

## Reproduction in *Agama aculeata aculeata* and *Agama planiceps planiceps* females from Windhoek, Namibia

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**Abstract.** *Agama aculeata aculeata* and *Agama planiceps planiceps* females were reproductively active during summer, which is the rainy season in Namibia. Both species were iteroparous; clutch size and relative clutch mass in the smaller *A. a. aculeata* were significantly larger than in *A. p. planiceps*. Egg and newborn hatchling size of *A. a. planiceps* on the other hand were significantly greater than in *A. a. aculeata*. It is suggested that these differences may have evolved as a result of different strategies which the two species possibly employ to cope with predation pressure, namely, evasion through crypsis in *A. a. aculeata* and through speed of escape in *A. p. planiceps*.

### Introduction

*Agama aculeata aculeata* and *Agama planiceps planiceps* are two diurnal oviparous lizard species found in Namibia. *Agama aculeata aculeata* is psammophilic and occurs in semi-desert and savanna type habitats throughout Namibia and also in western Botswana, southern Angola and in the Cape Province (South Africa) (McLachlan, 1981; Branch, 1988). *Agama planiceps planiceps* on the other hand is rupicolous and found in semi-desert and arid savanna habitats (Branch, 1988). Its more restricted range is given as Damara-land and the Kaokoveld in northern Namibia and the northern part of Namaqualand, South Africa, as well as the Windhoek, Okahandja and Omaruru areas (Mertens, 1955, 1971).

*Agama aculeata aculeata* is cryptically coloured, with a generally olive coloured body blending well with the surroundings. *Agama planiceps planiceps*, on the other hand, has more conspicuous body colouration, the head having lemon coloured spots while the body is grey to black with a larger orange spot on each shoulder blade.

The breeding biology of Namibian lizards has received scant attention and the few studies conducted deal mainly with species from the Namib Desert, e.g. *Pachydactylus laevigatus* (Werner, 1977), *Angolosaurus skoogi* (Mitchell et al., 1987), *Aporosaura anchietae*

and *Meroles cuneirostris* (Goldberg and Robinson 1979) and *Aporosaura anchietae* (Robinson, 1990). Brief comments on the reproductive biology of other southern African lizards may be found in the taxonomic works of Fitzsimons (1943) and Branch (1988).

One objective of reproductive studies in general is to gain an understanding of the reproductive strategy of organisms as well as the causal selective factors. This has, for example, led Tinkle (1969) to subdivide lizards into early maturing, multiple clutch, short-lived species and late maturing, single clutch, long-lived species. Various workers have searched for an accurate method of assessing reproductive effort in lizards, with the ratio of clutch mass to body mass and clutch calories to body calories being two methods used most frequently (Vitt, 1978; Shine, 1980). Hirshfield (1980), however, cautions that knowledge of an organism's food intake is fundamental in analysing its reproductive effort, and that a lack of knowledge of this currently represents a serious weakness of life history theory. Tuomi et al. (1983), for example, showed theoretically that reproduction need not always take place at the expense of somatic maintenance and therefore survival, but that its impact on the latter depends on the level of resource intake by the organism.

Most studies of the reproductive biology of lizards include an analysis of lipid cycles, as these usually provide useful information about reproductive strategies and ultimately life-histories (Derickson, 1976b; Taylor, 1986). Adiposectomy in female *Uta stansburiana* (Hahn and Tinkle, 1965), for example, resulted in a high incidence of follicular atresia and retarded vitellogenesis, suggesting a causal relationship between ovarian development and fat body condition. Lipid reserves can be used by lizards for mainly reproductive purposes (e.g. Castilla and Bauwens, 1990), or for winter nourishment (e.g. Loumbourdis and Kattoulas, 1985), or for both (e.g. Taylor, 1986). In some lizards, however, the function of the lipid reserves is not clear. Magnusson (1987), for example, found that the relative fat body size of certain teiid lizards from the Amazonian savanna varied little throughout the year with no apparent correlation between fat body size and gonad development.

The liver cycles of some lizards show a clear pattern, normally synchronised with those of the fat bodies (e.g. *Cnemidophorus sexlineatus*, Etheridge et al., 1986), but in others it shows no clear trend (e.g. *Agama atra*, van Wyk, 1984b). The depletion of liver glycogen in *Anolis carolinensis* during the first days without food led Gist (1972) to conclude that these reserves are used initially and preferentially as an energy source. As in the case of the fat bodies, the liver energy stores can be utilised for reproduction, winter maintenance or both, (e.g. Loumbourdis and Kattoulas, 1985).

The aims of the present study were as follows:

- (i) to analyse the reproductive cycles of *A. a. aculeata* and *A. p. planiceps* females;
- (ii) to compare their reproductive strategies in terms of the size and mass of the clutches, eggs and hatchlings they produce; and
- (iii) to determine the relationship between reproduction, and the abdominal fat bodies and liver condition in the two species.

## Material and methods

The study was conducted in Windhoek (22°34'S; 17°06'E), Namibia. Windhoek lies at an altitude of about 1725 m above sea-level in a cool steppe region where the vegetation is predominantly highland savanna.

The breeding cycles of the two species were analysed by monitoring the size and condition of their ovarian follicles on a monthly basis. The mean diameter of the five largest hydrated follicles was recorded for each female specimen during the non-breeding season, while the mean diameter of all vitellogenic follicles was recorded during the breeding season. These measurements were used to calculate a monthly follicle size index by dividing the mean follicle diameter by the snout-vent length. Clutch size and mass, as well as individual egg mass, were recorded. The former was determined by counting vitellogenic follicles and oviducal eggs in freshly dissected females. Clutch mass and egg mass indices were calculated by dividing by the corrected body mass, which in turn was obtained by subtracting the combined wet mass of the abdominal fat bodies, liver, ovaries and their accessory ducts from the original mass of the animal. Egg incubations were carried out in the laboratory to determine hatchling size and mass at birth. The eggs were placed in moist vermiculite and incubated at 26.5°C until they hatched. The total length and mass of each newborn hatchling was determined within 24 hours of its birth.

The monthly fluctuation in mass of the abdominal fat bodies and liver was expressed as indices of the corrected body mass. All the mass determinations were carried out with a Sartorius toploading balance.

A sample of 4 to 6 *A. a. aculeata* specimens was collected monthly from April 1987 to March 1990, and a sample of 4 to 8 *A. p. planiceps* specimens monthly from August 1988 to November 1990. All the specimens were captured using a noose. The lizards were killed within 24 hours of capture, by first being kept at 0°C for 30 minutes, and then subjected to an overdose of chloroform vapour.

All the data were expressed as means with one standard deviation. Student's t-test was performed on means and  $P < 0.05$  was considered as significant. An exponential curve was constructed from the monthly fat body mass indices, in order to determine their rate of change during the breeding season. Weather data were obtained from the Windhoek Weather Bureau.

## Results

### *Gonadosomatic indices*

The earliest appearance of vitellogenic follicles in both species was in September, suggesting that these females became reproductively active during late August-beginning September. The onset of breeding was not synchronised, as the ovaries of some females still appeared quiescent at this time.

Follicle diameter increased significantly in *A. a. aculeata* by October ( $P < 0.05$ , September vs. October, fig. 1a) and in *A. a. planiceps* by September ( $P < 0.05$ , August vs. September, fig. 1b). The breeding season overlapped with the rainfall season which stretches from October to May.

#### *Clutch size: vitellogenic follicles*

In both species the follicles of individual specimens were always similar in size, reflecting a synchronization of vitellogenesis. The mean number of vitellogenic follicles in *A. a. aculeata* (11.8;  $n = 37$ ) was significantly greater than the mean number in *A. p. planiceps* (6.8;  $n = 53$ ),  $P < 0.001$ , although their ranges overlapped (6-17 and 4-13, respectively).

#### *Clutch size: oviducal eggs*

Oviducal eggs were present in *A. a. aculeata* from November to February, and in *A. p. planiceps* from October to March. In both species the clutch size was smaller than the vitellogenic follicle count but not significantly so ( $P > 0.1$ ). Mean clutch size in *A. a. aculeata* (11.5;  $n = 15$ ) was significantly larger than that in *A. p. planiceps* (6.0;  $n = 31$ ),  $P < 0.001$ , although their ranges overlapped (8-17 and 4-9, respectively). Mean egg mass index of *A. p. planiceps* (0.044;  $n = 186$ ) was significantly greater than that of *A. a. aculeata* (0.039;  $n = 143$ ),  $P < 0.001$ . Mean clutch mass index in *A. a. aculeata* (0.419;  $n = 13$ ) was, however, significantly greater than in *A. p. planiceps* (0.253;  $n = 28$ ),  $P < 0.01$ .

#### *Hatchling morphometric data*

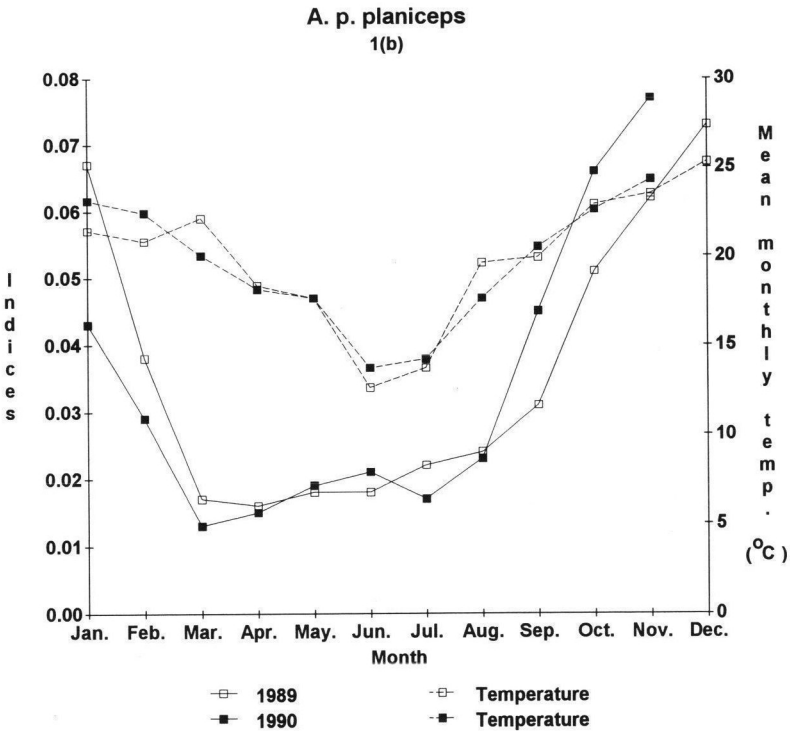
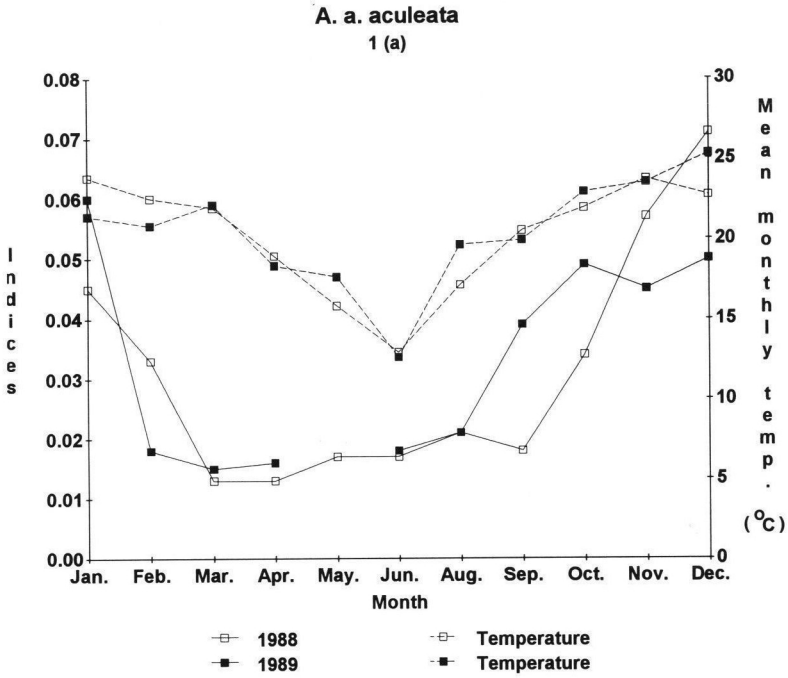
Mean newborn hatchling size of *A. p. planiceps* (74.6 mm;  $n = 12$ ) was significantly greater than that of *A. a. aculeata* (58.9;  $n = 30$ ),  $P < 0.001$ . Mean body mass did not, however, show a significant difference (0.99 and 1.04, respectively,  $P > 0.01$ ).

#### *Abdominal fat bodies*

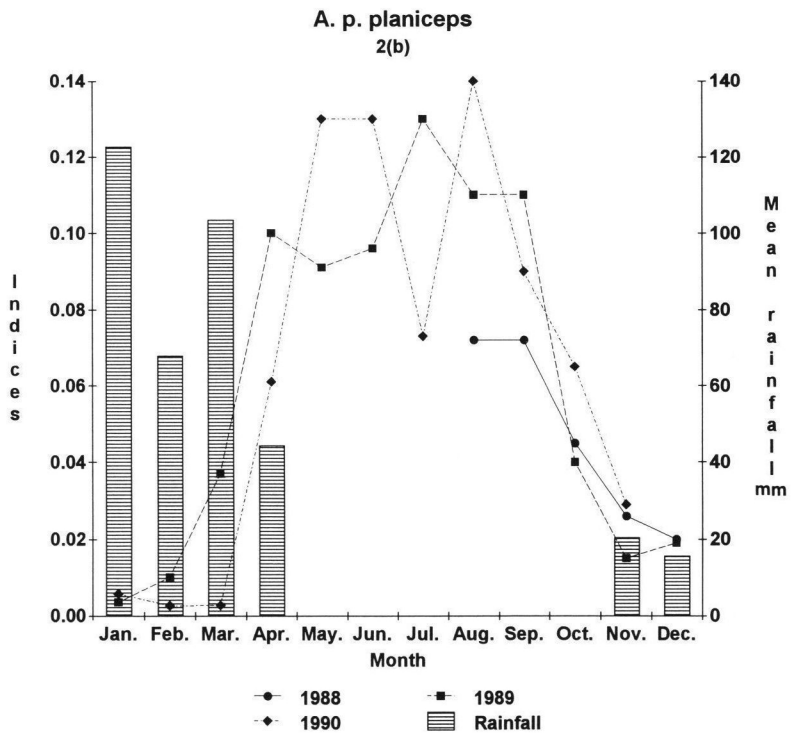
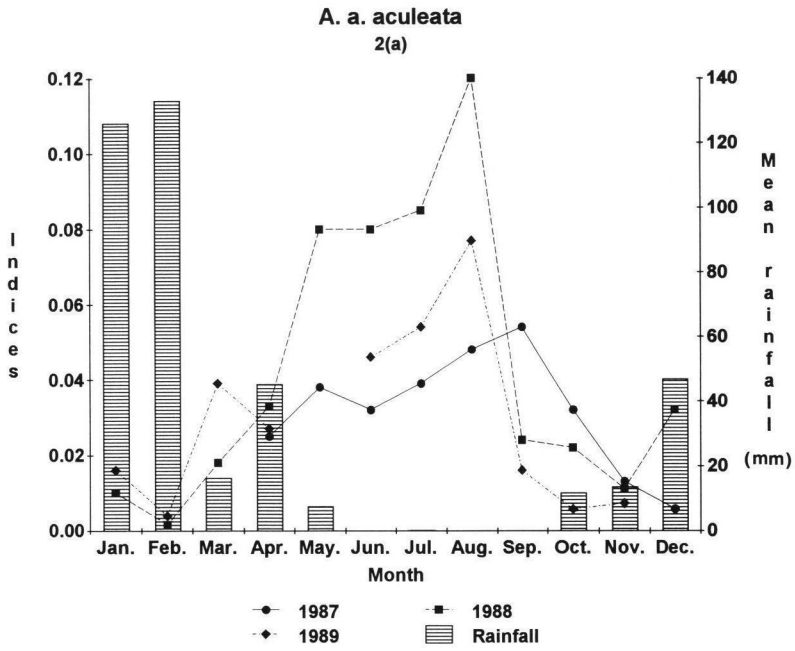
The monthly variation in mass of the abdominal fat bodies showed a seasonal pattern in both *A. a. aculeata* and *A. p. planiceps* (figs. 2a and 2b, respectively). In *A. a. aculeata* mean fat body mass peaked in August, the month when breeding commenced, while in *A. p. planiceps* females it peaked in June, about two months before breeding commenced. The rate at which the mass of the fat bodies decreased from maximum to minimum levels during the breeding season in *A. p. planiceps* ( $-0.0916$ ,  $r = 0.888$ ) was 1.36 times faster than in *A. a. aculeata* (0.0676,  $r = 0.936$ ).

#### *Liver*

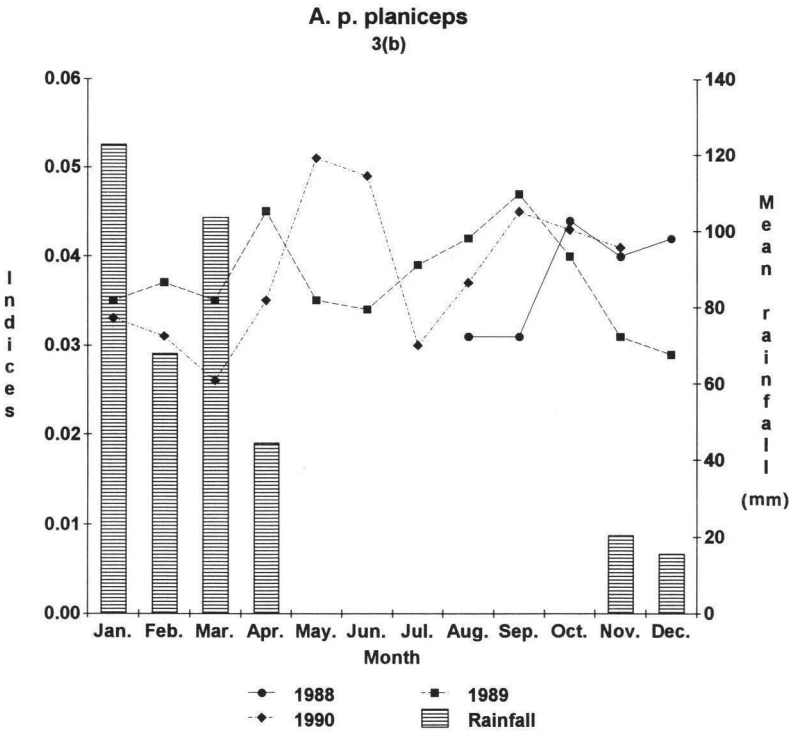
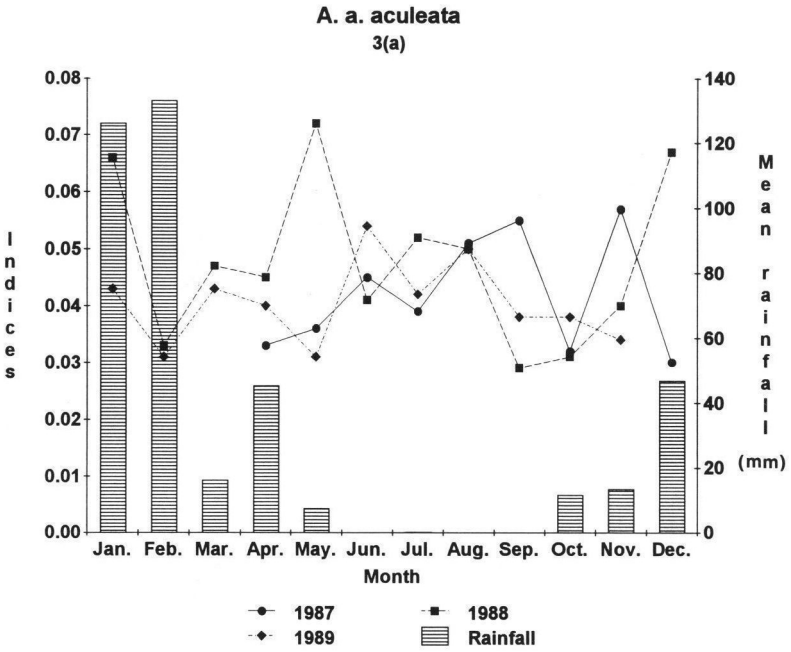
In contrast to the abdominal fat bodies, the monthly variation in mass of the liver in *A. a. aculeata* and *A. p. planiceps* did not reflect an obvious seasonal pattern (figs. 3a and 3b,



**Figures 1(a) and 1(b).** The mean monthly follicle diameter indices of *A. a. aculeata* and *A. p. planiceps* plotted against the mean monthly temperature.



**Figures 2(a) and 2(b).** The mean monthly abdominal fat body mass indices of *A. a. aculeata* and *A. p. planiceps* plotted against the collective mean monthly rainfall for the study period.



**Figures 3(a) and 3(b).** The mean monthly liver mass indices of *A. a. aculeata* and *A. p. planiceps* plotted against the collective mean monthly rainfall for the study period.

respectively). Furthermore, the mean liver mass during the breeding season did not differ significantly from that of the non-breeding season ( $P > 0.1$  in both species).

## Discussion

*Agama a. aculeata* and *A. p. planiceps* are summer breeders and oviposition and the appearance of their offspring coincides with the summer rains. The moist conditions are presumably essential for protecting the eggs, which are deposited in the soil, against desiccation and probably also ensure an abundance of insect food for the hatchlings. Janzen and Schoener (1986), for example, found a positive correlation between insect abundance and diversity, and moisture in tropical parts of Costa Rica. It is also reasonable to assume that breeding in these two species is stimulated by high ambient temperatures and long photoperiods prevailing in summer. Both species were iteroparous as indicated by the simultaneous occurrence of vitellogenic follicles and oviducal eggs or fresh corpora lutea in numerous specimens.

The two species clearly differ with respect to their reproductive strategies as is manifested by the significant differences in the size and mass of the clutches, eggs and hatchlings that they produce. Shine (1980) contends that fecundity and survivorship are likely to constitute the most important reproductive costs in lizards, rather than an energy allocation trade-off. According to Vitt and Price (1982) the relative clutch mass of a lizard should represent a trade-off between the advantage of investing heavily in reproduction at one time and the cost in terms of foraging efficiency and predator escape. Tinkle (1969) listed a series of factors that in his opinion increase the predation risk of lizards during breeding, and would therefore play an important role in shaping their reproductive strategies. These included conspicuous colouration, high relative clutch mass and the laying of multiple clutches. In a cryptic species speed is viewed as not essential for successful predator avoidance, and clutch mass is expected to be constrained by the degree to which it upsets the effectiveness of crypsis (Vitt and Congdon, 1978). In more conspicuous species the opposite is expected and clutch mass should be constrained by the degree to which it reduces the effectivity of running speed as a means of predator escape. The situation in *A. a. aculeata* and *A. p. planiceps* seems to conform to these hypotheses, as the former cryptic species carries clutches which in terms of their size and mass, are approximately double that of the latter more conspicuous species. These differences are further accentuated by the fact that *A. a. aculeata* is the smaller of the two lizard species (Fitzsimons 1943; Branch 1988). Although no quantitative comparisons of the running speeds of gravid and non-gravid females of the two species were made, gravid females were found to tire much quicker when chased and could be noosed with greater ease than non-gravid females in both cases (pers. obs.). Furthermore, it was not uncommon to encounter gravid *A. a. aculeata* females that could easily be caught by hand but this was not the case in *A. p. planiceps* (pers. obs.). Several studies have in fact shown that gravid female lizards have significantly slower running speeds than similar sized non-gravid ones (e.g. Shine, 1980; Cooper et al., 1990). The



relatively small clutch size of 5 to 7.5 eggs/clutch reported by Chapman and Chapman (1964) in the large, conspicuous rainbow lizard *Agama agama* of Ghana may therefore be linked to the maintenance of effective running speed.

The amount of energy invested per egg has an effect on the fitness of the offspring. *Agama p. planiceps* and *A. a. aculeata* clearly differ in this respect as relative egg size and relative egg mass was significantly larger in the former. On the basis of these differences, *A. p. planiceps* thus invests more energy per egg and therefore per offspring than *A. a. aculeata*. This is borne out by the fact that its hatchlings are significantly larger. The hatchlings of *A. p. planiceps* have the same conspicuous colouration as their maternal parent while the *A. a. aculeata* hatchlings resemble their parents in being cryptic. The significantly larger size of *A. p. planiceps* hatchlings may offset their assumed higher predation risk by enabling them to flee at great speed. Sinervo and Adolph (1989) found that the larger *Sceloporus occidentalis* hatchlings had higher sprint speeds than the smaller *Sceloporus graciosus* hatchlings, and suggested that the former may therefore be more adept at evading predators. Superior running ability in *A. p. planiceps* hatchlings may also bring about better foraging efficiency in comparison to their smaller *A. a. aculeata* counterparts by enabling them to not only capture fast moving prey but also larger prey which should provide them with greater energy gains per effort. A more energy-rich diet in the case of *A. p. planiceps* should promote a faster growth rate and therefore a quicker acquisition of reproductive maturity, factors that would benefit a species subjected to a high predation risk. Several other studies support the hypothesis that large hatchlings may have an advantage over small ones in terms of coping with predation pressure and in the attainment of reproductive maturity through more efficient foraging (e.g. Ferguson and Fox, 1984; Anderson and Karasov, 1988). The smaller *A. a. aculeata* hatchlings are presumably afforded adequate protection against predators by crypsis, and high foraging efficiency and fast growth rate may therefore be less critical for their survival. When approached they usually hug the ground and remain motionless, often only running off when an attempt is made to pick them up (pers. obs.).

The decrease in mass of the abdominal fat bodies during the breeding season in the two species suggests that these energy stores are utilized for reproduction in both. The rate of decrease of the fat bodies in *A. p. planiceps* was substantially faster than in *A. a. aculeata*, despite the fact that the latter invests substantially more energy per clutch. This may be due, at least partly, to their difference in social organization and behaviour during the breeding season. In the polygynous *A. p. planiceps*, the females maintain a rank order through aggressive behaviour such as combat and chasing, and compete for mating opportunities with the resident male through soliciting behaviour while in the monogamous *A. a. aculeata* this type of behaviour was not observed (Heideman, 1993). The higher breeding activity budget of the former as compared to the latter may therefore be partly responsible for the difference found. Finally, in terms of the scheme which Derickson (1876a) classified lizards according to the r-K selection theory, *A. p. planiceps* could be classified as a more r-selected species and *A. a. aculeata* as a more

K-selected species. This classification is based on the fact that the fat body mass index of *A. p. planiceps* was substantially higher than that of *A. a. aculeata* at the onset of breeding and that its utilization of these energy stores during breeding was faster.

The monthly fluctuation in the liver mass of both *A. a. aculeata* and *A. p. planiceps* showed no discernable seasonal pattern. Furthermore, mean liver mass did not show a significant difference between the non-breeding and breeding season in either species ( $P > 0.05$ ). The functions of the liver during breeding is thus not clear. Non-cyclicality of liver mass has also been found in *Agama atra* females by van Wyk (1984b). A number of studies nevertheless report a discernable pattern in monthly liver mass fluctuations (e.g. Selcer, 1987). In order to shed more light on the relationship between the liver and reproduction in *A. a. aculeata* and *A. p. planiceps*, metabolic studies monitoring fluctuations of liver metabolites during breeding will have to be conducted.

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