

What, if anything, is a ‘typical’ viper? Biological attributes of basal viperid snakes (genus *Causus* Wagler, 1830)

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For many major phylogenetic radiations of organisms, the available ecological knowledge is disproportionately derived from a small minority of taxa, and sometimes from organisms that are highly atypical. Viperid snakes provide a good example of this situation; high-latitude cold-climate taxa in northern Europe (vipers) and North America (rattlesnakes) have been studied intensively, but more speciose radiations in tropical Africa, Asia, and Central America remain poorly known. We dissected > 500 specimens (six species) of night adders (genus *Causus*), mostly from Cameroon (68%) in equatorial Africa, to quantify morphology, diets, and reproductive biology. By contrast to the ‘slow’ life-histories of cold-climate viperids, night adders feed frequently on frogs (rather than infrequently on mammals), and produce frequent large clutches of relatively small eggs (rather than infrequent small litters of relatively large live young). Thus, putatively ‘typical’ viperid attributes such as low fecundity, viviparity, and predation on mammals reflect adaptations to the invasion of cold environments by a small and perhaps atypical subset of viperid taxa. Our data on prey size suggest that one of the critical innovations of early viperids may have been an ability to subdue and ingest relatively large prey. © 2006 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2006, 89, 575–588.

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INTRODUCTION

Many major biological radiations have resulted in numerous species that are now distributed widely across the planet. However, for historical reasons, universities and research centres have been based in a highly nonrandom subset of countries, notably in relatively cool-climate northern lands in Europe and North America. Accordingly, intensive ecological research has been conducted primarily in those countries. An inevitable result has been that, for many biological lineages, our knowledge is based upon a small and potentially nonrepresentative sample of taxa. This limitation of available information severely com-

promises our ability to make valid generalizations about major adaptive radiations.

One spectacular adaptive radiation that fits this description comprises the venomous snakes of the family Viperidae: vipers, rattlesnakes, bushmasters, water moccasins, lanceheads, and their allies. Snakes of this family are abundant and conspicuous elements of the reptile fauna over most of the world’s continents, especially in Africa (*Adenorhinos*, *Atheris*, *Bitis*, *Causus*, *Cerastes*, *Echis*, *Macrovipera*, *Montatheris*, *Proatheris*, *Vipera*), Asia (*Azemiops*, *Calloselasma*, *Daboia*, *Deinagkistrodon*, *Echis*, *Eristicophis*, *Gloydus*, *Hypnale*, *Macrovipera*, *Ovophis*, *Protobothrops*, *Pseudocerastes*, *Triceratolepidophis*, *Trimeresurus*, *Tropidolaemus*, *Vipera*, *Zhaoermia*), and Central and South America (*Agkistrodon*, *Atropoides*, *Bothriechis*,

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Bothriopsis, *Bothrocophias*, *Bothrops*, *Cerrophidion*, *Crotalus*, *Lachesis*, *Ophryacus*, *Porthidium*, *Sistrurus*). However, detailed ecological data are lacking on almost all of these taxa. For example, despite recent detailed field studies on Nigerian vipers (Luiselli & Akani, 1998, 2003; Luiselli *et al.*, 1998, 2004; Luiselli, Angelici & Akani, 2000; Angelici *et al.*, 2000; Akani *et al.*, 2001, 2002), ecological data are fragmentary for most African viperid snakes (but see Bodbijn, 1994; Chevalier, 1997). By contrast, the two viperid species found in northern Europe (*Vipera aspis* and *Vipera berus*) rank among the most intensively studied snake species worldwide (Saint Girons, 1957; Madsen & Shine, 1994; Naulleau, 1997; Zuffi, Giudici & Iolae, 1999; Bonnet *et al.*, 2002). A similar situation occurs North America (USA and Canada, exclusive of Mexico), with a radiation of 18 species within three genera of pit-vipers (*Agkistrodon*, *Crotalus*, *Sistrurus*). Although the number of pit-viper species in North America (exclusive of Mexico: *Agkistrodon contortrix*, *Agkistrodon piscivorus*, *Crotalus adamanteus*, *Crotalus atrox*, *Crotalus cerastes*, *Crotalus horridus*, *Crotalus lepidus*, *Crotalus mitchellii*, *Crotalus molossus*, *Crotalus oreganos*, *Crotalus pricei*, *Crotalus rubber*, *Crotalus scutulatus*, *Crotalus tigris*, *Crotalus viridis*, *Crotalus willardi*, *Sistrurus catenatus*, *Sistrurus miliarius*; Ernst & Ernst, 2003) and Europe (*Gloydius halys*) combined ($N = 18$ and 1 , respectively) comprises only approximately 10% of all pit-vipers worldwide ($N = 166$ species), these cold-climate taxa have attracted almost all of the ecological research devoted to crotaline snakes (Fitch, 1970; Parker & Plummer, 1987). Thus, we know a great deal about a relatively small number of cool-climate species, and almost nothing about the rest of the Viperidae.

If we are to understand why viperid snakes have been so spectacularly successful across so much of the world, the ecological traits of cool-climate species may provide a poor guide. The extensive literature on these taxa paints a consistent scenario of ambush predators that specialize upon small mammals, often feeding infrequently (Fitch, 1960; Bea *et al.*, 1992; Brown, 1993). Perhaps reflecting these low rates of food intake, European vipers and North American rattlesnakes generally exhibit slow growth, delayed maturation (often, at > 4 years of age: Saint Girons, 1957; Martin, 1993), and infrequent female reproduction (typically, less than once every 3 years: Saint Girons, 1957; Brown, 1993; Martin, 1993). All of these taxa are viviparous, presumably reflecting the cool climates in which they live (Neil, 1964; Shine, 1983). Indeed, the familial descriptor Viperidae comes from this mode of reproduction (Gaffiot, 2000). However, some viperids from warmer climates are oviparous (Fitch, 1970). Clearly, before we can frame valid generalizations about viperid ecology, we need more information on

the ecological traits of other species, especially taxa basal to the radiation, whose ecological traits may more closely resemble those of ancestral vipers. Only then can we interpret the phylogenetic history of viperid snakes in ecological terms. The present study was designed to provide information of this kind, focused on a 'primitive' (phylogenetically basal) group: African 'night adders' of the genus *Causus*.

MATERIAL AND METHODS

STUDY SPECIES

Recent phylogenetic reconstructions agree that *Causus* should be included within the Viperidae (Cadle, 1992; Underwood, 1999; Lenk *et al.*, 2001; Parkinson, Campbell & Chippindale, 2003; Nagy *et al.*, 2005). The genus *Causus*, as presently considered, comprises six recognized species and at least one undescribed species (Pitman, 1974; Audiens, 1978; Branch, 1998; de Massary, 1993; Chippaux, 2001):

Causus bilineatus (Boulenger, 1905)

This species is clearly related to *Causus rhombeatus* and, until recently, was considered as one of its subspecies. Its limited distribution includes the Democratic Republic of Congo, Rwanda, Angola, and Zambia (David & Ineich, 1999). Growing to 65 cm in snout-vent length (SVL), this taxon appears to be restricted to moist savannah habitats at elevations from 800 to 1800 m asl (Spawls *et al.*, 2001).

Causus defilippii (Jan, 1863)

With an average SVL of approximately 40 cm (Branch, 1998; Spawls *et al.*, 2001), this small species occupies moist and dry savannas from sea level to approximately 1800 m in eastern and southern Africa from Tanzania and Kenya to the Republic of South Africa.

Causus lichtensteinii (Jan, 1859)

This medium-sized (up to 70 cm SVL) species occurs in forest habitats from Guinea through Cameroon, Gabon, the Democratic Republic of Congo and east to Uganda, Kenya, Zambia, and Angola (David & Ineich, 1999). The species lives in dense evergreen forests as well as mosaic forest-savannas (recently deforested areas) from sea level to approximately 2100 m asl.

Causus maculatus (Hallowell, 1842)

With a mean SVL of approximately 40 cm, this is the most widespread and abundant species within the genus. It is present in most of subtropical Africa from Mauritania in the west through Ethiopia and as far south as the Democratic Republic of Congo, Angola, and Uganda (Hughes, 1977; David & Ineich, 1999). The species lives in forested areas and agricultural

areas as well as in savannas, and from around sea level to nearly 2000 m asl.

Causus resimus (Peters, 1862)

This taxon (approximately 50 cm in mean adult length) occurs in two disjunct populations, which our unpublished data (I. Ineich, X. Bonnet, R. Shine, T. Shine, F. Brischoux, M. Lebreton & L. Chirio, unpubl. data) suggest may belong to two different species. The eastern populations live in humid mountains of east Africa (Uganda, Rwanda, Burundi, Democratic Republic of Congo, and Ethiopia) and their coloration in life is light green (David & Ineich, 1999). The western populations inhabit savanna regions of western and central Africa from Nigeria and Cameroon through the Central African Republic (CAR), Chad, and Sudan; their coloration in life is light brown. They are found at elevations of 150–500 m asl.

Causus rhombeatus (Lichtenstein, 1823)

The longest species of the genus reaches 83 cm SVL (Branch, 1998) and occupies mesic savannas. It appears to be found only in the eastern regions of southern Africa but its northern limit is unclear. Reports from western, central, and eastern Africa correspond to another species that, here, we call *Causus sp.*, which is easily distinguished from *C. rhombeatus* by its higher number of ventral scales.

Causus sp.

This as yet undescribed taxon (I. Ineich, X. Bonnet, R. Shine, T. Shine, F. Brischoux, M. Lebreton & L. Chirio, unpubl. data) is endemic to high-elevation savannas of central Cameroon and the western CAR. Another population related to this species occurs in the Kerouane area of south-eastern Guinea. Although eastern African populations clearly do not belong to the 'true' *C. rhombeatus*, whether or not they are conspecific with the western and central African populations has yet to be assessed. For the present study, we treat all those populations (except 'true' *C. rhombeatus* from southern Africa) as conspecific. This species is found in humid lowlands and small rivers, at elevations of 700–1950 m asl in Cameroon.

COLLECTION OF SNAKES

Although *Causus* are relatively well represented in museum collections, an ecological analysis ideally requires a large series of animals from restricted localities, killed soon after collection (so that gut contents remain undigested) and with reliable dates of collection. To obtain samples of this kind, L. Chirio and M. LeBreton arranged for local villagers in Cameroon (and to a lesser extent from the Central African Republic) to collect and preserve snakes encountered

in the course of the villagers' daily activities from October 1990 to December 2002. The snakes were killed immediately after capture and preserved in drums of formalin left at each village for subsequent collection. All the specimens were deposited in the Paris Natural History Museum collections (MNHN). For this study, we also used previous collections of the MNHN, from localities with large series of specimens for the most common species (*C. maculatus*), and all available specimens for the other species.

DATA COLLECTION

For each snake, we measured the following morphological attributes: SVL, maximum body diameter, tail length, jaw length (snout to quadrato-articular articulation), maximum head width, eye diameter, and distance between nostrils. We then made a mid-ventral incision on each snake to determine sex and reproductive status. We counted the number of follicles and/or ovulated eggs, and scored the epididymial ducts in males as convoluted (i.e. containing sperm) vs. transparent (empty of sperm). Inspection of the digestive tract revealed three types of prey remains: amphibians in the stomach, insect fragments in the stomach, or well-digested faecal material in the hindgut. Because we never found intact insects, we interpret the insect fragments as secondary prey items (i.e. from inside the stomachs of digested frogs). We identified prey remains to the lowest possible taxonomic level at the MNHN with the help of Renaud Boistel (PhD student at Université Paris Sud – Centre Scientifique d'Orsay).

RESULTS

SAMPLE SIZES

Our sample sizes are highest for four taxa from Cameroon; one of these species (*C. maculatus*) was obtained in reasonable numbers in the Central African Republic as well (Table 1). Although we had very small samples for two taxa, we report these data because they are among the first for these poorly-known animals. Because some specimens were damaged during collection, our data sets are incomplete for some variables for some animals.

MORPHOLOGY

Significant interspecific differences were apparent for all traits that we measured (Table 2). This was true for overall mean body sizes as well as for morphological traits correlated with body size (Table 2). *Causus defilippii* was the smallest species, three other taxa averaged 40–48 cm SVL as adults ($P < 0.001$ for these post-hoc tests; Table 2). In terms of body proportions (body

Table 1. List of locations of origin of the *Causus* specimens examined for the present study

	<i>Causus defilippii</i>	<i>Causus lichtensteinii</i>	<i>Causus maculatus</i>	<i>Causus resimus</i>	<i>Causus sp.</i>	<i>Causus rhombeatus</i>	Total
Cameroon	0	28	224	61	37	0	350
Central African Republic	0	59	2	0	1	0	62
Senegal	0	0	19	0	0	0	19
Zaire	0	1	0	0	16	0	17
Congo	0	14	0	0	0	0	14
Others	14	9	11	0	13	7	54
All regions	14	111	256	61	67	7	516

'Others' represents localities where less than ten specimens were collected (Kenya: eight *C. sp.*; Republic of South Africa: seven *C. rhombeatus*; Gaboon: six *C. lichtensteinii*; Mali: five *C. maculatus*; Tanganyika: five *C. defilippii*; Ethiopia: four *C. sp.*; East Africa: three *C. defilippii*; Mozambique: three *C. defilippii*; Burkina: two *C. maculatus*; Guinea: one *C. lichtensteinii* and one *C. sp.*; Liberia: two *C. lichtensteinii*; Benin: one *C. maculatus*; Chad: one *C. maculatus*; Great lakes: one *C. defilippii*; Mauritania: one *C. maculatus*; Togo: one *C. maculatus*; Zambezi: one *C. defilippii*; Zanzibar: one *C. defilippii*).

Table 2. Morphological characteristics of adult specimens of the six species of *Causus* examined in the present study

Species	Snout-vent length (cm)	Tail length (cm)	Jaw length (mm)	Head width (mm)	Body diameter (mm)	Eye diameter (mm)
<i>Causus defilippii</i>	30.3 ± 1.9 (8)	2.8 ± 0.2 (8)	17.0 ± 1.1 (7)	7.4 ± 0.5 (7)	12.5 ± 1.1 (8)	3.3 ± 0.2 (8)
<i>Causus lichtensteinii</i>	39.7 ± 5.1 (84)	4.3 ± 0.8 (83)	19.3 ± 2.4 (71)	7.0 ± 0.7 (74)	10.7 ± 1.8 (84)	4.2 ± 0.5 (78)
<i>Causus maculatus</i>	40.4 ± 6.2 (165)	3.9 ± 0.7 (166)	22.3 ± 2.8 (150)	7.6 ± 0.7 (141)	13.6 ± 2.5 (165)	3.9 ± 0.5 (154)
<i>Causus resimus</i>	47.2 ± 10.4 (53)	4.8 ± 1.1 (51)	23.0 ± 4.2 (48)	7.9 ± 1.1 (46)	16.3 ± 4.3 (50)	3.5 ± 0.6 (47)
<i>Causus rhombeatus</i>	39.9 ± 10.5 (6)	5.2 ± 0.7 (6)	25.7 ± 5.1 (6)	8.7 ± 1.2 (6)	15.4 ± 3.7 (6)	3.9 ± 0.5 (6)
<i>Causus sp.</i>	47.5 ± 10.8 (33)	5.1 ± 1.2 (33)	25.5 ± 4.3 (28)	8.1 ± 1.2 (29)	13.4 ± 3.0 (33)	3.9 ± 0.6 (30)
<i>F</i>	16.46	23.1	23.3	13.1	27.6	15.6
d.f.	5, 343	5, 341	5, 304	5, 297	5, 340	5, 317
<i>P</i>	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001

Data are the mean values with the associated standard errors, and sample size in parentheses. Statistical results are derived from one-way analysis of variance with species as the factor. d.f., degrees of freedom.

size corrected traits), we also found significant differences among the species (Table 3). *Causus rhombeatus* was the most stockily built species, with a relatively large head and a long tail ($P < 0.001$ in the post-hoc tests). By contrast, *C. lichtensteinii* was the most slender-bodied, and had relatively larger eyes than any of the other taxa ($P < 0.001$ in the post-hoc tests).

SEX RATIO AND AGE STRUCTURE

Sex ratios were similar among species ($\chi^2 = 5.52$, d.f. = 5, $P = 0.36$; Table 4). Approximately two-thirds

of the collected snakes were adults, but the exact proportions differed among species (comparing the species: $\chi^2 = 27.9$, d.f. = 5, $P < 0.001$; Table 4).

SEXUAL DIMORPHISM

The degree of sexual size dimorphism (SSD) varied among species [analysis of variance (ANOVA) with sex and species as the factors and SVL as the dependent variable; interaction between species and sex: $F_{5,481} = 4.16$, $P < 0.0001$; Table 5]. Three of the species (*C. lichtensteinii*, *C. resimus*, *C. sp.*) displayed similar

Table 3. Body proportions of the six *Causus* species examined in the present study

Species	Tail length (cm)*	Jaw length (mm)*	Head width (mm)*	Body diameter (mm)*	Eye diameter (mm)**
<i>Causus defilippii</i>	3.4 ± 0.1 (14)	19.1 ± 0.4 (13)	7.5 ± 0.2 (13)	13.2 ± 0.5 (14)	3.3 ± 0.1 (13)
<i>Causus lichtensteinii</i>	3.9 ± 0.1 (109)	18.1 ± 0.2 (94)	6.6 ± 0.1 (96)	9.8 ± 0.2 (110)	4.3 ± 0.0 (97)
<i>Causus maculatus</i>	3.4 ± 0.0 (247)	20.6 ± 0.1 (222)	7.1 ± 0.0 (208)	12.4 ± 0.1 (240)	3.7 ± 0.0 (208)
<i>Causus resimus</i>	3.7 ± 0.1 (58)	18.5 ± 0.2 (55)	6.8 ± 0.1 (53)	12.9 ± 0.3 (57)	3.2 ± 0.1 (52)
<i>Causus rhombeatus</i>	4.9 ± 0.2 (7)	23.8 ± 0.6 (7)	8.1 ± 0.2 (7)	14.1 ± 0.7 (6)	3.4 ± 0.2 (7)
<i>Causus sp.</i>	3.9 ± 0.1 (66)	20.7 ± 0.2 (56)	7.0 ± 0.1 (58)	10.6 ± 0.2 (66)	3.6 ± 0.1 (58)
<i>F</i>	21.8	54.4	16.4	45.3	48.1
d.f.	5, 494	5, 440	5, 428	5, 487	5, 428
<i>P</i>	0.0001	0.0001	0.0001	0.0001	0.0001

Data for snakes of all age classes were included in these calculations. Data are adjusted means [*relative to snout-vent length (SVL), **relative to head width] with standard errors and sample size. Statistical analysis: results are derived from analysis of variance with species as the factor, the trait under focus as the dependent variable, and SVL (*) or head width as a covariate. d.f., degrees of freedom.

Table 4. Sex ratios and age structures (proportion of juveniles) of *Causus* species examined in the present study

	<i>Causus defilippii</i>	<i>Causus lichtensteinii</i>	<i>Causus maculatus</i>	<i>Causus resimus</i>	<i>Causus rhombeatus</i>	<i>Causus sp.</i>	Total
Males	10	59	110	29	4	29	241
Females	4	52	130	31	3	38	258
Sex ratio (% female)	(29)	(47)	(54)	(52)	(43)	(57)	(52)
Adults	8	84	170	53	6	33	354
Juveniles	6	26	83	7	1	34	157
Proportion of juveniles (%)	(43)	(24)	(33)	(12)	(14)	(51)	(31)

mean adult body sizes in males and females; one species (*C. maculatus*) had females larger than males, and two (*C. defilippii*, *C. rhombeatus*) had males growing significantly larger than females (Table 5).

Males tended to have longer tails than same-sized females in all species (sex $F_{1,473} = 54.52$, $P < 0.0001$; Table 5), although the degree of this sex divergence varied interspecifically (interaction between sex and species; $F_{5,473} = 4.42$, $P < 0.0001$). At the same body length, female *Causus resimus* had wider heads than did conspecific males (sex effect: $F_{1,420} = 19.08$, $P < 0.0001$, see Table 5) and in three species (*C. maculatus*, *C. lichtensteinii*, *C. sp.*, Table 5), females had longer jaws than did conspecific males at the same SVL. However, the degree of sexual dimorphism in this latter trait also varied among

species (interaction between sex and species; $F_{5,420} = 2.60$, $P < 0.02$). No significant sexual dimorphism was apparent for any of the other traits (all $P > 0.05$).

REPRODUCTION

Proportion of reproductive individuals

Most adult-sized individuals were reproductive, in all species [range 85–96% in males, 50–89% in females (excluding small sample sizes); Fig. 1]. Nonetheless, significant interspecific differences were apparent in the percentage of reproductive individuals among adults ($\chi^2 = 13.53$, d.f. = 5, $P = 0.019$). Abdominal fat bodies were not notably enlarged or depleted in females with vitellogenic follicles compared to other

Table 5. Sexual dimorphism in six species of viperid snakes of the genus *Causus*

Trait	Sex	<i>Causus deflippii</i>	<i>Causus lichtensteinii</i>	<i>Causus maculatus</i>	<i>Causus resimus</i>	<i>Causus rhombeatus</i>	<i>Causus sp.</i>
Snout-vent length	F	19.0 ± 5.0 (4)	36.2 ± 1.4 (52)	38.1 ± 0.9* (126)	44.7 ± 1.5 (31)	30.3 ± 4.9* (4)	36.2 ± 1.6 (38)
	M	27.7 ± 3.1* (10)	38.4 ± 1.3 (58)	33.6 ± 0.9 (109)	45.1 ± 1.8 (29)	44.1 ± 5.7* (3)	39.3 ± 1.8 (29)
Tail length*	F	2.04 ± 0.10 (4)	3.77 ± 0.08 (52)	3.19 ± 0.03 (125)	3.94 ± 0.08 (29)	4.91 ± 0.17* (3)	3.71 ± 0.08 (37)
	M	2.21 ± 0.08 (10)	4.25 ± 0.08* (57)	3.70 ± 0.04* (107)	4.97 ± 0.08* (29)	5.07 ± 0.14* (4)	4.43 ± 0.10* (29)
Jaw length*	F	14.7 ± 0.6 (4)	19.1 ± 0.2* (45)	20.8 ± 0.12* (109)	22.0 ± 0.4 (28)	26.4 ± 1.2* (3)	22.0 ± 0.3* (33)
	M	13.6 ± 0.4 (9)	17.9 ± 0.2 (49)	20.2 ± 0.13 (99)	22.1 ± 0.4 (27)	23.6 ± 1.1* (4)	20.6 ± 0.3 (23)
Head width*	F	6.29 ± 0.18 (4)	6.82 ± 0.10 (46)	7.06 ± 0.05 (102)	7.87 ± 0.12* (24)	8.86 ± 0.66* (3)	7.26 ± 0.11 (32)
	M	6.04 ± 0.13 (9)	6.69 ± 0.09 (50)	7.17 ± 0.05 (93)	7.46 ± 0.11 (29)	7.99 ± 0.61* (4)	7.02 ± 0.12 (26)
Body diameter*	F	9.4 ± 0.4 (4)	9.9 ± 0.2 (52)	12.1 ± 0.2 (120)	15.2 ± 0.4 (28)	14.5 ± 1.0* (3)	11.4 ± 0.3 (37)
	M	9.3 ± 0.3 (10)	10.2 ± 0.2 (58)	12.6 ± 0.2 (107)	15.5 ± 0.4 (29)	15.1 ± 0.9* (4)	10.7 ± 0.4 (29)
Eye diameter†	F	2.87 ± 0.08 (4)	4.09 ± 0.07 (46)	3.62 ± 0.04 (101)	3.43 ± 0.10 (28)	4.14 ± 0.17* (3)	3.55 ± 0.07 (32)
	M	2.89 ± 0.06 (9)	4.08 ± 0.06 (51)	3.70 ± 0.05 (94)	3.38 ± 0.11 (23)	3.50 ± 0.15* (v4)	3.61 ± 0.07 (26)
Nostril separation†	F	3.28 ± 0.15 (4)	3.67 ± 0.08 (46)	3.97 ± 0.04 (101)	4.51 ± 0.08 (28)	4.72 ± 0.31* (3)	3.76 ± 0.07 (32)
	M	3.18 ± 0.10 (9)	3.78 ± 0.08 (48)	3.91 ± 0.04 (92)	4.36 ± 0.09 (24)	4.20 ± 0.29* (4)	3.73 ± 0.08 (26)

Traits other than overall body size (snout-vent length) were adjusted, *relative to snout-vent length, †relative to head width. Data are means with standard errors (*N*). Data for the larger sex are indicated by an asterisk (*) if the difference in mean values between the sexes was statistically significant ($P < 0.05$). F, female; M, male.

segments of the population (ANOVA with fat score as the dependent variable, species and follicular stage as the factors, $F_{7,142} = 0.82$, $P = 0.58$, excluding *C. deflippii* due to small sample size; this result remained unchanged when all the species were pooled: $F_{2,153} = 1.38$, $P = 0.25$). This result suggests that female reproductive output may not be necessarily closely linked to maternal energy reserves. In support of this inference, several vitellogenic females (*C. maculatus*, $N = 10$; *C. lichtensteinii*, $N = 17$; *C. resimus*, $N = 2$; *C. rhombeatus*, $N = 1$) lacked detectable fat body reserves. Thus, females may have the ability to fuel vitellogenesis from current feeding rather than long-term energy stores. The smallest SVLs for reproductively mature individuals were 29.5 and 30.0 cm for females and males, respectively, for *C. lichtensteinii*; 30.7 and 27.7 cm for *C. maculatus*; 29.0 and 27.0 cm for *C. resimus*; 40.5 and 23.7 cm for *C. rhombeatus*; and 29.0 and 28.10 cm for *C. sp.*

Seasonal patterns

Vitellogenesis was observed all year round (comparing among months, $\chi^2 = 49.5$, d.f. = 55, $P = 0.68$), and ovulation was not limited to a single period (Fig. 2). Similarly, males with convoluted ducts were observed at most times of the year ($\chi^2 = 69.6$, d.f. = 55, $P = 0.09$). Overall, no clear seasonal pattern was apparent for either male or female reproductive cycles (Fig. 2). One female *C. maculatus* (545 cm SVL) contained both oviductal eggs ($N = 12$, mean diameter 13 mm) and enlarged vitellogenic ovarian follicles ($N = 8$, mean diameter 4 mm), indicating rapid production of successive clutches.

Fecundity

We found shelled oviductal eggs in females of *C. maculatus*, *C. lichtensteinii*, *C. resimus*, *C. rhombeatus*, and *C. sp.*, confirming previous reports of oviparous reproduction in this group

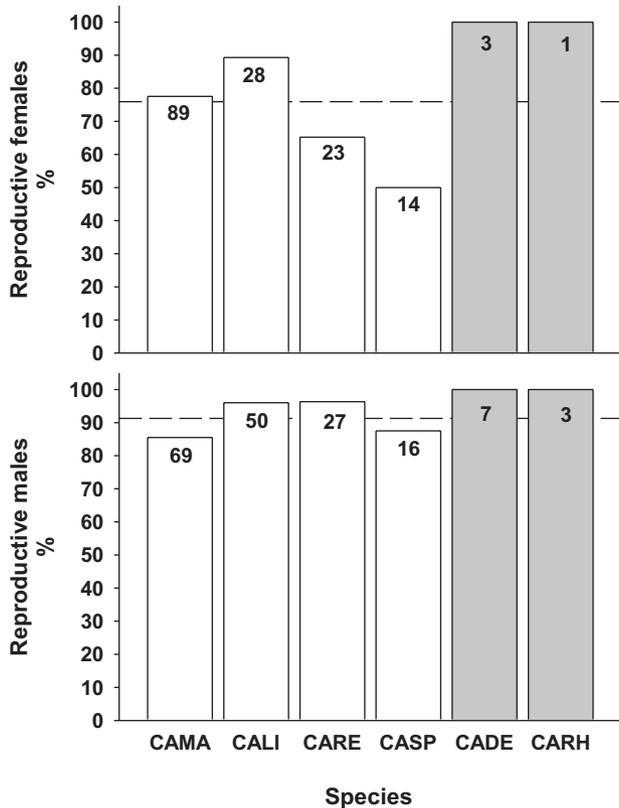


Figure 1. Reproductive frequencies in *Causus* species. The upper graph shows the proportion of adult female snakes with vitellogenic follicles or oviductal eggs, whereas the lower graph shows the proportions of adult male snakes with convoluted epididymial ducts. Grey bars indicate taxa with small sample sizes. CAMA, *Causus maculatus*; CALI, *Causus lichtensteinii*; CARE, *Causus resimus*; CASP, *Causus* sp.; CADE, *Causus defilippii*; CARH, *Causus rhombeatus*.

(FitzSimons, 1962; Fitch, 1970; Botha, 1984). For all species combined, eggs varied from 13.3–30.0 mm in length, and from 7.5–14.5 mm in diameter ($N = 11$ clutches). In species for which we have large samples, the body sizes of the smallest field-collected animals may provide an indication of size at hatching. Among such samples, the smallest individuals that we recorded were 12.0 cm SVL (*C. maculatus*) to 22.9 cm SVL (*C. rhombeatus*). Mean clutch sizes differed among species, ranging from 1 to 26 (ANOVA with clutch size as the dependent variable, species as the factor; $F_{5,83} = 10.3$, $P < 0.0001$; Table 6). Fecundity increased with maternal body size [analysis of covariance (ANCOVA) with clutch size as the dependent variable, species as the factor and SVL as the covariate; effect of size: $F_{1,81} = 59.2$, $P < 0.0001$; Fig. 3]. Relative to maternal SVL, mean clutch sizes differed significantly among species

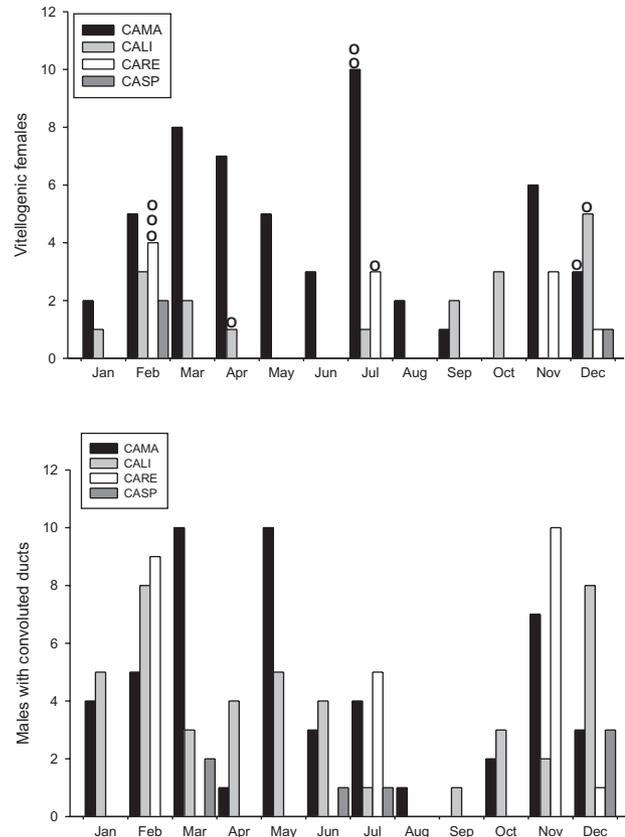


Figure 2. Seasonal patterns of reproduction in *Causus* species. Females were classified as vitellogenic if they contained vitellogenic (> 10 mm diameter). ‘O’ refers to females with oviductal eggs. Males with convoluted epididymial ducts were considered as potentially sexually active. CAMA, *Causus maculatus*; CALI, *Causus lichtensteinii*; CARE, *Causus resimus*; CASP, *Causus* sp.

(effect of species: $F_{5,81} = 5.6$, $P < 0.001$, Table 6); for example, female *C. rhombeatus* produced more eggs than did female *C. lichtensteinii* at the same body length (Fig. 3).

FEEDING HABITS

Prey type

The only prey remains found in *Causus* guts were anurans and insect fragments (Table 7). Several of the prey taxa that we found had not previously been recorded from these snakes (Table 7).

Proportion of fed individuals

We found prey or evidence of a recent meal (frogs, insect fragments or faeces) in most of the snakes that we examined (Fig. 4). The proportion of snakes containing prey varied from 67–86% (comparing among species, $\chi^2 = 14.0$, d.f. = 5, $P = 0.016$). Even if the anal-

Table 6. Fecundity of six species of snakes of the genus *Causus*

	<i>Causus defilippii</i>	<i>Causus lichtensteinii</i>	<i>Causus maculatus</i>	<i>Causus resimus</i>	<i>Causus rhombeatus</i>	<i>Causus sp.</i>
Mean clutch size	7.0 (1)	5.7 ± 0.8 (23)	8.5 ± 0.6 (47)	14.2 ± 1.2 (10)	18.5 (2)	12.5 ± 1.6 (6)
Relative clutch size	12.3 (1)	7.2 ± 0.6 (23)	9.6 ± 0.5 (46)	10.9 ± 1.0 (10)	17.2 (2)	9.2 ± 1.3 (6)

Mean clutch size and relative clutch size (adjusted to snout–vent length using analysis of covariance) in the six species are shown. Data are means with standard errors (*N*).

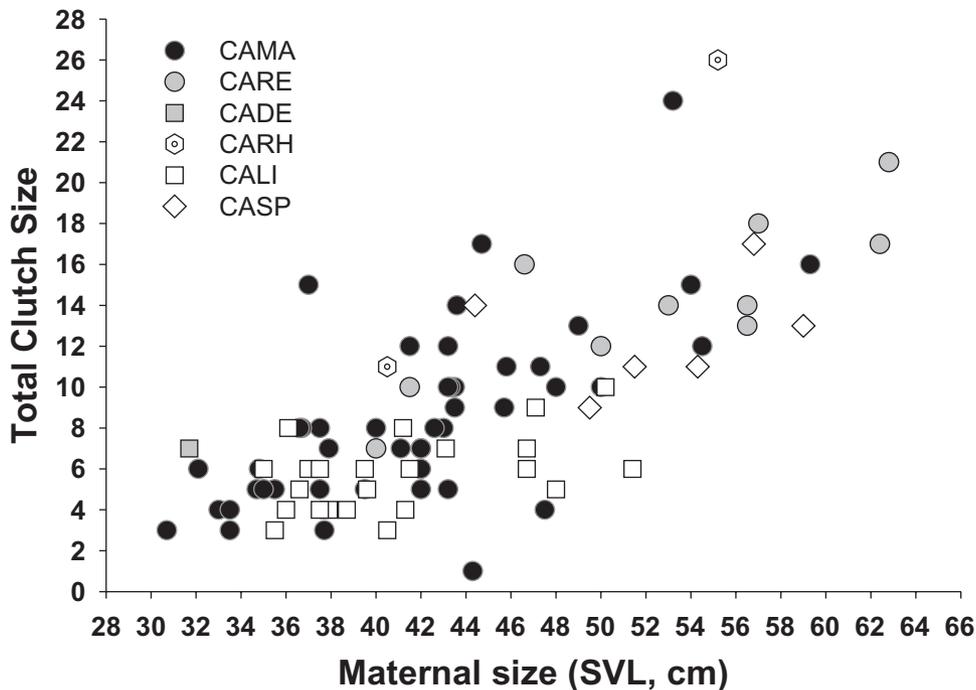


Figure 3. Relationship between maternal body size and total clutch size in six species of night adders. CAMA, *Causus maculatus*; CARE, *Causus resimus*; CADE, *Causus defilippii*; CARH, *Causus rhombeatus*; CALI, *Causus lichtensteinii*; CASP, *Causus sp.*

ysis is restricted to freshly ingested prey (relatively undigested anuran remains), the proportion of recently fed snakes averaged 34% (Fig. 4). Females containing oviductal eggs also frequently contained prey (79 of 108 specimens; 68%); thus, analysis did not reveal any significant decrease in feeding rate associated with reproduction ($\chi^2 = 0.45$, d.f. = 2, $P = 0.80$). We rarely found undigested frogs and insect fragments in the gut simultaneously, and snakes with insect fragments in the stomach rarely contained faeces in the hindgut. However, intact prey items were often found in the stomachs of snakes whose hindguts contained faeces ($\chi^2 = 27.00$, d.f. = 1, $P < 0.001$; Fig. 5). These patterns suggest frequent feeding and rapid passage of prey items through the digestive tract.

Relationship between snake body size and prey size
Causus often contained large prey. In many cases, the diameter of a prey item ($N = 63$) exceeded the jaw length and/or body diameter of the snake that had ingested it (Fig. 6). For 11 frogs for which we could confidently measure or estimate prey mass prior to ingestion, the ratio of prey mass to predator mass was in the range 7–150% (mean = 51%, SD = 44%).

Larger snakes consumed larger prey items (ANCOVA with prey diameter as the dependent variable, species as the factor and jaw length as the covariate; effect of jaw size: $F_{1,52} = 24.1$, $P < 0.0001$; Fig. 6). Larger snakes not only took larger prey, but also ceased feeding upon small prey (note the absence of records of small prey items in large snakes in Fig. 6).

Table 7. Composition of the diet of six species of *Causus* inferred from the analysis of stomach contents of museum specimens

Prey taxon	<i>Causus deflippii</i>	<i>Causus lichtensteinii</i>	<i>Causus maculatus</i>	<i>Causus resimus</i>	<i>Causus rhombeatus</i>	<i>Causus sp.</i>
Anura	8	14	38	10		17
Bufonidae						
<i>Bufo</i> sp.		8	12	1		4
<i>Bufo regularis</i>		1	7	1		2
<i>Bufo camerounensis</i>		1*				
<i>Bufo maculatus</i>		1*				
Ranidae						
<i>Pyxicephalus edulis</i>				1*		
<i>Ptychadaena</i> sp.		1*	1*			
<i>Ptychadaena mascareniensis</i>				2*		
Rhacophoridae						
<i>Chiromantis rufescens</i>		1*				
Hyperoliidae						
<i>Kassina</i> sp.				1*		
<i>Kassina senegalensis</i>				1*		
Arthroleptidae						1*
<i>Cardioglossa</i> sp.		4*	2*			
<i>Cardioglossa leucomystax</i>		2*	2*			
<i>Leptodactylodon</i> sp.		2*				
Insect fragments	3	50	34	14	6	31

*A new (previously unrecorded) prey type for the species in question.

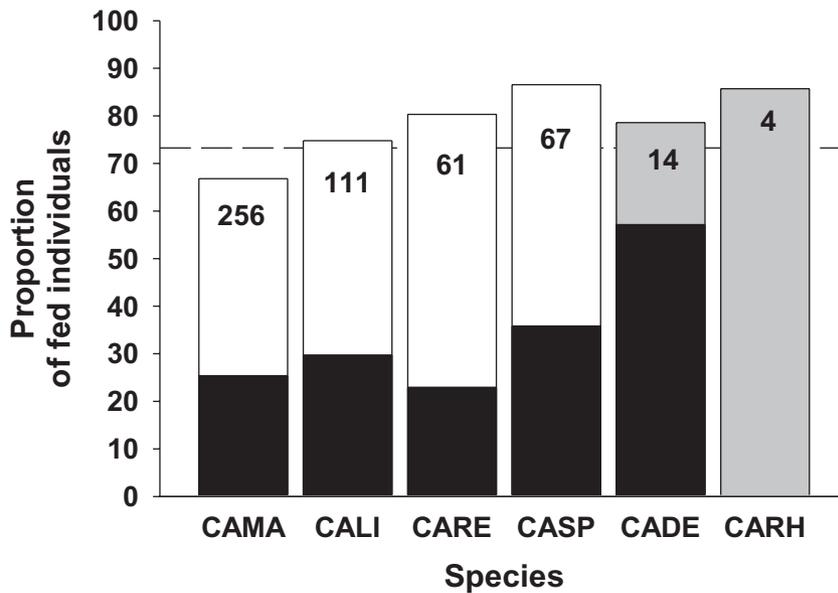


Figure 4. Proportion of snakes found with an indication of a recent meal (combined information from frog, insects, or faeces) and proportion of snakes with a frog in the stomach (black bars). Numbers provide sample sizes. Grey bars indicate small sample sizes. CAMA, *Causus maculatus*; CALI, *Causus lichtensteinii*; CARE, *Causus resimus*; CASP, *Causus sp.*; CADE, *Causus deflippii*; CARH, *Causus rhombeatus*.

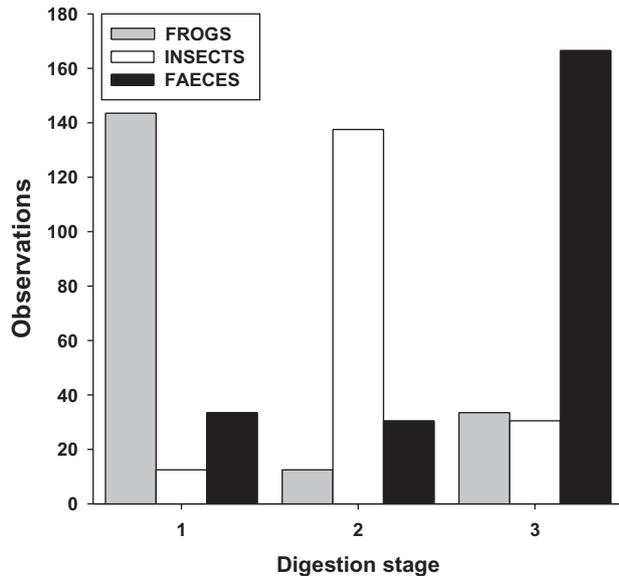


Figure 5. Prey items found in the digestive tract of six species of *Causus*. On the x-axis, each number corresponds to one of three stages in digestion: 1, snakes that contained recently ingested (hence undigested) anuran prey in the stomach rarely also had insect fragments in the stomach, but a few had small quantities of faeces in the hindgut; 2, of the snakes without identifiable anurans in the stomach, many had many insects fragments that presumably had been part of the stomach contents of digested anurans; 3, snakes that abundant faecal material in the hindgut often lacked any identifiable prey items in the stomach.

Prey sizes relative to predator size differed significantly among species (ANCOVAs with prey diameter as the dependent variable, species as the factor: $F_{4,57} = 5.83$, $P < 0.001$ with SVL as the covariate; $F_{4,52} = 2.73$, $P = 0.04$ with jaw length as the covariate; and $F_{4,57} = 2.38$, $P = 0.06$ with body diameter as the covariate).

DISCUSSION

Although our sample sizes are small for some taxa, the overall sample is relatively large ($N = 516$) and most of these animals were killed and preserved immediately after capture. Thus, our data set provides a more detailed insight into the natural history of *Causus* than has been available from any previous work. Despite significant interspecific divergences in some traits (such as the direction and degree of sexual size dimorphism), many common features were apparent. For example, absolute mean body sizes were relatively similar across taxa; all are oviparous, producing large clutches of relatively small eggs; most adult-size females and all adult-size males were reproductive when collected; and approximately one-third of the

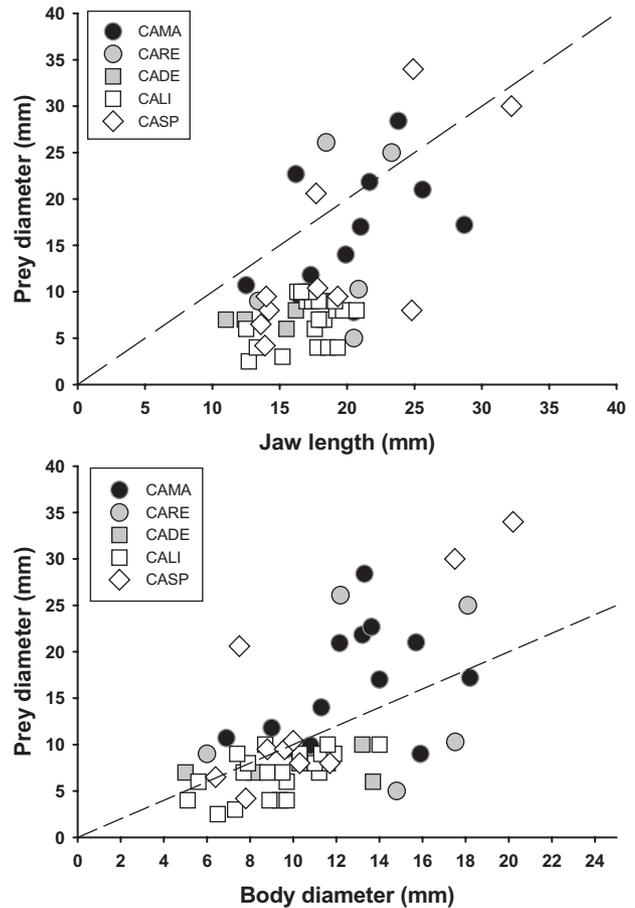


Figure 6. Relationship between prey size and snake jaw size (upper graph) or snake body diameter (lower graph). The dotted line indicates equality, where the prey dimension equals the snake dimension. CAMA, *Causus maculatus*; CARE, *Causus resimus*; CADE, *Causus defilippii*; CALI, *Causus lichtensteinii*; CASP, *Causus sp.*

snakes were juveniles, consistent with high and relatively aseasonal reproductive activity. The alimentary tracts of most of the snakes contained evidence of freshly ingested frogs and toads, suggesting a high frequency of feeding.

In all of these respects, night adders differ significantly from the cool-climate (European and North American) viperid species that have been the focus of previous study. Below, we compare our data on *Causus* with previously published data on other viperid taxa.

SEXUAL DIMORPHISM

Comparative analyses have shown that the direction of SSD among snakes is related to the mating system: males grow larger than females in species in which rival males engage in physical combat, and thus benefit from larger size via sexual selection

(Shine, 1994a). Male–male combat has been reported in three species of the genus *Causus* (*C. defilippii*, *C. lichtensteinii*, *C. maculatus*; O’Shea, 2003) and may well occur in all taxa (Shine, 1994b; Schuett, Gergus & Kraus, 2001; Pearson, Shine & Williams, 2002b). The opposing force of fecundity selection, whereby a larger body size significantly enhances reproductive output, favours large body size in females relative to males (Darwin, 1871; Andersson, 1994). The balance between these forces, in combination with other factors (e.g. food availability; Pearson, Shine & How, 2002a; Pearson *et al.*, 2002b) determines the direction and the degree of SSD (Shine, 1991). Thus, it is interesting to note geographical variation in patterns of SSD within major viperid lineages. All species of North American rattlesnakes except the sidewinder (*C. cerastes*) have males larger than females, and to approximately the same degree (Klauber, 1956). Conversely, females are the larger sex in the cool-climate European species of the genus *Vipera* (Saint Girons, 1952). Thus, although male–male combat occurs and larger female body size enhances fecundity in all three of these viperid lineages (*Vipera* in northern Europe; *Crotalus* in North America; *Causus* in Africa: Klauber, 1956; Branch, 1998; Shine, 1991; present study), the equilibrium between these selective forces has generated different patterns: male-biased SSD in rattlesnakes, female-biased SSD in northern European vipers, and interspecifically variable SSD within *Causus*. Males averaged larger than conspecific females in all taxa except *C. maculatus*, but females grew significantly larger than males in the latter taxon (Table 2).

Causus also display significant sexual divergence in body proportions; males of all species have longer tails and smaller heads than females of the same SVL, although the magnitude of this sex disparity varies among species (Table 3). Increased tail length in male snakes relative to females has been attributed to several selective forces, including sexual selection on males and fecundity selection on females (King, 1989; Shine & Shetty, 2001). The sex-based divergence in head sizes is more likely to involve food habits, especially prey size: a larger head enables these gape-limited predators to ingest larger prey (Shine, 1991; Pearson *et al.*, 2002a, b). In some intensively studied species of snakes from other lineages, the sex with the larger relative head size (generally the female) does indeed consume larger prey (Houston & Shine, 1993).

REPRODUCTIVE BIOLOGY

Published reviews of squamate life-histories have identified a consistent suite of traits in viperid snakes from Europe and North America (Parker & Plummer, 1987; Dunham, Miles & Reznick, 1988). These include

slow growth, late maturation (> 4 years), infrequent and highly seasonal reproduction, viviparity, large offspring size relative to maternal size, and small litter size (Parker & Plummer, 1987). For example, female timber rattlesnakes (*C. horridus*) mature at approximately 7–13 years of age, and produce a litter of approximately six to ten neonates, each approximately 32% of maternal SVL, at intervals of 2–3 years (Brown, 1993; Ernst & Ernst, 2003). Similarly, female asp viper (*Vipera aspis*) reproduce on a 3-yearly basis (Naulleau & Bonnet, 1996).

Although dissections of freshly-killed specimens cannot provide the same degree of insight as long-term mark-recapture studies, our data reveal that the life-history of *Causus* differs substantially from that described above. Given the warm climate, high rates of feeding and large prey sizes of *Causus*, these animals are likely to grow rapidly and thus, attain sexual maturity at relatively young ages (by analogy with other tropical snakes; Brown & Shine, 2002). The co-occurrence of oviductal eggs and vitellogenic ovarian follicles suggests that some females, at least, produce clutches of eggs in rapid succession. This ability has been reported in captive *C. rhombeatus*, with one animal producing more than seven clutches, each of 11–18 eggs, in quick succession (at intervals of 3–5 weeks; Woodward, 1933). Oviparity rather than viviparity is the mode of reproduction for all of the *Causus* for which data are available (Tinkle & Gibbons, 1977). The same ecological conditions allow *Causus* to reproduce year-round, whereas seasonal shifts in temperature constrain reproduction to the summer months in most temperate-zone reptiles (Fitch, 1970, 1982). Night adders also produce larger clutches of smaller offspring than have been reported for most other viperid species. Optimal offspring sizes may be constrained by the size spectra of available prey items (Nussbaum, 1985), and amphibian-eaters such as *Causus* species may have access to a wider range of small prey items (and hence be able to ‘afford’ a smaller size at hatching) than would be true for a mammal-specialist like many of the north-temperate viperid species.

The presence of vitellogenic follicles in female night adders regardless of the volume of their abdominal fat bodies (energy reserves) suggests that these animals may combine ‘income’ and ‘capital’ breeding tactics rather than relying solely upon stored body reserves to fuel reproductive expenditure (Drent & Daan, 1980; Jönsson, 1997; Bonnet, Bradshaw & Shine, 1998). This hypothesis accords well with the apparently rapid reproductive rate of female night adders. Because ‘capital breeders’ must necessarily delay the next clutch until they have accumulated sufficient energy reserves, they typically reproduce only at long intervals (Bonnet *et al.*, 2002). Similarly, the fact that

female night adders continue to feed even when carrying oviductal eggs stands in sharp contrast to many other snake species in which females (and often, males) forego feeding during the reproductive season (Madsen & Shine, 1993). The anorexia of gravid females may reflect conflicts between feeding and careful thermoregulation, with females in cool climates selecting sites that provide optimal basking opportunities but no access to food (Shine, 1980; Lourdais, Bonnet & Doughty, 2002). The easy access to high ambient temperatures in tropical Africa may weaken or remove such a conflict, allowing females to continue feeding year-round.

FOOD HABITS

Our study extends considerably the diversity of prey items consumed by night adders, both in terms of prey species and in terms of a snake's diet (Table 7). Nonetheless, we found only amphibians as food items, in contrast to previous reports of mammals and reptiles as prey items for *Causus* (Spawls & Branch, 1995; Luiselli *et al.*, 2004). However, amphibians also represent the majority of prey items in these previous studies. Anurans are a common prey type for snakes of many phylogenetic lineages worldwide, including many viperid species (Mori, Toda & Ota, 2002), but *Causus* in our study are somewhat unusual in feeding entirely on anurans. Many anuran-eating snake species also take occasional prey of other types, and frequently display an ontogenetic shift from anurans to mammals with increasing body size (Shine, 1994b). Most anuran-specialist snakes are relatively small-bodied, such as *Causus*, so that the predominance of mammal-specialization in many species of European vipers and North American rattlesnakes may reflect the large body sizes attained by these animals, as well as the diverse and abundant rodent resources of north-temperate grasslands and forests (Saint Girons, 1952). However, some aspects of the trophic relationships of *Causus* resemble those of previously studied viperids from other parts of the world. For example, a trend for larger snakes to forego smaller prey items, as seen in *Causus* (Fig. 6), has also been reported in rattlesnakes that feed on mammals (Reynolds & Scott, 1982) and Chinese vipers that eat birds (Shine & Sun, 2003).

In summary, our data paint a picture of a tropical snake lineage that differs in fundamental ways from its better-studied relatives in cooler parts of the world. Those differences are profound, ranging from general morphology through to reproductive biology, life-history, and trophic ecology. Many of the distinctive ecological characteristics of night adders may be direct effects of their environment; for example, year-round high temperatures and abundant amphibian prey may

directly induce a 'faster' life-history than seen in cooler-climate taxa (Adolph & Porter, 1991). Other aspects, such as reproductive modes and output (clutch and offspring sizes), must reflect genetic factors, and presumably are adaptive.

In many respects, night adders resemble colubrid snakes rather than other viperids. The most obvious traits are morphological; for example, entire (rather than fragmented) cephalic shields, round pupils, a relatively slender body form, and a relatively small head. To this list, we can add ecological traits such as reliance on amphibian prey, and frequent reproduction with large clutches of small eggs (for a comparison of viperid vs. colubrid reproductive tactics, see Parker & Plummer, 1987; Naulleau & Bonnet, 1995). Prey size is an ecological attribute in which *Causus* is distinctly viper-like rather than colubrid-like. *Causus* often consume anurans that are very large relative to the size of the predator; some prey items weighed as much as the snakes that consumed them (Fig. 6). The literature reports such high relative prey masses primarily in viperid snakes rather than colubrids (Greene, 1997).

Thus, we suggest that the key innovation in early vipers may have involved modifications of head morphology that facilitated the capture, subdugation, and ingestion of remarkably large prey items. Clearly, macrostomate (large-gape) feeding habits arose very early in snake phylogeny, well before the origin of the Viperidae (Haas, 1952; Greene, 1983, 1997; Wilcox *et al.*, 2002). However, early viperids may have refined such abilities even more than the colubroid stock from which they arose. By providing access to large (and thus nutrient-rich) prey types inaccessible to similar-sized snakes of other lineages, these traits may have allowed proto-vipers to extend their range across many habitat types. Because they encountered rodent-rich habitats of the temperate zone, vipers accumulated a series of secondary adaptations (such as viviparity, capital breeding, and large offspring size) that enhanced their ability to exploit these distinctive areas. However, regardless of the validity of this speculation, our study shows that any generalizations about viperid snakes must be wary with respect to zoogeographical (and hence phylogenetic) biases in the existing database.

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