Paradoxical reproduction and body size in the rock lizard, *Agama atra atra*, in Namaqualand, South Africa

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The rock lizard *Agama atra atra* from Namaqualand differs in both body size and reproduction from other populations of this species occurring elsewhere in southern Africa. Both sexes from Namaqualand are significantly larger than their counterparts in the south-western Cape. While reproduction in this species is strongly seasonal elsewhere, it is apparently continuous in Namaqualand. Females with vitellogenic ovarian follicles and/or oviducal eggs were collected during the winter months, a time when females are typically reproductively quiescent in other populations. Aseasonal reproduction and large body size of this species in Namaqualand do not correlate with prevailing environmental conditions in the area. The presence of at least one other species with continuous reproduction and two others with tropical affinities in the same general area, suggests that the Namaqualand population of *A. a. atra* may be a tropical relict.

Die bloukopkoggelmander, *Agama atra atra*, wat in Namakwaland voorkom, verskil in beide liggaamsgrootte en voortplanting van ander populasies van hierdie spesie wat elders in suidelike Afrika aangetref word. Beide geslagte van die Namakwalandse vorm is aansienlik groter as hul eweknieë elders. Voortplanting by hierdie spesie is elders uitgesproke seisoenaal, maar in Namakwaland is dit oënskynlik aaneenlopend. Wyfies met vitellogenetiese follikels en/of eiers in die ovidukte, is gedurende die wintermaande hier versamel, 'n tyd van die jaar wanneer wyfies tipies in 'n reproduktiewe rusfase verkeer in ander populasies. Aaneenlopende voortplanting en groot liggaamsgrootte van hierdie spesie in Namakwaland korreleer nie met heersende omgewingstoestande in die gebied nie. Die teenwoordigheid van ten minste een ander spesie met aaneenlopende voortplanting en twee ander met tropiese verwantskappe in dieselfde algemene gebied, dui daarop dat die Namakwaland populasie van *A. a. atra* moontlik 'n tropiese oorblyfsel mag wees.

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Reproduction in reptiles is generally closely co-ordinated with the environment (Fitch 1970; James & Shine 1985). In temperate zone forms, reproduction is typically seasonal with distinct periods of activity followed by periods of quiescence (Fitch 1970; Heatwole 1976; Fox 1977; Duvall, Guillette & Jones 1982). Various patterns of seasonal or discontinous reproductive activity have been reported, the most common being that in which males and females exhibit spring gonadogenesis, followed by courtship, mating and oviposition (Fitch 1970; Duvall et al. 1982; Ficht 1984; Lofts 1985; Mendez de la Cruz, Guillette, Santa Cruz & Casas-Andrew 1988; Guillette & Mendez de la Cruz 1993). The latter discontinuous pattern is especially dominant among oviparous species (Fitch 1970). In tropical forms, on the other hand, reproduction is often aseasonal or continuous, although many forms exhibit cyclical reproductive patterns (Fitch 1970; Sherbrooke 1975; Guillette & Mendez de la Cruz 1993).

The agamids are a diverse family of Old World lizards often regarded as the counterparts of the New World iguanids. Nearly all are oviparous and most agamas studied to date show a well defined breeding season, even in the tropics (Fitch 1970; Van Wyk 1983; James & Shine 1985; Jacobsen 1989; Heideman 1992; Mouton & Van Wyk 1993). The southern rock agama, *Agama atra* Daudin 1802, is a medium sized southern African lizard which occurs throughout the Cape Province, Orange Free State, south-western Transvaal, southern Namibia, Lesotho, Transkei and southern Natal (FitzSimons 1943; Branch 1988a). An isolated population also occurs on the Transvaal escarpment (Branch 1988a; Jacobsen 1989). This species is a diurnal oviparous lizard which inhabits rocky areas, from sea level to high elevation (± 2000 m above sea level). Two races are recognized but these are poorly delimited (Branch 1988b). The typical race, *A. a. atra*, has an extensive range in southern Africa, whereas *A. a. knobelli* is restricted to southern Namibia (Branch 1988a).

As is typical of temperate zone oviparous forms, *A. a. atra* exhibits spring gonadogenesis over most of its range (Van Wyk 1983; Branch 1988a; Jacobsen 1989; Mouton & Van Wyk 1993; Flemming pers. comm.). Recent surveys, however, revealed that *A. a. atra* from Namaqualand in the Cape Province (Figure 1) is not only apparently much larger in body size, but its reproductive cycle also differs substantially from that recorded for this species elsewhere in southern Africa. We provide preliminary data demonstrating the paradoxial nature of body size and reproduction in Namaqualand *A. a. atra* and briefly discuss the implications of our observations.

Material and Methods

During 1992 several localities in Namaqualand were visited from which specimens of *A. a. atra* were collected (Figure 1). Other material from various localities in the south-western Cape, excluding Namaqualand (Figure 1), was also

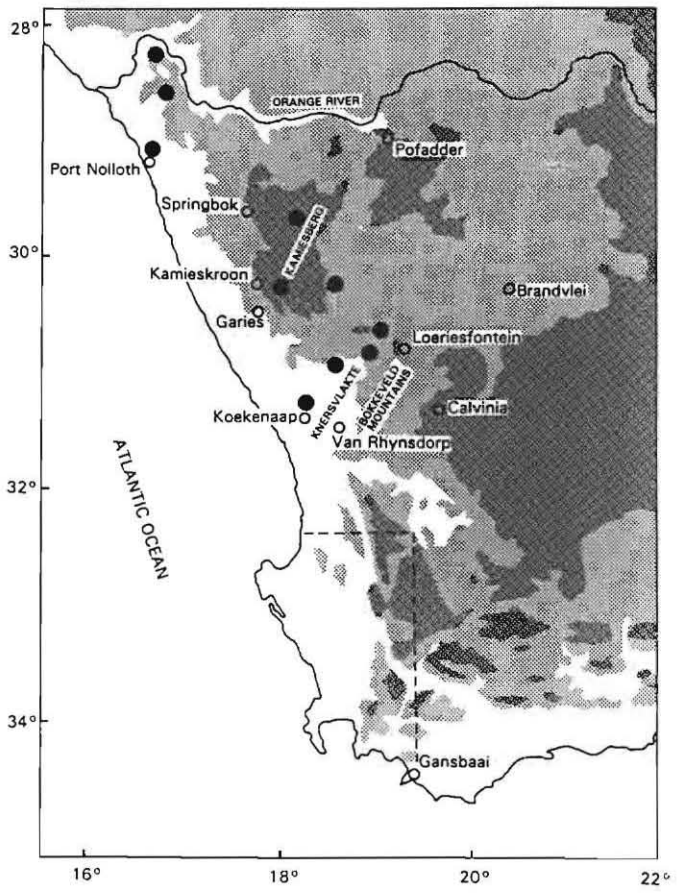

Figure 1 Localities in Namaqualand from which *Agama atra atra* of large body size and with apparent continuous reproduction, were collected (shaded circles). Major towns in the area are represented by open circles. The 400 m and 1000 m contours are shaded. The area in the south-western Cape from where additional material was examined, is also indicated.

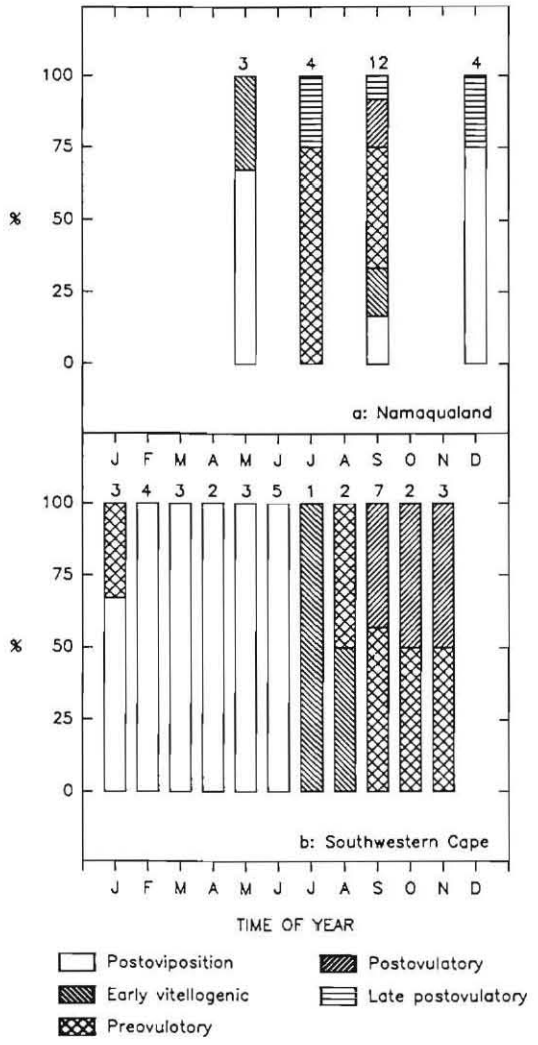

Figure 2 Stacked bar diagrams showing the percentage of females of *Agama atra atra* in the various reproductive stages at different times of the year for (a) Namaqualand and (b) the south-western Cape [see Van Wyk (1983) for a full description of the stages]. The monthly sample sizes appear above the bars.

examined to determine differences in body size and timing of reproductive events among the Namaqualand and south-western Cape populations. All material used in this study is housed in the Ellerman Museum of the University of Stellenbosch.

Snout-vent length (SVL) was measured from preserved specimens to the nearest 0,1 mm using digital vernier calipers. The right ovary and oviduct of all females were removed and the mean diameter of the three largest follicles in each ovary measured to the nearest 0,01 mm. The reproductive stages proposed by Van Wyk (1983) for *A. a. atra* were used to qualitatively describe the reproductive condition of the females (Figure 2). The right testis of all males examined was removed. The longest and shortest axes of the testes were measured to the nearest 0,01 mm. Testicular volume was calculated as being ellipsoid. Paraffin sections (4–7 μm) were taken from the middle of the testes and stained with hematoxylin and eosin. Spermatogenic activity was assessed using the classification of Licht (1967).

The Mann-Whitney *U* test (Zar 1984) was used to test for significant differences in body size between animals collected in Namaqualand and those collected elsewhere in the south-western Cape ($p < 0,05$ considered as significant). Owing to considerable sexual dimorphism in body size, males and females from the two regions were compared separately.

Results

The reproductive stages of female *A. a. atra* collected in Namaqualand are listed in Figure 2a. Data were available only for the months May, July, September and December. During all four months gravid females (with oviducal eggs) or females with vitellogenic ovarian follicles were present in the samples. During early September all five reproductive stages were recorded among the females examined. In contrast, all the south-western Cape females collected during the period February to June ($n = 17$) were reproductively quiescent, i.e. with hydration stage follicles and without oviducal eggs (Figure 2b). All south-western Cape females ($n = 19$) collected during the period mid-July to mid-January were reproductively active, displaying either vitellogenic follicles or oviducal eggs (Figure 2b). Vitellogenesis starts from late July to early August, with ovulation occurring from mid-September onwards. Females with oviducal eggs

were collected from mid-September until mid-January, but not later.

Data for Namaqualand males were available only for the months April, May, July, September and December. Testicular volume remained fairly constant during this period (Figure 3a), while histological examination showed that spermatids and spermatozoa were abundant in the seminiferous tubules of males collected during these months (Figure 4a). South-western Cape males, in contrast, showed a distinct period of testicular regression from the end of January until April, as is evident from a decrease in testicular volume (Figure 3b). Histological examination showed that during this period the seminiferous tubules are involuted with only spermatogonia present (Figure 4b). Towards the end of April an abrupt increase in testicular volume is evident in south-western Cape males (Figure 3b). From this time onwards until mid-January, both spermatids and spermatozoa are present in the seminiferous tubules.

The body size (SVL) distribution of female and male samples of *A. a. atra* from Namaqualand and the south-western Cape is shown in Figure 5a and 5b, respectively. The Mann-Whitney *U* test showed that both males and females collected in Namaqualand attain significantly larger body sizes than males and females collected elsewhere in the south-western Cape ($p < 0,05$).

The range of the large Namaqualand agama with apparent continuous reproduction seems to be well delimited by the Knersvlakte in the south and the Bokkeveld Mountains in the south-east (Figure 1) as specimens from the Matsikamma Mountains near Van Rhynsdorp and the Bokkeveld Mountains near Nieuwoudtville fall within the normal size range recorded elsewhere for this species. Along the coast the southern-most locality where this large agama was collected, is near Koekenaap (Figure 1). The Bushmanland flatlands apparently form the eastern border of its range. The situation to the north of the Orange River and to the north-east (Figure 1) is not clear at present. In the southern and eastern parts of its range its distribution seems to be closely associated with the occurrence of granite.

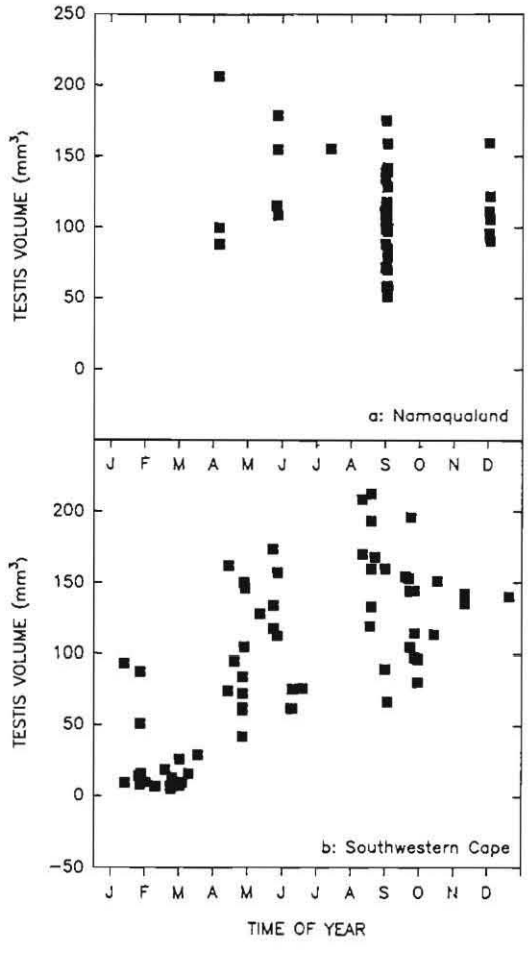

Figure 3 Scatterplots of testicular volume against time of the year for *Agama atra atra* males from (a) Namaqualand and (b) the south-western Cape.

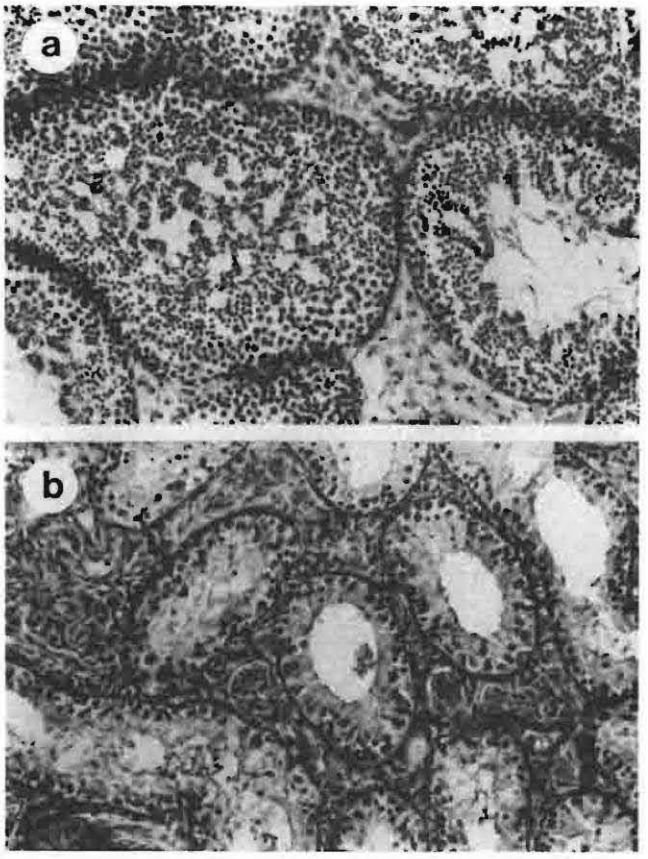

Figure 4 Cross sections through the testes of *Agama atra atra* males: (a) collected in Namaqualand at the beginning of April, showing seminiferous tubules with spermatids as well as spermatozoa, (b) collected in the south-western Cape during March, showing seminiferous tubules with spermatogonia only.

Discussion

Elsewhere in southern Africa the reproductive cycle of female *A. a. atra* is discontinuous and reproductive activity is restricted to the late winter and summer months, i.e. from late July to January (Van Wyk 1983, 1984a, b; Jacobsen 1989; Mouton & Van Wyk 1993; Flemming, pers. comm.). Furthermore, the timing of reproductive events among females present at any locality is normally well synchronized. The timing of events also seems to be remarkably conservative geographically as no significant differences were noted among populations as far apart as the south-western Cape, Transvaal, Orange Free State and the Lesotho

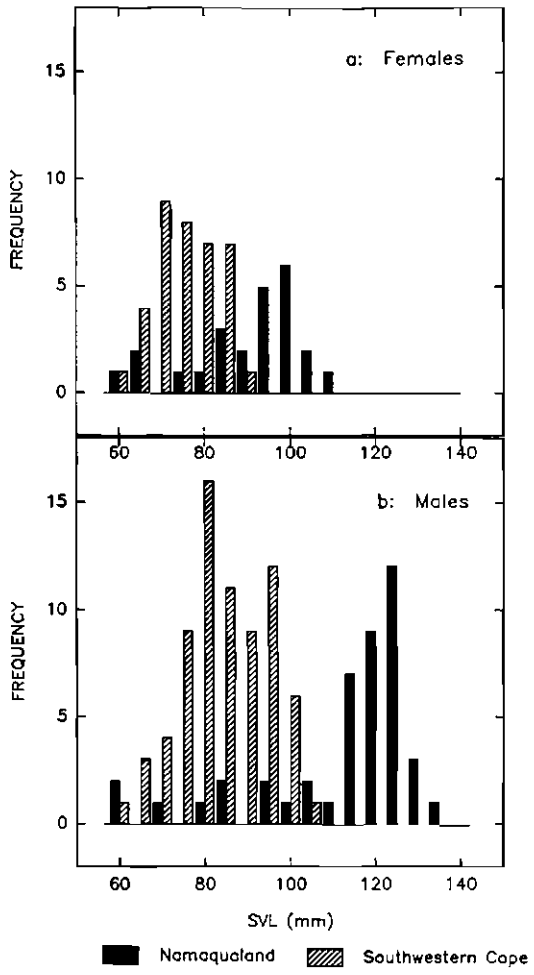

Figure 5 Frequency histograms showing differences in size classes between Namaqualand and south-western Cape populations of *Agama atra atra*, for (a) females and (b) males.

Highlands (Van Wyk 1983; Jacobsen 1989; Mouton & Van Wyk 1993; Flemming, pers. comm.). Data presented here, however, show that the female reproductive cycle of *A. a. atra* in Namaqualand differs from the female cycle recorded elsewhere in South Africa in that reproductive activity apparently does not cease during the autumn and winter months. Furthermore, unlike elsewhere, the timing of reproductive events seems to be poorly synchronized among females.

Results obtained in this study for south-western Cape *A. a. atra*, as well as data available for other regions (Jacobsen 1989; Mouton & Van Wyk 1993; Van Wyk, unpublished data for Orange Free State), suggest that male reproductive activity, typical of temperate zone oviparous species, is also seasonal over the greater part of the range. Lack of data for the months February and March, the period when testicular regression is particularly evident elsewhere within the range of this species (Figure 3b), does not allow definite conclusions to be reached regarding reproductive activity in male *A. a. atra* from Namaqualand. Nevertheless, the presence of only reproductively active males in a sample collected at the beginning of April (Figures 3 & 4), indicates the possibility that in Namaqualand, males may be reproductively active throughout the year. More detailed investigations are, however, needed to confirm this.

Food availability is an important determinant of life history attributes such as body size and reproductive effort (Case 1978; Schwaner 1985; Plummer 1987; Peters 1983; Brown, Marquet & Taper 1993). The relationship between body size and allocation of energy to reproduction is also well documented (see, e.g. Harvey, Read & Promislow 1989; Reiss 1989; Charnov 1991). Thus in temperate areas with seasonal climates, where resources may be limited during certain times of the year, reproduction would typically be discontinuous (Fitch 1970; James & Shine 1985; Guillette & Mendez de la Cruz 1993). Furthermore, in order to maintain the required reproductive output, less energy may be invested in growth in temperate areas (see, e.g. Fitch 1978). The climate in Namaqualand, as elsewhere within the range of *A. a. atra* is seasonal (Schulze & McGee 1978). Steep gradients in most climatic paramaters occur from the coast to the interior so that *A. a. atra* is here subjected to a broad range of environmental conditions. That *A. a. atra* should display 'tropical' life history attributes in this temperate area is therefore surprising.

There are two possible explanations for the paradoxical body size and reproduction of *A. a. atra* in Namaqualand and clues in this regard are provided by other species in the area. Firstly, Goldberg & Robinson (1979) reported that reproduction in the lacertid lizard *Meroles anchietae*, occurring in the Namib Desert, is also aseasonal. They concluded that the perennial availability of windblown seeds allows this omnivorous species to obtain enough energy for year-round production. The possibility thus exists that in the case of *A. a. atra* some unknown environmental factor may directly or indirectly influence food availability resulting in an all-year-round supply. Secondly, at least two lizard species with tropical affinities are endemic to the Namaqualand area. The Namaqua day gecko, *Phelsuma ocellata* is the only species of this tropical genus occurring on the mainland of Africa; the other ± 25 species occurring on Madagascar and other tropical islands in the Indian Ocean (Welch 1982). The Cape flat lizard, *Platysaurus capensis* is the only species in the genus present in the western parts of southern Africa, the other 11 species occurring in the subtropical north-eastern parts of the southern subcontinent (Broadley 1966; Branch 1988a). The presence of these two species in the same general area as the large agama suggests that they may all share the same biogeographical history, i.e. they may be tropical leftovers in what is now a temperate region.

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