8	1860	2537

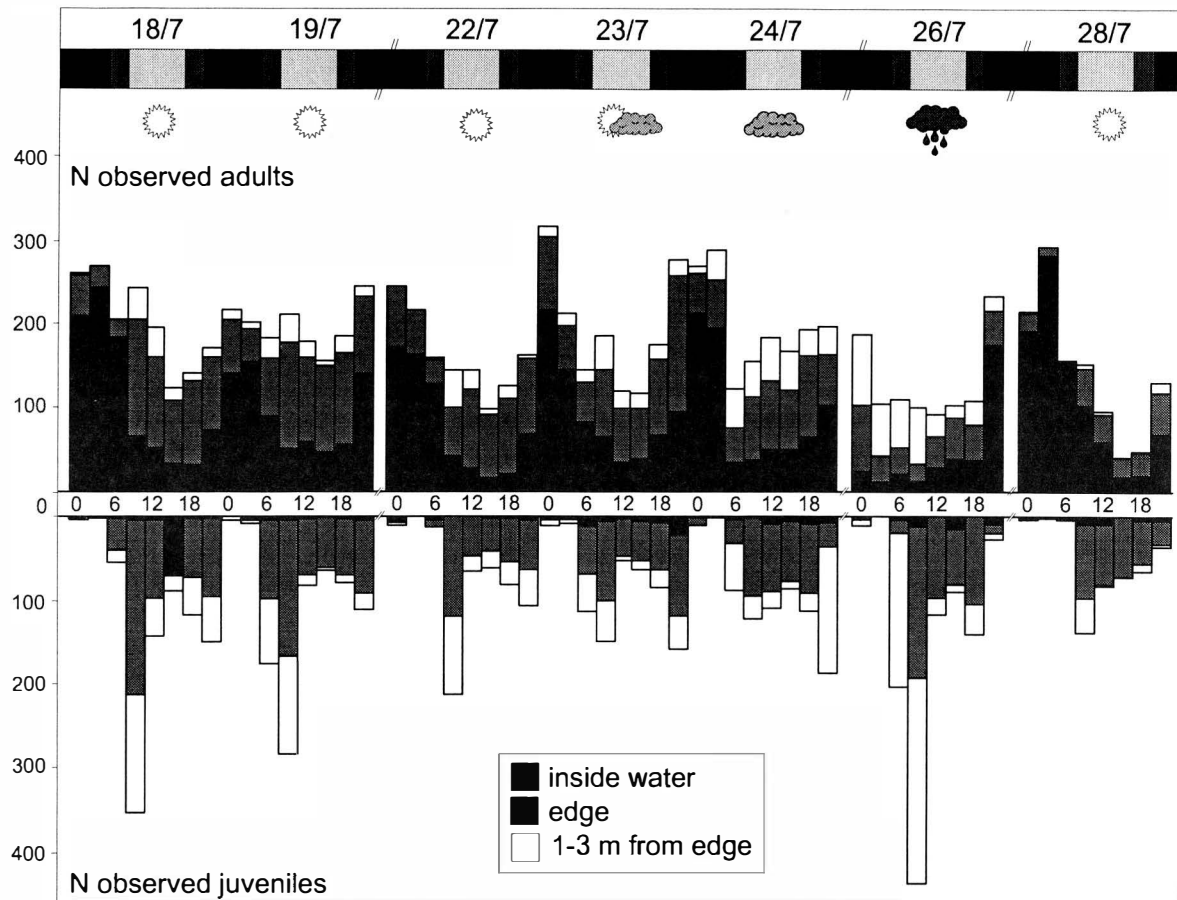


FIG. 1. Activity (total number of observed frogs, separately for adults and juveniles) of *Rana temporaria* as recorded during 3hr-interval surveys on 7 days and nights around the Ibón de las Ranas pond. The upper bar gives approximate timing of light, dusk/dawn and darkness, and general meteorological conditions.

area except for 'scattered pines'. In 'scree' and 'boulders', only one or two individuals were observed (Table 1). Total numbers of observations (adults + juveniles) in the different microhabitats were not directly related to the area covered by each microhabitat type. This result is highly supported by the statistical analysis ($\chi^2=70691.5$, $df=10$, $P<0.0001$; microhabitat type 'scattered pines' excluded from analysis). Considering adults and juveniles together, many more specimens than expected by chance alone were observed in the microhabitats 'pond shore', 'rocky pond shore', 'marsh/puddles', 'brooks' and 'dry brooks'. On the contrary, fewer individuals than expected were seen in the microhabitats 'pastures', 'subalpine shrubs', 'boulders', 'scree' and 'rock surface'. Highly significant differences were found when comparing the numbers of adults and juveniles found in each microhabitat type ($\chi^2=21250.1$, $df=8$, $P<0.0001$; microhabitat types 'scattered pines', 'boulders' and 'scree' excluded from analysis). Most adults were observed in the 'pond' microhabitat (43% of the observations) which harboured almost no juveniles (1%). On the other hand, juveniles were mainly observed in the 'marsh/puddles' (38%) and 'brooks' (24%) microhabitats which were used only by a few adults (7% and 4%, respectively).

Ivlev's electivity indices are summarized in Table 2. They indicate the degree to which the number of frogs observed in a certain microhabitat differs from the number expected from the area covered by this

microhabitat when assuming a random distribution of frogs. In adult *R. temporaria* the highest values were those of the microhabitats 'marsh/puddles', followed by 'pond shore', 'rocky pond shore', 'brooks' and 'pond surface'. The remaining microhabitat types were used less frequently than expected (Ivlev's indices <0). In juveniles, 'marsh/puddles' and 'brooks' had the highest indices, followed by 'dry brooks' and 'pond shore'; all other microhabitat types had negative indices. The main differences between adults and juveniles were the negative values of 'pond surface' and 'rocky pond shore' in juveniles (positive values in adults) and the negative value of 'dry brooks' in adults (positive value in juveniles).

ACTIVITY

During the seven survey days, we made a total of 14755 observations (9695 adults, 5060 juveniles). The recorded absolute numbers of adult and juvenile frogs in each time interval are shown in Fig. 1. The percentages of adults (Fig. 2) and juveniles (Fig. 3) active in water, at the pond edge, and at 1-3 m distance from the pond edge is given separately for the six days without rainfall and for the single 24 hr period in which precipitation was recorded. Adults were active at night as well as during the day, with the highest numbers recorded during the night and early morning (before dawn). The number of adult frogs seen at night (sum of numbers at 2100 hr, 0000 hr, 0300 hr, 0600 hr: 5752 specimens)

TABLE 2. Ivlev's electivity index (Ivlev 1961) of microhabitat types, calculated for adult and juvenile *Rana temporaria* in the study area (from total numbers of adults and juveniles in Table 1).

microhabitat	adults	juveniles
pastures	- 0.69	- 0.46
scree	- 0.98	-
pond surface	+ 0.48	- 0.92
rock surface	- 0.95	- 0.96
boulders	- 0.89	-
subalpine shrubs	- 0.50	- 0.98
pond shore	+ 0.84	+ 0.72
dry brooks	- 0.11	+ 0.76
scattered pines	-	-
rocky pond shore	+ 0.80	- 0.19
brooks	+ 0.67	+ 0.94
marsh/puddles	+ 0.89	+ 0.98

was significantly higher ($\chi^2=337.5$, $df=1$, $P<0.0001$) than that observed during the day (sum of numbers at 0900 hr, 1200 hr, 1500 hr, 1800 hr: 3943 specimens). At night, a higher percentage of frogs was seen in the water (3739 out of 5752 individuals; 65%) than during the day (1192 out of 3943; 30%); the difference was highly significant ($\chi^2=2095.8$, $df=1$, $P<0.0001$).

The water temperature of the pond was rather stable in the study period, with recorded temperatures in shallow areas near the shore between 15.8 and 22.5°C. According to the data in Table 3, the difference between minimum and maximum water temperatures in the seven study days (mean=4.37°C, SD=1.37°C, range=1.8-5.0°C) was much smaller than the difference

between minimum and maximum air temperatures (mean=8.94°C, SD=3.08°C, range=5.8-13.8°C) as recorded by the Respomuso meteorological station (Mann-Whitney *U*-test, $P<0.01$). Minimum air temperatures were always lower than minimum water temperatures (mean difference=6.5°C, SD=2.39°C, range=4.2-9.6°C). Water and air temperatures generally reached their minimum values in the early morning (0600 hr) according to our personal observations. The percentage of adult frogs observed in the water at that time (Table 3) was negatively correlated with the minimum air temperature ($r=-0.87$; $P<0.05$; Fig. 4).

The highest numbers of frogs 1-3 m from the shore was observed in the morning at 0900 hr on four out of the five cloudless days (Figs. 1-2). On the single rainy day, the activity of the adult frogs changed markedly, with an overall higher percentage of active frogs out of the water, and less difference in observed numbers between day and night (Fig. 2).

Juveniles showed a distinct difference in activity between day and night. Numbers of juveniles observed during the six sunny days decreased by 94% from 2100 hr to 0000 hr (748 observed specimens at 2100 hr; 46 observed specimens at 0000 hr). The number of juveniles seen at night (sum of numbers at 2100 hr, 0000 hr, 0300 hr, 0600 hr: 1507 specimens) was significantly lower ($\chi^2=989$, $df=1$, $P<0.0001$) than during the day (sum of numbers at 0900 hr, 1200 hr, 1500 hr, 1800 hr: 3553 specimens). Observed number of juveniles was highest on the single rainy day (Fig. 1), but the reduction in activity at night was similarly drastic. No relevant differences were observed in percentages of juveniles in the water, at the shore or 1-3 m from the

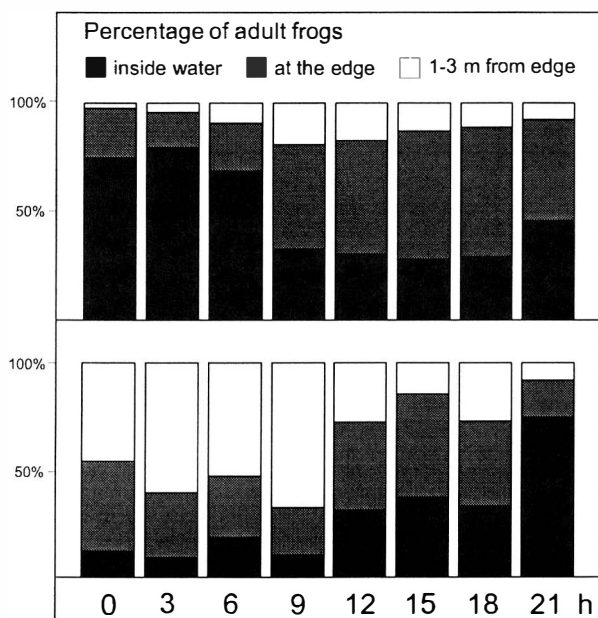


FIG. 2. Percentage of adult *Rana temporaria* in water (black), at the pond edge (grey) and 1-3 m from pond edge (white) recorded in each 3h-interval survey around the Ibón de las Ranas pond. The upper bars indicate the percentages summarized for the six cloudless days and nights (18, 19, 22, 23, 24 and 28 July) and the lower bars indicate the percentages on one rainy day and night (26 July).

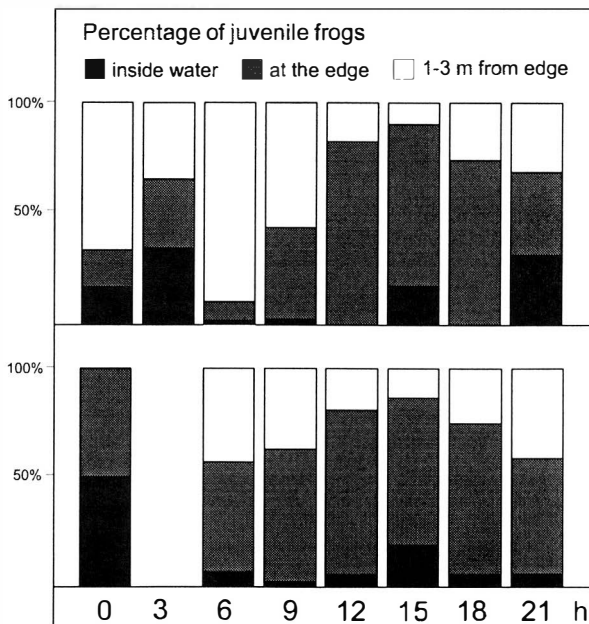


FIG. 3. Percentage of juvenile *Rana temporaria* in water (black), at the pond edge (grey) and 1-3 m from pond edge (white) recorded in each 3h-interval survey around the Ibón de las Ranas pond. The upper bars indicate the percentages summarized for the six cloudless days and nights (18, 19, 22, 23, 24 and 28 July) and the lower bars indicate the percentages on one rainy day and night (26 July). No juveniles were found during the 0300 survey on 26 July.

TABLE 3. Number and percentage of adult frogs observed in the water at 0600 hr (relative to total number of frogs observed at that time) over the seven study days. Minimum and maximum temperatures of water (own measurements in a shallow area near the shore of the Ibón de las Ranas) and air (Respomuso meteorological station) are given for the preceding 24 hours.

	18 July	19 July	22 July	23 July	24 July	26 July	28 July
T _{max} (water)	20.9°C	21.9°C	21.4°C	20.5°C	19.5°C	22.5°C	20.5°C
T _{max} (air)	19.0°C	19.6°C	20.0°C	17.0°C	19.6°C	20.0°C	20.0°C
T _{min} (water)	15.9°C	17.1°C	16.9°C	16.9°C	17.8°C	16.3°C	15.8°C
T _{min} (air)	10.0°C	12.0°C	7.6°C	11.2°C	13.6°C	12.0°C	6.2°C
Total no. observed frogs (0600 hr)	204	181	159	144	121	108	155
Percent frogs in water (0600 hr)	88.7%	48.6%	79.9%	56.3%	27.3%	18.5%	99.4%

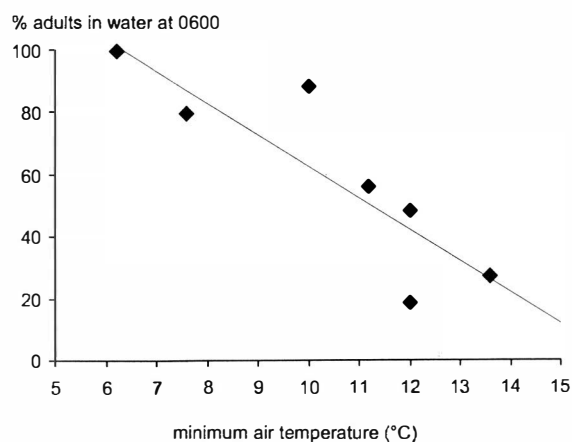


FIG. 4. Scatterplot of the percentage of adult *Rana temporaria* observed in water at 0600 hr vs. minimum air temperature as recorded by the Respomuso meteorological station on the corresponding night (regression analysis: $y=10.21x + 165.7$; $r^2=0.76$, $df=1,6$; $F=15.84$, $P<0.05$).

shore between the six cloudless days and the single rainy day (Fig.3).

Some of these activity patterns of adults (higher percentage of specimens in the pond at night) and juveniles (almost exclusively diurnal activity) were also evident among the four surveys done for the microhabitat preference analysis (see Table 1).

DISCUSSION

In the study area and period, adult and juvenile *Rana temporaria* were largely dependent on aquatic or moist microhabitat types. The poorly used microhabitats (see Table 2) were in a very dry condition in July 1998. A temporary reduction in activity, or aestivation, may not be advantageous in the Circo de Piedrafita area considering the shortness of the activity period in montane areas (see Elmberg & Lundberg, 1991). The frogs were therefore probably forced to remain active in the brook and dry book areas, marshes, puddles, and in and around the pond. The adults especially used the pond as summer habitat, and showed more aquatic habits during the night than during the day. According to the mark-recapture data of Vences *et al.* (1999), about 770 adults were present in and around the pond during the study period, of which by far the majority (93%) were males.

Despite the rather low sample size (data only available for seven days), our results indicated that the

percentage of adult frogs active in the pond at night increased as air temperature decreased. Water temperature was less variable than air temperature, and minimum air temperature values were clearly lower than minimum water temperatures. In the Circo de Piedrafita, night-time temperatures may drop to values around 0°C even in summer. The Respomuso meteorological station recorded 3.0°C on 2 July 1998. It can therefore be concluded that the adult frogs appear to use the pond at least partly as a refuge from the cold. Also, the rather high degree of diurnal activity of adults at the Ibón de las Ranas (not found by Loman, 1980, in a low altitude population) may be explained by the relatively low temperatures at night.

The juveniles differed both in microhabitat choice and activity from the adults. The pond was used very little by juveniles, and their activity was almost exclusively diurnal. This corresponds partly with the observations of Loman (1980) who also found largely diurnal activity in juvenile *R. temporaria*. There are several possible reasons underlying this niche segregation of adults and juveniles. (1) Adults and juveniles of the same frog species may differ in prey preference. Since we did not study prey availability in the different microhabitat types, no statements are currently possible concerning this factor. (2) Predator avoidance may also influence juvenile activity cycles. The niche segregation may even be related to cannibalism; in several analysed stomach contents of adult *R. temporaria* from the Ibón de las Ranas, we found juvenile frogs (D. R. Vieites & S. Nieto, pers. obs. in 1998). Considering the high population density of adults, they may constitute one of the most important predators of the juvenile frogs. (3) It also may be important that *R. temporaria* tadpoles are largely day-active (Griffiths, 1985; Piqué *et al.*, in press), as with many pond dwelling anuran larvae which generally show a positive phototaxis (Duellman & Trueb, 1986). The possibility therefore cannot be excluded that frogs may only change later in development to a more nocturnal activity pattern. (4) Most probably, the activity patterns of juveniles are heavily influenced by climatic factors. Juvenile frogs are clearly more sensitive to rapid air temperature decreases with the risk of freezing (Pasanen & Karhapää, 1997). Also, they are less mobile than adult frogs, and may thus not be able to reach soon enough larger, warm water bodies when temperatures begin to decrease

quickly. It may therefore be an advantage for juveniles to shelter soon after dusk to avoid the danger of freezing.

Some information is available on the fact that high-mountain populations of *R. temporaria* can be aquatic all-year-round (Combes, 1967; Nöllert & Nöllert, 1992; Serra-Cobo *et al.*, 1998). However, often the pattern observed in lowland areas (spring and occasional autumn migration to the breeding site; terrestrial summer habitat; see Loman, 1978; Strijbosch, 1980; Verrell & Halliday, 1985; Hintermann, 1984; Ryser, 1986; Kneitz, 1998) is believed to be typical for the species (e.g. Esteban, 1997). Many of the habitat types generally used by the common frog in lowlands, such as meadows and forest (Loman, 1978), forest, coppice strips, pastures and meadows (Strijbosch, 1980), gardens, chalk, greensands, deciduous woods (Beebee, 1985), meadows and leaf litter (Galán, 1989) and coniferous forest (Pasanen *et al.*, 1993) are not found or are less common in alpine environments.

As a conclusion from the results presented here, literature data, and our own, informal observations on many additional populations, adult common frogs at high altitudes tend to have rather aquatic habits during summer, and to show a high degree of daytime activity. These patterns may be a response to (1) increased aridity of the terrestrial environments at high altitudes where no forest cover with associated leaf litter layer is present, and (2) the low nocturnal air temperatures and the danger of a sudden drop in temperature in an unpredictable environment.

The differences between montane and lowland populations of *Rana temporaria*, however, do not only extend to microhabitat choice and activity of adults. Montane populations show an accelerated larval development at certain temperatures (Aebli, 1966; Angelier & Angelier, 1968; Brand & Grossenbacher, 1979) which probably leads to differences in tadpole morphology (Vences *et al.*, 1998), differences in colour pattern (increased number and size of black spots: Nöllert & Nöllert, 1992), shorter hindlimbs (e.g. Vences *et al.*, 1998), modified time allocation during the breeding period (Elmberg & Lundberg, 1991), and older age at maturity (Miaud *et al.*, 1999). This variation, at least in the Pyrenees, does not appear to be correlated with relevant genetic differentiation (unpublished allozyme data of M. Veith and M. Vences). Detailed long-term comparative studies on neighbouring high- and low-altitude populations of *Rana temporaria* will therefore probably allow the identification of further morphological, ecological and ethological adaptational responses of anurans to the selective pressures of alpine environmental conditions.

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ASSESSING BODY MASS CONDITION IN THE TORTOISE *TESTUDO HERMANNI*

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Condition in the tortoise *Testudo hermanni* was assessed using the ratio of observed mass (M) to that predicted (M') from the allometric relationship $M=aL^b$, where L is body length. A condition index (CI) was based on regressions of $\log M$ on $\log L$ in July (taken as a standard); these regressions differed significantly between females and males. The CI $\log M/M'$ was slightly left-skewed, but was preferred to the simple ratio M/M' for ease of analysis of interaction effects. $\log M/M'$ ranged from approximately -0.1 to $+0.1$ in the wild, equivalent to observed mass of 80-120% of predicted mass. Condition varied seasonally, being low after emergence from hibernation, maximal in spring (April to June), and decreasing in autumn. The detailed pattern of seasonal variation differed significantly between adult females, adult males, and subadults. Regression equations for $\log M$ on $\log L$ in different months are provided for a seasonally-adjusted condition index (CI_s), to assess the relative condition of individuals and annual samples measured in different months.

Key words: allometry, condition index, season, *Testudo*, tortoise

INTRODUCTION

The ability to measure the condition of a tortoise is of interest to both field workers and those who keep chelonians in captivity. Physiological parameters such as lipid stores (Pond & Mattacks, 1984; Kwan, 1994) offer perhaps the best criteria, but are often impractical to measure in the field or involve distressing the animal. Considerable information on condition can, however, be obtained from body mass (M) in relation to length (L). Such body mass condition may be difficult to interpret as it may vary due to gut contents or the presence of eggs rather than with the condition of the soma (i.e. the body as such, excluding gut contents and eggs), but has the advantage of minimal disturbance to the animal. Body mass condition may also be calculated retrospectively from measurements collected routinely during field studies. The ratio M/L has been found to be useful for the examination of captive tortoises (Jackson, 1978, 1980), extreme low or high values indicating poor health. Nevertheless, this ratio changes with size, as pointed out by Meek (1982), who suggested the allometric equation $L=aM^b$, conventionally used to describe the mean mass-length relationship. The inverse relationship is even more useful - fluctuation of mass is of interest for condition, so that mass should be the dependent variable; $M=a^bL$.

The measurement of condition has been neglected in studies of reptiles but has a long history in fish ecology (Weatherley & Gill, 1987). The condition factor K is based on the assumption that body shape is constant with size; that is, where $b=3$. This holds approximately for salmonid fish, which were the early focus of interest for economic reasons, but is less appropriate for other animals. If b is not equal to 3, then K will change with size, with the same problems of interpretation as M/L .

Le Cren (1951) suggested the relative condition factor $K_b=M/M'$, where M' is the predicted mass, i.e. that calculated for a given length from the allometric equation. M' will be influenced by the condition of the individuals used to determine the baseline relationship, which in practice requires a large sample size for the allometric equation to be a valid reference.

The ratio M/M' (expressed as a percentage) has been used to measure condition in female *Testudo hermanni* in relation to reproduction (Hailey & Loumbourdis, 1990). An allometric relationship is linearized by plotting $\log M$ on $\log L$, so that $\log M$ would be expected to be normally distributed around the regression line. In that case $\log M/M'$ should be a preferable condition index (CI), since this equals residuals from the regression (i.e. $\log M - \log M'$), giving a symmetrical distribution best suited for statistical analysis. This paper uses measurements of wild *T. hermanni* to find a suitable index of body mass condition for field studies, and to assess low-condition criteria for captive animals.

METHODS

Field data were from approximately 5650 individual *T. hermanni* marked at Alyki in northern Greece from 1980 to 1999. The site has been described by Stubbs, Swingland, Hailey & Pulford (1985). Tortoises were located by walking through the habitat, measured in the field (Stubbs, Hailey, Pulford & Tyler, 1984), and released immediately afterwards at the point of capture. Length was measured to the nearest 1 mm on a flat-bed scale. The measure is thus the horizontal straight distance between the front and rear of the carapace with the plastron flat on the substrate (not the maximum straight distance, which is given by tilting the animal forwards slightly). Mass was measured with a 100 g, 1 kg or 2.5 kg Pesola spring balance, depending on size. Sex was determined by plastral concavity and larger tails in males; only sexable animals (those larger than

10 cm carapace length) are considered here. Sexual maturity was based on body size criteria; males of 13 cm and females of 15 cm or more are considered to be adults (Hailey, 1990; Hailey & Loumbourdis, 1990). Each individual was permanently marked with a unique code by notching the marginal scutes with a hacksaw blade. Tortoises were also temporarily marked with a waterproof pen on a lightly-pigmented area. These marks served to avoid disturbance of frequently encountered individuals, which were not reweighed, so that most condition values were at intervals of a few months or more.

The allometric relationship $M=aL^b$ was found by linear regression of log-transformed values, giving $\log M=a+b\log L$. To minimize seasonal variability, the reference equations (for females and for males) used measurements only from July (Hailey & Loumbourdis, 1990) since this is the time after females have laid eggs but before the dry months when activity (and thus possibly condition) varies substantially with rainfall (Hailey, 1989). Only the first mass measurement for each individual in July was used in the reference curves, and those for females and males were compared with analysis of covariance (ANCOVA). Statistical

analysis used MINITAB and SPSS, and values of $\log M/M'$ and M/M' for other months were calculated using FORTRAN programs. Only the first condition value for each individual in each category (month x sex) was used in analysis of variance (ANOVA) of seasonal differences.

RESULTS

The mass-length relationships for females and males larger than 10 cm measured in July are shown in Fig. 1. Females were slightly (on average about 4%) heavier than males of the same length, and ANCOVA showed that mass varied significantly between the sexes after allowing for length as a covariate ($F_{1,1462}=104.9$, $P<0.001$). Expected mass M' and thus condition was therefore calculated separately for females and males. Two features of the mass-length relationships in Fig. 1 are particularly suitable for measurement of condition: there are no changes of slope, as occur in some reptiles when shape changes at maturity (e.g. Fig. 4 of Hailey & Davies, 1987), and the deviations around the regression line are rather constant throughout the size range, so that animals of different sizes may be compared directly.

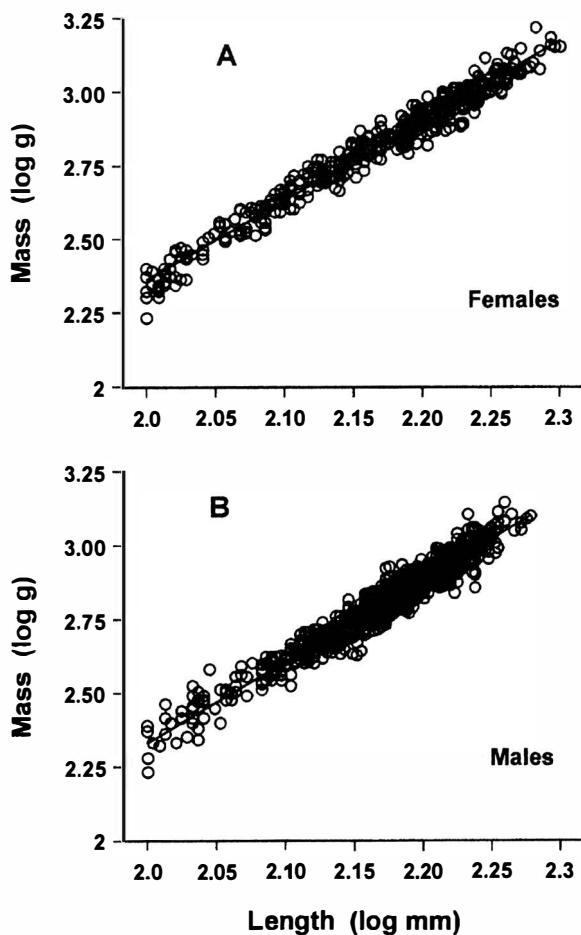


FIG. 1. The allometric relationship between mass and carapace length in *T. hermanni* larger than 100 mm, measured in July. Regression equations are given in Table 2.

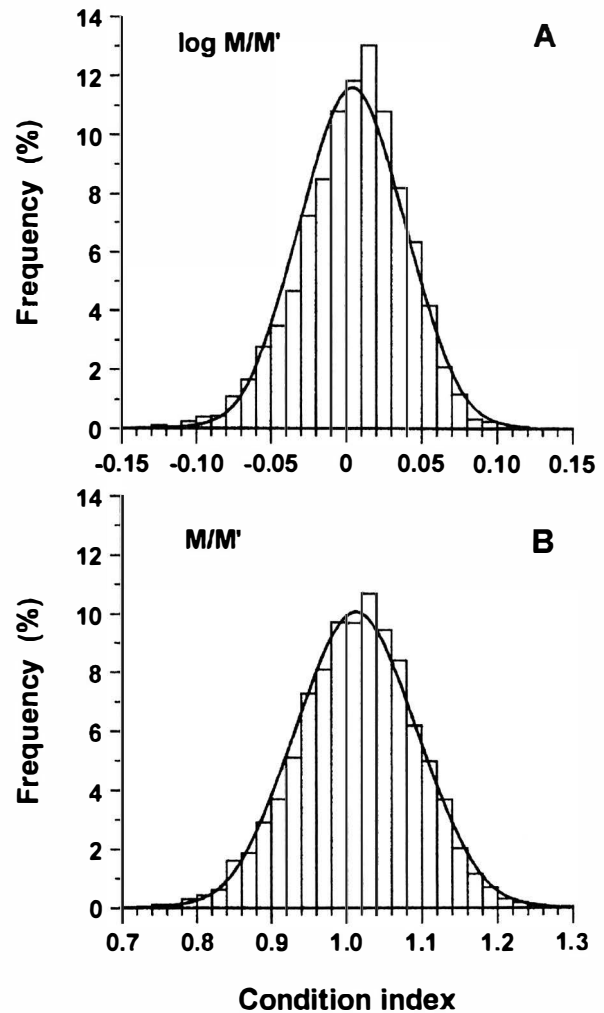


FIG. 2. Frequency distributions of condition index in male *T. hermanni*, measured throughout the year. (A) $\log M/M'$; (B) M/M' . Fitted normal curves are also shown (parameters in Table 1).

TABLE 1. Parameters of condition in wild *T. hermanni* measured by $\log M/M'$ and M/M' . The SE of skewness is the same for both measures because this is based on the normal curve and calculated solely from sample size (P. Rothery, personal communication).

	$\log M/M'$		M/M'	
	Females	Males	Females	Males
<i>n</i>	3686	7888	3686	7888
Mean	0.0048	0.0043	1.0140	1.0131
SD	0.0330	0.0346	0.0762	0.0798
Skewness	-0.376	-0.348	-0.092	-0.063
SE skewness	0.040	0.028	0.040	0.028

The condition index $\log M/M'$ was approximately normally distributed in both males (Fig. 2a) and females. There was a slight skewing to the left in both sexes, that is with the left tail of the distribution more drawn out and the peak shifted to the right, relative to the normal curves (Sokal & Rohlf, 1981). The degree of skewness was similar in both sexes (Table 1). The condition index M/M' was less skewed and fitted a normal

curve even better in both males (Fig. 2b) and females (skewness in Table 1). Nevertheless, the advantage of the log ratio for analysis of interaction effects in ANOVA outweighs the potential disadvantage of the slight skewness (P. Rothery, personal communication), and $\log M/M'$ was therefore used as the CI here. Values of $\log M/M'$ fell within the approximate limits -0.1 to +0.1, equivalent to M/M' of 0.8 to 1.2 (Fig. 2), that is with observed mass within 20% of the predicted value. The variability of $\log M/M'$ was similar in both sexes, as shown by the standard deviations (Table 1).

Seasonal variation in the CI was examined in adults and subadults of both sexes using two-way ANOVA of the months March to October; a small number of captures in November were pooled with those from October. There was significant variation with month in all four groups (all $P < 0.001$). The pattern of seasonal variation of CI was broadly similar in all groups (Fig. 3a), with low values following emergence from hibernation in March, highest values in spring (April to June), a decrease through summer to September and an increase before hibernation. Differences in the seasonal pattern of CI among groups were tested by the month x group interaction term of the ANOVA; there was significant variation among the four groups ($F_{21,9081} = 6.05$, $P < 0.001$). There was no significant difference between subadult females and subadult males ($F_{7,1798} = 1.07$, $P = 0.382$), which were therefore pooled. There were significant differences among ($F_{14,9089} = 8.56$, $P < 0.001$) and between the remaining three groups; adult females with subadults, $F_{7,3689} = 2.23$, $P = 0.029$; adult males with subadults, $F_{7,7206} = 8.34$, $P < 0.001$; adult males with adult females, $F_{7,7283} = 12.2$, $P < 0.001$.

DISCUSSION

CONDITION INDEX

$\log M/M'$ was only slightly skewed, and is thus the preferred index of body mass condition. Other possible indices have shortcomings such as systematic variation with size (M/L or K), or difficulty of interpretation of interaction effects (M/M'). The difference $M-M'$ has also been used successfully as a measure of body mass condition for *T. hermanni* (S. Longepierre & C. Grenot, personal communication). This CI is useful over small size ranges but makes comparisons between individu-

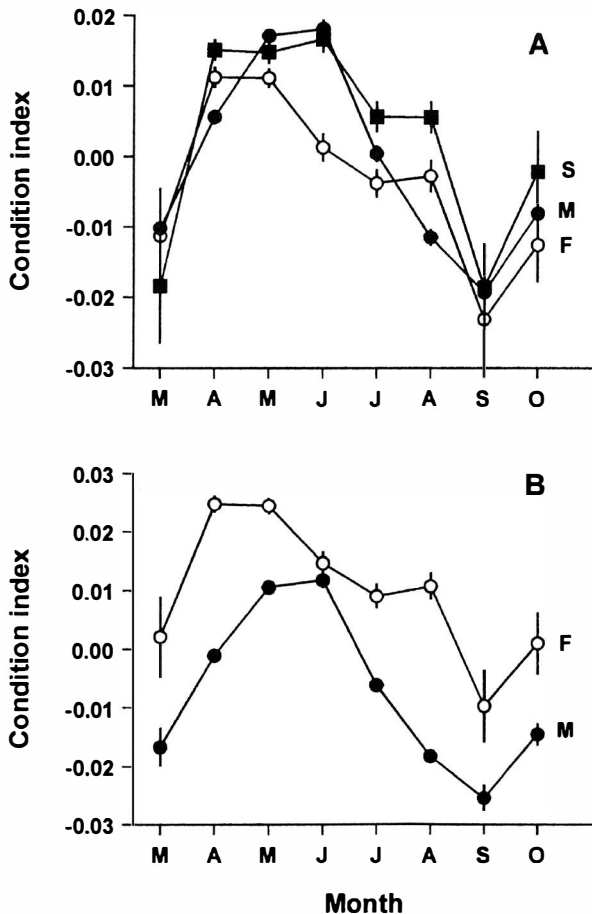


FIG. 3. Seasonal variation in condition index ($\log M/M'$) of *T. hermanni* at Alyki. October and November combined; bars show \pm SE. A, Comparison of adult females (F), adult males (M) and subadults (S). $n=9113$ measurements; no replication of individuals within groups. B, Comparison of adult females and males calculated from the pooled regression equation $\log M = -3.116 + 2.729 \log L$ ($n=1465$, $r^2=95.0\%$); this spuriously shows females in better condition, as described in the Discussion.

Table 2. Seasonal regression equations for *T. hermanni*. Values are shown \pm SE; a and b are the intercept and slope, respectively of the regression of $\log M$ (g) on $\log L$ (mm), n is the number of individuals, and r^2 is the coefficient of variation (%).

	Females				Males			
	a	b	n	r^2	a	b	n	r^2
March	-3.420 \pm 0.177	2.868 \pm 0.081	30	97.8	-2.960 \pm 0.208	2.650 \pm 0.095	110	87.8
April	-3.091 \pm 0.039	2.729 \pm 0.018	748	96.8	-2.964 \pm 0.037	2.659 \pm 0.017	1415	94.6
May	-3.080 \pm 0.036	2.724 \pm 0.016	714	97.5	-3.138 \pm 0.037	2.744 \pm 0.017	1119	96.0
June	-2.951 \pm 0.050	2.662 \pm 0.023	385	97.2	-3.101 \pm 0.043	2.728 \pm 0.020	670	96.7
July	-3.056 \pm 0.048	2.708 \pm 0.022	468	96.9	-3.197 \pm 0.048	2.763 \pm 0.022	997	94.0
August	-3.000 \pm 0.062	2.682 \pm 0.028	379	95.9	-2.992 \pm 0.048	2.665 \pm 0.022	1004	93.5
September	-3.024 \pm 0.153	2.684 \pm 0.070	69	95.6	-3.322 \pm 0.123	2.811 \pm 0.056	280	89.9
October	-2.887 \pm 0.149	2.625 \pm 0.068	96	94.1	-3.151 \pm 0.098	2.739 \pm 0.045	372	91.0

als or populations of differing body sizes difficult, and *T. hermanni* shows a particularly large size range among populations (Willemsen & Hailey, 1999).

The seasonal variation of condition was broadly similar in subadults and adults of both sexes, with lowest condition after emergence from hibernation in March, and at the peak of the summer drought in September. Condition increased in October/November, presumably as preparation for hibernation; mass is known to decrease during hibernation in *Testudo* (Gilles-Baillien, 1974). Kirsche (1971) noted that mass of captive *T. hermanni* increased considerably immediately after hibernation, and that monthly mass increases were greatest in spring up to the end of June, the time of peak condition in the wild.

Variation among the seasonal patterns of CI in adult females, adult males, and subadults must be interpreted in relation to the activity of these groups, which will be considered in detail elsewhere. The most notable differences were the decrease in CI between May and June in adult females, and between July and August in adult males, which may be due to the end of the nesting season and a period of high courtship activity, respectively. It is notable that the nesting season (May and June) did not cause an increase in CI of adult females compared to April or to subadults and males. This pattern supports previous conclusions that the presence of eggs is not associated with increased mass in female tortoises, unlike the situation in other reptiles (for example Madsen & Shine, 1999). Females with and without shelled eggs cannot be separated on the basis of body mass during the nesting season (Hailey & Loumbourdis, 1990). Clutch size is probably limited by the volume of the carapace (Hailey & Loumbourdis, 1988), and the presence of shelled eggs may cause reduced food intake (Meienberger, Wallis & Nagy, 1993) so that the mass of eggs is offset by reduced gut contents.

Previous studies of condition in chelonians have pooled the sexes (for example Jackson, 1980). The regressions of $\log M$ on $\log L$ in July were similar in males and females, with slopes not significantly different (ANCOVA, $F_{1,1461}=3.10$, $P>0.05$), and the pooled regression could be used to calculate a rough measure

of condition. It is worth using the separate regressions, however, because otherwise condition of females will appear to be higher than that of males (Fig. 3b). This result occurs because females are on average heavier than males of the same length, because of their carapace and plastron shape, and therefore appear to be in higher condition if this is calculated from a pooled regression equation. The variability of the CI was similar in the two sexes (Table 1) so that condition values may, however, be pooled for analysis after calculation from separate equations.

The lower threshold of $\log M/M'$ observed in the field was about -0.1, equivalent to M/M' of 0.8. This corresponds well with Jackson's threshold of "dangerously low" weight for length ratio, which was at about 80% of the mean (Fig. 1 in Jackson, 1985). Condition this low or lower was very rarely observed in the field (0.6% of observations), and it would seem advisable to seek veterinary attention for tortoises with such low condition unless this is due to known acute factors (such as dehydration) or unusual carapace shape (particularly narrow or flat individuals). Overweight captive tortoises, with unusually high condition values, should also be a cause of concern, because of the possible association with oedema, egg peritonitis or liver disease (Jackson, 1980; Lawrence, 1985).

SEASONALLY-ADJUSTED CONDITION

The condition index calculated from a common reference (July) varied through the year. There is little doubt that this reflects real differences in the absolute condition of the tortoises. Thus, those handled after emergence from hibernation in March, or at the height of the Mediterranean summer drought in September, are actually in poorer condition than those feeding on lush herbs in spring. This absolute CI is of limited usefulness in field studies, however, unless samples can always be made at the same time of year. Most tortoise populations occur at low population density so that sampling has to continue over long periods. A relative CI is therefore necessary to combine measurements made in different months; for example to compare year-to-year variation of condition with annual rainfall,

or to examine the correlation between condition and survival rate among individuals.

The mean CI values in Fig. 3a could be used for this purpose, by subtracting the mean for the appropriate month and group from each CI measurement. Nevertheless, the significantly different seasonal patterns in tortoises of different sizes (i.e. adults and subadults) show that the slopes of $\log M$ on $\log L$ vary among months. A better method of seasonal adjustment is therefore to calculate M' using separate regression equations for each month, rather than from the July reference. The equations in Table 2 can be used to calculate M' to give a seasonally-adjusted condition index (CI_s), to compare relative condition of tortoises independently of when they were handled. Use of separate regressions for each month will, however, obscure the seasonal change of body mass condition, for which the CI calculated from a single reference is necessary.

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THE DIET OF COEXISTING SPECIES OF AMPHIBIANS IN CANADIAN JACK PINE FORESTS

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Diets of adults of amphibian species coexisting in the boreal forest are poorly understood. We quantified and compared the diets of adult amphibians from four jack pine (*Pinus banksiana*) forests in east-central Canada. Results showed that American toads (*Bufo americanus*) and northern redback salamanders (*Plethodon cinereus*) were predominantly ant-eaters; blue-spotted salamanders (*Ambystoma laterale*) fed mainly on snails, beetles, and insect larvae; spring peepers (*Pseudacris crucifer*) took primarily spiders and wasps; and wood frogs (*Rana sylvatica*) took a variety of alternative prey and had the highest dietary diversity. Diets of these amphibians differed significantly among the species in all study sites. Discriminant analyses showed species separation based on food type, the variable representing the proportion of ants in stomach contents being the major contributor to the discriminant functions in all assemblages.

Key words: frog, salamander, diet, feeding behaviour

INTRODUCTION

Amphibians play a key role in forest food webs, foraging on small invertebrates and serving as food to a variety of vertebrate predators (Burton & Likens, 1975; Pough *et al.*, 1987). However, amphibian ecology in general, and feeding ecology in particular, are poorly understood in boreal forest ecosystems. There is evidence that timber harvesting reduces amphibian populations (e.g. Petranka *et al.*, 1993; Dupuis *et al.*, 1995), and that habitat destruction and deforestation are factors implicated in the decline of amphibian populations worldwide (Wake, 1991). Jack pine (*Pinus banksiana*) dominates large areas of the southern boreal region in Canada and is one of the most important species in lumber and pulp production. Consequently, jack pine plantations are part of the matrix of commercially utilized forest that is subject to perturbations due to forestry practices. An understanding of the natural history and ecology of animal species inhabiting the forest is fundamental to the development of ecologically sound forest management.

Descriptions of animal diets are of general interest in natural history, and are useful for identifying food requirements of species and for understanding how animals utilize food resources. Although diets of adult amphibians have been described in both temperate (e.g. Bury & Martin, 1973) and tropical (e.g. Toft & Duellman, 1979) assemblages, most work deals with the larval stage (Wilbur, 1984 and references therein). Studies of the diets of adult amphibians, based largely on Toft's contributions (see Toft, 1985), showed that amphibians feed largely on arthropods and that species differ in their feeding strategy and degree of specialization. A very limited number of studies conducted in temperate regions suggests that frogs are opportunistic feeders (Stewart & Sandison 1972). A few studies have

reported on the diets of adults of coexisting species of amphibians in some localities within the boreal region in the Nearctic (Moore & Strickland, 1955; McAlpine & Dilworth, 1989); however, we are not aware of similar studies in jack pine forests.

Here, we quantify and compare the diets of adult American toads (*Bufo americanus*), wood frogs (*Rana sylvatica*), spring peepers (*Pseudacris crucifer*), northern redback salamanders (*Plethodon cinereus*), and blue-spotted salamanders (*Ambystoma laterale*) in four assemblages in jack pine forests. We identify their primary food and estimated the overall diet for each species. Additionally, we test whether amphibian species can be differentiated by food type in each assemblage, and identify the prey that allows separation among amphibian species based on food type.

MATERIALS AND METHODS

The study area is located in the southern boreal forest, approximately 30 km south of Gogama (47°31'N; 81°40'W), Ontario, Canada, where jack pine dominates. The area is composed of extensive monospecific forests, ranging in age from 1 year to more than 60 years, as a result of artificial regeneration following clearcutting or wildfire. Mixed coniferous-deciduous forests are also present in the area. We studied the diets of adult amphibians from four jack pine forests: a 6-year old stand (Stand 1), a 35-year old stand (Stand 2), and two stands over 60 years of age (Stands 3 and 4). Different stand ages provide different assemblages of amphibians. Understorey vegetation was composed of herbs and shrubs in Stand 1 and of mosses, herbs, and shrubs in Stands 2-4. Vegetation covered 64% of the ground in Stand 1, 59% in Stand 2, 71% in Stand 3, and 72% in Stand 4.

Amphibians were collected from pitfall traps during July and August 1994. These traps (one-quarter filled with water) were set to collect insects and accidentally captured amphibians as well because of their depth (ca. 20 cm). Rather than destroying valuable material, we used the latter to analyse gut contents. However, this

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TABLE 1. Species composition and mean head-body length (\pm SD) of amphibians in four jack pine forests in the southern boreal region of east-central Canada. An "x" means that the species was in the site but the number of individuals caught was not sufficient to provide a good representation of the diet. A capital "X" means that the diet of the species was described.

Species	Head-body length (cm)	Stand 1	Stand 2	Stand 3	Stand 4
<i>Bufo americanus</i>	1.44 \pm 0.44	X	X	X	
<i>Rana sylvatica</i>	2.30 \pm 0.43	X	X	x	X
<i>Pseudacris crucifer</i>	1.64 \pm 0.07	x	X	x	x
<i>Rana septentrionalis</i>		x			
<i>Ambystoma laterale</i>	4.69 \pm 0.81	X	X		
<i>Plethodon cinereus</i>	3.81 \pm 0.32	X		X	
<i>Ambystoma maculatum</i>		x			
<i>Notophthalmus viridescens</i>		x			

approach is not recommended for sampling and the use of shallower pans (ca. 5 cm) appears now to prevent such accidental captures. Amphibian abundance was not addressed in this paper because specimens found alive in the traps were set free, and that would bias any estimate. It is unlikely that captured amphibians fed while in the pitfall traps because terrestrial species search for live prey (insects usually die shortly after falling into the trap), which are unlikely to be found in the traps.

In Stand 1, pitfall traps (15 m apart) were established in two grids (approximately 500 m apart) following a 7 x 7 point pattern. They operated over six consecutive days every two to three weeks and were checked at the end of each sampling period. In Stand 2, two lines (approximately 400 m apart) of 25 traps each were established, and a single similar trap line was set in Stands 3 and 4. In Stands 2, 3, and 4, traps were checked weekly and operated continuously. Amphibians caught by pitfall traps were placed in labelled plastic bags and frozen for later dissection.

A total of eight species of amphibian was found in pitfall traps, six in Stand 1, five in Stand 2, four in Stand 3, and three in Stand 4 (Table 1). Given the number of available stomachs, we were able to describe the diet of five out of eight captured species, and for 11 out of the 18 possible species and site combinations (Table 1).

Amphibians were identified and the head-body length was measured. Stomach contents were removed and preserved in 50% alcohol, and they were analysed under the microscope. Prey items were identified to the level of Order in most cases. Larvae and adult insects were considered separate food items because their habitat, mobility, and caloric contents are usually different. Stomach contents were quantified by counting the number of individuals of each food type. Number of individuals was recorded rather than volume because we wanted to test whether amphibian species could be separated by the type of food they ate and not whether their bioenergetics differed. We took a conservative approach by estimating the minimum number of food items per stomach (Jaeger & Barnard, 1981), and only those stomachs containing three or more individual food items were considered in the analysis. We estimated the percentage frequency of each type of food

for each stomach ($\%n_i$ = number of individual items of food type i in a stomach/total number of individual food items x 100), and summarized data for each amphibian species and site as the average percentage frequency of each type of food ($\%n$). We estimated the percentage frequency of occurrence for each type of food ($\%f$) as the number of stomachs in which each food type was found over the total number of stomachs examined multiplied by 100. The cumulative frequency of new food types appearing in the diet as a function of the number of stomachs analysed indicated that three to eight stomachs were sufficient to account for most food types represented in diets for the different combinations of species and sites (Heck *et al.*, 1975). To take a conservative approach, however, a species was excluded from the analysis when fewer than five specimens were available.

Stepwise discriminant analysis (BMDP software, 7M procedure) was performed to test whether coexisting species of amphibians could be distinguished by the types of food found in their stomachs, and to identify the types of food that reflected species differences. The variables used in the multivariate analysis were the percentage frequencies of the total number of prey items found in the stomachs of individual amphibians ($\%n_i$). Larvae of Coleoptera (beetles), Lepidoptera (caterpillars), Diptera (maggots), and the unidentified insect larvae were pooled in a single food category (insect larvae). The adults of Lepidoptera (moths), Hemiptera (bugs), Homoptera (hoppers, aphids), Protura (telson tails), Thysanoptera (thrips), Myriapoda (centipedes, millipedes), and Pseudoscorpionida (false scorpions) were not included as variables because they occurred only occasionally in stomachs (representing all together 1.7%-15.5% of the average diets), and their frequency distributions did not reach normality even after data transformation. Thus, nine food type variables were considered to represent the most common food types: insect larvae (LAR), Coleoptera (COL, beetles), Diptera (DIP, flies), Formicidae (FOR, ants), Other Hymenoptera (HYM, wasps), Collembola (COLL, springtails), Acari (ACA, mites), Araneae (ARA, spiders), and Gastropoda (GAS, snails). Log- and square-root transformations were the most effective to satisfactorily normalize variable distributions.

TABLE 2. Overall average percentage frequency of the total number of prey items (% n) and percentage frequency of occurrence of prey items (% f) in stomachs of five amphibian species (*Bufo americanus*, *Rana sylvatica*, *Pseudacris crucifer*, *Plethodon cinereus*, and *Ambystoma laterale*) in Canadian jack pine forests. *n*: number of stomachs analysed; *H'*: Shannon-Wiener diversity index.

Prey type:	<i>Bufo</i> (<i>n</i> =36)		<i>Rana</i> (<i>n</i> =41)		<i>Pseudacris</i> (<i>n</i> =5)		<i>Plethodon</i> (<i>n</i> =43)		<i>Ambystoma</i> (<i>n</i> =12)	
	% n	% f	% n	% f	% n	% f	% n	% f	% n	% f
<i>Insect larvae:</i>										
Coleoptera	0.8	13.6	2.6	21.9	2.2	20.0	4.1	27.9	12.2	41.7
Lepidoptera	1.4	11.1	3.2	24.4	8.1	60.0	0.9	4.6	1.2	8.3
Diptera	0	0	1.3	9.7	1.7	20.0	0.3	2.3	0	0
Unidentified	1.2	25.0	3.4	21.9	0	0	3.5	27.9	8.0	33.3
<i>Adult insects:</i>										
Coleoptera	10.5	75.0	10.2	58.5	3.9	40.0	6.1	53.5	15.9	58.3
Lepidoptera	0.3	25.0	4.6	21.9	0	0	0.3	2.3	7.1	25.0
Diptera	4.6	58.3	10.5	63.4	17.0	100.0	2.4	27.9	9.6	58.3
Formicidae	37.9	88.9	6.6	36.6	5.3	40.0	25.7	83.7	4.5	16.7
Other Hymenoptera	13.6	88.9	15.1	82.9	25.4	100.0	10.8	60.5	7.3	41.7
Hemiptera	2.4	27.8	4.7	39.0	0	0	1.6	18.6	0.5	16.7
Homoptera	1.1	8.3	3.2	29.3	1.7	20.0	0.5	6.9	0.5	8.3
Protura	1.0	8.3	0.4	4.9	0	0	0.2	2.3	0	0
Collembola	9.6	47.2	7.3	48.8	0	0	14.7	37.2	1.3	16.7
Thysanoptera	0	0	0	0	0	0	1.0	2.3	0	0
<i>Other arthropods:</i>										
Myriapoda	0.3	5.6	0.2	4.9	0	0	0.3	4.6	0	0
Acarina	8.5	52.7	7.3	46.3	2.2	20.0	14.2	58.1	0.5	8.3
Araneae	4.2	55.5	13.8	73.2	30.8	100.0	8.8	48.8	5.9	33.3
Pseudoscorpionida	0.5	8.3	0.1	2.4	0	0	0.3	6.9	0.8	8.3
<i>Other invertebrates:</i>										
Gastropoda	2.1	27.8	5.5	46.3	1.7	20.0	4.3	53.5	24.8	66.7
Total no. of food items	745		498		49		3244		80	
<i>H'</i>	0.896		1.113		0.814		0.986		0.971	
Richness of food items	17		18		11		19		15	

Discriminant analysis was performed separately for each site, and species was the discriminator variable. The Shannon-Wiener index (Colwell & Futuyma, 1971) estimated dietary diversity.

RESULTS AND DISCUSSION

Most amphibian species differed in their primary food type (Table 2). Ants were the primary food of *Bufo*, occurring in 88.9% of the 36 stomachs analysed and representing 37.9% of all invertebrate food items; other prey types such as wasps and beetles were also found in toad stomachs. The diet of *Rana* showed the highest dietary diversity, in agreement with previous studies that have classified ranids as opportunistic feeders in temperate regions (Stewart & Sandison, 1972; McAlpine & Dilworth, 1989). We found that wasps, spiders, flies, and beetles were the most common prey in the stomachs of *R. sylvatica* whereas Moore & Strickland (1955) found beetles and flies to be the most common prey of this species in Alberta; differences in the consumption of primary food by *R. sylvatica* may

reflect differences in prey availability. *Pseudacris* was captured by pitfall traps in low numbers in the four study sites, and we were able to describe its diet based only on five individuals trapped in Stand 2. This species seems to feed primarily on spiders, wasps, and flies, whereas ants represented only a low proportion of the stomach contents as in *Rana*.

The two salamander species differed in the proportion of food types consumed (Table 2). We found that *A. laterale* (large size) fed mainly on snails and beetles whereas *P. cinereus* (small size) consumed primarily ants and mites. Salamanders have been identified as opportunistic feeders in which food size is more important than food type (Toft, 1985). Variations in body size among sympatric salamanders have been correlated with differences in diet (Jaeger, 1972). A study conducted by Maglia (1996) in mixed deciduous forests found that *P. cinereus* fed mainly on mites and spiders, and that the abundance of prey types in the diet differed little among populations or sites, in agreement with our findings (Table 3). *Ambystoma* had the highest percent-

TABLE 3. Average percentage frequency of the total number of individual prey items (% *n*) and percentage frequency of occurrence of prey items (% *f*) in the stomachs of amphibian species (*Bufo americanus*, *Rana sylvatica*, *Pseudacris crucifer*, *Plethodon cinereus*, and *Ambystoma laterale*) coexisting in four Canadian jack pine forests. *n*: number of stomachs analysed; *H'*: Shannon-Wiener diversity index.

Prey type:	Young stand				Mid-age stand					
	<i>Bufo</i> (<i>n</i> =11)		<i>Rana</i> (<i>n</i> =12)		<i>Bufo</i> (<i>n</i> =5)		<i>Rana</i> (<i>n</i> =23)		<i>Pseudacris</i> (<i>n</i> =5)	
	% <i>n</i>	% <i>f</i>	% <i>n</i>	% <i>f</i>	% <i>n</i>	% <i>f</i>	% <i>n</i>	% <i>f</i>	% <i>n</i>	% <i>f</i>
<i>Insect larvae:</i>										
Coleoptera	0.0	0.0	4.0	25.0	0.7	20.0	2.4	17.4	2.2	20.0
Lepidoptera	0.6	9.1	3.6	33.3	0.0	0.0	2.2	17.4	8.1	60.0
Diptera	0.0	0.0	3.1	16.7	0.0	0.0	0.0	0.0	1.6	20.0
Unidentified	0.9	45.4	0.0	0.0	0.6	20.0	4.1	26.1	0.0	0.0
<i>Adult insects:</i>										
Coleoptera	14.6	100.0	8.8	50.0	7.9	60.0	9.5	56.5	3.9	40.0
Lepidoptera	0.0	0.0	0.0	0.0	1.5	20.0	8.0	43.5	0.0	0.0
Diptera	4.6	54.5	12.4	58.3	2.1	40.0	10.5	65.2	17.0	100.0
Formicidae	43.0	100.0	16.2	75.0	66.6	100.0	2.7	21.7	5.3	40.0
Other Hymenoptera	11.7	90.9	21.3	91.6	8.8	100.0	10.9	78.3	25.4	100.0
Hemiptera	1.4	18.2	4.6	41.7	0.5	20.0	5.1	34.8	0.0	0.0
Homoptera	0.6	9.1	4.0	25.0	0.7	20.0	2.3	21.7	1.7	20.0
Protura	0.0	0.0	0.8	8.3	0.0	0.0	0.0	0.0	0.0	0.0
Collembola	14.1	63.6	5.0	41.7	1.8	20.0	9.9	56.5	0.0	0.0
Thysanoptera	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Other arthropods:</i>										
Myriapoda	0.8	9.1	0.0	0.0	0.0	0.0	0.1	4.3	0.0	0.0
Acarina	2.7	36.4	7.1	33.3	2.9	20.0	8.5	56.5	2.2	20.0
Araneae	2.5	54.5	7.4	50.0	2.8	40.0	15.7	78.3	30.8	100.0
Pseudoscorpionida	0.8	18.2	0.5	8.3	0.3	20.0	0.0	0.0	0.0	0.0
<i>Other invertebrates:</i>										
Gastropoda	0.6	9.1	1.2	16.7	3.1	40.0	8.1	60.9	1.7	20.0
Total no. of food items	216		106		138		309		49	
<i>H'</i>	0.770		1.030		0.589		1.079		0.812	

age of insect larvae (with 83% of the stomachs containing this food type) compared to the other amphibian species (Table 2). The primary food of this species of ambystomatid seems to be snails. When the stomachs of *A. jeffersonianum* (Jefferson's salamander) collected in deciduous forests were analysed, it was found that their diet also was comprised basically of snails and orthopterans (Judd, 1957).

Diet differed among amphibian species and ants were the main food type that was distinct among the species (Table 3). Discriminant analysis showed that coexisting individuals of *Bufo* and *Rana* differed in the type of food found in their stomachs in Stand 1 (eigenvalue=0.5341, Wilks' Lambda $F_{1,20}=10.683$, $P=0.004$). Most individuals (86.4% of the total cases, canonical correlation=0.590) were correctly assigned to species by the single discriminant function based on ants (variable FOR). *Bufo* (species centroid=0.7) tended to feed more and *Rana* (species centroid=-0.7) less on ants. In Stand 2, results showed significant dif-

ferences in diet among amphibian species (Wilks' Lambda $F_{8,116}=11.237$, $P<0.0001$) (Table 3). The first and second discriminant functions accounted for 95.3% and 4.7% of the total variance, respectively (canonical correlation of the first and second function was 0.808 and 0.292, respectively). Discriminant functions correctly classified 53.1% of the total cases to the actual species. Food type variables representing ants (FOR) and insect larvae (LAR) contributed the most to the functions (Fig. 1). Amphibian species coexisting in Stands 3 and 4 also differed in the proportion of food types found in their stomachs (Stand 3: eigenvalue=1.2865, Wilks' Lambda $F_{2,24}=15.438$, $P<0.0001$; Stand 4: eigenvalue=0.3377, Wilks' Lambda $F_{1,21}=7.092$, $P=0.0145$; Table 3). In Stand 3, 88.9% of the individuals could be correctly classified by the discriminant function as either *Bufo* or *Ambystoma* (canonical correlation=0.750). The proportion of ants and mites (variable ACA) in the diets was the major contributor to the discriminant function, in

TABLE 3 (continued...)

	Mid-age stand				Mature stand 1				Mature stand 2			
	<i>Plethodon</i> (n=26)		<i>Ambystoma</i> (n=5)		<i>Bufo</i> (n=20)		<i>Ambystoma</i> (n=7)		<i>Rana</i> (n=7)		<i>Plethodon</i> (n=17)	
Prey type:	% n	% f	% n	% f	% n	% f	% n	% f	% n	% f	% n	% f
<i>Insect larvae:</i>												
Coleoptera	4.3	23.1	14.6	60.0	1.2	20.0	0.2	28.6	0.9	16.7	3.7	29.4
Lepidoptera	0.0	0.0	2.9	20.0	2.2	15.0	0.0	0.0	5.6	16.7	2.2	11.8
Diptera	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.9	33.3	0.8	5.9
Unidentified	3.2	30.8	5.0	20.0	1.0	15.0	10.1	92.9	7.4	50.0	4.1	23.5
<i>Adult insects:</i>												
Coleoptera	5.2	42.3	13.8	60.0	8.8	65.0	17.4	57.1	15.8	83.3	7.6	64.7
Lepidoptera	0.5	3.8	5.4	20.0	0.1	5.0	8.3	28.6	1.0	16.7	0.0	0.0
Diptera	2.0	30.8	9.9	60.0	5.3	65.0	9.5	57.1	6.9	66.7	3.0	23.5
Formicidae	26.4	92.3	4.0	20.0	28.0	80.0	4.8	14.3	2.4	16.7	24.6	70.6
Other Hymen.	10.1	53.8	4.7	40.0	15.8	90.0	9.2	42.9	18.7	83.3	12.0	70.6
Hemiptera	0.5	11.5	0.0	0.0	3.5	35.0	0.9	14.3	3.6	50.0	3.3	29.4
Homoptera	0.4	7.7	0.0	0.0	1.5	5.0	0.9	14.3	5.1	66.7	0.7	5.9
Protura	0.3	3.8	0.0	0.0	1.8	15.0	0.0	0.0	1.0	16.7	0.0	0.0
Collembola	17.4	46.2	1.8	20.0	9.2	45.0	0.9	14.3	1.8	33.3	10.7	23.5
Thysanoptera	1.6	3.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Other arthropoda:</i>												
Myriapoda	0.1	3.8	0.0	0.0	0.1	5.0	0.0	0.0	1.0	16.7	0.5	5.9
Acarina	16.8	69.2	0.0	0.0	13.1	70.0	0.9	14.3	2.2	33.3	10.2	41.2
Araneae	8.3	53.8	4.9	40.0	5.4	60.0	6.5	28.6	19.7	100.0	9.4	52.9
Pseudoscorpions	0.6	11.5	2.0	20.0	0.3	5.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Other invertebrates:</i>												
Gastropoda	2.4	26.9	31.0	80.0	2.6	35.0	20.4	57.1	14.2	50.0	7.2	35.3
Total no. of food items	2010		34		391		46		83		1234	
H'	0.934		0.924		0.965		0.875		1.104		1.013	

which the diet of *Bufo* (species centroid=0.65) showed a high percentage of ants and mites compared to *Ambystoma* (species centroid=-1.84). In Stand 4, ants (FOR) contributed the most to the discriminant function that correctly classified 73.9% of individuals into *Rana* or *Plethodon* (canonical correlation=0.502). *Rana* (species centroid=-0.93) showed low and *Plethodon* high (species centroid=0.33) values of the canonical variable.

The diets of some amphibian species differed among stands (Table 3). Ants comprised a higher percentage of the diet of *Bufo* in Stand 2 than in the other stands; dietary diversity of this species was also lower in Stand 2. Some differences in the proportion of food types in stomachs of *Rana* occurred between sites; the proportion of ants in the diet was lower and that of spiders higher in Stand 2 than in the other sites. The diet of *Ambystoma* was similar in Stands 2 and 3, whereas the diet of *Plethodon* was also similar in Stands 2 and 4. Differences in diet between the sites may be due to factors such as prey availability and interspecific

competition. The age of the stand creates different environmental conditions (e.g. shaded conditions, amount of woody debris) that influence insect communities and thus, food availability for insectivorous vertebrates. However, some amphibian species (e.g. *Bufo*) seem more likely to have different dietary contributions depending on the site than others (e.g. *Plethodon*), and this may be related to the individual species with which they are associated. Different amphibian assemblages also occurred at the different sites (Table 1).

Most amphibian species coexisting in jack pine stands were distinguished from each other based on the type of food they ate. However, that does not necessarily mean that they actually discriminate food by type because differences in diet may reflect differences in microhabitats. Based on her extensive review of resource partitioning in amphibians and reptiles, Toft (1985) found that 100% and 94% of the studies she reviewed demonstrated that salamanders and frogs, respectively, partitioned food resources. She also pointed out that salamanders tend to be opportunistic

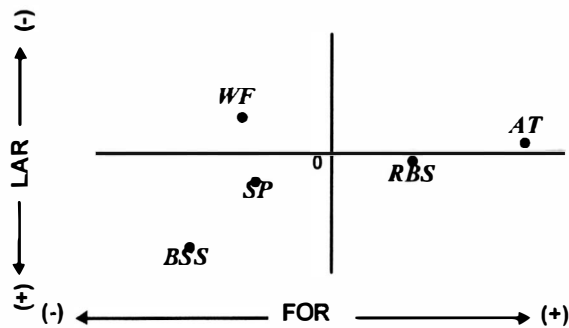


FIG. 1. Position of species centroids in the discriminant space showing differentiation among American toad (AT), wood frog (WF), redback salamander (RBS), spring peeper (SP) and blue-spotted salamander (BSS) based on food type consumed in a jack pine forest (Stand 2).

feeders that discriminate food by size, and that often the differences in prey type are those attributable to habitat. Frogs seem to partition food type more strongly than salamanders (Toft, 1985); however, they vary in size and occupy many kinds of habitat (more than salamanders do), which contribute to differences in diet among species. In eastern Canada, McAlpine & Dilworth (1989) found significant differences in prey size between sympatric *Rana clamitans* (green frog) and *R. catesbeiana* (bullfrog) but not between *R. clamitans* and *R. pipiens* (leopard frog). These authors assumed that food type would reflect the microhabitat used by ranids rather than a case of food partitioning *per se*. In our study, the primary food type differed among species except for the ant-eating *Bufo* and *Plethodon*. These two species were found coexisting in only one out of the four study sites, and - in that case - *Bufo* was present in low numbers (unpublished data). In the remaining assemblages, only one ant-eating species was represented.

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SHORT NOTES

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**A NEW SPECIES OF *SCUTIGER*
(ANURA: MEGOPHRYIDAE) FROM
NAGALAND, NORTH-EASTERN
INDIA**

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Key words: *Scutigera*, anuran, new species

The anuran genus *Scutigera*, assigned by some (e.g. Frost, 1985 and Duellman, 1993) to the family Pelobatidae, and by other more recent workers (e.g. Fu *et al.*, 1997; Fu & Murphy, 1997) to Megophryidae, contains 32 nominal species. While the apparent centre of radiation of the genus is China, three species (*S. nyingchiensis* Fei, 1977; *S. occidentalis* Dubois, 1977 and *S. sikimensis* Blyth, 1854) have been recorded from India (Inger & Dutta, 1986; Dutta, 1997). Until now, a single species, *S. sikimensis*, has been recorded from the north-eastern region of India (see Chanda, 1994). A well-preserved adult male *Scutigera* received by the Zoological Survey of India serves as the basis for the description of a new species. The material was collected from Nagaland, in north-eastern India.

Measurements were taken with a Mitutoyo™ dial vernier calliper (to the nearest 0.1 mm) from specimens in 70 per cent ethanol. The following measurements were taken: snout-vent length, SVL (from tip of snout to vent); tibia length, TBL (distance between surface of knee to surface of heel, with both tibia and tarsus flexed); trunk length, TL (distance between posterior edge of forelimb at its insertion to body to anterior edge of hind limb at its insertion to body); head length, HL (distance between angle of jaws and snout-tip); head width, HW (measured at angle of jaws); head depth, HD (greatest transverse depth of head, taken at the posterior of the orbital region); eye diameter, ED (diameter of eye); interorbital width, IO (least distance between upper eyelids); internarial distance, IN (distance between nostrils); eye to snout-tip distance, E-S (distance between anterior-most point of eyes to tip of snout); eye to nostril distance, E-N (distance between anterior-most point of eyes and nostrils); and diameter of disk on finger II, FIID (width of disk at tip of finger II).

Measurements of fingers and toes were taken from base of each phalange to tip, on right fore and hind limbs, respectively. Sex was determined through examination of gonad.

SCUTIGER MOKOKCHUNGENSIS SP. NOV.

Holotype. ZSI A 8889 (adult male, with enlarged testes), from Mokokchung (26° 20'N; 94° 30'E), alt. ca. 1200 m above msl., Nagaland State, north-eastern India. Coll. Veena Tandon, 1996.

Diagnosis. A large species of *Scutigera* (SVL 87.2 mm in a mature male), that shows the following characteristics: interorbital region lacking tubercles; eye diameter about twice orbit-nostril distance; tongue small, oval; no spinous processes on tubercles of dorsum; undersurface of tibia without tubercles; a single pair of smooth, subtriangular axillary glands; nuptial pads absent; toes with large subarticular tubercles; toe IV webbing, on inner side, broadly to basal subarticular tubercle, reaching base of digit tip as a fringe, and on outer side, as a fringe of skin to base of digit tip; elongated, compressed, inner metatarsal tubercle; and maxillary and vomerine teeth present.

Description. Large body size (SVL 87.2 mm); habitus robust, bufonid-like, with a relatively narrow waist; head wide (HW/SVL ratio 0.36), exceeding length (HL/HW ratio 0.78), snout flattened (HL/HD ratio 0.33), rounded, projecting beyond mandible; nostrils equidistant from snout tip and orbit (E-N/E-S ratio 0.51); canthus rostralis sloping; lores not flattened. Eye large (ED/HL ratio 0.35), eye diameter about twice orbit-nostril distance (ED/E-N ratio 1.98), interorbital distance nearly twice width of upper eyelid (IO/UE ratio 1.94); no dermal fold in interorbital region; internarial region wide (IN/ED ratio 0.91); supratympanic fold glandular, commencing from the posterior border of orbit to a little over the forearm; tympanum absent; nares dorso-laterally oriented, protuberant, and slit-like in shape. Vomerine teeth in two oblique series, in a line between median-posterior of choanae, separated by a distance less than length of each group (vomerine length 2.2 mm; intervomerine distance 1.8 mm). Inferior aspect of snout weakly nicked; inner margin of mandible juncture with a slight w-shaped notch, without two sharp odontoids near symphysis. Tongue small (18.2 mm in length), oval (14.8 mm in width), its dorsal surface covered with papillae; weakly bifid, free posteriorly for 45.1 per cent of length. Vocal sac single, median, subgular. Sternum ossified, rounded posteriorly.

Forearm robust; tips of fingers swollen, but not dilated into disks; fingers free; relative lengths of fingers (measurements in parentheses; in mm): 3 (17.9) > 4 (13.8) > 2 (13.0) > 1 (10.7). Thigh muscular; tibia robust, long (TBL/SVL ratio 0.52); tips of toes weakly swollen but not disk-like; large, oval subarticular tubercles on hand and foot. Webbing reaches: toe I (outer) broadly to base of digit tip; (inner) as fringe to base of

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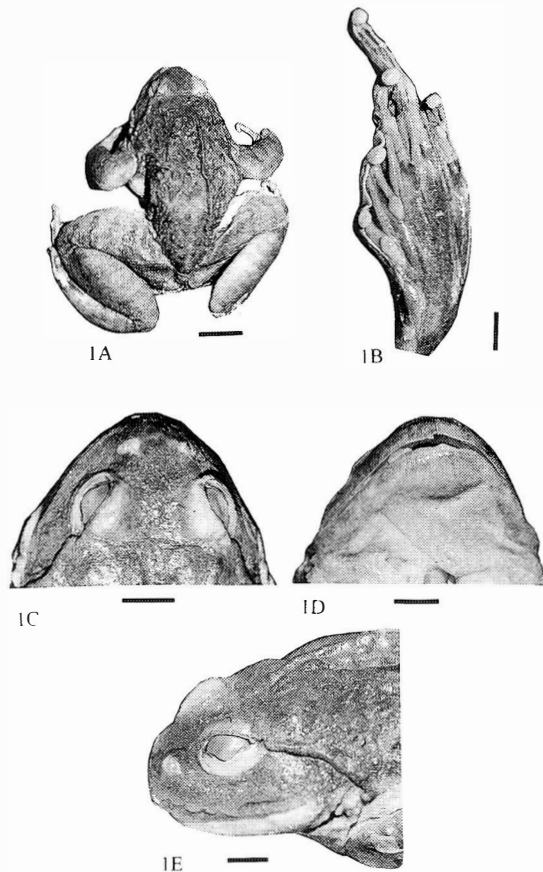


FIG. 1. Holotype of *Scutigera mokokchungensis* (ZSI A 8889). 1A: Body in dorsal view (scale = 15 mm); 1B: Hind limb, showing extent of webbing (scale = 5 mm); 1C: Head in dorsal view (scale = 5 mm); 1D: head in ventral view (scale = 5 mm); and 1E: Head in lateral view (scale = 5 mm).

digit tip; II (outer) broadly to base of digit tip; (inner) broadly to base of digit tip; III (outer) broadly to penultimate subarticular tubercle, reaching base of digit tip as a fringe; (inner) broadly to base of digit tip; IV (outer) broadly to the middle subarticular tubercles, reaching the base of digit tip as a fringe of skin; (inner) broadly to basal subarticular tubercle, reaching base of digit tip as a fringe; V (outer) as a fringe to base of digit tip; and (inner) broadly to penultimate subarticular tubercle; reaching base of digit tip as a fringe of skin. Tarsal fold absent. No outer metatarsal tubercle; elongated, compressed, inner metatarsal tubercle; relative lengths of toes (measurements in parentheses; in mm): 4 (35.1) > 3 (24.7) > 5 (24.4) > 2 (18.1) > 1 (12.7).

Dorsum of body with large scattered conical tubercles, especially beyond sagittal region to level of axilla, with interspaces larger than tubercles that lack spinous processes; upper eyelids smooth; upper surface of thighs tuberculate, tubercles arranged in a linear series; around cloaca, tubercles distinctly clustered. Throat and pectoral region smooth; lower part of venter up to inguinal region smooth; thigh venter smooth. Paired subtriangular, axillary glands at the pectoral region smooth. Undersurface of forelimbs and rest of hind

limbs smooth. Cloacal opening directed postero-ventrally, on upper level of thighs.

Coloration (in preservative). Dorsum unpatterned grey, thighs with diffused bands, upper eyelids yellowish-grey, mandible light grey; ventrum, including throat, pectoral region and abdomen cream with greyish variegations. Subarticular tubercles dark grey.

Measurements (in mm). SVL 87.2; BL 31.2; TBL 45.0; HL 24.3; HW 31.2; HD 13.2; IO 10.1; IN 7.7; UE 5.2; ED 8.5; E-N 4.3; E-S 8.4.

Natural history. No ecological data are associated with the unique holotype. The relatively long tibia (TBL/SVL ratio 51.6) and highly webbed hindlimbs are suggestive of the utilization of lotic habitats, such as streams, rather than smaller mountain torrents (Ohler & Dubois, 1992).

The hills of Mokokchung, the home of the Ao Naga tribesmen, have altitudinal elevations between 1000 and 1400 m above msl. Average annual precipitation is high, with a protracted wet season (the South-West Monsoons) between May and October (extending in some years to December). The temperature range of the locality is 8.6–25° C.

Comparisons. We assign the specimen to the genus *Scutigera* Theobald, 1868 (type species: *Bombinator sikimensis* Blyth, 1854, by monotypy) within the family Megophryidae for the following characteristics that are considered diagnostic of the genus by Dubois (1980; “1986” 1987; Ohler & Dubois, 1992): rough dorsal skin; presence of axillary glands; absence of tympanum; oval tongue that is slightly notched posteriorly; median internal vocal sac in adult male; glandular tubercles on dorsum; snout exceeding mandible; tips of digits without expanded disks; and jaws lacking spinous border. In addition, along with *S. adungensis* Dubois, 1979 (Dubois, 1979), *S. mokokchungensis* shows maxillary teeth, a feature that, along with the lack of a tympanum, was used by Myers and Leviton (1962) to diagnose the megophryid genus *Oreolalax* Myers and Leviton, 1962; and by Dubois (“1986” 1987) to diagnose the subgenus *Aelurolalax* within *Scutigera*. The separation of the subgenera *Scutigera* and *Oreolalax* is supported by both morphological and karyological data (see Li *et al.*, 1990). China is apparently the centre of diversity of both megophryid genera (Fei & Ye, 1989; Frost, 1985; Zhao & Adler, 1993).

In the following section, we compare *S. mokokchungensis* with congeners from the Indian region (India and Nepal), in addition to adjacent parts of eastern Asia, including northern Myanmar (formerly Burma) and south-western China. We list characters in these species that separate them from the species from the Naga Hills.

Scutigera nepalensis Dubois, 1974 (distribution: western Nepal): interorbital region smooth, lacking tubercles; tubercles on dorsum with spinous processes;

toes free; subarticular tubercles on toes absent; and undersurface of tibia with tubercles. *S. occidentalis* Dubois, 1978 (distribution: Kashmir and Ladakh [northern India]): tubercles on dorsum with spinous processes; double pair of smooth, subtriangular axillary glands; eye-snout distance exceeds eye diameter; nuptial pads present (although it is possible that the holotype of the new species was taken outside of the breeding season, at which time a regression of this secondary sexual character may have occurred); both inner and outer metatarsal tubercles present; finger II without subarticular tubercle; inner edge of finger I with a fringe of skin; back of forearm with tubercles; subarticular tubercles absent; rounded metatarsal tubercle; undersurface of tibia with tubercles; and toes 1/3 webbed. *S. sikimensis* (Blyth, 1854) (distribution: Nepal, Sikkim and north-eastern India and southern Tibet [China]; the record from Kashmir by Ahmed ("1945" 1946 requires verification): toes with a vestige of webbing; subarticular tubercles indistinct; tongue elongate; warts larger laterally than on dorsum; undersurface of tibia with tubercles; two pairs of axillary glands; and smaller male SVL (that of ZSI 9854, a syntype of *Cophophryne sikimensis* Blyth, 1854, an adult male, 54.4 mm). *S. boulengeri* (Bedriaga, 1898), (including its synonym *S. alticola* Procter, 1922; distribution: Tibet [= Xizang, south-western China] and north-western Nepal): subarticular tubercles absent; outer edge of toe IV without a sheath of skin; tubercles on dorsum with spinules; and belly and undersurface of tibia with tubercles. *S. nyingchiensis* Fei, 1977 (distribution: Tibet [China] and Kashmir and Ladakh [northern India]): smaller size (SVL 52.0-73.0 mm); toes 1/2 to 1/3 webbed; and tubercles on dorsum with spinules. *S. adungensis* Dubois, 1979 (distribution: northern Myanmar [formerly Burma]): eye-snout distance exceeds eye diameter; axillary patch isolated, not in contact with forelimb; nuptial pad present; toes with a vestige of webbing; metatarsal tubercle oval in shape; and subarticular tubercle absent. *S. glandulosus* (Liu, 1950) (distribution: Western Sichuan and north-western Yunnan, China): male SVL 58-78 (mean 67) mm; maxillary and vomerine teeth absent; eye diameter approximately equal to eye-nostril distance, upperlips pink; and dorsum with brick-red blotches. *S. gongshanensis* Yang and Su, 1979 (distribution: Western Yunnan, China): male SVL 47-57 (mean 51.7) mm; dorsum without conical tubercles; toes webbed at base; eye diameter approximately equal to eye nostril distance; and tips of digits pink. *S. mammatus* (Günther, 1896) (distribution: Yunnan, Sichuan, Qinghai and Xizang [= Tibet], China): male SVL 61-85 (mean 71.1) mm; maxillary and vomerine teeth absent; slender habitus; toes half webbed; eye diameter approximately equal to eye nostril distance; and dorsum with dark brown blotches. *S. mokochungensis* further differs from all described species of *Scutiger* in showing vomerine teeth, a feature that, within the megophryids,

is found only within certain (though not all) species of the genus *Megophrys* (see Dubois, 1980).

In the absence of an existing phylogeny, we speculate that *Scutiger mokochungensis* is most closely related to the northern Burmese *S. adungensis*, with which it shares many phenetic characters, in addition to showing maxillary teeth, which, among congeners, is found only in the species from Myanmar. The type locality of *S. adungensis* lies about 415 km to the north-east of Mokochung (the type locality of *S. mokochungensis*).

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SKIN POCKETS AND THE LOCATION OF ECTOPARASITIC MITES ON LIZARDS OF BAJA CALIFORNIA

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Key words: ectoparasites, lizards, *Sceloporus*, *Petrosaurus*

The presence of skin invaginations in some lizards and their possible relationship with ectoparasites has been the subject of recent research interest. These invaginations, or pockets, often contain mites or ticks (Acarina), and it has been suggested that the concentration of ectoparasites in these pockets reduces their harmful effects (Arnold, 1986). This hypothesis has been challenged by some authors (Bauer, Russell & Dollahon, 1990), but the scarcity of empirical evidence in favour of each hypothesis leaves the controversy open. Experimental blocking of *Psammodromus algirus* pockets in the field induced a redistribution of ticks on their lizard host, with most ticks fixed to ears and axillae, reducing the lizard's mobility and survival. These results strongly suggest a functional role for skin pockets (Salvador, Veiga & Civantos, 1999). However, the kinds of harmful effect induced by ticks are probably different from those induced by other ectoparasites, so it cannot be concluded that the functional value suggested for *P. algirus* pockets may also apply in other ectoparasite-lizard interactions.

The presence of chiggers (Trombiculidae) on lizards has been examined in a few field studies (Allred & Beck, 1962; Arnold, 1986; Goldberg & Bursley 1991a, 1991b, 1994; Smith 1996). There is, however, scant information on ectoparasite distribution on lizards' bodies and on the factors that affect it. This information, though, may be a first step towards understanding the functional role of skin pockets. In this paper, we focus on the distribution of chiggers in three species of iguanian lizards. We investigate whether chiggers attach preferentially in pockets or are also found in other parts of the body and whether lizard size affects chigger distribution. As the capacity of pockets for sheltering mites is limited, we predict that their efficiency may vary with lizard's body size. We also examine variation

among species which differ in body size and pocket size. To eliminate macrohabitat and seasonal effects, the three species have been examined at the same site and during the same time of the year (end of the wet season).

This study was conducted at Cañón de San Dionisio, Sierra de La Laguna, Baja California Sur, Mexico. Vegetation at 300-800 m altitude is arid tropical, and includes 32 species of tree and 60 species of shrub. Dominant plants are palo blanco (*Lysiloma candida*), mauto (*Lysiloma divaricata*), palo zorrillo (*Cassia emarginata*), cajalosuchil (*Plumeria acutifolia*), copal (*Bursera hindsiana*), palo de arco (*Tecoma stans*) and several species of morning glory (*Ipomoea* sp.) (León de la luz, Domínguez-Cadena, & Coria-Benet, 1988). Mean annual precipitation is 765 mm, mostly occurring during July-October (Coria-Benet, 1988). Between 5 and 14 October 1998, we noosed lizards from 0900 to 1300 hrs at both sides of the trail (elevation 400 m) between Las Veredas and San Dionisio ranches. Our sample includes immature and adult males and females of three species: *Sceloporus hunsakeri*, *Sceloporus licki* and *Petrosaurus thalassinus*. We measured the snout-vent length (SVL) of each lizard to the nearest mm using a ruler. We also noted the positions of chiggers on every lizard. Lizards were released at the capture site after examination.

To analyse whether chigger distribution on lizards' bodies occurred randomly or whether ectoparasites prefer to attach inside or outside pockets, we performed a logistic regression using a maximum likelihood model and including interactions between independent variables.

We captured 16 *S. hunsakeri*, 17 *S. licki* and 31 *P. thalassinus* whose SVLs were, respectively, 46-85 mm (mean=70.5 mm, SE=3.0), 46-85 mm (mean=70.6 mm, SE=2.6) and 67-170 mm (mean=107.6 mm, SE=6.2). A comparison of the mean SVL's of - on the one hand - lizards with mites in pockets only, and - on the other - those with them in pockets and other body locations, showed that, in *S. hunsakeri* and *S. licki*, individuals with mites only in pockets were larger than individuals with mites also in other body locations, although the differences were only significant in the latter species (Table 1). The opposite tendency was recorded for *P. thalassinus*, but the differences were not significant. However, a logistic-regression showed that chigger distribution within and outside pockets was not random, and depended on lizard species (-2logLR=7.53, $P=0.02$), snout-vent length (-2logLR=4.38, $P=0.03$), and their interaction (-2logLR=7.27, $P=0.02$). In both species of *Sceloporus*, chiggers were mostly attached to pockets in lizards with larger SVL, whereas chiggers were attached not only to pockets but also to other sites in lizards with smaller SVL. In contrast, chiggers were mainly attached to pockets in smaller SVL individuals of *P. thalassinus*, whereas chiggers were more evenly distributed between pockets and other body parts in larger individuals (Table 1).

TABLE 1. Snout-vent lengths (mean \pm SE) of lizards with mites in pockets only and those with them in pockets and other body locations.

	Pockets only	<i>n</i>	Pockets and others	<i>n</i>	<i>t</i> -test	<i>P</i>
<i>Sceloporus hunsakeri</i>	71.4 \pm 3.2	13	66.3 \pm 9.3	3	0.65	0.53
<i>Sceloporus licki</i>	75.5 \pm 1.8	10	63.6 \pm 4.7	7	2.68	0.017
<i>Petrosaurus thalassinus</i>	104.7 \pm 7.7	22	114.6 \pm 10.7	9	0.72	0.48

It is possible that the pockets of small individuals of the two *Sceloporus* species studied here are not able to shelter many mites, so that these were found attached also at other body sites. On the contrary, adult *Sceloporus* seems to be able to provide space in their well-developed pockets for most mites. Explanations for chigger position based on body size differences in *Sceloporus* species fail to account for observations on *P. thalassinus*. On one hand, differences between *P. thalassinus* and *Sceloporus* could be explained by the smaller body size and the larger, well-developed pockets observed in *Sceloporus*. However, *S. licki* is semi-arboreal and is also found in rocks, and *S. hunsakeri* is associated with rocky habitats, whereas *Petrosaurus* is found on larger rocks (Alvarez-Cárdenas, Galina-Tessaro, González-Romero & Ortega-Rubio, 1988). Hence, differences between species in chigger distribution could reflect microhabitat effects, as mites may be associated with some microhabitat types (Allred & Beck, 1962).

Integumentary pockets may have arisen *de novo* in some lizard species, but in others their position suggests that they may be remnants of structures with a different function. In the lacertid lizard *Psammotromus algirus*, there is experimental evidence that pockets may redistribute ticks and prevent attachment in functionally important areas (Salvador, Veiga & Civantos, 1999). Although the conclusions of this particular study cannot be directly generalized to other species, pockets are located near legs and ears in most species, suggesting that a possible function of these invaginations is to prevent attachment of ectoparasites at sites where they could affect locomotion or hearing.

In conclusion, our results show that mites tend to concentrate in pockets rather than in other body parts, though there is considerable variation with lizard size and species. Although we have not counted the total numbers of mites on lizards, it seems that the presence of pockets may help to reduce the presence of mites in parts of the body where they could have a harmful effect. These results are in accordance with the hypothesis that proposes a functional value for the skin pockets. Additional work is, however, needed to reveal with more detail the role of pockets in the relationship between mites and lizards in these iguanian species.

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**PRELIMINARY DATA ON THE DIET
OF JUVENILE *VARANUS
EXANTHEMATICUS* (SAURIA:
VARANIDAE) IN THE COASTAL
PLAIN OF GHANA**

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Key words: Bosc's monitor lizard, diet, predation, stomach-flushing

Monitor lizards show very large differences in size from juvenile to adult that are sometimes accompanied by a shift in diet to larger prey. The most extreme example is *Varanus komodoensis*, in which juveniles are insectivorous whilst adults sometimes kill prey weighing more than 500 kg (Auffenberg, 1981). Despite their relatively large size, most adult monitor lizards feed mainly on small prey (Losos & Greene, 1988). There have been few investigations into the diets of juvenile monitor lizards. Auffenberg & Ipe (1983) and Auffenberg (1994) examined the gut contents of 92 juvenile (defined as less than one year old) *Varanus bengalensis* from various locations in the Indian sub-continent and found mainly ants, beetles, isopterans, fly larvae and orthopterans. Adults took greater quantities of the same prey (except ants), along with lesser numbers of crabs, mammals, reptiles and amphibians. Angelici & Luiselli (1999) reported no difference in diet composition of adult and juvenile *Varanus niloticus ornatus* in south-eastern Nigeria.

Here I report on the diet of juvenile (six to seven months old) Bosc's monitor lizards (*V. exanthematicus*) in the Great Accra Region of Ghana, as determined by stomach flushing and faecal sampling. *V. exanthematicus* is a small monitor lizard, about 500 mm snout-vent length (SVL), that inhabits grasslands throughout West Africa. In the study area, reproduction occurs in November and December during the hot, dry season, and eggs hatch at the beginning of the rainy season in March and April (personal observation). Stomach flushings were taken from 16 animals caught on 13 September 1994 at Abokobi (5°E42' N, 0°E11' W) and 12 animals caught at Ayi Myensah (5°E46' N, 0°E10' W), on 14 September 1994. Both of these sites are located in southern Ghana, with Ayi Myensah lying about six miles to the north-east of Abokobi. Faecal samples were taken from 24 animals at Ayi Myensah on 28 and 29 August 1994. Animals were caught by excavating burrows in fields of cassava, maize, peppers

and tomatoes. Stomach flushings were obtained using a lubricated 7 mm diameter tube, inserted into the stomach via the oesophagus, through which a constant flow of water was passed until no more prey items were evacuated. Faecal samples were obtained by handling the animals after capture, usually for no more than a minute. Animals were marked and released after examination. The alimentary contents of two animals, killed accidentally during excavation at Ayi Myensah, were also examined. Prey items were identified to ordinal level and counted. All fragments other than single limbs were recorded as prey. Intact body mass of some prey types was estimated by comparison with specimens collected locally.

All samples reported upon here were collected from different animals. However, because of inconsistent labelling, samples could not be assigned with certainty to individual lizards within each location. There was no significant difference in mean SVL between the stomach-flushed animals and those from which faecal samples were collected (mean±SD= 179 mm±24.6 mm and 175 mm±21.6 mm, respectively). Body mass data are available for stomach-flushed animals only: mean body mass± SD= 109±32 g, range 56-175 g, *n*= 26). Dissected animals weighed 97 g (SVL= 147 mm) and 60 g (SVL= 145 mm).

Orthopterans were the most common prey in both stomach flushings and faeces, representing 76% and 85% of prey overall (Table 1), followed by scorpions (10% in both samples) and coleopterans (7% and 3%, respectively). Frogs were not detected in faeces, but represent 5% of prey in stomach flushings. Hymenoptera accounted for 2% of prey in both samples. Twenty-four stomach flushings (86%) and 25 faecal samples (100%) contained orthopterans; they included giant crickets (*Brachytrupes* sp.), locusts and small crickets. Locusts weighed 1-2 g, *Brachytrupes* 3-4 g and other crickets less than 0.5 g. In the field, *Brachytrupes* and locusts were usually encountered singly, but congregations of 5-20 or more small crickets were often found in burrows during searches for lizards. Eight faecal samples (32%) and six stomach flushings (21%) contained scorpions: one was a buthid, with an original mass of 1.5 g; the others were *Pandinus imperator*, weighing about 6-7 g. Three stomach-flushed animals (11%) had eaten unidentified ranid frogs weighing 12-15 g. Two faecal samples (8%) and four stomach flushings (14%) contained beetles of unknown types, all weighing less than 1 g. Three lizards had eaten wasps (8% of faecal samples and 4% of stomach flushings), for which no estimates of weight are available. Both dissected lizards contained pieces of shell of snails, for which no weights could be estimated. One of the dissected animals also contained a scorpion (*P. imperator*) and two orthopterans (a *Brachytrupes* and a small cricket); the other also contained three orthopterans (one *Brachytrupes* and two small crickets). Prey:predator mass ratios for the dissected lizards

TABLE 1. Diet of *Varanus exanthematicus* in Ghana, determined by stomach flushings and faecal samples.

Prey type	% of total prey items		% occurrence in samples	
	Faeces	Flushings	Faeces	Flushings
Orthopterans	85	76	100	86
Scorpions	10	10	32	21
Coleopterans	3	7	8	14
Frogs	0	5	0	11
Hymenopterans	2	2	8	4

were 0.08 and 0.11. There was no significant difference between the mean numbers of prey recorded from stomach flushings at Abokobi (mean no. prey items = 2.3, $n=16$) and Ayi Myensah (mean no. prey items = 1.9, $n=12$; $t=0.902$, $P>0.05$). Overall, however, faecal samples contained more prey items (mean=3.8) than stomach flushings (mean=2.1; $t=4.87$, $P<0.01$).

Amphibians were not found in faecal samples, but otherwise there were no obvious differences in relative proportions of prey recorded from stomach flushings and faecal samples. Others have also commented on an absence of amphibian parts from reptile faeces (e.g. Fitch, 1965). Frogs probably represent the largest size-class of prey which the juvenile lizards are able to consume, accounting for about 20% of the lizards' body mass. In lizards that had recently consumed amphibians the hind legs of the prey were observed protruding from the oesophagus into the mouth. That both dissected animals contained pieces of shell suggests that snails may constitute a common dietary item that is not detected in stomach flushings or faecal samples. However, it is possible that the snail shells had been lodged in the guts for some time. In both animals the fragments were found in the stomach, were perfectly clean and may have been too big to move into the small intestine.

Whereas juvenile *V. bengalensis* are entirely insectivorous (Auffenberg, 1994), the diet of juvenile *V. exanthematicus* also includes amphibians and snails. My results suggest that juvenile *V. exanthematicus* consume fewer but relatively larger prey than do juvenile *V. bengalensis*. The 92 juveniles examined by Auffenberg (1994) contained a total of 1,102 prey items, averaging nearly 12 per lizard. My data for *V. exanthematicus*, combining mean prey numbers in stomach flushings and faecal samples, suggest an average of about six prey items per lizard. Auffenberg (1994) reported a mean prey mass of 0.3 g for *V. bengalensis* of all age classes and a mean prey:predator mass ratio of 0.02 for juveniles (maximum ratio = 0.5). Although comparable figures cannot be calculated for *V. exanthematicus* from the available data, average prey mass was certainly greater than 1 g, and mean prey:predator mass ratio was not less than 0.05. For some lizards the ratio was higher than 0.3.

The only previous study of the diet of *V. exanthematicus* (Cisse, 1972) examined 28 animals, mainly adults, collected over a year in Senegal. Cisse did not find *Brachytrupes* in the diet and recorded only a single snail. Overall, orthopterans accounted for only

8.8% of prey items in Senegal, occurring in 35.7% of lizards. Coleopterans, myriapods and lepidopterans were the most important prey. Coleopterans were common in the diet in early winter and were replaced by orthopterans later in the season. Cisse (1972) stated (my translation) that *V. exanthematicus* finds its prey by active searching, with the eyes playing an essential role. My observations suggest that, other than locusts, all important food types of juvenile *V. exanthematicus* in my study area were nocturnal species that spend the day below ground. Therefore olfaction, rather than eyesight, may play the major role in prey location in this population.

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BOOK REVIEWS

Advances in Amphibian Research in the Former Soviet Union, vols 3 (1999) 245 pp. and 4 (1999) 239 pp. S. L. Kuzmin & C. K. Dodd (eds.). Pensoft, Sofia, Moscow. Subscription price: US\$ 29.00 per volume; single volume: US\$ 34.00 (cloth).

Considering the vastness of the area, the territory of the former Soviet Union is home to only a relatively small number of amphibian species. This periodical aims to publish original papers on the 41 or so species of frogs, toads and salamanders that occur in this region. Co-editor of the series is Dr Sergius Kuzmin, who recently published an English language book with the same publisher on the amphibians of the Former Soviet Union. Volumes 1 and 2 of 'Advances' appeared in 1996 and 1997 respectively, and if these books showed one thing, it was the great amount of work that a large number of 'former Soviet' researchers are carrying out and which they are now prepared to publish in English. This is a laudable aim of this series, which brings a large community of scientists in contact with the western world of herpetology. The volumes contain many figures and photographs, some of which are in colour. On the whole these are informative and interesting books to have in one's library.

Volume 3 contains papers on the distributions of *Ranodon sibiricus* and *Bufo danatensis*, developing limbs in hynobiids, the use of characters under selection in *Rana macrocnemis*, post-metamorphic growth in *Rana temporaria*, papers on different aspects of the morphology of *Triturus karelinii* and *Ranodon*, and notes on *Triturus vittatus* found in Armenia, giant larvae of *Mertensiella caucasica*, the current status of *Onychodactylus fischeri*, and some other communications. Book reviews and announcements conclude the issue.

Volume 4 is devoted exclusively to a monograph on the amphibians of the Caucasus, a very thorough treatise written by David N. Tarkhnishvili and Ramaz K. Gokhelasvili. The Caucasian region possesses a unique amphibian fauna, which is also one of the richest in the former Soviet Union. This publication is the first since A. M. Nikolsky (1913) to give a detailed treatment of the Caucasian amphibian fauna. The area contains 14 species, some of which are interesting endemics, such as *Mertensiella caucasica*, *Pelodytes caucasicus*, *Bufo verrucosissimus* and *Triturus vittatus ophryticus*. Morphology, systematics, distribution and ecology of each species are discussed in detail. The species chapters are subdivided as follows: synonymy, type locality, taxonomic position, distribution, landscape and vertical distribution, morphological description of adults, eggs and larvae, life mode, reproduction, embryonic and larval development, postmetamorphic development, feeding, predators,

parasites and defence, population structure and number dynamics, status and factors of mortality, concluding with a paragraph on conservation. Each of these subsections ends with specific references. There is a chapter on the origin of the amphibian fauna of the Caucasus, followed by a chapter on amphibian assemblages of different Caucasian ecosystems and one on conservation. Besides giving a useful summary of existing information, the book contains a wealth of original material, collected by the authors during many years of work in the region. Ecological data on species occurring in the Caucasus are compared to data on the same species from Western Europe. The authors give due attention to unresolved taxonomic problems and explain the arguments on which they have based their decisions. The book concludes with a rich bibliography, followed by detailed distribution maps and a series of colour plates (which are unfortunately a little less attractive than is standard nowadays). The great merit of the monograph is that it makes available and discusses many interesting data, which were hitherto hidden in Russian language publications, and thus opens up an interesting area of research on which still few publications in Western European languages exist.

Max Sparreboom
The Hague

Handbuch der Paläoherpetologie. Part 4: Salientia. Borja Sanchiz. (1998). 276 pp. Verlag Dr. Friedrich Pfeil, München. DM 150 (cloth).

This long-awaited book represents the state of the art in anuran palaeoherpetology. Its title translates as *Encyclopaedia of Palaeoherpetology*, and this is a very apt description. It is part of a series of publications which collectively must have one of the longest gestation periods in herpetological publishing history. Nineteen volumes have been published since 1969, covering extinct and extant amphibian and reptile orders and suborders, from the Palaeozoic to the present day. Seven new volumes are in preparation. Part 4 (they are not published in order) is dedicated to the Salientia, essentially the Anura. Borja Sanchiz has surmounted the insurmountable by gathering, describing, evaluating, re-evaluating and synthesising the known global archive of fossil data on anurans, from their earliest origins to the present day. He has been aided by various learned collaborators along the way, but the production of this volume was undoubtedly no mean feat. Reading the individual accounts for each species reveals a level of scrutiny that is truly admirable.

The book is well-ordered and laid-out. It begins with a brief historical overview, followed by background on geochronology and anatomical nomenclature. The rest of the book is taken up by a systematic account of the fossil record for each anuran suborder, superfamily,

family, subfamily, genus and species. The fossil record is obviously incomplete, particularly so for less-populated areas of the world, and this book is limited to the data available. Nevertheless, it draws a line upon which new work can be built. It highlights the gaps in our knowledge, and sets out exactly what we do know.

The ancestral origins of the Anura can be traced back to the Early Triassic, some 220 million years ago, to the salamander-like but distinctly tailless *Triadobatrachus*. It is the sole taxon representing the order Proanura. The Anura *sensu stricto* have a fossil record spanning approximately the last 200 million years. Sanchiz tackles their family tree in a systematic fashion. Each account sets out the taxonomic and systematic status of the taxon, discusses its osteological diagnosis and lists the literature sources. There is fossil coverage of sixteen families, from the Ascaphidae to the Microhylidae, followed by a string of monotypic species that, due to their ambiguous affinities, are classed *incertae sedis*. Working on European herpetofaunas myself, I was particularly interested in the accounts for the living genera *Alytes*, *Bombina*, *Discoglossus*, *Pelobates*, *Pelodytes*, *Bufo*, *Hyla* and *Rana*. There is also good detail on the extinct pipoid family Palaeobatrachidae, an example of which - *Pliobatrachus langhae* - survived in central Europe until the Middle Pleistocene. Likewise, the extinct European giant discoglossid genus *Latonina* has been well-recorded from Tertiary deposits. Fossil specimens of many taxa are illustrated, often beautifully. A useful series of maps also reconstructs the palaeogeography of the continents at various stages during the evolution and dispersal of the Anura.

A section on synonyms follows, and a *Nomina Dubia* section for dubiously-described taxa. This is an invaluable inclusion as it keeps a check on the palaeoherpetological 'splitters'. Then there is a *Nomina Vana* section, listing taxa which were correctly-described under standard zoological nomenclatural rules, but for which there is insufficient evidence to maintain the taxon, mostly through loss of type specimens. The *Nomina Nuda* section deals with taxa which have not been correctly described according to international rules, and 'Taxa Removed from Salientia' is the self-explanatory result of previous misidentifications. Sanchiz then lists all the fossil localities from his extensive literature search, and in the last text section discusses anuran phylogeny and evolution, illustrating cladistic relationships. Finally, the impressive bibliography lists 1600 references, occupying almost a quarter of the book. These are numbered and can be cross-referenced with both the systematic accounts and the site list. A notable feature throughout this book is the fastidious referral to - and critical appraisal of - previous literature. It gives the reader confidence that this piece of work has been thoroughly researched and well-executed.

This is a book that should appeal to a broad range of herpetologists, not just evolutionary biologists and pal-

aeontologists. It is an indispensable encyclopaedia, and an interesting reference book at the very least. It has been meticulously collated and serves its purpose well. The price is still quite high, even though prices for the whole *Handbuch der Paläoherpetologie* series were halved in 1998. However, it is a hardback, and with a bright orange cover it will not get lost on your bookshelf. The print run for Part 4 was a mere 300 copies, which goes some way to explaining the high price, and provides an incentive for you to purchase a copy soon!

Chris P. Gleed-Owen
Coventry University

Erpetologia del Piemonte e della Valle d'Aosta. Atlante degli Anfibi e dei Rettili. F. Andreone & R. Sindaco (eds.). (1998). Museo Regionale di Scienze Naturali di Torino, Monografia XXVI.

This volume is the result of an investigation carried out between 1985 and 1996, involving more than two hundred collaborators covering an area of 28 661 km², and the collection of more than seven thousand observations. The analysis of this original information, coupled with literature research and examination of museum collections, allowed the authors to confirm the presence in Piedmont and Aosta Valley (north-west Italy) of 21 native or acclimatized amphibians species and 17 reptiles species.

However, the aim of this book is not just to be a local atlas. In fact, it is something more much more comprehensive. The second chapter, for instance, describes the herpetological history in Piedmont and Aosta Valley and it is enriched by reproductions of some beautiful colour plates taken from the publications of Lessona (1823-1894), Camerano (1856-1917) and Peracca (1861-1923). These scientists, to whom the book is dedicated, have guided most of the Piedmontese herpetologists. Further, there is an interesting section with a biogeographic analysis of the area, and another one describing several aspects of herpetological population biology and species conservation. This includes an analysis of main threats to the species and an appraisal of the legislative protection currently existing in the region. Later on in the book, there is a historical study of distribution patterns and a comparison between historical and contemporary data is presented. Another chapter discusses and comments on cartographical aspects.

The book is pleasant to read, and will prove both interesting and useful to all people who have a passion for amphibians and reptiles as well as specialists. In the fifth chapter, for example, there is a dichotomous key, helpful for the recognition of adults of the species present in the study area; and a further key to identify amphibian larvae and eggs. Line drawings and photographs supplement the text. The tenth chapter offers

commentaries on every single species, written by specialists, describing aspects of their biology and ecology, emphasizing the need for conservation measures. These are accompanied by photographs and distribution maps. The volume is completed by a comprehensive bibliography, an analytic index and two appendices, the first one containing pictures of habitats of herpetological importance in Piedmont and Aosta Valley and photographs of amphibian larvae, the second one presenting historical distribution maps.

If the main aim of an atlas is to provide a better understanding of population status and ecology, with a view to producing effective conservation measures, the regional atlas part of this book is particularly useful for

two two reasons. Firstly, because the information provided is very detailed, and secondly, for the political impact that – hopefully – it will have. It is therefore an important tool for decision-makers and those who want to protect the Piedmontese herpetological fauna. All this assumes a greater meaning in a country such as Italy where there are few conservation laws and the Bern Convention has yet to be rigorously implemented.

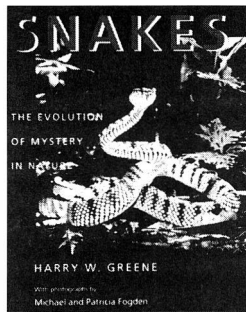
Those not familiar with the Italian language can read the abstracts in English and in French; the keys of all the figures and tables are also presented in English.

Laura Racca
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THE HERPETOLOGICAL JOURNAL

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(revised January 1999)

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Dunson, W. A. (1969a). Reptilian salt glands. In *Exocrine glands*, 83–101. Botelho, S. Y., Brooks, F. P. and Shelley, W. B. (Eds). Philadelphia: University of Pennsylvania Press.

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