

Observations on sexual dimorphism and social structure in the lizard *Angolosaurus skoogi* (Cordylidae) of the northern Namib Desert dunes

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Angolosaurus skoogi is a large, herbivorous lizard of the northern Namib dune sea. Adults are sexually dimorphic in body size and colouration and these differences may be related to social organization. Whether the observed dimorphism is a result of the mating system, as is the case with several other herbivorous lizards, is unresolved. A scale character is described that provides an external indication of sex in non-reproductive individuals and thus provides a means of investigating questions pertaining to sexual dimorphism and other population level questions.

Angolosaurus skoogi is 'n groot plantvretende akkedis van die noordelike Namib duinesee. Die volwasse diere is geslagtelik dimorfies in liggaamsgrootte en kleur en hierdie verskille blyk verband te hou met die sosiale organisasie in hierdie spesie. Of die opgemerkte tweevormigheid 'n gevolg van die paringstelsel is, soos in die geval van baie ander plantvretende akkedisse is onopgelos. 'n Skubpatroon word beskryf om 'n uitwendige aanduiding van geslag in onvolwasse individue te gee en dit voorsien 'n metode om vrae aangaande geslagtelike dimorfisme en ander vrae op bevolkingsvlak te ondersoek.

Sexual differences in morphology and/or behaviour are seemingly common and conspicuous in some environmental settings (e.g. tropical rainforests), among some taxa (e.g. birds), but may be comparatively rare in others. For many endemic inhabitants of the Namib Desert dune sea, external differences in sexually dimorphic characters are often subtle and are revealed only through careful examination (e.g. Penrith 1975); thus the occurrence of markedly dimorphic characters in the sexes of a sand dune inhabiting species is of interest. Such characters can provide not only insight into the biology of the species in question but also the methodological tools necessary for otherwise intractable studies.

Angolosaurus skoogi is a chthonic, herbivorous lizard species inhabiting the Namib Desert dunes of southern Angola and northern Namibia. Although the species was described more than half a century ago (Andersson 1916), it has received little attention until relatively recently [Hamilton & Coetsee 1969; Pietruszka, Hanrahan, Mitchell & Seely 1986; Pietruszka 1987; Mitchell, Seely, Roberts, Pietruszka, McClain, Griffin & Yeaton (in press), Seely, Mitchell, Roberts & McClain (in press)]. The purpose of this report is to add to the limited knowledge concerning this species. Here I focus on aspects of sexual dimorphism and the social system in *A. skoogi*. Two dimorphic characters are considered in relation to observations on *Angolosaurus* social interactions, and another sex-related trait which provides an external indication of sex in non-reproductive individuals is described.

Materials and Methods

Field work was conducted from 1983–1987 in an area located approximately 15 km inland along the south bank of the Unjab River in the northern Namib dunes (20°09'S / 13°14'E). This site, at the extreme southern

end of *Angolosaurus*' distribution, is characterized by barchanoid-type sand dunes and sparse vegetation consisting of a small number of persistent plant species. Perhaps the most important plant species, *Nara* (*Acanthosicyos horrida*), often is associated with sand dune slipfaces (Hanrahan & Yeaton 1987). Total vegetative cover in the area is less than 1% (Pietruszka *et al.* 1986).

Information on sexual dimorphism and aspects of *Angolosaurus* social organization was recorded at the site during the course of a number of studies concerning the biology, diet, and temperature regulation of *A. skoogi* (Pietruszka *et al.* 1986; Pietruszka 1987; Mitchell *et al.* in press; Seely *et al.* in press).

Early in these studies a scale character was noticed that appeared to vary systematically between the sexes. Therefore, a sample of 113 preserved specimens was obtained from the State Museum in Windhoek, S.W.A./Namibia, for a detailed examination of the apparently sex-linked scale trait. The sex of each specimen was predicted on the basis of scutellation alone and the snout–vent length (SVL) was recorded. The sex of each specimen was then determined by dissection and examination of the gonads in order to verify the accuracy of the external scale character in diagnosing sex.

Between 8 Jan. 1985 and 17 Dec. 1985, individual marks were permanently applied (by toe-clipping) to 145 *Angolosaurus* inhabiting a single dune (hereafter called camp slipface) at the Unjab River study site. Prior to marking, each lizard was sexed and its mass was determined to the nearest 0,1 g using a Pesola (TM) spring scale. Total length and SVL were measured to the nearest 0,5 mm using a metal mm rule. Notes on unusual colouration and tail breakage and regeneration also were recorded. During February and July 1985 and February 1986, approximately 120 h of observation on feeding, thermoregulatory and social behaviour were recorded.

Results and Discussion

Body size

As mature adults, the sexes of *A. skoogi* differ markedly and are easily distinguished in the field from a distance. Typically, adult males attain a larger body size and greater mass than adult females. A random sample of adult lizards (> 115,0 mm SVL) measured in the field yielded an average body SVL of 146,8 mm ($n = 28$; $SE = 1,9$ mm) for males and 129,8 mm ($n = 34$; $SE = 1,5$ mm) for females ($t = 6,659$; $df = 60$; $P < 0,00001$). Male mass for the sample (82,1 g; $SE = 3,4$ g) was also significantly greater than that for females (56,7 g; $SE = 2,5$ g; $t = 6,154$; $df = 60$; $P < 0,0001$). However, in a more general analysis using analysis of covariance (ANCOVA, Sokal & Rohlf 1981) to eliminate the effects of varying SVL, body mass was not found to differ between sexes ($F = 0,321$; $P > 0,5$; $n = 145$). This suggests that the relationship between body size and mass probably does not differ between the sexes. Rather, the size differences between adult male and female lizards are more likely to be due to differences in sex-specific growth rates. Presumably, males grow either for a longer time or at a faster rate before reaching their asymptotic maximum size, as has been shown for other lizard species (e.g. Dunham 1978; Van Devender 1978).

Colouration

Apart from size, the most striking sexual difference in adults of this species is colouration. This is in marked contrast to other sand dune associated species in the area (e.g. *Aporosaura anchietae*, *Meroles reticulata*, *Palmatogecko rangeii*) in which colouration is similar between the sexes. As noted by Fitzsimons (1953), adult male *A. skoogi* are characterized by an intense black colouration about the head and neck, chest and belly. In some individuals this colouration may continue onto the underside of the pelvic girdle, hind limbs and tail, and, in very large individuals (> 150 mm SVL), it often completely envelopes the head. In addition, the dorsum of male individuals is suffused with an irregular pattern of salmon (orange-pink, Steyn 1963) speckles between the

pectoral and pelvic girdles and extending onto the tail. Adult male colouration is generally well developed by a body size of 140,0 mm SVL but may not be apparent at body sizes below ca. 130,0 mm SVL. Once attained, male colouration does not vary seasonally and appears only to intensify with age.

In contrast, females retain the olive-beige ground colour of immature individuals and generally lack any of the speckling or intense melanistic colour seen in males. Some females acquire melanistic blotches on the head and neck similar to those of subadult males in the early stages of acquiring adult colouration. Based on their large body size (> 140 mm SVL) and their overall condition, females exhibiting secondary melanism generally appear to be older individuals, which suggests that such darkening may be age-related.

Sexual differences in scutellation

The only sexually related difference in scutellation noted by previous workers was a difference in the development of the femoral pores on the hind limbs (Steyn 1963). In many cordylid lizards, where femoral pores occur in males only (e.g. FitzSimons 1943; Mouton 1986), these are well developed in juveniles. In *A. skoogi*, however, femoral pores are large and well developed only in adult males and are rudimentary in females and immature individuals. Hence, this character is of limited use in diagnosing sex in young individuals. However, lying lateral to either side of the midline of the ventral surface of the tail and immediately posterior to the opening of the vent is a series of 2–3 postanal scales that provides an external indication of sex, almost irrespective of age. These scales are somewhat analogous to the postanal plates found in males of many of the North American iguanid species (Stebbins 1954) and teiid species of the genus *Cnemidophorus* (Pietruszka 1981). They arise from the first row of caudal scales posterior to the vent. The terminal scale in the series, which I term the spur scale, is triangular to pentangular in shape in males, ending in a distinct point that protrudes markedly from the cross-sectional curvature of the tail (Figure 1a). The base of the spur scale and the scale immediately

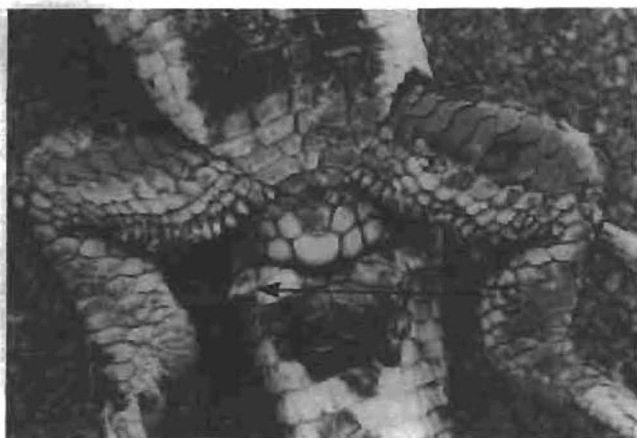


Figure 1 Sexual differences in scutellation in *Angolosaurus skoogi*. (A) Adult male and (B) adult female from the Unjab River, SWA/Namibia, showing fully developed spur scales. S — spur scales.

proximal to it lie directly over the internal position of the hemipenes in male lizards.

In females these postanal scales are considerably less well developed than in males. The spur scale does not terminate in a distinct point but rather is more rounded and spade-shaped and conforms to the cross-sectional curvature of the tail (Figure 1b).

The museum specimens examined spanned a range of body sizes (51,0–172,0 mm SVL) that included representatives of most of the size classes found in the field. Thus they provided a good vehicle for examining the degree of association of well developed spur scales with a single sex as gonadal sex could be obtained by dissection for verification purposes.

The efficacy of spur scale conformation in providing an external indication of sex is indicated by the fact that the sex of only 8 of 113 museum specimens could not be diagnosed accurately by scalation alone. If spur scales were randomly distributed with respect to sex, then one could expect to correctly diagnose the sex of an individual lizard only about half of the time using this character. In the total sample, the correct assignment of sex using scalation alone far surpassed this expectation (males: 89%, females 97%, Table 1). Indeed, six adult specimens originally labelled as females on field tags were found to be males on the basis of scalation (verified by gonadal examination).

With increasing body size the distinction between male and female scalation increases. In small specimens (< ca. 80 mm SVL) the spur scales tend to be rounded distally in both sexes, generally ending in a dull point. Among smaller males the distal portion of the spur scale is generally thickened, causing the scale to protrude slightly from the curvature of the tail. This is usually not the case in small female specimens and in these the spur scale conforms to the tail curvature as it does in adults. Thus, unlike similar characters in other species (Stebbins 1954; Pietruszka 1981), there is a clear allometric component to this scale character. This becomes particularly apparent by examining the character's effectiveness in diagnosing sex in relation to body size. Above a body size of about 80 mm SVL, the error rate in sex diagnosis was nil in a sample of 84 specimens ($P < 0,001$). Below this size, the error rate rose to 27,6% ($n = 29$), although even in small specimens there was a significant difference ($P < 0,05$) between the sexes in spur scale conformation.

Table 1 Results of χ^2 -tests (Sokal & Rohlf 1981) for a sexual association of scalation. M — Males, F — Females

Body size (SVL)	N M/F	Proportion correctly identified		χ^2	P
		M	F		
< 80 mm	16 / 13	0,625	0,846	4,084	< 0,05
> 80 mm	38 / 46	1,000	1,000	58,698	< 0,001
Overall	54 / 59	0,889	0,966	53,160	< 0,001

Despite some ambiguities in very small individuals, there remains a highly significant association between the presence or absence of enlarged spur scales and sex (Table 1). In general, sexual traits, such as spur scales, provide a means for studying such life-history characteristics as sex-specific survivorship, sex-specific growth rates and sex ratios among prereproductive individuals. These characteristics can be of critical importance to an understanding of population dynamics in unstable and/or unpredictable environments (Turner 1977). The dynamics of *A. skoogi* populations are, at present, unknown.

Sexual dimorphism and social structure

In reptiles, large male size relative to that of females is frequently associated with male combat behaviour, territoriality and/or some form of dominance hierarchy (Stamps 1977; Shine 1978; Van Devender 1978; Carothers 1984). Field observations of social interactions indicate that this may also be true of *A. skoogi*. If it is, the significance of sexual differences in adult body size and colouration may be closely tied to the social system of these lizards.

In the southern extreme of its distribution, at least, *A. skoogi* exhibits a seasonal social organization. During winter (July) few social interactions occur between adults and the primary activities revolve around feeding and thermoregulatory behaviour (Hamilton & Coetzee 1969; Seely *et al.* in press). Those that do take place appear to result from transient and highly localized dominance hierarchies stemming from patchy food resources (Mitchell *et al.* in press). Episodic interactions of this type, however, seem more common among juvenile individuals, particularly during foraging bouts at the base of the slipface. On the three occasions in which agonistic interactions were observed during winter (30,6 h of observation), all were of this local, episodic nature. In each case the dominance appeared to be size related: larger juveniles drove off smaller individuals from localized feeding areas at the avalanche base of the slipface.

During the breeding season (known from our studies to extend only from mid-January to the end of February), male *A. skoogi* establish territories around the perimeter of any Nara patch that is associated with the dune slipface. As the perimeter around a given Nara is limited, only dominant males are able to establish territories. At the camp slipface, for example, only 4 of 24 males in reproductive condition were able to establish and to hold breeding territories. The most active courting of females by males (as evidenced by shudder-bob displays, *sensu* Carpenter & Ferguson 1977) appears to centre around these territories (92%, $n = 28$). However, it is unclear whether females are actively choosing among these males as prospective mates, and, if so, what the selection criteria are.

During the territory establishment period and afterwards, there is generally intense male–male interaction around the Nara perimeter (Table 2). Among territory holders this is normally evidenced in ritualistic body posturing (*sensu* Carpenter & Ferguson

Table 2 Summary of aggressive interactions between males during the breeding season. Percentages based on 89,4 h of observation at two Unjab River slipfaces during February 1985 and February 1986. Total number of interactions = 124

	Frequency	%
Participants in interaction		
Territorial male vs. intruder male	69	55,6
Territorial male vs. territorial male	46	37,1
Among non-territorial males ¹	9	7,3
Type of interaction		
Posturing	41	33,1
Chases:		
by single males ²	68	54,8
by two males	6	4,8
by three males	3	2,4
Attacks	6	4,8

¹ — all interactions took place away from the Nara on the slipface.

² — includes chases initiated by territorial males + those between non-territorial males away from the Nara.

1977). At the camp slipface, for example, only one of the 38 agonistic encounters observed between adjacent territory holders did not involve posturing. Once territories have been established, territory holders repel other males attempting to enter the Nara. Chases of 'intruder' males by individual territory holders made up the vast majority (92,6%) of the 68 single male chases observed (Table 2). Only 7,4% of all chases were observed between non-territorial males on the dune crest. A small proportion of the interactions between territorial and intruding males (7,2%) actually involved two or three adjacent territorial males chasing an intruder in what appeared to be a 'joint' effort (Table 2). Alternatively, these simply may have been simultaneous independent responses to a common intruder and a function of the close packing of territories. Insufficient data exist at present, however, to distinguish between these alternatives.

Of the interactions between territorial males and intruders, a few (4,8%, Table 2) result in actual physical combat that can result in potentially serious injury to the unsuccessful combatant. In one particularly intense interaction at the camp slipface, a young adult male was viciously attacked and driven off by a territorial male (marked #12), losing its tail and part of a hind foot during the encounter.

Notably, only adult and subadult males (i.e. those just beginning to exhibit adult colouration) appear to be recognized and repelled; non-reproductive males and females are not. None of the 115 territorial interactions observed involved lizards that were not readily identifiable as males. This suggests that male colouration plays an important role in focusing male-male interactions. (Interactions with melanistic females have not been recorded.) That large body size in male *A.*

schoogi may influence the outcome of male-male interactions (and hence dominance status) is suggested by measurements made on two of the four territory-holding males on the camp slipface. These animals had the largest (164,0 mm SVL) and fourth largest (158,0 mm SVL) body sizes of the mature males marked at the camp slipface ($n = 24$) and bore the same size rankings among all lizards marked on that slipface ($n = 145$).

Current information on the social interactions of this markedly dimorphic species is limited. The observations reported here suggest that there may be a distinct seasonal and perhaps complex dominance hierarchy among male *A. schoogi*; however, few details concerning its nature are available. Nor is there adequate information on the criteria by which females select mates (if indeed they do). Nonetheless, the intensity of agonistic interactions among males during the breeding season suggests that there may be strong competition for breeding rights. For several other herbivorous lizard species there is evidence to suggest that sexual selection may have promoted size dimorphism through the population mating structure (Carothers 1984). Indeed, the present picture of *Angolosaurus* social organization is certainly consistent with such a hypothesis.

Alternatively, dimorphism in body size may simply be the result of the differential channelling of energy between the sexes. Energy diverted to egg production rather than growth in females can result in a larger average body size in males. Thus, whether intra-sexual competition stemming from the mating system has led to sexual dimorphism in *A. schoogi* or dimorphism has resulted from other factors and the mating system is simply a consequence of that dimorphism is, as yet, unclear. Fortunately, the presence of a character (spur scales) that can be used to distinguish sexes at a relatively early age provides an approach for resolving this question. It remains an open area of endeavour for future investigations.

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