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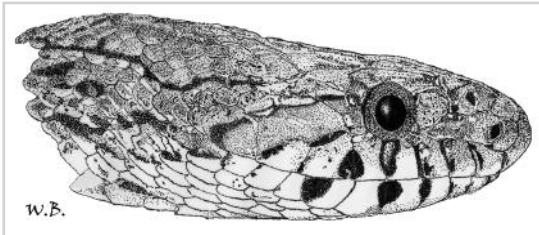
All submissions and correspondence arising from the Bulletin should be sent to the Editor, Peter Stafford, c/o Dept. of Botany, The Natural History Museum, Cromwell Road, London, SW7 5BD. *E-mail:* herpbulletin@thebhs.org

Front cover illustration. Bengal monitor (*Varanus bengalensis*) positioned at the entrance of its home-site at night in what may be 'sentinel' behaviour. Photograph © Edie Jolley. See article on page 31.

EDITORIAL

Correction

The caption to Will Brown's illustration of a Corn snake in *Herpetol Bull.* 94 (page 21) – reproduced again below – was incorrectly described as a 'photograph manipulated and enhanced using



digital imaging software'. In fact this was an original pen and ink illustration. The editor would like to apologise for this oversight.

Author's reprints

Due to rising postage costs and the increasing demand for electronic copies of articles, it has been decided that with effect from issue number 96 (Summer 2006), off-prints of articles published in the *Bulletin* will no longer be supplied to authors. All contributors, however, will continue to receive a complimentary printed copy of the issue in which their article is published. *Ed.*

Important announcement

The British Herpetological Society is preparing an online subscription for Institutions, Overseas and Full UK members, to be launched fully for 2007. From January 2007, the *Herpetological Journal* will be available as an online publication through our provider, Ingenta. Initially, only the *Herpetological Journal* will be available online; the *Herpetological Bulletin* will remain in hardcopy and be delivered via surface mail. It is planned to include the *Bulletin* in the online subscription by 2008/9. In brief, the advantages to members will be faster access to publications as they are released, access to all available back-copies, and cheaper subscription. Papers will of course be available as downloads, providing all the benefits that electronic access to documents brings, such as keyword searching, filing, etc. The Society will benefit from greater exposure of its content, including abstracts of all papers to non-members, and reduced printing and posting costs. In order for subscribing BHS members to test and check access to the services provided by Ingenta, all issues of the *Herpetological Journal* published during 2006 will be available online. Volume 15, No. 4 and Volume 16, No. 1 are available now. All BHS members (full inland, overseas and institutions) are invited to try this service to ensure error-free access. Please note you will need your membership number to gain access to online publications.

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Trevor Rose, BHS Secretary



Occurrence of the alien Bedriaga's frog (*Rana bedriagae*) Camerano, 1882 in the Maltese Islands, and implications for conservation

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ABSTRACT — We document the occurrence of Bedriaga's frog *Rana bedriagae* Camerano, 1882 in the freshwater pool of L-Ghadira ta' Sarraflu on the island of Gozo, one of the very few naturally occurring permanent bodies of water in the Maltese Islands, and a protected site. The frog is an alien species that appears to have been deliberately introduced in the late 1990s and to have established a breeding population at Ta' Sarraflu and possibly at two other sites on Gozo and at one site on Malta. Spread of the alien seems to be through human agency, not natural dispersal. Occurrence of the alien frog may have an impact on the only native amphibian, the Painted frog *Discoglossus pictus pictus* Otth, 1837, a protected species, as well as on the biota of the freshwater systems where the alien occurs, which are within or in close proximity to, protected sites and candidate Natura 2000 Special Areas of Conservation.

WHILE fossil remains of toads (*Bufo* spp.) have been recovered from Quaternary deposits in the Maltese Islands (reviewed by Hunt & Schembri, 1999), the only living amphibian that has ever been reported from the islands is the Painted frog, *Discoglossus pictus* Otth, 1837 (Lanza, 1973; Baldacchino & Schembri, 2002). This species is highly adapted to live in the semi-arid Maltese environment, where it thrives in spite of a dearth of freshwater (Sammut & Schembri, 1991). The Painted frog has a very limited distribution, with one subspecies (*Discoglossus pictus pictus*) occurring in Sicily and the Maltese Islands, and another (*Discoglossus pictus auritus*) in Algeria, although it has been introduced to parts of southern France and NE Spain (Lanza *et al.*, 1986).

Against this background, the discovery of a thriving population of a species of water frog in the permanent freshwater pool at Ta' Sarraflu on the island of Gozo was surprising. This population was discovered when one of us (AS) investigated the origin of strange calls that were being heard from the pool area. These peculiar calls were first noticed in mid-April 2000 but were initially

dismissed as those of a water bird; however, after they could not be assigned to any water bird that occurs in the Maltese Islands, more careful study showed them to be similar to those made by water frogs. Investigation of the water in the pool revealed the presence of the Painted frog, but also of a larger and different species that proved very difficult to observe since at the slightest movement individuals disappeared very rapidly under water and into the dense reed beds in the pool. It was only on 27th May 2004 that we managed to take photographs of this animal; the first specimens were captured on 5th September 2004 (Fig. 1).

Size, colour and morphology of the 'new' species from Ta' Sarraflu indicated it to belong to the southeastern European/northeastern African group of water frogs, possibly *Rana ridibunda*/R. *bedriagae* or a related species (Fred Kraus, pers. comm.; Ulrich Sinsch, pers. comm.). Because of the great morphological similarity in frogs within this group and the small sample size available for study, specific determination was made by Prof Ulrich Sinsch (Institut für Zoologie, Universität Bonn, Bonn, Germany) on the basis of analysis of eight male advertisement calls recorded in the

field on 29th March 2005. All calls analysed had 12–20 pulse groups per call and each pulse group had 6–8 pulses, which are coincident with reference calls from *Rana bedriagae* recorded from Egypt to Turkey (Ulrich Sinsch, personal communication; Schneider & Sinsch, 1992; 1999). We are therefore confident that the 'new' frog from Ta' Sarraflu is Bedriaga's frog, *Rana bedriagae* Camerano, 1882. The native distributional range of *Rana bedriagae* is Cyprus, Egypt, Greek islands close to the Turkish coast, Israel, Jordan, Lebanon, Syria and Turkey; it is also present in Iraq and possibly further east (Arnold & Ovenden, 2002; IUCN, 2004). This frog is not native to the Maltese Islands but has been introduced, probably sometime in the late 1990s. Given their larger size, different coloration and the very loud noises these frogs make, especially in spring and summer when the males establish territories and court females, it is unlikely that these animals would have been overlooked, especially given that many naturalists, including ourselves, visit Gozo regularly and that there are no other species present in the Maltese Islands that make comparable calls; in fact, it was the unusual calls from Ta' Sarraflu that alerted us to the presence of this species in the first place.

When first detected in 2000, some six individual males were heard calling at Ta' Sarraflu. At present (spring and summer of 2005) about 50 males can be heard calling at any one time. Eggs, tadpoles and froglets of the alien are also present in the pool. This suggests that *Rana bedriagae* has established an actively breeding population at Ta' Sarraflu and that this population has increased at least tenfold over a period of five years. Whether the carrying capacity of the pools has been reached or not is unknown.

How this species was introduced to Gozo is not clear, but in all probability it was introduced deliberately perhaps in a misguided attempt to 'embellish' the environment. Some farmers in the area whom we questioned are of the opinion that the frogs were obtained from overseas and released by a resident of Gozo in the early 1990s; however, we cannot confirm this since the person indicated is now deceased. Up until Malta's

accession to the European Union in 2004, the local Environment Protection Department (EPD) operated a system whereby any importation of biota from overseas required a permit from the EPD. These regulations were put in force specifically to control the entry of potentially problematic alien species into Malta. According to the records of the EPD, prior to 1st May 2004, requests for the importation of a number of species of *Rana* were received and processed by the Department, however, *Rana bedriagae* was not amongst these and no species of *Rana* was actually imported. After Malta's accession to the European Union on 1st May 2004, the requirement for an import permit for species originating from EU member states was abolished in accordance with the principle of free trade. However, as the alien species was already established by 2000, we exclude the possibility that the Ta' Sarraflu population originates from legally imported material.

The presence of *Rana bedriagae* in the pool at Ta' Sarraflu is of concern. L-Ghadira ta' Sarraflu (as the pool is known) is a very important habitat in the local context since it is one of very few pools where natural freshwater accumulates and persists throughout the year, even during the hot summer months when most other freshwater dries up (mean annual rainfall in Malta is ca 530 mm of which some 85% falls during the period October–March; Chetcuti *et al.*, 1992). A significant number of plant and animal species that require a perennial supply of freshwater occur there but are overall very rare in the Maltese Islands, as their habitat is rare. For this reason the pool at Ta' Sarraflu has been scheduled as a Level 1 Area of Ecological Importance and Site of Scientific Importance under the Development Planning Act of 1992 (Government Notice 288 of 1995), while the entire western coastal area of Gozo, including L-Ghadira ta' Sarraflu, has been declared a Candidate Special Area of Conservation of International Importance in the Flora, Fauna and Natural Habitats Protection Regulations, 2003 (Legal Notice 257 of 2003); these regulations transpose the requirements of the European Union's 'Habitats Directive' to local legislation.

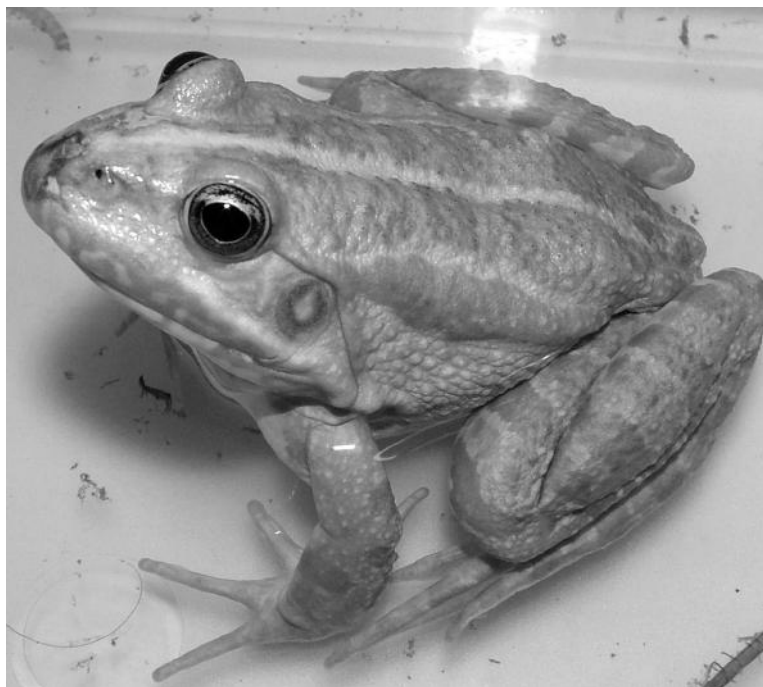


Figure 1. *Rana bedriagae* collected from the pool at Ta' Sarraflu in Gozo. Photograph © Arnold Sciberras.

What the impact of the alien water frog on the biota and ecology of the pool has been, or will be, is not known, but *Rana* are known to be voracious predators and to eat the tadpoles and froglets of smaller species as well as a large variety of invertebrates. In captivity, we observed *Rana bedriagae* from Ta' Sarraflu to be unselective feeders on beetles, dragonflies and cockroaches, as well as on bees and wasps (which *Discoglossus pictus* rejects). We have also observed predation by *Rana bedriagae* on larval and juvenile *Discoglossus* on numerous occasions and on two instances we observed a large individual of *Rana bedriagae* (>15 cm length) prey on the shrew *Crocidura sicula calypso* (a protected, endemic subspecies), and at another time an equally large *Rana bedriagae* preying on a juvenile House mouse (*Mus musculus*), close to the water's edge. On the other hand, on four occasions we observed large *Discoglossus* (one individual ca 8.5 cm, and three individuals ca 7 cm in length) feeding on *Rana* froglets (<3 cm length).

Rana bedriagae and *Discoglossus pictus* currently co-exist at Ta' Sarraflu. For the present, *Rana bedriagae* seems to be confined to the pool because of its requirements for water, however, the population of *Discoglossus* is probably replenished from the surrounding environment since the native frog is able to transverse large expanses of arid ground. Unlike *Discoglossus pictus*, which is active during the wet season (October to March), we observed *Rana bedriagae* to spend cold periods when the temperature falls below 15 Celsius in a state of quiescence under water and to become active during spring and summer, that is, at the tail end of

the wet season and during the dry season. Nonetheless, the impact of *Rana* on *Discoglossus* and on the pool and bank biota needs to be studied, especially given the status of L-Ghadira ta' Sarraflu as a protected area and of *Discoglossus pictus* as a locally protected species.

It is worrying that we have recently heard calls of what is probably *Rana bedriagae* from two other localities on Gozo: Il-Wied tax-Xlendi, where the calls came from dense reed beds in a wet and thickly vegetated part of the valley, and from a deep artificial pool at Nadur. We have yet to confirm the species here by actual specimens or acoustic characterisation. We have also seen what appears to be the same species in a reservoir within the grounds of a tourist complex at Mellieha Bay on the island of Malta. Additionally, we have information that what may be this species is also available from street markets on Malta. It is likely that the apparent spread of the alien frog on Gozo is more due to transport and release by humans than to natural dispersal; we have seen children at Ta' Sarraflu capturing the frogs with nets to be kept as 'pets'. The presence of an alien *Rana* at Il-Wied tax-Xlendi and at Mellieha Bay is

of particular concern since the areas where the frogs occur are in close proximity to ecologically important scheduled sites and within candidate NATURA 2000 sites. In this regards we recommend that measures be taken with urgency to prevent the further spread of the alien by humans and to control the populations where it has already established itself, especially at this early stage when the alien species is still present in a few, contained areas.

ACKNOWLEDGEMENTS

The authors thank Jonathan Abela, Nimrod Mifsud, Esther Schembri and Jeffery Sciberras for help with fieldwork, Dr Fred Kraus (Bishop Museum, Honolulu, Hawaii) for taxonomic advice and much other information, Prof. Ulrich Sinsch (Institut für Zoologie, Universität Bonn, Germany) for kindly identifying the species and other help, and Ms Charmaine Muscat (Environment Protection Department, Malta Environment and Planning Authority) for information about import permits.

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A review of morphological and pattern variation in the Painted turtle, *Chrysemys picta*, in Missouri, USA, with an alternate hypothesis of the origin of *Chrysemys picta marginata*

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THE Painted turtle, *Chrysemys picta*, as traditionally recognized, is composed of four distinct subspecies (Ernst, 1971; Ernst *et al.*, 1994). *Chrysemys picta picta*, the Eastern painted turtle, ranges from southeastern Canada through New England south along the Atlantic coastal plain to Georgia and west into eastern Alabama. It has the vertebral and pleural scutes of its carapace aligned (the only turtle with this condition) light borders along the carapace seams, a narrow light vertebral stripe, and a mostly unpatterned plastron (some dark spotting may occur). *Chrysemys p. dorsalis*, the Southern painted turtle, occurs from extreme southwestern Kentucky and southeastern Missouri southward in the Mississippi Valley to the Gulf Coast of Louisiana and eastward through Mississippi into Alabama, and formerly in a relict population in southeastern Oklahoma and adjacent Texas. It is distinguished by having a conspicuous, broad, red or yellow, vertebral stripe, light borders along the carapace seams, the vertebral and pleural scutes disaligned, and an unpatterned plastron. *Chrysemys p. marginata*, the Midland painted turtle, is found from southern Quebec and Ontario south in the central United States to Tennessee and northern Alabama. Its range is east of the Mississippi River, extending eastward to New England, Pennsylvania, Maryland, Virginia, and the Carolinas. It has disaligned pleural and vertebral scutes, dark or no border along the carapace seam, a narrow often interrupted or

absent vertebral stripe, and a variable dark pattern that is commonly less than half the width of the plastron. *Chrysemys p. bellii*, the Western painted turtle, ranges from western Ontario across southern Canada to British Columbia and south to Missouri, northern Oklahoma, eastern Colorado, Wyoming, Idaho, and northern Oregon. It also occurs in scattered localities in the southwestern United States and at one site in Chihuahua, Mexico. It is the largest subspecies (CL_{max} 25.1 cm), and has alternating vertebral and pleural scutes, a light reticulate pattern on the carapace, narrow light borders along the carapace seams, a narrow sometimes interrupted light vertebral stripe, and a plastron pattern which branches outward along the seams to occupy most of the plastron.

Where the ranges of the subspecies of *C. picta* meet, zones of intergradation occur, and these have been well studied at various areas of the geographical range. Data on intergradation are known from the Northeast and adjacent Canada (Babcock, 1933; Hartman, 1958; Waters, 1964, 1969; Pough & Pough, 1968; Klemens, 1978; Gordon, 1990; Rhodin & Butler, 1997; Wright & Andrews, 2002), Pennsylvania (Ernst & Ernst, 1971); Maryland (Groves, 1983), Kentucky and Tennessee (Johnson, 1954; Ernst, 1970), the southern Gulf states (Ernst, 1967; Muir, 1989), and the Upper Peninsula of Michigan (Ernst & Fowler, 1977). In addition, overall subspecific

variation in morphology and colour patterns has been examined by Bishop & Schmidt (1931), Hartweg (1934), Bleakney (1958), and Ultsch *et al.* (2001).

Bleakney (1958) proposed a theory as to the places of origin of the four subspecies, and how they subsequently migrated into their present geographical ranges after the Wisconsinian glacial period. He thought that at the end of the last North American glacial period painted turtles (*Chrysemys*) were divided into three separate populations, which may well have represented separate incipient species that had not yet evolved reproductive isolation: *C. picta* in the southeastern Atlantic coastal region, *C. dorsalis* in the lower Mississippi River Valley, and *C. bellii* in the Rio Grande River and Pecos River watersheds of New Mexico.

According to Bleakney, these three populations extended their ranges northward with the retreat of the glaciers. *Chrysemys dorsalis* moved up the Mississippi River and met *C. bellii* in the region of St. Louis 'near the Missouri-Mississippi-Ohio [rivers] junctures.' There, Bleakney hypothesized, the two hybridized and produced the species, *C. marginata*. *C. marginata* then spread up the Mississippi River and Ohio River watersheds, eventually reaching the northeastern United States and adjacent Canada. There it met and interbred with *C. picta*, which had migrated up the Atlantic Coast. It also met and interbred with *C. bellii* in Wisconsin and Michigan. Because the four 'species' had not evolved reproductive isolating mechanism to prevent gene exchange when their populations met, broad zones of intergradation were established.

Recently, Starkey *et al.* (2003) studied the molecular systematics of the four subspecies of *C. picta* by analyzing the variation in the rapidly evolving mitochondrial DNA control region. The genetic data gathered indicated that two monophyletic evolutionary clades exist in extant *Chrysemys*; one containing only *C. p. dorsalis*, and a second, extremely wide-ranging and genetically undifferentiated, clade that includes the other three subspecies. Based on this, Starkey

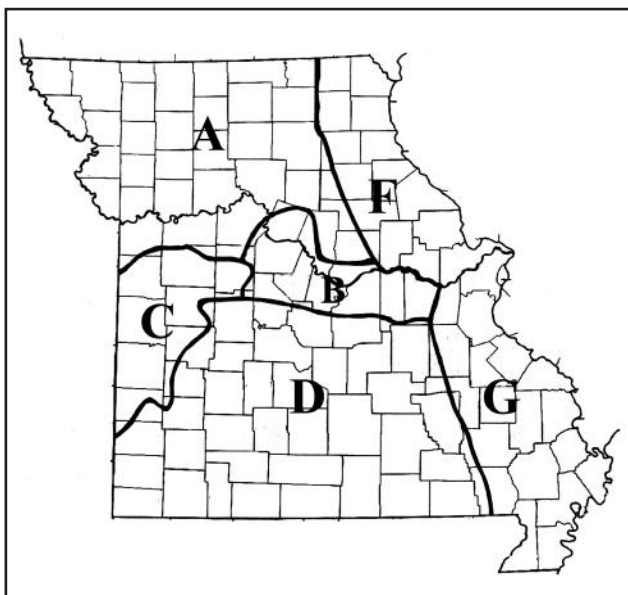


Figure 1. Map of Missouri, USA showing the Physiographic Provinces denoted by Thom & Wilson (1980), but with Province E deleted and intergrade Zones F and G inserted.

et al. concluded that *C. p. dorsalis* should be elevated to the full species *C. dorsalis*, and that the other three subspecies should remain within the current species *C. picta*.

We examined specimens of *C. picta* from throughout Missouri to document their subspecific status, and especially that of painted turtles from the St. Louis area, the proposed centre of hybrid origin of *C. p. marginata*. We present our results below, and offer an alternate hypothesis concerning the region of origin of *Chrysemys p. marginata*.

METHODS

A total of 195 specimens of *Chrysemys picta* from 58 counties in Missouri was examined. All were sexed using the characters of Ernst (1971), and their greatest carapace and plastron lengths recorded. All measurements were made with metric dial calipers accurate to 0.1 mm. Scute terminology used was that of Ernst *et al.* (1994).

The methods of measurement of Hartman (1958) were used to compare the degree of disalignment of the carapace laminal seams. When



Clockwise from top left: *Chrysemys picta belli* (adult), *C. p. belli* (juvenile), *C. p. marginata* (adult), *C. p. dorsalis* (male). Photographs © C. Ernst.

the seams between the central vertebral scutes and the lateral pleural scutes lie in the same transverse line, they were considered to be 0% disaligned; if the seams alternate exactly they were 100% disaligned. The base point for measuring is the inner end of the seam between the second and third pleural scutes. The imaginary line from the base point forward and parallel to the longitudinal axis of the carapace, to the point opposite the inner end of the seam between the first and second pleurals was measured, and was denoted 1a on the left side of the carapace, and 2a on the right side. The part of this same imaginary line starting at the base point between the second and third vertebrals was measured, and was denoted as 1b on the left side, and 2b on the right side. The average percent disalignment was then calculated as $1b/1a + 2b/2a$.

The light border of the anterior seam of the second pleural scute was measured at its widest

point and its colour noted. Red, orange, or yellow borders were considered characters of *C. dorsalis* and *C. p. belli*; black, olive, or no border pigmentation were considered characters of *C. p. marginata* (Ernst, 1971). The greatest width of the medial dorsal stripe on the carapace was measured on the second vertebral scute. Cagle (in Johnson, 1954) discovered the dorsal stripe to be wider than the widest foreleg stripe in *C. dorsalis*, but narrower in other subspecies of *C. picta*. The greatest width of the dorsal stripe was expressed as a percentage of the greatest width of the foreleg stripe. Percentages greater than 100 were regarded a character of *C. dorsalis*. The condition of the dorsal stripe was also noted. A complete, uninterrupted dorsal stripe was a character of *C. dorsalis* and *C. p. belli*, but a discontinuous, interrupted stripe was characteristic of *C. p. marginata*, as was also the absence of a dorsal stripe. The widths of both the pleural seam border and the dorsal stripe were scaled against the greatest carapace length of the turtle. In addition, the presence of (*C. p. belli*) or the absence of a

Zone	Plastron Mark	Character				
		Carapace Seam Disalignment	Carapace Seam Width	Carapace Stripe Condition	Carapace Stripe Width	Carapace Stripe/Foreleg Stripe
A <i>n</i> = 42	b = 40 (95.2%) b x m = 1 (2.4%) m = 1 (2.4%)	94.5% (70.3-104.4)	1.77 mm (0.6-4.0)	Cont. 25 (59.5%) Disc. 14 (33.3%) None 3 (7.1%)	0.63 mm (0-1.10)	47.9 (10.0 – 77.7)
B <i>n</i> = 25	b = 23 (92%) b x m = 2 (8%)	95.7% (93.4-98.3)	2.25 mm (0-4)	Cont. 25 (68%) Disc. 8 (32%)	1.13 mm (0.9-1.3)	64.4 (40.9-80.0)
C <i>n</i> = 14	b = 14 (100%)	91.1% (88.1-93.7)	1.95 mm (1.3-2.5)	Cont. 13 (93%) Disc. 1 (7%)	0.80 mm (0.50-1.10)	46.1 (27.7-64.7)
D <i>n</i> = 6	b = 6 (100%)	95.7% (93.4-98.3)	1.30 mm (1.0-1.5)	Cont. 2 (33.3%) Disc. 4 (66.7%)	0.7 mm (0.6-0.9)	35.9 (26.1-50.0)
F <i>n</i> = 41	b = 13 (31.7%) b x m = 20(48.7%) m = 8(19.5%)	95.6% (91-100)	1.4 mm (0-2.3)	Cont. 23 (56.1%) Disc. 17(41.5%) None 1 (2.4%)	1.03 mm (0.5-1.6)	54.8 (35.7-76.2)
G <i>n</i> = 23	d = 18 (78.3%) m x d = 2 (8.7%) m = 3 (13.0%)	76.6% (54.7-112.9)	2.68 mm (0-4.8)	Cont. 23 (100%)	2.8 mm (0.9-5.6)	161.1 (56.2-373.0)
Ky <i>n</i> = 96	m = 96 (100%)	36.8% (61.1-102.9)	1.68 mm (0.5-3.3)	Cont. 61 (63.5%) Disc. 31 (32.3%)	1.03 mm (0-2.0)	58.2 (1.1-100)
LM <i>n</i> = 80	d = 80 (100%)	54.8% (5.5-96.2)	1.70 mm (0.7-4.0)	Cont. 79 (98.8%) Disc. 1 (1-2%)	2.10 mm (1.0-3.8)	147.2 (70-345)
MN <i>n</i> = 61	b = 65 (100%)	93.5% (79.0-108.7)	1.99 mm (0.9-5.3)	Cont. 34 (55.7%) Disc. 22 (36.1%) None 5 (8.2%)	0.98 mm (0-2)	58.1 (24-100)

pattern of reticulating light lines on the carapace (*C. dorsalis*, *C. p. marginata*), were also noted.

Three patterns of dark markings occur on the plastron of the *Chrysemys* turtles (Bishop & Schmidt, 1931; Ernst, 1971). The pattern of each specimen was noted. The absence of a dark plastron pattern was considered a character of *C. dorsalis*. A large pattern of dark lines covering most of the plastron and extending outward from the centre along the seams was considered characteristics of *C. p. bellii*, and a more narrow central dark pattern lacking outward seam extensions was considered to be of *C. p. marginata*. Intermediate patterns between the latter two were considered intergrade, as was a pattern of only a few dark pigmented spots.

Data on Missouri *Chrysemys* were placed for comparison into five groups corresponding to the physiographic provinces of Missouri (Fig. 1) proposed by Thom & Wilson (1980) and described by Johnson (1987): A) The Glaciated Plains comprise the northern third of the state (28 counties sampled) and mark the southern-most

Table 1. Phenotypic characters by zones for Missouri *Chrysemys picta* (b = *bellii*, d = *dorsalis*, m = *marginata*, b x m = *bellii* x *marginata*, m x d = *marginata* x *dorsalis*).

limits of the Kansan Glacial Period. They feature rolling hills and wide flat valleys, with soils composed of glacial till and loess. Most of these occur within the Missouri River watershed, but waterways of the easternmost counties flow into the Mississippi River (Pflieger, 1975); B) The Ozark Border (14 counties sampled) forms a narrow system of river hills and sandstone bluffs, deciduous forests, wide river valleys, and deep soils along the lower Missouri River. Its southeasternmost watersheds flow into the Mississippi River (Pflieger, 1975); C) The Osage Plains (7 counties sampled) is an unglaciated region of rolling hills, streams, and tallgrass prairies with deep soils in west central Missouri. Waterways in most of the zone flow northeast into the Missouri River, but those of the southern portions drain southwestward out of the state

(Pflieger, 1975); D) The Ozark Plateau (4 counties sampled) is a rugged mountainous region of limestone bluffs, clear streams, and thin soils south of the Missouri River and east of the Ozark Plains. The northern counties drain into the Missouri River, waterways of the southwest flow out of the state in that direction, and the southern portions of the zone drain southward into Arkansas (Pflieger, 1975); and E) The Mississippi Lowlands (5 counties sampled) lie in the southeastern corner of the state on the floodplain of the Mississippi River, and contain swamps and bottomland hardwood forests.

In addition, 81 adult specimens of *Chrysemys dorsalis* from Louisiana and Mississippi, 99 adult specimens of *Chrysemys p. marginata* from Kentucky, and 61 adult specimens of *Chrysemys p. bellii* from southwestern Minnesota were included in the data set to ensure pure characters from these taxa for comparison with painted turtles from the supposed site of hybrid origin of *Chrysemys p. marginata* in the vicinity of St. Louis. These specimens were from localities outside the zones

Table 2. Classification by cross validation of individual turtles from zones F and G with complete data (b = *belli*, d = *dorsalis*, m = *marginata*, b x d = *bellii* x *dorsalis*, b x m = *belli* x *marginata*, and d x m = *dorsalis* x *marginata*).

of hybridization or intergradation between the respected taxa (Ernst, 1967, 1970; Ernst & Fowler, 1977).

Statistics were run using SAS package 8.2; levels of significance were set *a priori* at $P = 0.05$. To compare possible hybrids or intergrades, Fisher’s discriminant analysis was run on combined data from both sexes using the following nonsexually dimorphic variables: scute disalignment, seam width, carapace stripe width, and the width of the foreleg stripe. Normality was checked visually using probability plots. To analyze the data, first, a training data set was created using data from the known pure taxa (Ultsch *et al.* 2001, Starkey *et al.* 2003) under investigation from Kentucky, Mississippi and Louisiana, and Minnesota. The remaining specimens (from eventually newly created zones F and G) were then compared and analyzed by comparing them with the training data set. Canonical discriminant analyses were performed on grouped data from each of the five physiographic zones. Cross validation was then used to test the taxonomic identification of each individual in each physiographic zone which had complete data (some specimens lacked soft parts or parts of the shell making statistical comparisons difficult).

Taxon Frequency							
Zone	b	d	m	b x d	b x m	d x m	Total
F	10	0	5	0	22	0	37
G	0	9	0	9	2	3	23
Total	10	9	5	9	24	3	60

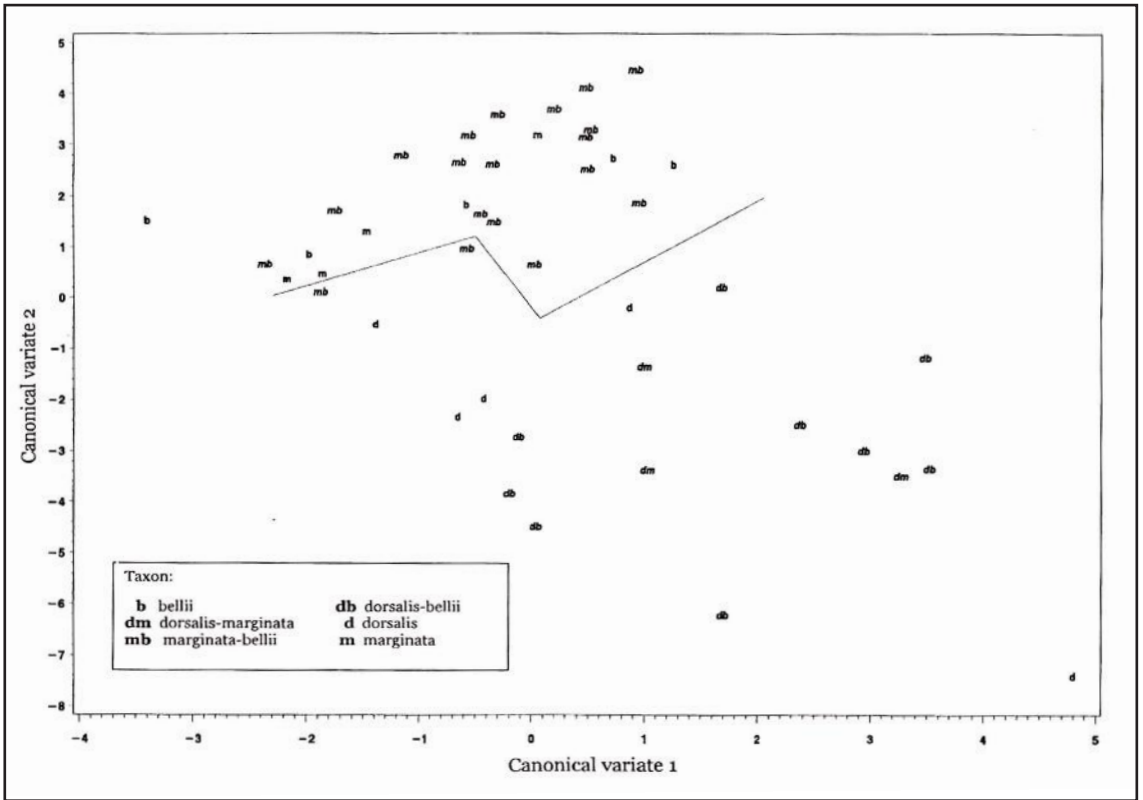


Figure 2. Discriminant analysis of individuals of *Chrysemys* in Zones F (above) and G (below).

RESULTS

Plastron pattern was different by frequency for all zones (Table 1). Examination of the phenotypic characters of colour and shell patterns, and of carapace seam alignment of each specimen, showed that 100 percent of the individuals from populations of *Chrysemys* in the Osage Plains (C) and Ozark Plateau (D) zones could be assigned to the subspecies *C. p. bellii* (Table 1). However, the Glaciated Plains (A), Ozark Border (B), and Mississippi Lowlands (E) zones contained hybrid specimens of *C. p. bellii* X *C. dorsalis* (zone B, 7/65, 10.8%; zone E, 8/34, 23.5%) and *C. p. marginata* X *C. dorsalis* X (zone B, 1/65, 1.5%; zone E, 10/34, 29.4%), and intergrade specimens of *C. p. bellii* X *C. p. marginata* (zone A, 12/73, 16.4%; zone B, 13/65, 20%). *Chrysemys p. marginata* patterns were found in only a few individuals (zone A, 1/73, 1.4%; zone B, 5/65, 7.7%). Individuals of *Chrysemys p. marginata* totaled only 6/195 turtles (3.1%) examined from Missouri, and they were from eastern counties north of the Missouri River.

All but two of the intergrade individuals (Fig. 2, Table 1) were from eastern counties where the waterways flow primarily into the Mississippi River (Pflieger, 1975). The other two intergrade specimens were from Franklin and Montgomery counties, respectively, on the plateau of the Ozark Border just west of the Mississippi floodplain. These data indicate that eastern Missouri has received genes of *C. dorsalis*, *C. p. bellii*, and *C. p. marginata* to form a *Chrysemys* population with a mixed genotype in an extensive hybrid/intergrade zone along the western floodplain of the Mississippi River. North of the confluence of the Missouri and Mississippi rivers the intergrades are *C. p. bellii* X *C. p. marginata*, as determined by variation in the dark plastron mark, absence or interruption of the vertebral stripe, and the presence or absence of reticulate light markings on the carapace. South of the

Missouri River *C. dorsalis*, *C. p. bellii*, and *C. p. marginata* have each contributed genes to the mixed swarm, as indicated by the presence or absence of a dark plastron mark and, if present, variation in it; the degree of prominence and width of the vertebral stripe; disruption of the vertebral stripe in some specimens; the width of the light seam border on between pleural scutes 2 and 3; and the presence or absence of light reticulations on the carapace.

In view of the apparent interbreeding based on shell morphology and colour patterns, and for more meaningful comparisons, we removed the eastern intergrade populations from the Glaciated Plains (A) and Ozark Plateau (B), but retained the nonintergrade populations in them. We designated the intergrade populations in 6 counties occurring north of the Missouri River the Northeastern Intergrade Zone (F), and combined those occurring in 3 counties south of the Missouri River with turtles from the original 5 counties of the Mississippi Lowlands zone (E) into a second Southeastern Intergrade Zone (G), abandoning the original designation of zone E for the Mississippi Lowlands (Table 1). Results of cross validation for the new zones F and G are presented in Table 2.

DISCUSSION

Ultsch *et al.* (2001) conducted a study of *Chrysemys* from throughout the genus' geographic range in an attempt to better define the morphological phenotypes of its four morphs. Their data revealed no reason to accept or reject Bleakney's (1958) theory of the distribution of the subspecies of *C. picta* at the height of the Wisconsinian glaciation, or Bleakney's conjecture that *C. marginata* was derived from hybridization between *C. bellii* and *C. dorsalis*. They speculated that, if *C. marginata* is a hybrid, it could have originated as one between *C. bellii* and *C. picta*; however, nowhere at present do the ranges of *bellii* and *picta* meet, and, although they may possibly have in the past, there is no supporting fossil evidence. Unfortunately, the possible flaw in their hypothesis that *C. marginata* may be a hybrid of *C. bellii* and *C. dorsalis* is that Ultsch *et al.* (2001) examined no specimens from Missouri or adjacent

Illinois. If the centre of origin of *C. marginata* is in the St. Louis area, than pure *marginata* specimens should be present there today in identifiable numbers.

Figure 2 and Tables 1 and 2 indicate that this is not the case. Only 5 (11.6%) of the 43 turtles from the Northeastern Intergrade Zone (F), which includes the St. Louis area, could be assigned to *C. p. marginata*. A sixth specimen of *C. p. marginata* was recorded from Audrain County, just west of the Northeastern Intergrade Zone. Phenotypic *marginata* characters were also found in 24 (55.8%) *C. p. bellii* x *C. p. marginata* from the Northeastern Intergrade Zone (F) and one turtle showing phenotypic *marginata* characters was recorded in each of Franklin and Montgomery counties on the Ozark Border just west of Zone F. Under cross validation of the 37 turtles in Zone F having complete data 5 (13.5%) were classified as *C. p. marginata*, 10 (27.0%) were classified as *C. p. bellii* and 22 (59.4%) as *C. p. bellii* x *C. p. marginata* (Table 2). No turtle from north of the Missouri River possessed *C. dorsalis* characters, which is to be expected if *C. p. marginata* is a hybrid creation between *C. dorsalis* and *C. p. bellii*, as proposed by Bleakney (1958).

In addition, only 3 (13%) turtles from the Southeastern Intergrade Zone (G) had a phenotype like *C. p. marginata*, 2 (8.7%) individuals were *C. dorsalis* x *C. p. marginata*, and the remaining 18 (78.3%) turtles were *C. dorsalis* (Table 1). Under cross validation of the 23 turtles from Zone G with complete data, none were classified as *C. p. marginata*, 2 (8.7%) were *C. p. bellii* x *C. p. marginata*, 9 (39.1%) were classified as *C. dorsalis*, and 9 (39.1%) were *C. dorsalis* x *C. p. bellii* (Table 2). Individuals with a phenotype like that of *C. p. marginata* comprised only 12.4% (11/89) of the *Chrysemys* turtles examined from the Mississippi watershed in eastern Missouri, 9% (8/89) from localities north of the Missouri River (F) and 3.4% (3/89) from south of that river (G) (Table 1). Cross validation only classified 8.3% (5/60) turtles as *C. p. marginata* in the Mississippi watershed in eastern Missouri, 13.5% (5/37) from localities north of the Missouri River (F) and none from localities south of the Missouri River (Table

2). If the hybrid creation of *C. p. marginata* proposed by Bleakney (1958) occurred south of the Missouri River, some pure *C. p. marginata* should probably be present, but our data do not show this.

Hartweg (1934) surmised that “west of the Mississippi River little *marginata* influence can be detected except in the region of St. Louis. Our data agree, but evidence supporting Bleakney’s (1958) theory is very weak at best. Our data indicate that those watersheds flowing into the Mississippi River in eastern Missouri (F, G) can be interpreted as containing a narrow north-south hybrid/intergrade swarm (Fig. 2) that has received genes from southern *C. dorsalis*, western *C. p. bellii*, and eastern *C. p. marginata*, and not as the region of hybrid origin of *C. p. marginata*. Where then did *Chrysemys p. marginata* originate?”

Fossil evidence (Holman, 1995) supports the proposed centres of origin of Bleakney for both *C. bellii* and *C. picta*, but fossils are lacking in the area of Louisiana and Mississippi where he thought *C. dorsalis* originated.

Is there fossil evidence to support another region of origin of *C. marginata*? If *C. marginata* invaded Missouri from its present eastward range, we should look for evidence of its possible origin east or southeast of the Mississippi River. At its maximum, the Laurentide ice sheet of the late Wisconsinian did not reach the vicinity of the present channel of the Ohio River. Remains of turtles referable to the genus *Chrysemys* have been found at several Pleistocene sites in the Tennessee River watershed. The Blackbelt Complex of fossil sites in northeastern Mississippi has yielded remains of *Chrysemys* that date to the Sangamonian interglacial age and the Wisconsinian glacial stage (Holman, 1995). Fossil *Chrysemys* have also been found in Bell Cave, Colbert County, Alabama, which date to between 11,800-26,500 YBP (Holman *et al.*, 1990), and Guy Wilson Cave, Sullivan County, Tennessee has yielded fossil *Chrysemys* that date from about 19,700 YBP (Fay, *in* Holman, 1995). In addition, late Wisconsinian remains of *Chrysemys* have been uncovered at Ladds Quarry, Bartow County, in northwestern Georgia (Holman, 1985a, 1985b,

1995). These fossils show that turtles of the genus *Chrysemys* occupied the Tennessee River watershed at the same time as other *Chrysemys* occurred at the sites proposed by Bleakney (1958) as the centres of origin of both *C. bellii* and *C. picta* (Holman, 1995). If *C. marginata* originated in the region of the Tennessee River Valley, it could easily have migrated north, then west and east into its present geographical range, forming the present intergrade zones where it met *C. bellii*, *C. dorsalis* and *C. picta* (Hartweg, 1934; Cagle, 1954; Carr, 1952; Ernst, 1971; Ernst & Fowler, 1977; Conant & Collins, 1998; Ernst *et al.* 1994). The geological history of the Tennessee River Basin presented in Fitzpatrick (1986) also supports this conclusion. Therefore, we believe that the Tennessee River Valley is a more plausible centre of origin of the population of *C. picta* that eventually evolved into the subspecies *C. p. marginata*.

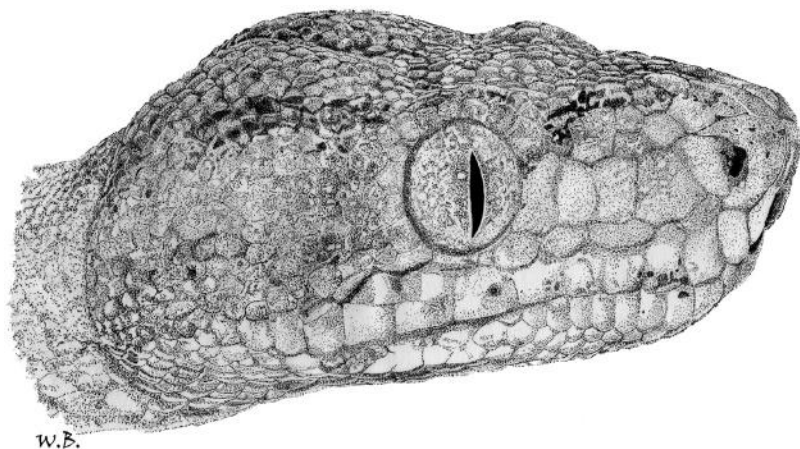
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Amazon tree boa, *Corallus hortulanus*. Pen and ink illustration by Will Brown.
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Male-male ritualized combat in the Brazilian rainbow boa, *Epicrates cenchria crassus*

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MALE-male combat is a ritualized behaviour occurring mainly during the mating season (Greene, 1997; Schuett, 1997; Schuett *et al.*, 2001) which is widespread among snake families including Boidae, Elapidae, Viperidae and Colubridae (Shine, 1978, 1994). Male-male combat is an example of intrasexual selection in which males compete for access to females. Typically, the two opponents attempt to physically subdue one another by exerting pressures (e.g., pushing, flipping, entwining) on the anterior part of their body in an attempt to bring their adversary to the ground. (Carpenter, 1977). Among boid snakes male-male combat is recorded in only one erycinae (*Eryx colubrinus* – see Schuett *et al.*, 2001), 21 pythoninae (see Shine, 1994; Schuett *et al.*, 2001) and 14 boinae species – nine of these being Neotropical (see Shine, 1994; Schuett *et al.*, 2001). The genus *Epicrates* includes ten species and combat is recorded for six, including the Brazilian *E. c. cenchria* (Shine, 1994; Schuett & Schuett, 1995; Schuett *et al.*, 2001). Despite the existence of many records in boid snakes, detailed descriptions of combat behaviour are only available for the pythoninae (*Python molurus*; Baker *et al.*, 1979) and the boinae *Sanzinia madagascariensis*.

Here we provide a description of combat in three captive male *Epicrates cenchria crassus*. This mainly terrestrial species feeds on small mammals (Pizzatto L., unpubl. data), and inhabits the Brazilian cerrado, a savanna-like vegetation, where it is probably associated with riparian forests (Peters *et al.*, 1986; Henderson *et al.*, 1995).

The three snakes came from unknown localities in São Paulo State, southeastern Brazil and were maintained in captivity in Bandeirantes city (-50°03'W, -23°02'S), Paraná State, southern Brazil. Male 1 and male 2 were obtained in 1999 and male 3 was obtained in early 2001. These snakes were maintained in individual cages (1.0 m x 0.50 m x 0.40 m) made of wood with screen in the front. Cages were contiguous and disposed side by side in the same room, thereby preventing visual contacts between the experimental subjects. Room temperature was ca. 30–32°C in spring/summer and 22–25°C in autumn/winter. We used heating pads when the temperature fell below 25°C, and sprayed the cages with water when the humidity was low. Water was provided ad libitum, and snakes were fed once a week (one or two young rats). We measured each snake in June 2004: Male 1 was 1130 mm in SVL and weighed 845 g, male 2 was 910 mm in SVL and 800 g, and male 3 was 1060 mm SVL and 910 g. All males were adults (L. Pizzatto, unpl. data). We used the terminology used by Carpenter *et al.* (1976) for the combat phases.

In April/May in 2001, we observed high snake activity in the cages and decided to introduce males to one another, simultaneously, in the same cage. Then, male 1 and 3 started a combat behaviour. Although male 2 was in the cage with the other 2 snakes it did not engage in combat. The end of the combat was initiated when the loser (male 3) withdrew itself from the fight and became inactive. After trials, all snakes were returned to their individual cages.

In April/May 2002, snakes became very active again. Male 3 was continuously forcing the cage wall towards the cage of male 1 until it broke the cage and entered male's 1 cage, probably attracted by chemical cues. The three snakes were put together again and exhibited combat behaviour. Again, male 2 did not engage in combat. But, in contrast to year 2001, male 3 became dominant over male 1. The same behaviour combat was recorded again in 2003 and 2004 with male 3 being the dominant. During these four years combat occurred from April to June.

The following description is based on two combat events that occurred between 11 and 12-June 2004: in the evening (the main period of activity for this species) we placed the three snakes together in an arena (1.3 m x 1.1 m x 0.7 m) and recorded combat behaviour using a JVC VHS model GR-AX827. As observed in the previous years, only male 1 and 3 engaged in combat. Below, we provide a detailed description of the combat phases:

Recognition-investigation phase – When male 3 and male 1 approached each other they tongue-flicked frontally, male 3 getting the /anterior part of its body in a 15° elevated S-shape, and moved toward the head of males 1. They tongue-flicked and crawled rapidly over each other. This phase lasted 10 sec in each combat event.

Ascent-alignment-orientation – Male 3 moved forward over the dorsum of male 1, and the snakes aligned their bodies and heads. Both males ascended the 1/3 anterior part of their body while keeping the posterior parts in contact. Male 3 had the anterior trunk more elevated and placed anteriorly relative to male 1, and they kept moving.

Topping – Male 3 entwined its 1/3 anterior trunk with the 1/3 anterior trunk of male 1, and forced it to the ground. The remainder of the bodies was loosely entwined. Heads were kept in a vertical position when the trunks were elevated and many times the posterior trunks were firmly entwined (Fig. 1). Sometimes snakes had the whole bodies entwined spinning on the longitudinal axes. Frequently, these males were completely entwined, constricting each other vigorously (Fig.

2) and male 3 pressed the anterior trunk of male 1 against the ground (Fig. 3). In most cases the 1/3 anterior trunks and heads were elevated in a vertical position (Fig. 1).

Submission – Male 1 moved far away from male 3, with head on the ground, showing a submissive position. This behaviour occurred many times, with male 1 chasing male 3.

On the first day, topping was mixed with submissive behaviour but it was more vigorous. After several minutes of submission the ascent-alignment-orientation started again and combat resumed. Combat lasted about 28 min interspersed with 18 mins of intervals.

On the second day, topping was less vigorous, 31 minutes elapsed between the start and the end of the combat. Topping behaviour was interrupted many times because male 1 assumed a submissive position, trying to escape, and male 3 chased it. Total topping time was 12 minutes. Male 2 never engaged in combat. On the first day, male 1 approached male 2 from behind, crawling rapidly forward over the body of its opponent. Male 1 tongue flicked on the dorsum of male 2, moving quickly and anteriorly above the other, apparently trying to align its body with the other snake. Male 2 fled in the other direction. Then, both snakes tongue flicked frontally once again, and male 3 raised its /anterior part of its body in the form of an S-shape at an 15° angle, and moved rapidly over male 2, their bodies facing opposite directions. During the most of this time male 2 continued to move away.

Carpenter *et al.* (1976) suggested that aggressive behaviour in boine and pythonine snakes lacks the vertical components exhibited by viperids. In addition, Greene (1997) pointed out that, in these subfamilies, combat frequently occurs with the bodies on the ground. However, *Sanzinia madagascariensis* use their anterior bodies only to maintain a purchase on limbs and branches (Carpenter *et al.*, 1978). Similar to the Indian python (*Python molurus*) and other Rainbow boas (*E. c. cenchria*, *E. inornatus* and *E. angulifer*), *E. c. crassus* exhibited elevation of the head and anterior body part, and this combat

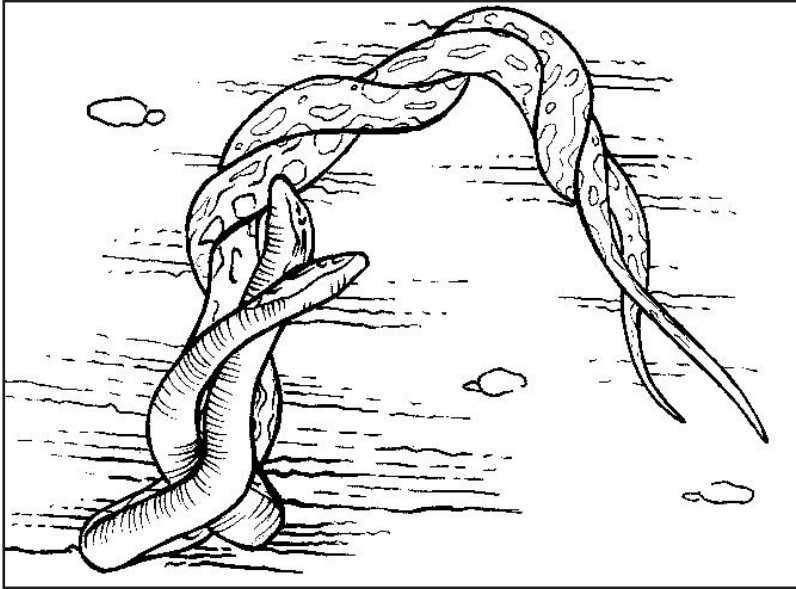
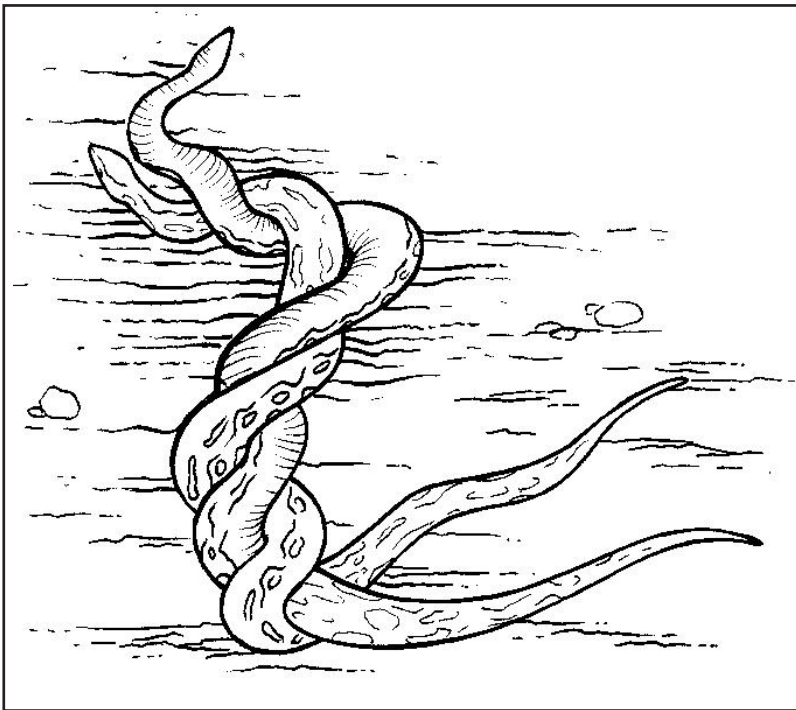


Figure 1 (above). Topping phase in *Epicrates c. crassus* showing males with 1/3 anterior trunk elevated, heads in vertical position and the posterior trunks firmly entwined. Dominant males maintain head more elevated.

Figure 2 (below). Topping phase in *E. c. crassus* showing males completely entwined, spinning and constricting each other vigorously (subordinate male is beneath dominant).



behaviour is synchronized with mating (Barker *et al.*, 1979; Schuett & Schuett, 1995). In addition, constriction during entwining is another component of boid combat behaviour, at least in *P. molurus* and *Corallus caninus* (Barker *et al.*, 1979; Osborne, 1984), and we also observed this behaviour in our study. Spur use has been recorded in courtship and combat in boine and pythonine snakes. However, we never observed this behaviour in the present work or in *E. c. cenchria* combat (Schuett & Schuett, 1995). There are at least two possibilities for this: spur use occurs but the captive conditions and small size of spurs in this species did not permit its observation, or it does not occur in this species.

Within *Epicrates*, male competition for females during the reproductive season can occur, at least in two forms: the ritualized combat, as described here, or an intense aggression which includes biting and other kinds of injury (Tolson, 1992).

Combat bouts in *Epicrates c. crassus* were always recorded during Autumn. It coincides with gonadal size increase (L. Pizzatto, unpubl. data) which reflects testes activity (Volsøe, 1944; Fox, 1952; Shine, 1977). Testosterone is produced during spermatogenesis and the level of this hormone is related to agonistic behaviour

in males *Epicrates striatus* (Teubner; in Tolson, 1992). Larger males of *E. striatus* have higher testosterone levels and deter smaller ones, frequently being dominant in combats bouts. In addition, testosterone levels of subordinates increase after the dominant's courtship and mating (Teubner; in Tolson, 1992). Thus, it is

possible that large dominant males delay gonadal recrudescence in smaller and less aggressive males (Tolson, 1992). In our study, the two largest males (1 and 3) were indeed competitive. Their hierarchical rank varied among years, while the smallest (male 2) always showed a submissive behaviour. Therefore, it is possible that males 1 and 3 had higher levels of testosterone that unchained combat behaviour and repressed male 2.

Our observations point out that chemical cues play an important role in initiating combat behaviour in *Epicrates c. crassus*. Pheromones may be a mediator of this behaviour, since males were not in visual contact before the combat. Many studies have recorded combat occurring in the presence of females (Carpenter *et al.*, 1978; Osborne, 1984; Schuett & Schuett, 1995) but it is apparently not essential in *E. c. crassus*, since no females were held captive in the same room.

There are four patterns of combat described for snakes (Bogert & Roth, 1966; Carpenter & Ferguson, 1977). The observed combat in *E. c. crassus* has characteristics of two; patterns four (viperids) and one (colubrids). The main characteristic of pattern four is that males are oriented in the same direction, upraise and intertwine loosely their anterior trunks and maintain heads tilted or in a vertical position. However, they frequently entwine most of their body, specifically the posterior ends, and keep their heads close together, barely raised from the ground (pattern one) (Bogert & Roth, 1966; Carpenter & Ferguson, 1977).

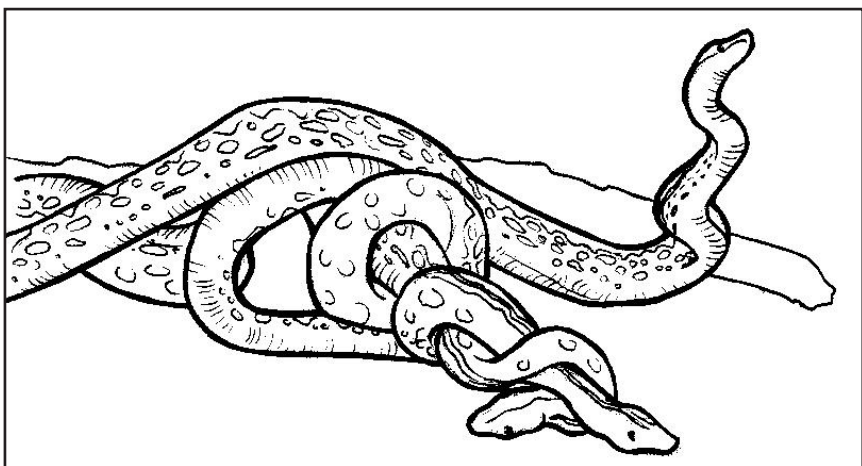


Figure 3. Topping phase in *Epicrates c. crassus* showing males with anterior trunk firmly entwined and posterior trunk loosely entwined. Dominant male is pressing the head of the subordinate male on the ground. The elevated male (male 2) is fleeing from the others and never engaged in combat.

Detailed descriptions of boid combat are scarce and current records include only four species: *Corallus caninus* (Osborne, 1984), *Epicrates c. cenchria* (Schuett & Schuett, 1995), *Epicrates angulifer* (Tolson & Henderson, 1993) and *Sanzinia madagascariensis* (Carpenter *et al.*, 1978). The latter species seems to present special adaptations of combat behaviour to the arboreal lifestyle which can not be a common pattern in this family (Carpenter *et al.*, 1978). The present work shows that *Epicrates c. crassus* combat is very similar to that of *Python molurus*, showing an anterior trunk and head elevation but lacking the spur use and biting (Barker *et al.*, 1979). *Epicrates angulifer* combatants also entwine their bodies and elevate part of the anterior trunk (see pictures in Tolson & Henderson, 1993). In conclusion, boid combat seems to be a mixed type that includes the vertical component of the anterior bodies and heads, and the entwinement of most portions of bodies with heads low to the ground and strong constriction and spinning. Mixed type of combat behaviour also occurs in the Neotropical colubrid *Chironius bicarinatus* (Almeida-Santos & Marques, 2002) and more studies can elucidate if it is common among less studied groups, such as the boids and colubrids.

ACKNOWLEDGEMENTS

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Body temperatures of the Common toad, *Bufo bufo*, in the Vendee, France

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ABSTRACT — Field body temperatures of nocturnally active Common toads (*Bufo bufo*) ranged from 11.7–18.9°C and from 27.8–34.2°C when in daytime retreats or abroad. The lowest body temperatures of individual toads were recorded during March and November. Body temperatures had good associations with air and substrate temperatures during nocturnal activity but were significantly lower than air temperatures in open areas during the day.

IT is well known that temperature influences the behaviour and metabolism of ectotherms and therefore field body temperatures are critical for physiological processes and for survivorship (Hutchison & Dupre, 1992). Thermal studies have largely concerned reptiles; less attention has been paid to the amphibia which often undergo sustained activity in the field, for instance during migratory behaviour (e.g. Oldham, 1967; Szatecsny & Schabetsberger, 2005) or in conflicts over territory or mates (e.g. Wiewandt, 1969). The field body temperatures of nocturnally active anurans are of interest as they may define the thermal niche of a species and determine when and where a species is active. Except for temperatures recorded during migratory movements there appears to be little information on body temperatures of the common European toad, *Bufo bufo* (eg Wisniewski *et al.*, 1981; Reading & Clark, 1995). A recent major review (Beebe & Griffiths, 2000) records a decline in activity below 5–6°C (Slater *et al.*, 1985) but it appears there is no information on temperatures throughout the active year. In this paper, we present such information on the annual activity body temperatures of *B. bufo* in France.

METHODS AND MATERIALS

Information was gathered during 2003 and 2004 in the Vendee region of France. Most data ($n = 143$) were recorded when searching fields and gardens at night, apparently whilst they were foraging in

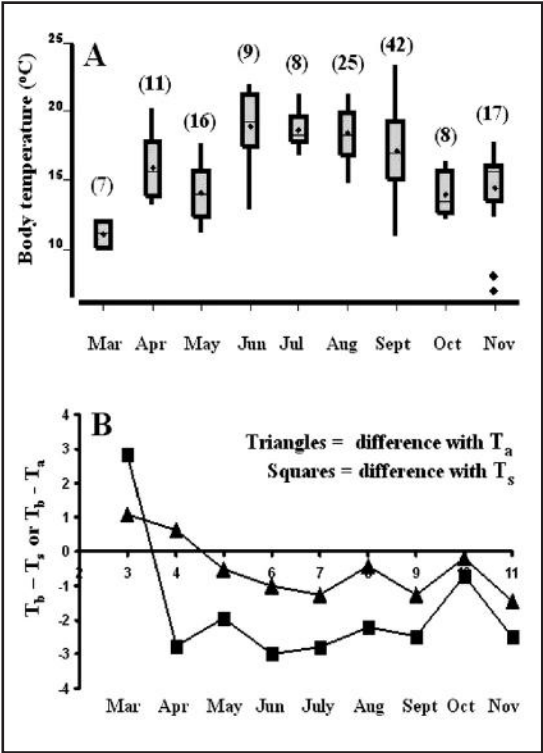
terrestrial home ranges or engaged in post breeding wandering. Some individuals were found during the day ($n = 15$) but as far as we could ascertain, no animals were involved in breeding migration. Body temperature (T_b) was measured using a Digitron infra-red pyrometer and here defined as the skin surface temperature taken at less than 5 cm from the skin surface. Skin surface temperature may only differ by small amounts from cloacal temperature in anurans ($mean = 0.46^\circ\text{C}$) but handling the animals may result in considerably raised body temperature (Fouquette, 1980). Thus, no animals were handled during sampling. The default error on the detector is 0.01°C . The emissivity was set at 0.95, an estimated value for the dry skin of toads that we assumed is close to the value for reptiles (emissivity of reptiles = 0.95 (Tracy, 1982)). Hence, there may be a small degree of error in the readings. Simultaneously to body temperatures, air temperatures (T_a) were recorded 10–15 cm above the surface where the toad was located and substrate temperatures (T_s) by directing the Pyrometer at the substrate surface. Humidity was recorded with a L'atelier humidity meter.

RESULTS

Nocturnal body temperatures. Active toads were observed between March and November. Figure 1 A shows monthly body temperatures of animals active after dark. Mean nocturnal T_b ranged from 11.7–18.9°C with the highest means recorded in

June, July and August (means of 18.9, 18.7 and 18.4°C respectively). Body temperatures were significantly higher than T_a or T_s only during March (two sample t -tests: versus T_s , $t = 8.2$, $p < 0.0001$, $d.f. = 8$; versus T_a , $t = 2.8$, $p = 0.02$, $d.f. = 10$). In general, mean monthly T_b ($15.8 \pm 2.6^\circ\text{C}$) was lower than mean monthly T_a ($16.1 \pm 3.3^\circ\text{C}$) and mean monthly T_s ($17.4 \pm 4.3^\circ\text{C}$) but the differences were not significant (two sample t -tests $p > 0.05$). A plot of the differences can be seen in Fig 1B. Coefficients of determination (r^2) have

Figure 1. Graphs of monthly body temperatures in *B. bufo*. Fig. 1A shows box plots of monthly means and distributions of body temperatures. The boxes represent the interquartile ranges, the means are shown as diamonds and the medians as horizontal bars. Vertical lines either side of the interquartile ranges represent the general ranges but the large diamonds for November (Fig1A) represent outliers - data that are between 1.5–3 times from the interquartile range. Numbers in parenthesis indicate sample sizes. Fig 1B shows the monthly differences between mean body temperatures and mean air or substrate temperatures.



been calculated to estimate the variation in body temperature that can be explained either by variation in air or substrate temperatures. The results suggest association of body temperature with both environmental temperatures (substrate $r^2 = 70.8\%$, air $r^2 = 70.6\%$) but not with humidity recorded at the time of capture (mean humidity = $80.3 \pm 9.9\%$, $r^2 = 0.3\%$). Nor were mean monthly body temperatures associated with the mean number of sightings per month (mean sightings = 15.8 ± 11.4 , range = 7–42, $r^2 = 6.9\%$) or the mean monthly humidity levels (mean of the monthly means = $80.9 \pm 5.2\%$, $r^2 = 3.3\%$).

Diurnal body temperatures. Fifteen individuals were found during daylight hours in what appeared to be either sentinel activity ($n = 4$; see Fig 2 for an example) or in hide areas. Body temperatures ranged from 27.8–34.2°C (mean = $30.2 \pm 2.2^\circ\text{C}$) and were significantly lower than mean substrate temperatures in the open (mean = $41.3 \pm 2.3^\circ\text{C}$, $t = 11.1$, $p < 0.0001$, $d.f. = 25$), significantly higher than shaded substrate temperatures (mean = $28.4 \pm 2.7^\circ\text{C}$, $t = 2.03$, $p = 0.05$, $d.f. = 26$) but not significantly different from shaded air temperatures (mean = $28.8 \pm 2.5^\circ\text{C}$, $t = 1.6$, $p = 0.11$, $d.f. = 28$).

DISCUSSION

The toads measured in this study were active over broadly a similar period of time as those studied elsewhere (e.g. Wisniewski *et al.*, 1981; Slater, *et al.*, 1985 and review in Beebee & Griffiths, 2000) and over a wide range of body temperatures. The lowest nocturnal body temperatures were found during November but March temperatures were also low and just above ambient temperatures of 2–4°C when activity apparently ceases in other areas (Wisniewski *et al.*, 1981). It may be that the higher than environment temperatures in March were achieved by the toads seeking out higher microhabitat temperatures and although the differences were small may be significant for an individual toad. Research on UK populations has suggested that the temperatures required for activity may be population specific (e.g. Frazer, 1966; Wisniewski *et al.*, 1981). Although we

found no statistical association between toad activity or T_b with humidity, it is likely that humidity is important for activity at certain times of the year. For example, although temperature may be the critical factor for long distance migration in the UK (R.A. Griffiths, pers. comm.) current work in the Vendée suggests there is the possibility, based on road mortality counts, that such movement in late October and November may in part be rainfall dependent.

The Vendée area is well known for hot, very dry summers with daytime humidity dropping to around 20% increasing to 80–90% in the hours after dusk; daytime retreats when found, were under sheets of plastic, canvas and cardboard. These were locations where temperatures and humidity were high and presumably enhance digestion efficiency and reduce dehydration. Daytime activity abroad may concern sit-and wait predation (Fig. 2) but could also be examples of mosaic basking (R. Avery, pers. comm.). However, it is unknown whether diurnal activity is common but difficult to detect, or simply infrequent. The high body temperatures recorded for diurnal activity are in good agreement with those found in other day active anurans (Carey, 1978) and, perhaps surprisingly, comparable with those in deserts (eg *Bufo mauritanicus* and *Rana perezi*; Meek, 1983) which are close to the lethal temperatures for toads of around 38°C (Brattstrom, 1979; Hutchinson & Dupre, 1992). Evaporative cooling should enable basking anurans to maintain relatively low body temperatures as evaporative losses increase at higher air temperatures stabilising body temperature (Shoemaker, *et al.*, 1987; Buttemer & Thomas, 2003). Indeed, certain anurans are active abroad even when the environment may be too hot for reptiles (Meek, 1983). Laboratory studies on



Figure 2. Diurnal sentinel behaviour/ mosaic basking in *B. bufo*. This individual was found in June 2004 when air temperatures were above 30°C.

bufonids have shown a strong correlation of field selected body temperatures with physiological performance (e.g. Putnam & Bennett, 1981) indicating the importance of body temperature for activity.

Nocturnal activity may partly involve the avoidance of predators. Ten captured snakes in the area – (nine *Natrix natrix* and one *N. maura*) regurgitated Common toads suggesting they are major predators in the Vendée as they are elsewhere (Reading & Davies, 1996; Arnold & Ovenden, 2002). Both snakes are common, diurnally active and widely foraging and hence, for toads, minimising diurnal activity may be adaptive in that it reduces predator encounter frequency, although it may be that the snakes search toad daytime retreats. Interestingly, if this small sample of snake feeding behaviour is representative, it could indicate that the more diurnally abundant green frogs (*Rana esculenta/lessonea* complex) are largely ignored because they bask extensively, have high body temperature and hence presumably have greater agility and speed compared to *B. bufo*.

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The colouration and displays of venomous reptiles: a review

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SOME years ago, my friend Malcolm Coe inadvertently stepped on a large Gaboon viper (*Bitis gabonica*) whilst scrambling along a narrow track up Mount Cameroon. Fortunately for Malcolm, the snake was apparently as anxious as he was to terminate their brief encounter as quickly as possible. It slithered away down the slope without making any attempt to strike at him. In captivity, Gaboon vipers show dramatic colouration – beige, browns, yellow, purple and black are interwoven in a manner that has been described as having the effect of an oriental carpet. These bright colours are disruptive (Mehrtens, 1987), and in their normal environment Gaboon vipers – like the majority of venomous snakes – are extremely cryptic. Their silvery eyes are located at the apex of black or dark brown cheek patches (Fig. 1). This marking not only disguises the eyes but it also conceals the mouth very effectively! (Cloudsley-Thompson, 1999a).

The thesis of the argument outlined below is that venomous snakes are almost always, if not invariably cryptic (Cott, 1940). None of the species illustrated by Greene (1957), Mattison (1986) or Mehrtens (1987) for example shows aposematic (conspicuous or warning) colouration with the exception of sea snakes and coral snakes which appear to be special cases. Other possible exceptions may include the juveniles of a few species such as the King cobra (*Ophiophagus hannah*) which have black and white stripes and the Bandy-bandy (*Vermicella annulata*) (see below). The rarity of warning colouration in venomous snakes was first emphasised by Poulton (1890) and by Hingston (1933).

Concealing colours

Back in 1890, E. B. Poulton concluded that whereas it may be 'to the advantage of certain venomous snakes to advertise publicly the fact that they are dangerous, retaining the poison to use if

necessary; and others would gain by concealing themselves by Protective Resemblance, while they also use their poison fangs if detected and attacked'. On balance, crypsis is more beneficial than aposematism in assisting venomous reptiles to avoid attack (Ruxton *et al.*, 2004).

According to Cott (1940) the methods by which concealment is obtained in nature are: (1) General colour resemblance to the environment, (2) Variable colour resemblance, (3) Obliterative countershading, (4) Disruptive colouration, (5) Coincident disruptive colouration and (6) Concealment of shadow. Not all of these are found among venomous reptiles. When present, their function may be concealment in defence, in offence so that they are not seen by the prey, or both. Good examples of the latter are provided by Green mambas (*Dendroaspis viridis*) and the vine snakes, of which four distantly related genera are known. They are all 'sit and wait' foragers which stalk their prey with lateral swinging of the head: they are generally extremely cryptic and difficult to see (Cloudsley-Thompson, 1989; Henderson & Binder, 1980). More common among venomous reptiles than general colour resemblance to the environment are obliterate countershading and disruptive colouration. Light and shade make objects apparent even when seen against backgrounds whose colour and texture exactly match their own. For this reason the ventral surfaces of nearly all animals are lighter in colour than the rest of their bodies. Concealment of shadow is achieved by pressing the body onto the substrate whenever possible. The Sidewinder (*Crotalus cerastes*) illustrated in Fig. 2 is doing this. As well as to day-active snakes, cryptic colouration is important to nocturnal species, such as the Horned adder (*Bitis caudalis*) (Fig. 3) and the Saw-scaled viper (*Echis carinatus*) (Fig. 4). Even these may bask in the sunshine during the hours of daylight and many snakes, nocturnal during the summer, become day-active in winter.

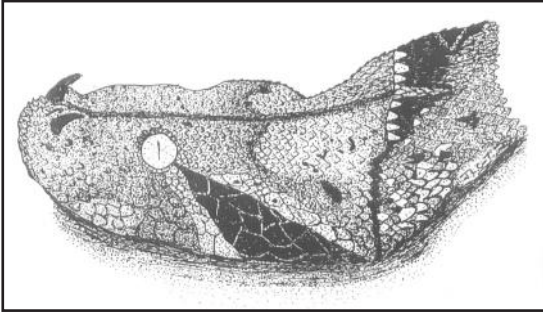


Figure 1. Head of Gaboon viper (*Bitis gabonica*).



Figure 2. Sidewinder (*Crotalus cerastes*).



Figure 3. Horned adder (*Bitis caudalis*).



Figure 4. Saw-scaled viper (*Echis carinatus*).

Few venomous snakes are able to adjust their colour rapidly to match their environment, but the Western rattlesnake (*Crotalus viridis*) has been reported to become lighter or darker within a minute or two, while the European adder (*Vipera berus*) becomes brighter after sloughing its skin prior to the breeding season (Ernst & Zug, 1996).

Warning colours

The most venomous lizards, the Gila monster (*Heloderma suspectum*) (Fig. 5) and the Mexican beaded lizard (*H. horridum*) provide striking contrast to other lizards which depend for safety upon cryptic colouration, alertness and speed. Not only are they brightly coloured, but they are slow, defiant, and defend themselves with their powerful jaws and poisonous bite (Cloudsley-Thompson, 1999). According to Greene (1988), the black and yellow colour pattern of *H. horridum* is primitively cryptic, whereas the black and pink colouration of *H. suspectum* is derived and probably aposematic. The Komodo dragon (*Varanus komodoensis*) is not only venomous but its bite is poisonous and often lethal to the prey on account of toxins and the noxious bacteria in its saliva (Fry *et al.*, 2006, summarised in *The Natterjack* No. 131: 4–5, December 2005). Whether or not the same is true of the Perentie (*Varanus giganteus*) does not appear to be known but, like those of the Lace monitor (*V. varius*), its bright colours could well be aposematic. In the course of my research in Sudan during the 1960s I was not infrequently bitten without ill effects by young Nile monitors (*V. niloticus*) which, likewise are brightly coloured (Fig. 6). In threat (see below) monitors of several species rear up to display alternatively dark and light stripes on much of their belly surfaces (Hingston, 1933).

Possibly the only adult venomous snakes with brilliant body colours whose function may be to warn possible predators that they are dangerous are sea snakes (*Pelamis platurus*) and coral snakes of the genera *Micrurus* and *Micruroides* (Elapidae). Not only are these readily detected but they have burrowing habits, dull sight, and are not stirred to irritability unless restrained (Ditmars, 1944). Not surprisingly, they are mimicked by various harmless or mildly poisonous ‘false’ coral



Figure 5. Gila monster (*Heloderma suspectum*).



Figure 6. Nile monitor (*Varanus niloticus*).

snakes (e.g. *Atractus*, *Erythrolamprus*, *Lampropeltis*, *Pseudoboa* and *Rhinobothryum* spp.; Colubridae). Coral snakes are so deadly that some investigators have expressed doubts as to whether they could actually serve as models, since potential predators are almost invariably killed and therefore never learn to avoid them. Alternatively, Mertens (1966) suggested that rear-fanged and mildly venomous species of snakes with coral snake patterns may be the models while nonvenomous and front-fanged species are respectively their Batesian and Müllerian mimics. The name Mertensian mimicry has been applied to this hypothesis (Wickler, 1986). It is doubtful, however, whether any snake is so venomous that all animals bitten by it are invariably killed. Moreover, many predators have both natural and acquired mimicry against snake and other venoms (Cloudsley-Thompson, 1994, 1999a). The paradox of the deadly model has also been discussed by Cloudsley-Thompson (1994), Engelmann & Obst (1984), Greene & McDiamid (1981), Mattison (1986), Pough (1988) and Roze (1996) among others. Mertensian mimicry is now generally regarded as a version of Müllerian and not as a completely different category of mimicry. The relationships are evidently extremely complicated and some 'false' coral snakes are found in regions where there are no venomous models. Since scavenging birds, which quickly consume other snakes killed on the roads, apparently leave the corpses of coral snakes undisturbed it may well be that their aposematic colouration is related more to distastefulness or an unpleasant smell than to venom (Cloudsley-Thompson, 1999a). Perhaps 'false' coral snakes and the most venomous

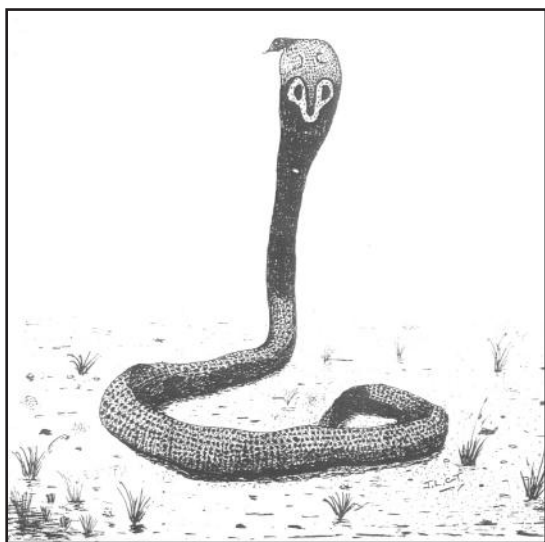


Figure 7. Indian cobra (*Naja naja*).



Figure 8. Rattlesnake (*Crotalus* sp.).

species both display the simple Müllerian mimicry of distasteful species.

Snakes are probably vulnerable to different predators at different times and under different conditions. Defence may be effective in some

cases, but none is invariably successful except possibly that of the aposematically coloured sea snake (*Pelamis platurus*) mentioned above. This is very conspicuous when not floating in the debris of drift-lines, its distinctive tail being especially noticeable. Greene (1997) suggested that this species might be one of the few vertebrates with no regular enemies – even among predators such as sea eagles that regularly feed on other marine elapids (Healwale, 1987). Seabirds occasionally seize but invariably drop them. Under experimental conditions Pacific Ocean fish rejected them as food and, although naïve Atlantic Ocean fishes ate them, they were later regurgitated (Rubinoff & Kropache, 1970).

Startling behaviour

When discovered by an enemy, many animals respond by adopting intimidating postures or making sudden, threatening sounds. Such behaviour is known as 'deimatic' (from the Greek word meaning 'I frighten') (Edmunds, 1974). Deimatic behaviour is extremely common among cryptic venomous snakes. Before striking in defence, most adopt characteristic positions. The Indian cobra (*Naja naja*), for instance, rears up with its conspicuous hood spread (Fig. 7), thereby increasing its apparent size. The hood of the Black-necked 'spitting' cobra (*Naja nigricollis*) has scarlet patches on its ventral side, while the ventral part of the body of Ringhal's cobra (*Hemachatus haemachatus*) displays black and white stripes below its black hood when the snake rears up.

Expansion of the neck region may be horizontal, as in cobras, or vertically as in the gular expansion of the Twig snake (*Thelotornis kirtlandii*) which flattens its head like an ace-of-spades. It is usually accompanied by the sudden exhibition of conspicuous colouration. Apparent increase in size is not limited to the hoods of cobras, however. The Boomslang (*Dispholidus typus*) can inflate its trachea and lung until it looks like an enormous sausage, the Eastern diamondback rattlesnake (*Crotalus admanteus*) to a lesser extent and the same kind of device is practised by numerous other animals (Cott, 1940). Defensive reactions of rattlesnakes such as *Crotalus cerastes* (Fig 3) and *C. viridis* in the presence of King-snakes

(*Lampropeltis getulus*) may consist of the formation of a broad loop or band in the body which is then lifted from the ground (Cowles, 1938). The Australian Bandy-bandy (*Vermicella annulata*), so named from its conspicuous white bands on a black body, elevates single or multiple body loops which are held immobile. Burrowing elapids, these snakes only emerge at night or after rain when their colouration may be aposematic.

The tongue and lining of the mouth are often brightly coloured among lizards and snakes. This internal colouration is associated with opening the jaws widely when threatened. Examples among venomous species include Hog-nosed snakes (*Heterodon* spp.), the Vine snake (*Oxybelis acuminatus*), the Long-nosed tree snake (*Ahaetulla prasinus*) and the Fer-de-Lance (*Bothrops atrox*) which have brightly coloured linings to their mouths, and the Cottonmouth (*Agkistrodon piscivorus*) in which it is white. Among venomous species, deimatic exposure of mouth colours may serve as a threat but, in harmless species, it is just bluff (Cloudsley-Thompson, 1994). Defensive tail displays are characteristic of rattlesnakes, coral snakes, sea snakes and other venomous serpents (Greene, 1988).

The Shield-nosed 'cobra' or Cape coral snake (*Aspidelaps lubricus*) rears the forepart of the body and neck when molested, thereby exposing a row of black and yellow bands. It does not have a hood as do true cobras, but is capable of producing extremely loud hisses accompanied by an exhalation of air that is quite explosive (Mehrtens, 1987). The King cobra or Hamadryad (*Ophiophagus hannah*) has a narrower hood than those of other true cobras. Whereas the hisses of most snakes are in the region of 3,000-13,000 Hertz, with a dominant frequency of 7,500 Hz, however, the 'growl' of the King cobra consists entirely of frequencies below 2,500 Hz with a dominant frequency near to 600 Hz. This sound is produced by tracheal diverticula functioning as low-frequency resonating chambers (*The NatterJack* No. 128, 3-4; Sept 2005).

Instead of hissing, a few venomous snakes stridulate by rubbing together the modified lateral scales of the trunk. Deimatic sounds are produced in this way by Saw-scaled vipers (*Echis* spp.) (Fig.

4), Horned vipers (*Cerastes cerastes*) and the Sand viper (*C. vipera*) of North Africa. They enable acoustic warning to be produced without the loss of respiratory water as occurs in hissing (Cloudsley-Thompson, 1999a) and are characteristic of desert species. Rattlesnakes (Fig. 8) also produce warning sounds without loss of water. A comparison of the power spectra and intensity of rattling in six species revealed conformation to the same general pattern – medium density broad-band sounds (2–20 k Hz) (Fenton & Licht, 1990). By drawing the attention of enemies or potential prey to their conspicuous tails, rattlesnakes must increase the chance of success when their heads strike unexpectedly from the opposite end of their bodies.

Vine snakes produce warning sounds by vibrating their tails in the vegetation, as does the Bushmaster (*Lachesis muta*) and other ground living snakes when they rattle their tails among dry leaves. Among the strangest sounds made by a snake are the cloacal ‘pops’ of the Sonoran coral snake (*Micruroides euryxanthus*) (Ernst & Zug, 1996). These are evenly spaced, of low amplitude (c. 50 decibels) and limited in pitch (442–5523 Hz) and frequency. They are made by contracting the cloacal sphincter and expelling air. Multiple pops are created by relaxing the sphincter, drawing air in, and contracting the sphincter again (*The NatterJack* No. 128, 11; Sept. 2005).

The similarity of deimatic sounds throughout the animal kingdom may well result from Müllerian mimicry, so common in warning colouration. In addition to the usual repertoire of visual displays and sounds, some venomous snakes are able to jump – not only for the capture of prey but also in defence. Examples include *Porthidium [Bothrops] nummifer* (Crotalinae) and various *Bitis* spp. This type of behaviour also occurs among non-venomous snakes (Cloudsley-Thompson, 1996; 1999a). In this context, the flight of back-fanged tree snakes of the genus *Chrysopelia* deserve mention, but this is a way of escaping or merely travelling rather than deimatic display. The defences of reptiles have been reviewed by Bellairs (1969), Cloudsley-Thompson (1994; 1999a) and Greene (1988) among others.

DISCUSSION

Evolutionary adaptations resulting from natural selection are often the result of more than one factor. This is particularly apparent in the adaptive colouration of animals. The colours of reptiles may, for instance, combine elements of crypsis, aposematism (based on formidable defences of which venoms are the more important, mimicry, or both), epigamic display and climatic factors (Cloudsley-Thompson, 1999b). Deimatic displays may be bluff, based on real threats or mimicry or either of these. Moreover, selection may be influenced overwhelmingly by factors that operate only for a brief period during the life of an animal – for example, during the breeding season or in twilight (Cott, 1940). Thus, the colour pattern of *Echis carinatus* (Fig. 4) has multiple functions. Initially it is cryptic but, after the viper has been annoyed and begins coiling around itself and stridulating, its colours become aposematic and have a warning function. The light coloured lines that cross the black are outlined by black scales. These, and the pale dorsal patches, render the Saw-scaled viper more conspicuous than snakes with unicoloured dark patches on a light background; while inflation of the body emphasises the contrast of the cross bands (Cloudsley-Thompson, 1994).

The functions of the colours of venomous reptiles are not always obvious. Frequently they can only be interpreted by herpetologists who have practical experience and knowledge of the animals in their natural environments. Some Egyptian cobras (*Naja haje*) are banded, some are black, and some uniformly brown. At night, the banded form is almost invisible, but the significance of the other colours is uncertain. Furthermore, different colour patterns may be found among siblings from the same batch of eggs. Beaded lizards (*Heloderma horridum*) too are very variable in colour. In general, snakes with horizontal stripes tend to be harmless, whilst banded snakes are dangerous. Stripes are less distinct among the snakes that inhabit regions with luxuriant vegetation than among those of more open country (Cloudsley-Thompson, 1994).

In this short review, an attempt has been made to draw attention to some of the outstanding problems presented by the colouration of

venomous reptiles. The solutions to these can only be supplied by herpetologists familiar with the animals concerned, and particularly those working in the field.

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**VARANUS BENGALENSIS (Bengal monitor):
UNUSUAL BEHAVIOUR AND FEEDING.**

During July 2005, as part of the Knuckles Expedition (De Silva, 2005), we conducted field studies on thermoregulation in *Calotes versicolor* at Hettipola (Meek *et al.*, in press), an area that lies on a flat plain at the edge of the Knuckles Massif in Central Province, Sri Lanka. At the time of our study, it was the dry season and operative temperatures exceeded 40°C daily. We frequently observed foraging *V. bengalensis* in the study area and all the observations reported here relate to this study site. Most sightings were after midday when they appeared to be searching for prey species. One lizard with an s.v. length of approximately 25 cm had a home site across from our hotel where we often saw it return either mid-afternoon or evening. This individual was easily recognised because of a damaged tail. One evening, an hour or so after dark, one of us (E.J.) saw this individual sitting partly outside its burrow in what appeared to be a type of sentinel behaviour (see cover illustration). It remained in this posture for some time and never ventured from its home-site. The lizard was approached (by E.J.) to a distance of about 0.5 metre, but it made no effort to escape and remained in its position. Air temperatures were around 30°C and within normal body temperature ranges recorded for this species (Meek, 1978; Wikramanayake & Green, 1993; review in Bennett, 1998).

The Bengal monitor is a typical varanid in that it forages diurnally for a wide variety of animal prey often over large distances (Auffenberg, 1994). Our observations at Hettipola indicated that they foraged in both terrestrial and arboreal microhabitats (Fig. 1). Dave (1960) observed movement at night but in an extensive study and review Auffenberg (1994) was unable to confirm this although he refers to an observation by a Mr Sanjeevaraj in Madras, India of a *V. bengalensis* foraging at 02:00 hrs for toads under a street light. We cannot confirm any feeding behaviour after dark, but it is difficult to imagine the lizard ignoring a prey animal if it wandered within striking distance.

On the afternoon of July 22nd we were alerted by hotel staff to a sub adult *V. bengalensis* (s.v. length approximately 15 cm) that had captured an adult Cricket frog or Paddie-field frog (*Limnonectes limnocharis*) at the front of the hotel and was in the process of swallowing it (Fig. 2). The frog was swallowed initially by continually being pushed against the ground then finally by inertia movements. This is the usual method employed by Varanids when the prey is large relative to body size. Apparently, vertebrate prey is comparatively rare in *V. bengalensis* (Bennett, 1998) and although is known to include frogs, there are no records of *L. limnocharis* as a prey species (Auffenberg, 1994). We observed another individual (s.v. length approximately 20 cm) eating six snails of an unknown species. Before swallowing the lizard crushed the shells by mastication then forced them into the stomach by the usual inertia movements. Hard-shelled prey is taken by adult Nile monitors (*V. niloticus*) and are crushed before swallowing. There are ontogenetic changes in the dentition for this dietary shift, where the teeth become broader and molar-like (e.g. Rieppel & Labhardt, 1979). We are not aware of this condition in *V. bengalensis*.

Finally, on two occasions we fed dead bats to foraging *V. bengalensis* (Fig. 3), one of which had just previously been foraging on the branches of a tree (Fig. 1). These were readily accepted suggesting the lizards consume just about any prey animal they come across. After consuming the bat (at around 14:00 hrs), the first animal immediately



Figure 1. Arboreal foraging in *Varanus bengalensis*.



Figure 2. Subadult *V. bengalensis* consuming an adult *Limnonectes limnocharis*.



Figure 3. One of two specimens of *V. bengalensis* consuming a dead bat offered by the authors.

retreated to what appeared to be its home site where it remained for the rest of the day. This may have concerned digestion as the general environmental temperatures at the time were high – even at midnight air temperatures were in the region of 28°C and by early morning still around 25°C, so basking to raise body temperatures may have been unnecessary.

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Amendment

When considering the significance of the colours of venomous reptiles (*Herpetol. Bull.* **95**, 25–30, 2006), I suggested that possibly the only adult venomous snakes with conspicuous coloration whose function might be to warn possible predators to leave them alone are sea snakes (*Pelamis platurus* and *Laticauda* spp.), coral snakes of the genus *Micrurus* and *Micruroides* and the burrowing Australian bandy bandy (*Vermicella anulata*). In this context I should also have mentioned the kraits (*Bungarus fasciatus* and *B. multicinctus*). The avoidance of coral snake banded patterns by free-ranging avian predators in Costa Rica was recorded by E. D. Brodie (1993, *Evolution* **47**, 227–235).

John Cloudsley-Thompson