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Sexual dimorphism in two girdled lizard species, *Cordylus niger* and *Cordylus cordylus*

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The extent of sexual selection in two girdled lizard species was evaluated by measuring sexual dimorphism in those characters normally affected by sexual selection. Neither *Cordylus niger*, a cool-adapted species, nor *C. cordylus*, a warm-adapted species, displayed any notable sexual differences in asymptotic body sizes, but both species displayed slight dimorphism in head size measurements. The *C. niger* sample contained more large males than large females, which may be attributed to a lower growth rate in females. In the cool Saldanha area, females of both species lack generation glands. In the warmer Gansbaai area, these glands are present in females of *C. cordylus*, but in lower numbers than in males. Sex ratios favouring females, have been recorded for both species. The observed sexual dimorphism in the two species seems to be mainly the result of differential energy allocation by females, and not of sexual selection *per se*.

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Introduction

Sexual dimorphism is a common phenomenon among reptiles (Carothers 1984; Vitt & Cooper 1985; Vial & Stewart 1989; Mouton & van Wyk 1993; Perez-Mellado & De La Riva 1993). Where the dimorphism has a genetic basis, two contrasting hypotheses are usually put forward to explain it, namely sexual selection and natural selection (Darwin 1859, 1871; Vitt & Cooper 1985; Koenig & Albano 1986). Although sexual selection is usually regarded as the prime causal factor of sexual differences in body size, head size and body coloration (Stamps 1983), many studies have shown that dimorphism in these characters can also result from natural selection (Anderson & Vitt 1990). Differential energy allocation by females as an adaptation to different climatic regimes, may, for example, affect their growth patterns and social behaviour and lead to dimorphism in any one or a combination of these characters (Fitch 1978; Carothers 1984; Cooper & Vitt 1989; Vial & Stewart 1989; Mouton & van Wyk 1993; Ruby & Baird 1994). On the other hand, sexual dimorphism does not necessarily have to have a genetic basis and can also result from a wide array of local environmental processes (Gibbons, Semlitsch, Greene & Schubauer 1981; Gibbons & Lovich 1990; Shine 1990). Adult growth and survival rates, for example, may vary from locality to locality, resulting in varying sexual differences in mean body size (Stamps 1993).

While sexual dimorphism is well-documented in many reptile groups, the family Cordylidae, which is endemic to Africa, has received little attention in this regard (Lang 1991; van Wyk 1992; Mouton & van Wyk 1993). Although limited information is presently available, there seems to be an evolutionary trend in this family in the degree to which sexual dimorphism is developed (Mouton & van Wyk 1992, 1993). In all species of *Platysaurus*, the most highly derived genus in the family (Lang 1991; Herselman 1991), sexual dimorphism, especially in body colour, is well developed (FitzSimons 1943; Broadley 1978; Jacobsen & Newbery 1989). In the genus *Pseudocordylus*, presently assumed to be more derived than *Cordylus*, sexual dimorphism in colour, body size and head dimensions is well developed in one of the more recent species, *P. melanotus* (Mouton & van Wyk 1993), while moderately developed or absent in the remainder of the genus (FitzSimons 1943; Loveridge 1944; Sachse pers. comm.). In *Chamaesaura* and *Cordylus*, the two basal genera in the family (Lang 1991), pronounced sexual dimorphism in these characters has not been reported as yet, apart from slight female-plus dimorphism in body size in *Cordylus giganteus* (van Wyk 1992).

All indications are that in *Platysaurus* and *Pseudocordylus* the observed sexual dimorphism is mainly the result of sexual selection (Mouton & van Wyk 1993). Mouton & van Wyk (1992, 1993) concluded that, because of certain phylogenetic constraints, sexual selection will not result in pronounced sexual dimorphism in members of *Chamaesaura* and *Cordylus*. All indications are that most species in the genus *Cordylus* are territorial and follow a sit-and-wait feeding strategy (FitzSimons 1943; Branch 1988; Cooper & van Wyk 1994; Cooper, van Wyk & Mouton 1995), characteristics which should be highly inducive to sexual selection and resultant sexual dimorphism (Stamps 1983). Detailed information on sexual dimorphism in this genus is available for only one species, *C. giganteus* (van Wyk 1992), and information for more representatives is needed to evaluate the statements of Mouton & van Wyk (1993).

We selected two *Cordylus* species for a detailed study of sexual dimorphism. Both these species are monomorphic in body colour. *C. niger* is a melanistic species, occurring in the Cape Peninsula and the Saldanha Bay region in association with upwelling zones of cold water in the Atlantic Ocean (Mouton 1987; Badenhorst 1990; Figure 1). *C. cordylus*, on the other hand, is a non-melanistic species, which has an extensive distribution in the south-western Cape (Mouton 1987; Figure 1) and is considered to be a warm-adapted form (Mouton & Oelofsen 1988). These two species are allopatric in their distribution, apart from a small area north of Saldanha Bay where they occur parapatrically and over a short distance of roughly 250 m, also sympatrically (Mouton 1987; van Heerden, Mouton & van Wyk 1992; Cordes 1995). The Saldanha Bay area provides an ideal opportunity to compare life history attributes of two closely related species, the one

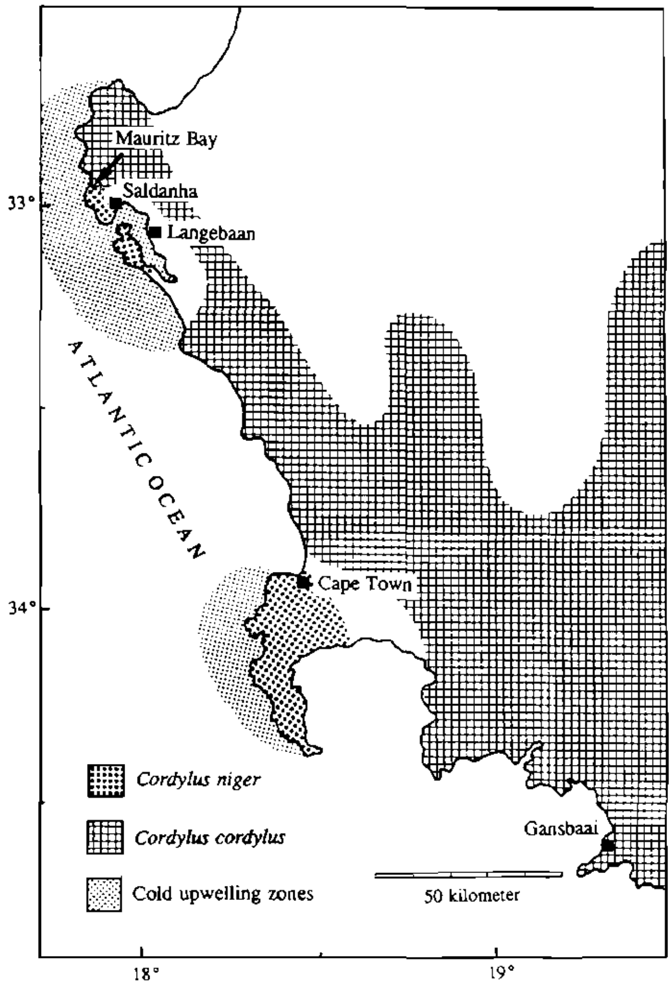

Figure 1 A map of the south-western Cape showing the distribution of *C. cordylus* and *C. niger* and the upwelling zones of cold water along the west coast.

cool-adapted and the other warm-adapted.

The aims of the present study were threefold: firstly, to evaluate the extent of sexual selection in members of the genus *Cordylus* by measuring the degree of sexual dimorphism displayed in characters normally affected by sexual selection, such as body size and head size; secondly, to compare the extent of sexual selection in a cool-adapted and a warm-adapted species subjected to the same environmental conditions; and thirdly, to obtain baseline information on sexually dimorphic characters other than size-related ones. To evaluate the possibility of geographical variation in the expression of sexual dimorphism in C. cordylus, a population outside the Saldanha Bay area was included in the analysis.

Materials and methods

Study areas

Saldanha-Langebaan area

The Saldanha-Langebaan area in the Western Cape, i.e. the area stretching from Langebaan in the south to Stompneus Bay in the north, including the Langebaan Peninsula, was selected as one study area (Figure 1). In this area, the climate is strongly influenced by the cold Benguela Current, which flows along the coast in a northerly direction. The result of this cold current is a cooler zone along the coast (Schulze 1965; Meigs 1966; Brown & Jarman 1978; Badenhorst 1990), with effective temperatures of 14–15°C, as indicated on the effective temperature map of Stuckenberg (1969). Upwelling of cold water from the depths of the Atlantic Ocean adjacent to this area adds to the cooling influence of the current (Hart & Currie 1960; Figure 1). A direct result of this upwelling zone is the formation of fog when warm inshore surface water mixes with the upwelling cold water (Schulze & McGee 1978). Not less than 128 misty days have been registered per year at Saldanha Bay, with the highest incidence in March (Thomas 1973; Badenhorst 1990). As a result of the frequent fog and cloud cover along the coast line, the area receives less sunshine (6–8 h per day) than the coastal lowland areas further inland, with 8–9,5 h per day (Badenhorst 1990). Owing to the proximity of the ocean, extreme daily or seasonal fluctuations in temperature do not occur (Visser & Schoch 1973; Flemming & van Wyk 1992).

Gansbaai area

The second study area is situated in the Gansbaai area on the southern coast of the Cape Province (Figure 1). In contrast to the situation along the western coast, where the Benguela Current has a cooling effect on the climate, the coastal region in the Gansbaai area is not directly subjected to the influence of the relatively warm Agulhas Current. Small branches of this current, however, regularly reach the area and probably have an effect on the climate (Isaac 1949; Brown & Jarman 1978). Although greater seasonal fluctuations occur, with relatively large and sometimes rapid temperature changes (Isaac 1949; Brown & Jarman 1978; van Wyk 1983), the climate is generally warmer than in the Saldanha area (see van Wyk 1983; Flemming & van Wyk 1992), with effective temperatures of 15–16°C (Isaac 1949; Stuckenberg 1969). Owing to the relatively high temperatures of the surrounding water, the pronounced formation of fog is not induced (Badenhorst 1990).

Material

C. niger specimens (*n* = 206) were collected at two localities in the Saldanha-Langebaan area, namely Mauritz Bay (32°59'S/17°52'E) north of Saldanha, and Postberg Nature Reserve (33°06'S/18°00'E), situated on the distal end of the Langebaan Peninsula (Figure 1). One of the two *C. cordylus* samples (*n* = 313) was also obtained from several localities in the Saldanha-Langebaan area. All localities are near the coast and therefore in the area that is affected by the cold upwelling zone and the Benguela Current (Figure 1). The contact zone between *C. niger* and *C. cordylus* at Mauritz Bay (Figure 1) offered good opportunity to compare the two closely related species, which are here subjected to the same environmental conditions. Seventy per cent of the specimens were collected in the immediate vicinity of the contact zone and on a nearby limestone hill (Kliprug: 32°58'S/17°57'E), 2 km east of Mauritz Bay.

The second *C. cordylus* sample (*n* = 143) consisted of specimens from the Gansbaai area, collected at six localities: De Kelders (34°32'S/19°22'E), Danger Point (34°37'S/19°19'E), Franskraal (34°35'S/19°23'E), Strandskloof (34°34'S/19° 26'E), Byeneskranskop (34°34'S/19°28'E) and Witkrans Mountains (34°32'S/19°25'E). Eighty per cent of the material came from the two coastal localities, De Kelders and Danger Point.

Morphological data

Measurements were based on alcohol-preserved material from the J. Ellerman Museum of the University of Stellenbosch (304 specimens), as well as live specimens collected during the study (358 specimens). Lizards were captured by hand or with a noose and were subjected to measurement immediately after capture. After all the morphometric data had been recorded, the lizards were marked with water resistant ink and released at the site of capture. All individuals were sexed by assessing for the presence of hemipenes and the presence of generation glands. These are holocrine glands occurring on the ventral aspect of the thigh, anterior to the femoral glands (van Wyk & Mouton 1992).

The following morphological measurements were recorded for all specimens, using a digital caliper: snout-vent length (SVL) from the tip of the snout to the anterior edge of the vent; head width at the widest point of the head; head length from the anterior edge of the tympanic opening to the tip of the snout. All body parts were measured to the nearest 0,01 mm. In all specimens the number of femoral glands was recorded. Generation glands were also counted in those specimens where they were present. The presence or absence of scars on the tail and on the rest of the body was noted. Cases where tails were freshly autotomized were ignored, owing to the possibility that tailbreaks may have occurred during capture of the lizard or handling of the preserved material.

Data analysis

Lizards were classified as either adults (sexually mature), or juveniles. Minimum size at sexual maturity was estimated for females as the SVL of the smallest female containing oviductal eggs or vitellogenic follicles, and for males based on the smallest male that had enlarged testes and sperm in the vas deferens, during the time when spermiogenesis is assumed to reach its peak in the two species.

To ensure unbiased samples, all lizards sighted, irrespective of size, were collected and measured. It was assumed that the museum collection also contains unbiased samples. To determine the sex ratio (ratio of adult males to adult females), all adult specimens were included in the counts.

Head and body size measurements were tested for homogeneity of variances using Bartlett's test (Zar 1984). Where data sets were abnormally distributed, the Mann-Whitney U test was used to compare sets, otherwise Student's t test was used. Least square regression analysis of log-transformed SVL and head sizes was used to determine the allometry of head growth with increasing body size. Regressions between adult females and adult males, and between adults of each sex and all juveniles, were tested for differences by the comparison-of-two-slopes method (Zar 1984, p. 292). An index of head size dimorphism (D) was calculated as female regression slope/male regression slope for the specific parameter. The mean SVL of the 20 largest specimens of each sex was used to compare sexual differences in asymptotic size among species. A size dimorphism ratio was calculated as mean male SVL/ mean female SVL. Percentage dimorphism was taken as the absolute value of [(dimorphism ratio – 1,000) × 100] (Levenson 1990). The standard criterion for significance was $p < 0,05$ in all statistical tests.

Results

Size at sexual maturity

In both species the smallest female containing oviductal eggs or enlarged vitellogenic follicles, and the smallest male that had enlarged testes and sperm in the vas deferens during the late winter and spring months, when both sexes are expected to be reproductively active (S. Jacobs, unpublished data), had a SVL of approximately 55 mm, which was taken as minimum size at sexual maturity. The individuals with a SVL of less than 55 mm were not sexed and were collectively classified as juveniles.

Sex ratio

The ratio of adult males (n = 63) to adult females (n = 107) for *C. niger* was 0,59:1, for *C. cordylus* from the Saldanha area 0,74:1 (males: n = 108; females: n = 146), and for *C. cordylus* from the Gansbaai area 0,63:1 (males: n = 47; females: n = 75).

Body and head size

The distribution of body size (SVL) for adult male and female samples of *C. niger* and *C. cordylus* is shown in Figure 2. SVL of 170 *C. niger* specimens ranged from 55–92 mm and that of 254 *C. cordylus* specimens from the Saldanha area and 122 from the Gansbaai area from 55–87 mm. The Mann-Whitney U test showed that the *C. niger* sample contained significantly more males of large body size than females ($p <$ 0,001). The largest specimens collected, however, were females (Figure 2). The dimorphism ratio for the *C. niger* population is 0,98, and the percentage dimorphism 2%. No significant sexual differences in body size were noted for either of the two *C. cordylus* populations (Table 1). The dimorphism ratio for the Saldanha population is 0,99, with a dimorphism percentage of 1%. The dimorphism ratio for the Gansbaai population is 1,01 and the dimorphism percentage 1%. The Gansbaai sample contained significantly more specimens of larger body size than the Saldanha sample in the case of both sexes ($p < 0,05$; Table 2).

The regression slopes of head width and head length *versus* SVL, to show the trends in head allometry, are shown in Figures 3 and 4, and the statistics are given in Table 3. Table 4 shows the results for the comparison of the slopes, indicating the differences in the rate of head growth between adult males and females, and between juveniles and adults. In both *C. cordylus* samples, growth rate of head dimensions relative to SVL was significantly higher in adult males than in adult females ($p < 0,001$). The regression slopes showed that allometric growth in head width of males did not differ much from that of juveniles, while in females the growth rate in head width decreased after sexual maturity was reached. On the other hand, head length seems to grow at a faster rate after sexual maturity in males while it stays more or less the same in females (Table 3). In juveniles, allometric growth was positive for head width (regression slope > 1), and negative for head length (regression slope < 1). Dimorphism indices (D) for head size parameters are listed in Table 4. In *C. niger* no

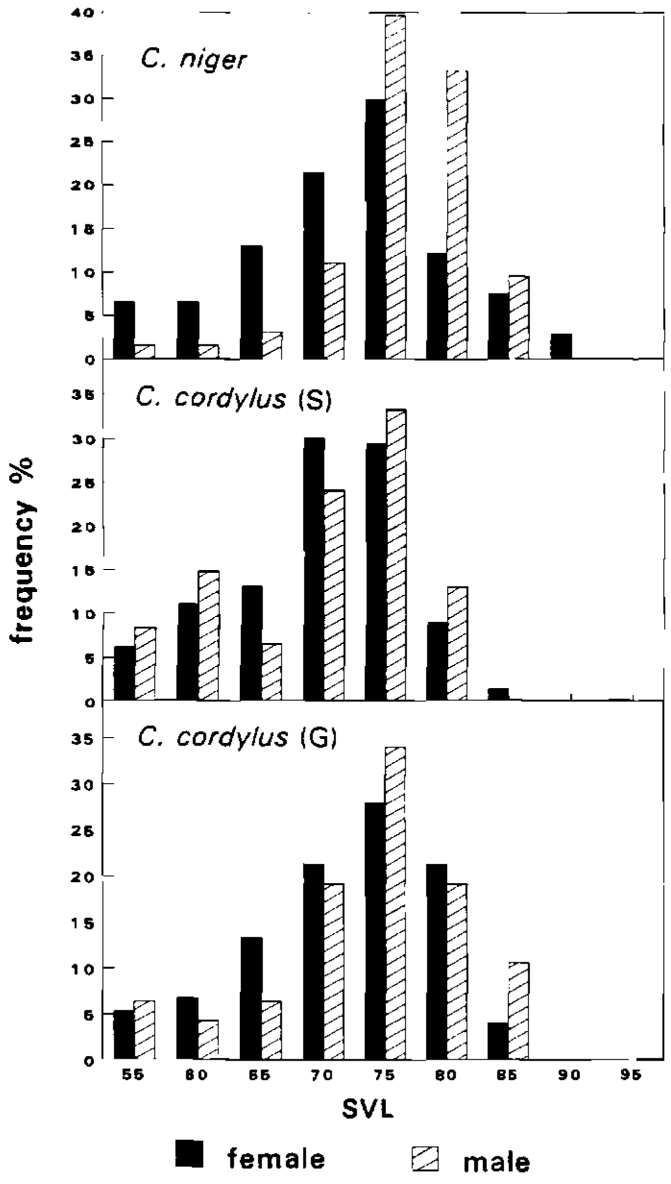

Figure 2 Body size distributions (SVL) for male and female *C. niger*, and *C. cordylus* from the Saldanha area, and *C. cordylus* from the Gansbaai area.

significant difference was apparent between male and female regression slopes for head size *versus* SVL, apart from slight dimorphism in head length (Table 3). Sexual dimorphism in both head dimensions relative to SVL is therefore present in *C. cordylus*, but only in head length in *C. niger*.

Epidermal glands

In *C. niger*, generation glands were only present in males. In the *C. cordylus* population from the Saldanha area, generation glands were also only present in males, but in specimens from Gansbaai they occurred in both sexes. The Mann-Whitney *U* test showed that at Gansbaai, males had significantly more generation glands than females ($p < 0,001$; Table 5). The number of generation glands did not correlate with SVL in any of the samples, and considerable variance was recorded.

Likewise there was no correlation between femoral gland count and SVL. In both species, femoral glands were present in males and females. Male and female counts in *C. niger* were significantly higher than in *C. cordylus* from both localities (Mann-Whitney *U* test, $p < 0,001$). However, no significant difference in the number of femoral glands between males and females has been established for *C. niger*, while in *C. cordylus* males have significantly more femoral glands than females at both localities ($p < 0,001$; Table 5). There was no significant difference in femoral gland counts between juveniles and adults in any of the samples. Although not measured, the size of the glands appeared to be larger in males than in females, and very small in juveniles.

Table 1 Comparison of body size (SVL), head width (HW) and head length (HL), between adult males and adult females, and the index of size dimorphism (D = mean SVL female/ mean SVL male) in *C. niger*, *C. cordylus* (Gansbaai), and *C. cordylus* (Saldanha). Statistics are based on the Mann-Whitney *U* test (z-value)

		n	Mean ± *SD*	*z*	*p*	D
C. niger						
SVL	male	63	78,8 ± 5,0	3,85	< 0,001	0,94
	female	107	74,4 ± 8,4			
HW	male	63	18,8 ± 1,5	6,98	< 0,001	
	female	107	16,6 ± 1,8			
HL	male	63	22,8 ± 1,5	7,63	< 0,001	
	female	107	20,3 ± 2,0			
C. cordylus (Saldanha)						
SVL	male	108	72,5 ± 7,7	0,94	> 0, 05	0,99
	female	146	72,4 ± 6,7			
HW	male	108	18,1 ± 2,4	5,34	< 0,001	
	female	146	16,8 ± 1,6			
HL	male	108	20,8 ± 2,4	5,76	< 0,001	
	female	146	19,5 ± 1,5			
C. cordylus (Gansbaai)						
SVL	male	47	76,0 ± 7,7	1,44	> 0,05	0,98
	female	75	74,4 ± 7,1			
HW	male	47	18,9 ± 2,2	5,12	< 0,001	
	female	75	17,1 ± 1,5			
HL	male	47	22,8 ± 2,4	4,70	< 0,001	
	female	75	20,9 ± 1,7			

Table 2 Comparison of adult body size (SVL) between the *C. cordylus* samples from the Gansbaai area and from the Saldanha area

	n	Mean ± *SD*	*z*	*p*
Male SVL				
Gansbaai	47	76,0 ± 7,7	2,11	< 0,05
Saldanha	108	72,5 ± 7,7		
Female SVL				
Gansbaai	75	74,4 ± 7,1	2,59	< 0,05
Saldanha	146	72,4 ± 6,7		

Scar frequency

Scar frequency did not vary considerably among the species.

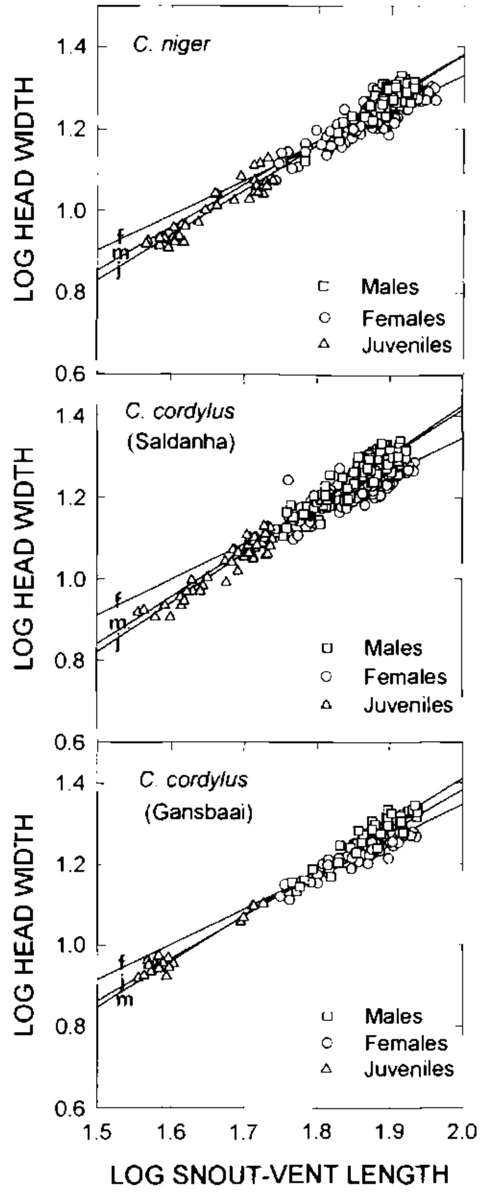

Figure 3 Regression of head width on snout-vent length (SVL) for adult males, adult females and juveniles of *C. niger*, and *C. cordylus* from the Saldanha area and *C. cordylus* from the Gansbaai area.

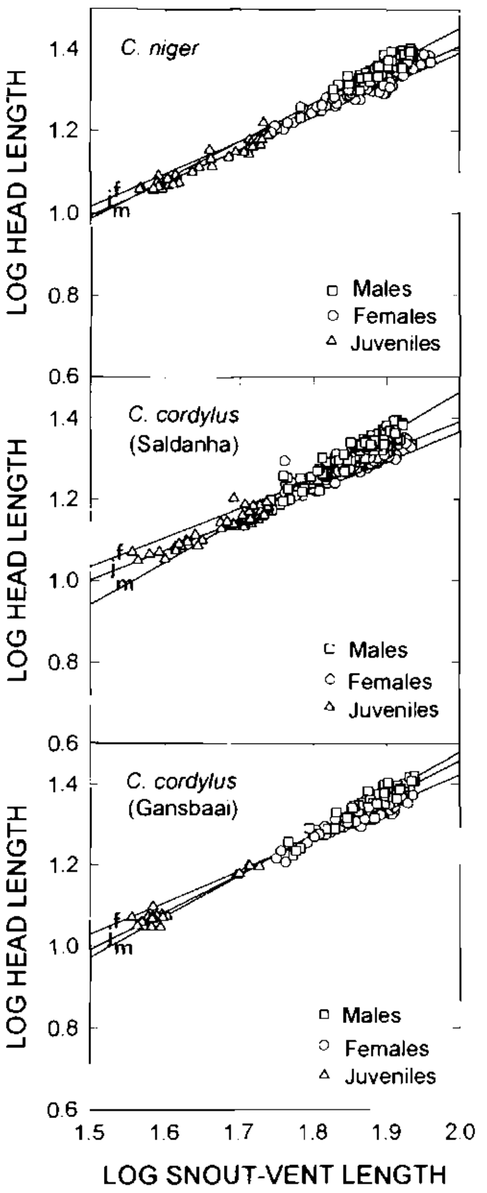

Figure 4 Regression of head length on snout-vent lenth (SVL) for adult females and juveniles of *C. niger* and *C. cordylus* from the Saldanha area and *C. cordylus* from the Gansbaai area.

Of all adults that were examined, 37,7% of C. cordylus (Saldanha) (n = 252), 40,6% of C. cordylus (Gansbaai) (n = 101) and 39,6% of C. niger (n = 170) had one or more scars on the body. In C. cordylus (at both localities), females displayed more scars than males. Of 146 females from Saldanha, 41% had one or more scars, compared to 32,1% in the males (n = 106). Most of the scars were on the tail (females: 82,0%; males: 82,4%), while the other scars included missing digits or limbs, and occasionally scars to the head or body. Of the 54 females from Gansbaai, 40,7% had scars (77,3% tail scars), while 38,3% of the 47 males displayed one or more scars (55,6% tail scars). In C. niger, males (n = 63) displayed more scars (49,2%) than females (n = 107; 35,5%). Of those scars, 80,6% were on the tail in males, and 76,3% in females.

Discussion

Sexual dimorphism in body and head size

We have demonstrated that both C. niger and C. cordylus exhibit sexual dimorphism, but in different characters; C. niger in mean body size and head length, and C. cordylus in head width and head length. Furthermore, we have shown that C. niger and C. cordylus from the Saldanha area, despite being subject to the same environmental conditions, differ in the degree and nature of sexual dimorphism displayed. FitzSimons (1943) considered C. niger a local colour variant of C. cordylus, while Loveridge (1944) and Branch (1988), more formally, listed it as a subspecies of C. cordylus. As the differences we recorded here may be a manifestation of different evolutionary histories, they support the elevation of C. niger to full species by Mouton & van Wyk (1990). Support for specific status for C. niger was also provided through an electrophoretic analysis by Brody, Mouton & Grant (1993).

Our results show that individuals of both *C. niger* and *C. cordylus* mature at a small size and then continue to grow to a larger asymptotic size. Asymptotic growth after maturity is typical of most poikilothermic vertebrates (Ware 1980;

Table 3 Regression statistics comparing the relationships between head dimensions (head width = HW; head length = HL) and SVL of adult males, adult females and juveniles for *C. niger*, *C. cordylus* (Saldanha), and *C. cordylus* (Gansbaai)

	r^2	*F*	*d.f.*	*p*	slope	intercept
C. niger						
HW male	68,5	132,5	61	< 0,001	1,06	-0,73
female	75,8	328,4	105	< 0,001	0,85	-0,38
juvenile	88,4	259,0	34	< 0,001	1,10	-0,82
HL male	82,0	278,3	61	< 0,001	0,93	-0,41
female	86,3	661,6	105	< 0,001	0,78	-0,16
juvenile	92,8	434,8	34	< 0,001	0,79	-0,20
***C. cordylus* (Saldanha)**						
HW male	84,7	586,3	106	< 0,001	1,15	-0,89
female	69,4	327,1	144	< 0,001	0,87	-0,39
juvenile	90,2	523,4	57	< 0,001	1,21	-1,00
HL male	91,1	1078,6	106	< 0,001	1,04	-0,62
female	78,0	509,8	144	< 0,001	0,71	-0,03
juvenile	86,4	362,8	57	< 0,001	0,73	-0,09
***C. cordylus* (Gansbaai)**						
HW male	88,2	336,8	45	< 0,001	1,13	-0,85
female	84,6	401,4	73	< 0,001	0,87	-0,39
juvenile	94,2	307,0	19	< 0,001	1,04	-0,70
HL male	89,8	395,0	45	< 0,001	1,01	-0,55
female	85,8	439,1	73	< 0,001	0,79	-0,15
juvenile	93,7	280,8	19	< 0,001	0,93	-0,41

Table 4 Test statistics for comparison of slopes of head width and head length *versus* SVL, and the index of dimorphism (D = slope female / slope male) of *C. niger*, *C. cordylus* (Saldanha) and *C. cordylus* (Gansbaai)

	t	d.f.	p	D
C. niger				
Head width				
Adult females *vs.* adult males	1,82	166	> 0,05	0,81
Juveniles *vs.* adult males	0,40	95	> 0,05	–
Juveniles *vs.* adult females	2,96	139	< 0,005	–
Head length				
Adult females *vs.* adult males	2,12	166	< 0,05	0,84
Juveniles *vs.* adult males	2,03	95	< 0,05	–
Juveniles *vs.* adult females	0,23	139	> 0,05	–
C. cordylus (Saldanha)				
Head width				
Adult females *vs.* adult males	4,15	250	< 0,001	0,76
Juveniles *vs.* adult males	0,82	163	> 0,05	–
Juveniles *vs.* adult females	4,50	201	< 0,001	–
Head length				
Adult females *vs.* adult males	7,40	250	< 0,001	0,68
Juveniles *vs.* adult males	6,18	163	< 0,001	–
Juveniles *vs.* adult females	0,30	201	> 0,05	–
C. cordylus (Gansbaai)				
Head width				
Adult females *vs.* adult males	3,65	118	< 0,001	0,77
Juveniles *vs.* adult males	0,96	64	> 0,05	–
Juveniles *vs.* adult females	2,35	92	< 0,05	
Head length				
Adult females *vs.* adult males	3,64	118	< 0,001	0,78
Juveniles *vs.* adult males	1,02	64	> 0,05	–
Juveniles *vs.* adult females	2,18	92	< 0, 05	–

Kusano 1982; Andrews 1982). No distinct sexual differences in asymptotic size were recorded for any of the three populations studied. This is in sharp contrast to the situation in *Pseudocordylus melanotus*, where males reach much larger asymptotic sizes than females (Mouton & van Wyk 1993). The percentage difference between the mean body size of the 20 largest males and females, which we used as an indicator of sexual differences in asymptotic size, is in the order of 16% in *P. melanotus*, while only between 1–2% in *C. niger* and *C. cordylus*.

In species where sexual dimorphism in body size is the result of sexual selection, one expects dimorphism to be manifested as differences in asymptotic size because the advantages of a specific body size will be important throughout adult life. Within the context of sexual selection, two such advantages are usually advanced to explain differences in body size in lizards (Shine 1989; Anderson & Vitt 1990). The first hypothesis predicts an advantage for large adult males in male-male aggressive encounters, with resulting greater access to females (Cooper 1977; Ruby 1978; Carothers 1984; Cooper & Vitt 1987). Shine (1978) and Fitch (1981), for example, pointed out that larger males are common among species that exhibit combat behaviour. The second hypothesis suggests non-random mating owing to mate choice by females, in that they may prefer larger males (Trivers 1972).

Sexual dimorphism in body size caused by sexual selection, has been found to be the greatest in territorial species with a polygynous mating structure (Stamps 1983). Anecdotal information suggests that most *Cordylus* species follow a sit-and-wait foraging strategy and are territorial to various degrees (FitzSimons 1943; Loveridge 1944; Burrage 1974; Branch 1988; Cooper & van Wyk 1994; Cooper *et al.* 1995), but there are no indications that any *Cordylus* species has a polygynous mating structure similar to that recorded for *P. melanotus* (Mouton & van Wyk 1993). In fact, the available data suggest that most *Cordylus* species probably have a mating system which is very near to a monogamous one (see Burrage 1974; van Wyk 1992). In behavioural studies done at our laboratories (Cordes 1995), the reactions of both sexes of *C. niger* and *C. cordylus* indicated territorial behaviour (see also Wirminghaus 1990). The sex ratio, favouring females in both species, however, suggests low levels of competition among males, and therefore a lower probability of sexual selection. Owing to the absence of sexual differences in scar frequency, no deductions can be made regarding the frequency of intrasexual aggressive encounters. In the light of the lack of clear sexual differences in asymptotic size and the indications of a monogamous mating structure, our preliminary conclusion is that sexual selection for a larger body size in males is not operative in either *C. niger* or *C. cordylus*.

Table 5 Comparison of the number of epidermal glands between adult males and females of *C. niger*, *C. cordylus* (Saldanha) and *C. cordylus* (Gansbaai)

	n	Mean ± *SD*	*z*	*p*
Generation glands				
C. cordylus (Gansbaai)				
Male	35	12,8 ± 4,78	5,59	< 0,001
Female	45	6,62 ± 2,96		
Femoral glands				
C. niger				
Male	63	17,38 ± 1,44	-1,18	> 0,05
Female	105	16,96 ± 1,89		
C. cordylus (Saldanha)				
Male	106	14,22 ± 1,22	-5,16	< 0,001
Female	138	13,18 ± 1,52		
C. cordylus (Gansbaai)				
Male	35	14,71 ± 1,66	4,07	< 0,001
Female	48	13,13 ± 1,52		

For reasons given above and mainly because there seems to be no sexual difference in asymptotic size, we are of the opinion that the sexual dimorphism in mean body size that we have recorded for *C. niger* in the Saldanha area, has nothing to do with sexual selection. In species exhibiting asymptotic growth after maturity, a wide range of processes can affect the size distribution of the adult males and females in a sample, for example, sexual differences in age or size at maturity, adult growth rates and survival rates (Gibbons & Lovich 1990; Shine 1990; Stamps 1993). Although a conclusive interpretation of sexual dimorphism in mean body size in *C. niger* will only be possible when data on growth and maturation are available (see Stamps 1993), we must point out that the size distribution in *C. niger*, where there are more large males than females in the sample, is exactly what one would predict for a cool-adapted species. In the south-western Cape there is a distinct correlation between the occurrence of melanistic cordylid populations and a high incidence of fog and cloud cover (Badenhorst 1990). Since lizards are ectothermic, these unfavourable conditions are likely to have a considerable impact on energy allocation and, owing to reproductive demands, the impact may be greater in females than in males. It would probably be more advantageous to the species if females invest a greater proportion of their available energy in reproduction than in growth (see Fitch 1978; Mouton & van Wyk 1993). Thus females will grow at a slower rate than males and will take a longer time to reach asymptotic size. Mouton & van Wyk (1993) pointed out the possibility that differential energy allocation by females in cool environments may lead to a change in the social structure from a monogamous mating system to a polygynous one. An increase in the degree of polygyny will then lead to an increase in the degree of sexual dimorphism. Although all indications are that *C. niger* had been subjected to cool climatic conditions for thousands of years (Mouton & Oelofsen 1988; Brody *et al.* 1993), this is not manifested in the degree of sexual dimorphism displayed.

It has been demonstrated that *C. niger* is an archaic species (Herselman 1991) and that the population in the Saldanha area is a relict population (Mouton & Oelofsen 1988; Brody *et al.* 1993). The fact that *C. niger* and *C. cordylus* occur in the same general area may suggest that the difference in patterns of body size dimorphism between these two species has a genetic basis. We suggest that growth patterns in the two species in the Saldanha area be investigated in detail, as such data may help to unravel the evolutionary history of melanistic cordylid species in the south-western Cape.

In species where male combat is involved, sexual selection usually also results in an increase in the size of the head or jaws (Carpenter & Ferguson 1977) and in many cases also in bright body coloration in males (Stamps 1977, 1983). The lack of bright body colours in males of *C. niger* and *C. cordylus*, and the absence of sexual differences in asymptotic body size, may serve as indicators that sexual selection, as far as head size is concerned, is, as in the case of body size, probably not operative in these two species. Increased head width is caused by the hypertrophy of the pterygoideus and temporalis jaw muscles, resulting in an increase in bite strength. Increase in head length results in an increase in gape size. It is therefore assumed that an increase in head size may be an advantage in winning male-male agonistic encounters (Vitt & Cooper 1985).

From the regression analyses of head width against SVL (Table 3) it is clear that, in both species, head width in males continues to increase at more or less the same rate as in juveniles, but that in females a decrease in growth rate occurs. Such a decrease has also been reported for *P. melanotus* (Mouton & van Wyk 1993) and *C. giganteus* (van Wyk 1992) and also for other lizard species (see Cooper & Vitt 1989; Vial & Stewart 1989). According to Cooper & Vitt (1989) the most feasible explanation for this phenomenon is that females allocate relatively more energy to reproduction after reaching sexual maturity than to characters less directly tied to reproductive success. The sexual dimorphism in head width in *C. cordylus*, however, differs from that recorded in *P. melanotus* in that in the latter there is a considerable increase in growth rate of head size in males, so that sexual head size dimorphism in this species is the result of both an increase in growth rate in males and a decrease in females after sexual maturity is reached. Sexual dimorphism in head width in *C. cordylus* thus seems to be only a function of energy allocation in females and not of sexual selection.

Results obtained in the regression analysis of head length against SVL show, that in the *C. cordylus* population at Saldanha, head length in adult males increases at a considerably higher rate than in juveniles. Such an increase may hint at sexual selection, but it is unclear as to why head width and head length do not show concordant patterns of increase in this population. In the highly dimorphic species, *P. melanotus*, there is a concordant increase in growth rate of head length and head width in males after maturity is reached (Mouton & van Wyk 1993). Thus, while sexual dimorphism in head width seems to be the result of energy allocation by females, the dimorphism in head length seems to result from selection for larger heads in males. The observed dimorphism in head size, with the exception of head length in the

Saldanha population of *C. niger*, is, however, small when compared to that exhibited by *P. melanotus* (Mouton & van Wyk 1993).

In summary, when compared to *P. melanotus* (Mouton & van Wyk 1993), *C. niger* and *C. cordylus* display low levels of sexual dimorphism in those characters usually affected by sexual selection. Males of both species lack bright body coloration, and sexual differences in asymptotic body size seem to be absent. The limited information available suggests that the sexual dimorphism in body size and head width in these species is mainly the result of energy allocation by females and not of sexual selection. Detailed studies on growth patterns and the social structure in the two species are necessary for the final interpretation of the observed sexual dimorphism.

Geographical variation in sexual dimorphism in *C. cordylus*

Although no apparent difference in the degree of sexual dimorphism between the Saldanha and Gansbaai *C. cordylus* populations was noted, both sexes from the former area were significantly smaller in body size than their counterparts from Gansbaai. This may be due to climatic differences between the two areas, the Saldanha area being relatively cooler with a higher incidence of mist (Stuckenberg 1969; Badenhorst 1990). Assuming that cooler climates will affect food availability, this will have a direct influence on growth rates and adult body size (see Madsen & Shine 1993). All the material collected from the two study areas during recent years (Mouton 1987; Brody *et al.* 1993) was included in this analysis and it is unlikely that the size differences between the two populations are related to different age structures caused by previous collecting of adult specimens. Many factors may, however, influence adult body size (e.g., Andrews 1976; Case 1978; Dunham, Tinkle & Gibbons 1978), and it will be premature to come to any final conclusions in this regard.

Sex ratio

A sex ratio favouring females has also been recorded for *C. giganteus* in the Free State (van Wyk 1991) and *C. macropholis* along the west coast (Wright & Mouton unpubl.). In an independant survey, Jacobs (unpublished data) also recorded a sex ratio favouring females for *C. cordylus* in the Gansbaai area. Flemming & van Wyk (1992), Mouton & van Wyk (1993) and Sachse (pers. comm.), however, recorded ratios of 1 : 1 for *C. polyzonus, Pseudocordylus melanotus* and *P. microlepidotus* respectively. The early indications are that the observed sex ratios for *C. niger* and *C. cordylus* are not a collecting artefact and that a ratio favouring females may be a wide spread phenomenon in the genus *Cordylus*. Female biased sex ratios are not uncommon among lizards and are usually ascribed to differential mortality of the sexes (Stamps 1983). Males must find and court females in the breeding season and higher activity rates by breeding males would increase their exposure to predators. Territorial defence by large males could also lead to differential mortality in small males (Stamps 1983). The sex ratio is considered an important variable determining the intensity of sexual selection, a sex ratio favouring females would mean that competition among males to obtain mating opportunities during the breeding season will be less (Stamps 1983).

Variation in generation and femoral glands

Within the Cordylidae there seems to be a temperature related pattern in the presence or absence of generation glands (Jacobs, unpublished data). In cool-adapted species, like montane species, females generally lack generation glands. In the high altitude species, *Pseudocordylus langi*, occurring in the Drakensberg Mountains, generation glands are even absent in males (Herselman 1991). Jacobs (unpublished data) found that the presence of generation glands in females may vary geographically in *C. cordylus*, being absent in highland areas and present in lowland areas. The observations made in this study, namely that females of both *C. niger* and *C. cordylus* lack generation glands in the cool Saldanha area, while they are present in females in the warmer Gansbaai region, agree with his findings.

At present, no data are available on the function of generation glands, but they probably play an important role in intraspecific communication. These glands are, for example, well developed in the highly territorial species, *Pseudocordylus microlepidotus*, and are not restricted to the femoral region, but also occur in the preanal region and on the back (van Wyk & Mouton 1992; Sachse, pers. comm.). The possibility exists that the presence or absence of generation glands in females is linked to the amount of energy females can afford to invest in territorial behaviour, which will be less in cooler areas. Males, that do not have the burden of reproduction like females, can invest energy in territorial behaviour, even in cool areas.

The observation made in this study that *C. niger* has more femoral glands than *C. cordylus*, probably has a phylogenetic connotation and is probably not directly linked to the environment. *C. niger* is considered a primitive species in the genus, sharing several plesiomorphies with the *Pseudocordylus* clade (Herselman 1991). One such plesiomorphy is the possession of a high number of femoral glands. As in the case of generation glands, femoral glands may be present or absent in females of the various species. However, there seems to be no clear geographical correlation in the presence of the femoral glands, unlike in the case of generation glands.

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