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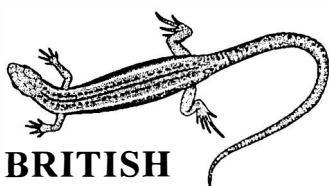
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FRONT COVER: Bush viper (*Atheris* sp.) with trematodes in buccal cavity (J. Cooper).

REVIEW: ORAL DISEASES OF REPTILES

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The oral cavity of reptiles shows a number of specialised features, some of which are relevant to the investigation and understanding of disease in these species. Oral diseases of reptiles may be infectious or non-infectious in origin. They can also be primary or secondary. Infectious agents associated with disease comprise bacteria, viruses, fungi and metazoan parasites. Non-infectious factors include trauma and burns, nutritional deficiencies and/or imbalances, neoplasms and developmental/genetic abnormalities. The investigation of oral diseases of reptiles requires an understanding of the normal morphology and function and a systematic approach to diagnosis.

INTRODUCTION

Oral disease is well recognised in reptiles and necrotic stomatitis ("mouth-rot" or "canker") is possibly the most prevalent disease of these species in captivity (Cooper & Jackson, 1981; Frye, 1991; Gabrisch & Zwart, 1985; Ippen, Schröder & Elze, 1985). Lesions of the oral cavity can lead to anorexia, ill-health and may prove fatal. Clinically affected reptiles frequently show evidence of pain or discomfort. There is often a need for rapid diagnosis and prompt treatment.

Data on oral disease in reptiles are scattered in the literature amongst herpetological and veterinary journals and various textbooks. Often descriptions are restricted to diagnosis and treatment and scant attention is paid to normal anatomy and function, despite the importance of this in terms of understanding pathogenesis and formulating preventive measures. Substantial data are available, however, on the normal features of the oral cavity of reptiles, largely because certain species play an important part as "models" in studying the evolution and development of dentition (Cooper, 1963, 1965; Westergaard & Ferguson, 1986, 1987). Recently there has been interest amongst medical researchers in the oral flora of venomous snakes because of an awareness that secondary bacterial infection can be a complication of snakebite (Cooper, 1991).

In this paper we describe the normal dentition and the other features of the oral cavity of reptiles and review the various diseases of this area which have been reported.

THE NORMAL ORAL CAVITY

GENERAL

In reptiles very little digestive or mechanical breakdown occurs in the mouth prior to swallowing (Davies, 1981). Methods of feeding vary widely. Examples include the chameleons (Chamaeleonidae) which catch their prey using their tongue, some snakes and lizards which immobilise their target species with venom, and carnivorous turtles which use gape and suck feeding in which the floor of the pharynx is lowered drawing water into the mouth, including their prey (Winokur, 1988). The teeth, if present, are generally used for grasping and tearing food items. Often they point caudally, preventing the escape of live prey. They are usually present in larger numbers than in mammals. For example, Owen (1866) identified 47-49 teeth in both upper and lower jaws of a lizard of the genus *Iguana*. The number of teeth is not usually fixed for a given species. Chelonians (tortoises, terrapins and turtles) do not have teeth (see later). As in mammals, the hard palate separates the oral and nasal cavities but in many species the hard palate is reduced in size and only in crocodilians is it complete. There are no definite lips in reptiles as there are in mammals. The glottis lies well forward in the oral cavity and, in snakes, is dorsal to the lingual sheath. When a snake consumes large food items, the glottis is extended to one side and the mandible is lowered to permit respiration. The glottis is circumscribed by two longitudinal and two transverse folds (Guibé, 1970). In some lizards and snakes (agamids, pythons) the ventral

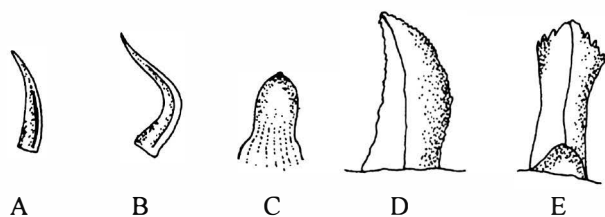


FIG. 1. The structural diversity of lizard and snake teeth. A, Gekkonidae (geckos); B, A tooth typical of snakes; C & D, Varanidae (monitor lizards); and E, Iguanidae (iguanas).

transverse fold is enlarged, continuous with a cranial projection of the cricoid cartilage, forming a lobe similar to the mammalian epiglottis (Guibé, 1970). In chelonians the glottis lies in a notch or cavity on the caudal margin of the tongue (Winokur, 1988).

TEETH

The teeth of reptiles are usually peg-like, showing little differentiation according to their position in the mouth (referred to as homodont), although the teeth of lizards show more diversity than those of snakes (Marcus, 1981) (see Fig. 1). They are generally longer than mammalian teeth. A few species show differentiation associated with feeding specialisations e.g. the venom-conducting fangs in many snakes and one genus of lizard (Edmund, 1969) (see Fig. 2) and the long teeth of bird-eating snakes which can penetrate feathers.

Teeth are present on the maxilla and mandible and, in many snakes, on the palatine and pterygoid bones. The premaxilla has teeth in lizards. Reptilian teeth are composed of enamel, cementum and dentine though the composition of these substances differs from that in mammals (Edmund, 1969).

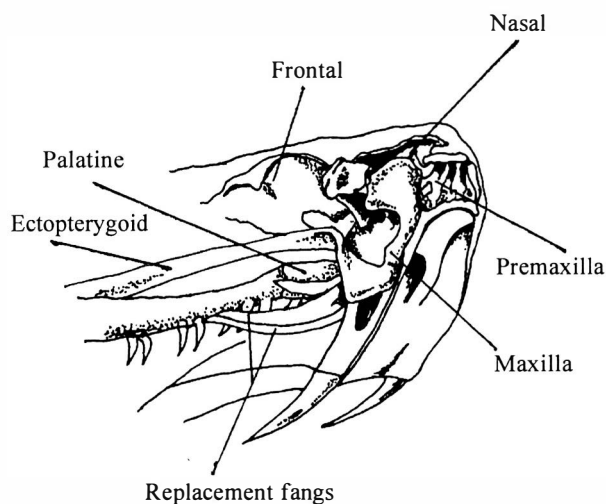


FIG. 2. The upper jaws and fangs of a rattlesnake (redrawn from Evans (1986)).

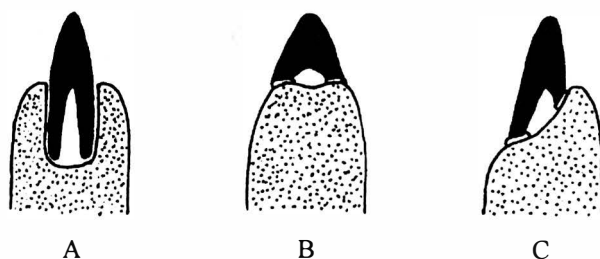


FIG. 3. The three basic types of tooth implantation in modern reptiles. A, Thecodont; B, Acrodont; C, Pleurodont; black = tooth; clear = bone of attachment; and stipples = jaw bone (redrawn from Parker (1977)).

There are three main types of tooth attachment in reptiles: pleurodont, acrodont and thecodont (see Fig. 3). In the pleurodont species (the majority of lizards and snakes) the tooth is attached to the lingual side of the jaw, while in acrodonts (chameleons) it is bound to the summit of the bone. Some lizards, such as the Agamidae, have teeth attached by both pleurodont and acrodont means (Edmund, 1969). The teeth of thecodonts (crocodilians) are set in alveolar sockets (gomphosis). Chelonians (tortoises, terrapins and turtles) do not have teeth (see later). In pleurodont reptiles replacement teeth develop lingually to their predecessors. In pleurodont and acrodont types of attachment the tooth is ankylosed by a substance similar to cementum. Therefore, healthy reptilian teeth are more difficult to remove surgically than similarly sized mammalian teeth. In thecodont reptiles there is no true periodontal membrane but soft tissue separates the cementum lining the alveolus and that on the tooth (Edmund, 1969).

Most reptiles shed and replace their teeth throughout life (polyphyodont) (Edmund, 1969; Bellairs & Attridge, 1975) and this allows the jaw to grow (teeth are present before hatching when the jaw is small). Consequently, the age of an animal cannot be determined by its dentition. Since there is no maternal feeding in reptiles, teeth must be present prior to hatching so that the young animals can immediately feed themselves. Replacement occurs in a definite but complicated sequence (Osborn, 1973) which ensures that there are as many functional teeth as possible. In lizards and all non-venomous snakes the sequence of replacement is disto-mesial but in most other elapids and all viperids this is reversed (Parker, 1977). However, replacement does not occur throughout life in acrodont reptiles (Edmund, 1969).

In oviparous reptiles a structure on the mesial end of the upper jaw serves to rupture the embryonic membranes and shells. In chelonians and crocodiles this structure is called the egg caruncle ("egg tooth") and is a horny epidermal point which is not a part of the true dentition. However, the egg tooth of lizards and snakes is a highly modified tooth belonging to the regular teeth on the premaxilla (Edmund, 1969). Many of the geckos are remarkable in having paired egg teeth.

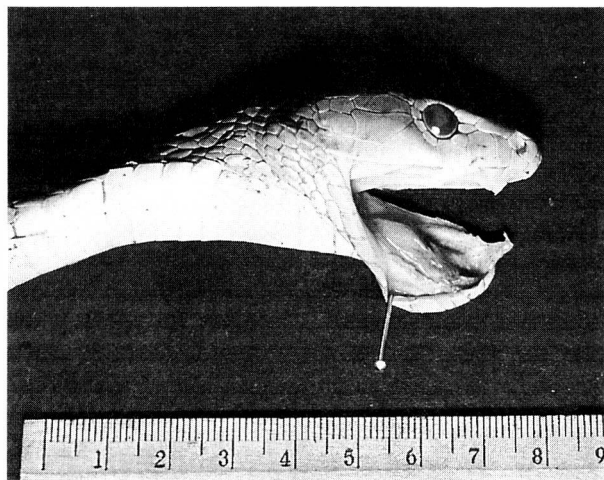


FIG. 4. Jameson's mamba (*Dendroaspis jamesoni*), showing short erect fangs.

Snakes. Most snakes have six rows of teeth attached to the maxillary, palatine and mandibular bones. The mandible is incomplete in the majority of snakes. All teeth are cemented to the rims of shallow crater-like depressions on the lingual surface of the bone (pleurodont), which are formed when a tooth has been shed. As teeth mature, dentine is deposited within and they become thicker. Prior to replacement, the tooth is resorbed from the base. The replacement tooth develops lingual or palatal to its predecessor, lying horizontally with its coronal tip pointing distally. When the old tooth has been completely resorbed the new tooth moves laterally into the tooth row. There is regular dental replacement; teeth that either fall or are torn out are replaced. The teeth are not used for chewing food but are simple, sharp, conical and curved, with the tips pointing distally to help retain prey items (Edmund, 1969). A few species of snake have no teeth. In *Dasypeltis*, an egg-eating snake, the eggshell is broken in the pharynx by ventral extensions of the cervical vertebrae (hypophyses) (Gans, 1974).

In venomous snakes the venom is delivered via specialised teeth or fangs. In some species these are grooved (rear-fanged or opisthoglyphous snakes e.g. the boomslang, *Dispholidus typus*), while in the proteroglyphous (cobras, mambas) and solenoglyphous (vipers), meaning tubular, snakes, the teeth are hollow. Members of the family Elapidae (cobras, kraits, mambas) have a pair of short, erect, rigid fangs in the mesial end of the upper jaw (Fig. 4), while the Viperidae (vipers and pit vipers) have long, curved, hinged fangs enclosed in a sheath at the distal end of the maxilla (Spence, 1986). These fangs can fold back when the mouth is closed and are erect when the snake strikes. The vipers can control their fangs individually (Marcus, 1981). In venomous species, those teeth which do not deliver venom are simple, as in other snakes.

Lizards. The mandible of lizards is complete and bears teeth that appear as a palisade. New tooth development can take place similarly to snakes (e.g. in monitors) or within the old teeth (e.g. in iguanas) (Guibé, 1970). In most lizards there is regular wave-like replacement which can take place up to four times a year. In those lizards with acrodont dentitions this replacement is suppressed after a certain age and no further teeth are produced (Edmund, 1969). Therefore the teeth of older individuals can be severely worn. In iguanas and geckos the replacement teeth lie in cavities on the lingual surface of the predecessor while in other lizards the replacement teeth lie lingually and slightly distally to the precursor (Parker, 1977).

Some lizards initially process their invertebrate prey by chewing prior to swallowing them. In herbivorous lizards, such as the iguana, the cheek teeth are distinguishable from the rostral, pointed, conical ones. The former have expanded crowns which are crenated (Owen, 1866). Thus, the incisors crop vegetation, while the cheek teeth crush and grind. Some monitors feed on molluscs and have broad, blunt teeth (Edmund, 1969). In all Varanidae, the teeth increase in size toward the pharynx. Geckos have large numbers of conical teeth. *Dracaena guianensis*, the Caiman lizard, has remarkable flat-cusped molar dentition well suited for crushing hard-shelled molluscs.

Two species of lizard (the Gila monster, *Heloderma suspectum* and the Mexican beaded lizard, *H. horridum*) have specialized teeth in the lower jaw for delivering venom (all fangs in snakes are in the upper jaw). The venom runs into the space between gums and teeth and rises by capillary action in grooves in the teeth. It is inoculated as the lizard chews on its victim (Marcus, 1981).

Chelonians. These do not have teeth but the heavily keratinized edges of the mandible and maxilla form a "beak" which can effectively cut food and grows throughout life (Evans, 1986). Many specialisations of the beak exist, for example, the herbivorous green turtle's (*Chelonia mydas*) upper beak has vertical ridges and a serrated lower beak for grazing while the desert tortoise (*Gopherus agassizi*) has serrated jaws for plant-shredding (Mahmoud & Klicka, 1979). The carnivorous soft-shelled turtles have very sharp jaws for cutting prey and *Dermochelys coriacea*, the leather-back turtle, has a hooked beak to aid in capturing prey (Mahmoud & Klicka, 1979). In snapping turtles, the mandible itself has a sharp tip and cutting edges (Evans, 1986). In the red-bellied turtle, *Pseudemys rubiventris*, the median ridges on the crushing surfaces are tuberculate, an adaptation for feeding on aquatic plants (Mahmoud & Klicka, 1979). **Crocodylians.** The teeth are generally homodont but the rostrally placed teeth are sharper than the distally placed ones and some teeth are enlarged (Edmund, 1969). When the mouth is closed, teeth in the lower jaw may sit in notches, grooves or cavities in the upper jaw. A good example is the fourth mandibular tooth of

true crocodiles, which is large and can be seen when the mouth is closed; in alligators, the fourth mandibular teeth fit into pits in the upper jaw and thus, are hidden from view. New teeth develop within the sockets of established ones and eventually displace them.

OTHER COMPONENTS OF THE ORAL CAVITY

The remaining parts of the oral cavity include the tongue, gingiva, and oral glands.

The tongue. The structure and function of the tongue vary enormously (Guibé, 1970). In snakes, the tongue is long, cylindrical and lies within a sheath ventral to the glottis. The tongue is usually lined with partially keratinised squamous epithelium and in species where it is fleshy (e.g. geckos), it contains many glands including mucous glands (Luppa, 1977). The sublingual glands in some lizards produce a swelling at the base of the tongue; these also contain mucous glands. The tongue is usually lined with many papillae on the dorsal surface but the sides and ventrum are smooth. The aquatic Chelonia either have small lingual papillae or lack them entirely, while terrestrial chelonia have many glandular papillae which produce mucus for lubrication (Winokur, 1988). In snakes and many lizards e.g. monitors, the tongue's function is solely for monitoring the chemical composition of the surroundings and is forked at the tip and retractable at its base. In chelonians and crocodiles, it has a mechanical function only but is relatively immobile in comparison with that of some species, especially certain lizards (e.g. chameleons) where it plays an important part in the capture of prey (Schwenk & Throckmorton, 1989). In

lizards the shape is variable and this characteristic is used taxonomically (Fig. 5). Taste buds are present on the tongues of some reptiles (Marcus, 1981).

The Jacobson's (vomeronasal) organ on the dorsal aspect of the oral cavity provides olfactory function. The forked tip of the tongue of snakes and some lizards slides into the ducts of this organ, carrying chemical particles with it.

Gingiva. A mucous membrane which largely consists of compound squamous, non-keratinized epithelium lines the oral cavity of most reptiles. In lizards this is replaced by a compound, ciliated, columnar epithelium, containing goblet cells, distally. The squamous epithelium is tougher and allows greater mechanical breakdown of food in the mouth (Luppa, 1977). In large sea turtles, the oropharyngeal and oesophageal epithelium has large numbers of long, conical, keratinized papillae that point distally, helping to retain food (Evans, 1986). Some chelonia have vascular, non-keratinized papillae which perform respiratory gas exchange (e.g. the soft-shelled turtles, Trionychidae (Winokur, 1988)). Taste buds occur within the epithelium of reptiles along with many types of glands, which are also found in the lamina propria (Luppa, 1977). In many snakes the gum forms a thick sheath which surrounds each tooth and conceals a large part of the base of that tooth (Owen, 1866).

Glands. In reptiles salivary gland secretions are mucous, have little digestive function, acting largely as lubricants. Venoms are an exception, being rich in proteolytic enzymes and other substances (Russell & Brodie, 1974).

There are a large number of glands in the oral region of reptiles (Fig. 6). The palatine glands are numerous and line the roof of the oral cavity of all reptiles apart from some turtles and lizards (Kochva, 1978). They may be simple crypts or relatively complex, multibranched tubules, which produce mucous

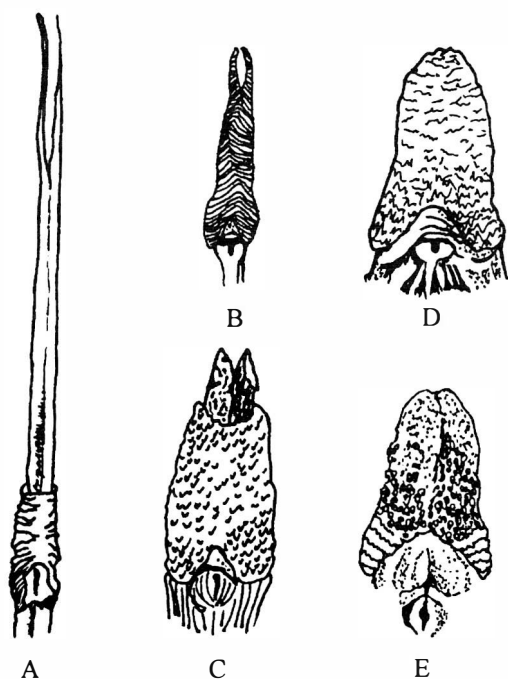


FIG. 5. Types of lizard tongues. A, Varanidae (monitors); B, Lacertidae; C, Anguidae; D, Agamidae (agamid lizards); E, Gekonidae (geckos) (redrawn from Guibé (1970)).

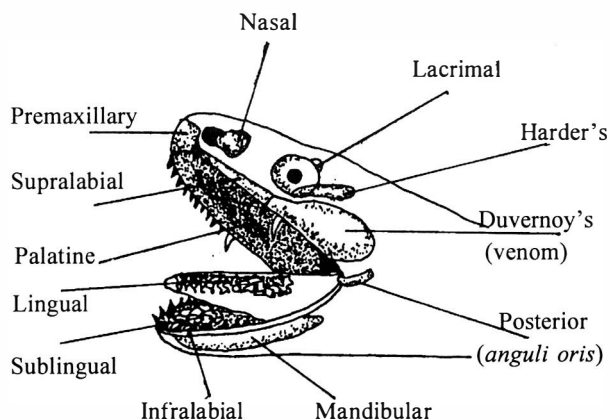


FIG. 6. The major glands of the reptilian head (redrawn from Kochva (1978)).

secretions. The sublingual glands lie in the base of the mouth and may fuse in the midline rostrally. They are similar in structure to the palatine glands. In true sea snakes (family Hydrophiidae) and the file snake (*Acrochordus granulatus*) the caudal sublingual gland is a salt gland (Dunson, 1976). Marine reptiles utilize salt glands for extra-renal excretion of electrolytes and specifically sodium chloride. The caudal sublingual salt gland encloses the lingual sheath. When the tongue is extended, fluid is expelled via multiple ducts into the tongue's sheath (Dunson, 1976). Lingual glands occur in the tongues of some lizards, Chelonians and crocodilians. They produce either mucous or serous secretions. They are absent in species where the tongue has mainly chemoreceptive functions (e.g. lizards, such as the Varanidae, and snakes).

In some crocodilians, the lingual glands are salt glands (Mazzotti & Dunson, 1989). In squamates, labial glands line the mouth edges and produce serous and mucous secretions.

The Gland of Gabe (Kochva, 1978) lies laterally to the mandible and ventrally to the labial glands. It only occurs in some anguimorph lizards. It has been suggested that this gland produces venom. The venom gland of snakes in the family Colubridae is called the Gland of Duvernoy (Kochva, 1978). It is located in the maxillary region, originating at the angle of the mouth and extending as far dorsally as the level of the eye. The surrounding muscles are believed to assist in emptying the gland but neuronal control may also occur. It is a branched tubular gland divided into two parts and many lobules, each opening into its own duct; these in turn feed a central duct.

Venom glands of Elapidae, Viperidae and *Atractaspis* are not called Duvernoy's glands. They differ considerably in size. The glands of the Elapidae are situated on the lateral side of the head. The gland is divided into an accessory gland and several lobules each containing many tubules. The secretory epithelium is columnar and serous apart from in the accessory gland where it is mucous. Muscular activity empties the gland. The Atractaspidinae have elongated glands which may extend up to one-sixth of the length of the body and do not have an accessory gland. The venom gland of the Viperidae is triangular and has an accessory gland. The capsule is thinner than in elapids. The function of the accessory gland is unknown. Viperidae tubules contain flattened, round and conical cells as well as columnar types.

DISEASES OF THE ORAL CAVITY

Oral diseases of reptiles can be categorised under two headings - (1) those conditions which primarily affect the oral cavity, and (2) diseases in which lesions or clinical signs involving the oral region occur but these are secondary to other changes. Necrotic stomatitis is an example of the former, bacterial septicaemia (with petechiae in the buccal mucosa) an example of the latter. In this review particular attention will be

paid to specific (primary) conditions of the oral cavity but mention will also be made of those in the second category where this is appropriate.

Oral diseases can be divided into two main groups: (a) Infectious - bacterial, viral, mycotic, and parasitic; and (b) Non-infectious - physical/traumatic, nutritional, neoplastic, and developmental/genetic.

This distinction is not absolute. Some conditions may be infectious in aetiology but non-infectious factors - for example, physical damage or nutritional deficiencies - can predispose to their development or spread. However, for convenience the two groups will be discussed separately.

INFECTIOUS

Bacterial. The most prevalent and well recognised oral disease of reptiles is probably necrotic stomatitis (commonly termed "mouth-rot" or "canker"). Its features have been discussed by many authors, amongst them Cooper & Jackson (1981), Frye (1991) and Hoff, Frye & Jacobson (1984). The condition may be acute or chronic. Snakes and chelonians (mainly tortoises) appear to be particularly susceptible (Fig. 7), lizards and crocodilians less so. The causal organisms are usually Gram-negative bacteria, especially *Pseudomonas* and *Aeromonas* spp., but other bacteria have occasionally been reported, amongst them a *Mycobacterium* sp. (Quesenberry, Jacobson, Allen & Cooley, 1986).

There has been considerable interest in the oral bacteria of reptiles (see for example, Cooper, 1981; Draper, Walker & Lawler, 1981; Goldstein, Agyare, Vagvolgy & Halpern, 1981) and the relationship between "normal flora" and infectious lesions such as stomatitis. Many of the organisms involved appear to be opportunists (Cooper, 1991). Factors that predispose to stomatitis probably include suboptimum temperatures and other stressors and a high challenge because of a build-up of bacteria in, for example, water containers. The inhalation of necrotic material and the



FIG. 7. Histological section of tongue of Mediterranean tortoise (*Testudo* sp.) with a bacterial glossitis. The mucosal surface is ulcerated and many bacteria are present.

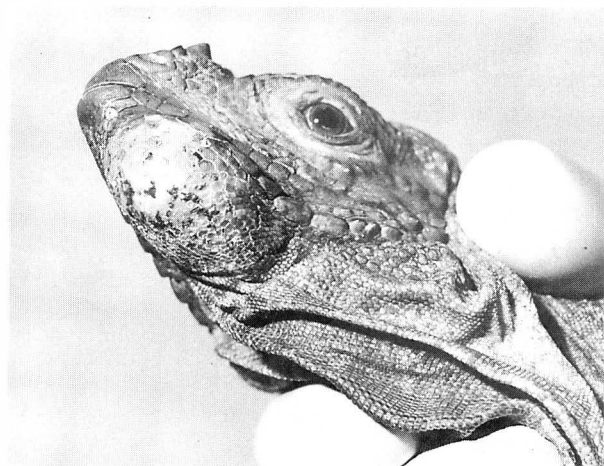


FIG. 8. Rhinoceros iguana, *Cyclura cornuta*, with a pronounced gular swelling. Radiography, histology and microbiology confirmed that this was an abscess.

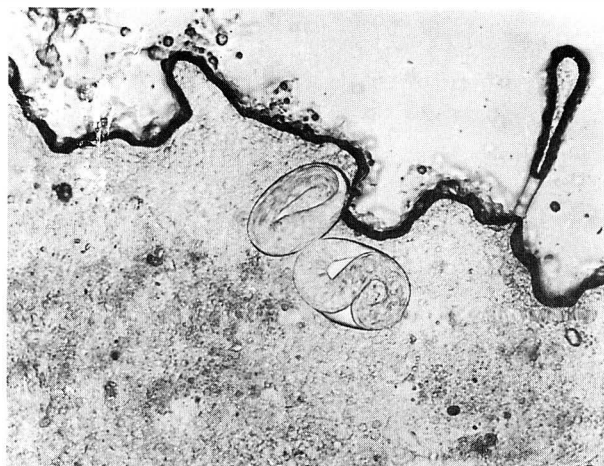


FIG. 9. Eggs of *Kalicephalus* in cellular debris from the upper oesophagus of a sand snake (*Psammophis*).

development of aspiration pneumonia is a common complication of necrotic stomatitis (Frye, 1991), particularly in chronic cases which progress to erosion, ulceration and fibrinous diphtheritic membrane formation.

Other bacterial infections of the oral region which have been reported include gular and parotid abscesses (Fig. 8) and cephalic cellulitis (Frye, 1991).

Reptiles with a bacterial septicaemia may exhibit petechiae of the buccal cavity. Similarly, cases of pneumonia may present with oedema of the mucosa and purulent exudate (from the lung or lungs) may be seen.

Viral. Herpesviruses have been isolated from the venom of elapid snakes and in the case of Siamese cobras (*Naja n. kaouthis*) were associated with venom gland infections (Simpson, Jacobson & Gaskin, 1979).

Herpes virus-like bodies were reported in Argentine tortoises (*Geochelone chilensis*), many of which died following severe stomatitis (Jacobson, Clubb & Gaskin, 1985).

An outbreak of stomatitis in Mediterranean tortoises (*Testudo graeca*) yielded a number of different bacteria including *Pseudomonas* spp., but there was no response to antimicrobial therapy. Transmission electronmicrography revealed virus particles, similar to a *Herpesvirus*, in two tortoises (Cooper, Gschmeissner & Bone, 1988). There have been subsequent reports of a glossitis and oesophagitis involving large numbers of Mediterranean tortoises (Müller, Sachsse & Zangger, 1990) and concern has been expressed recently that there may be a viral 'epidemic' in this genus in Europe (Cooper, Lawton, Jacobson & Zwart, 1991).

Mycotic. Several species of fungus have been reported from oral lesions in reptiles (Austwick & Keymer, 1981), including *Candida*, *Cladosporium*, *Trichosporon* and *Penicillium*. Others have not been fully

determined. Fungi have been associated with stomatitis and cephalic granulomata, although whether they are primary pathogens or secondary to (for example) a bacterial infection, nutritional deficiency or the use of antibiotics, remains unclear. Jacobson (1984) reported a case of chromomycosis and fibrosarcoma involving the intermandibular area of a mangrove snake (*Boiga dendrophila*).

Parasites. Ectoparasites are usually of little consequence insofar as the oral cavity is concerned, although ticks of various species occasionally attach to the skin around the mouth and leeches (e.g. *Placobdella* spp.) may be found on the buccal mucous membrane (Sawyer, 1986).

Three genera of nematodes, *Rhabdias*, *Entomelas*, and *Kalicephalus*, are sometimes associated with oral lesions. *Rhabdias* (in snakes) and *Entomelas* (in lizards) may cause oedema and inflammation while ulceration and accumulation of oesophageal debris are more typical of *Kalicephalus* (Cooper, 1971) (Fig. 9). Pentastomes (linguatulids) are primitive arthropod parasites which are usually associated with the lung and respiratory tract. Cellular debris is sometimes passed up the trachea and may be seen in the pharynx or buccal cavity.

Trematodes, usually of the genus *Ochetosoma*, are not uncommonly seen in the buccal cavity of snakes (Cooper, 1974; Pitman, 1974). They do not appear to be associated with oral lesions and can usually be removed with ease (Fig. 10).

NON-INFECTIOUS

Physical/traumatic. Captive reptiles are very prone to damage and this may have a number of different causes. Self-inflicted rostral abrasions are particularly prevalent in snakes and lizards which repeatedly rub themselves against the wall of their enclosure, especially if it is made of glass. The lesions become



FIG. 10. The buccal cavity of a bush viper (*Atheris* sp.) showing many trematodes. The sheathed fangs are also visible.

ulcerated and ultimately, if not treated or alleviated, chronic and granulomatous. Secondary bacterial infection may occur and osteolysis can be a sequel.

Teeth may break or be lost due to self-inflicted damage - for example, striking at the handler. It must be borne in mind that in most species teeth are shed regularly under natural conditions: the presence of teeth in the alimentary tract or faeces of a reptile does not therefore necessarily imply a physical injury or pathological process.

The keratinous "beak" of chelonians may become damaged (see later) or overgrown (Frye, 1981). Injuries can be repaired using a variety of techniques. Overgrown beaks can be trimmed and manicured.

Bite wounds are not uncommon in captive reptiles. Sometimes another reptile is responsible - for example, an adult male iguana may attack another - but more often the wound is inflicted by a predator, such as a dog, cat or other carnivore, or a rodent provided as food. The last of these can be avoided if only dead animals are used. The extent and significance of bite wounds vary considerably: sometimes severe damage ensues (e.g. fracture), but it must be remembered that even an apparently minor injury can result in anorexia and certain types of trauma (e.g. the loss of a snake's tongue), may have serious consequences.

Injuries to the oral cavity may also be caused by humans (intentional or accidental) and by accidents in the vivarium - for instance, a stone rolling on to a lizard, or a snake damaging its head because it slips or falls when trying to climb out of its enclosure. Burns may occur as a result of contact with heaters: although the body is most often affected, the head, including the oral cavity, may also be damaged. Chemical burns can occur if reptiles are housed in containers which have previously harboured or been cleaned with acids, alkalis or other irritant substances. Minor wounds affecting the oral cavity usually heal well but there is

always a danger of a secondary bacterial infection. Prompt attention to hygiene is important. Wounds can be treated topically: suturing may be necessary. More extensive damage such as fractures, may require specialist attention.

Long-term sequelae to traumatic lesions include granulation and fibrosis. Venom gland/duct damage can occur. Distortion of facial structures may make feeding difficult or predispose to desiccation/infection of oral mucous membranes.

Nutritional. Metabolic bone disease (MBD), or nutritional osteodystrophy due to a calcium:phosphorus imbalance, is a well recognised cause of oral changes (Lawton, 1991). Soft bones are a characteristic feature: in some cases the mandible and maxilla become pliable and easily distorted due to muscular action. Submandibular masses of fibrous tissue are common.

The only other nutritional deficiency which is unequivocally recognised in reptiles and which may have a direct effect on the oral cavity is vitamin A deficiency. The classical lesions in terrapins are swollen eyes associated with a build-up of keratinous debris (Elkan & Zwart, 1967), but some cases also show abrasions of the epithelium around the mouth and a tendency for the keratin to crumble and degenerate.

Vitamin C deficiency has been suggested as a predisposing factor in stomatitis (see earlier) (Wallach, 1969), but there is little evidence to support this claim. **Neoplastic.** Papillomata, probably caused by viruses (Cooper, Gschmeissner & Holt, 1982; Raynaud & Adrian, 1976), but occasionally associated with fungi and other organisms, occur in captive green lizards (*Lacerta viridis*) and may involve the animal's head and mucocutaneous junctions, including the "lips".

Carcinomas and sarcomas of various types have been recorded in reptiles (Jacobson, 1981): occasionally the buccal cavity may be affected. Careful differentiation from chronic inflammatory lesions may be necessary.

Developmental/genetic. Various developmental abnormalities have been recognised in reptiles (Bellairs, 1981). Prognathia and epignathia are not uncommon. Cleft lip/palate has been reported and axial bifurcation/conjoined twinning may result in duplication of all or part of the head and associated structures. The cause of these abnormalities is never easy to determine. Genetic factors may be involved, but there is also evidence for the role of an adverse environment - for example, eggs incubated at too high or too low a temperature (Frye, 1991).

DISCUSSION

Oral diseases are important in reptiles. Differential diagnosis requires an understanding of the normal anatomy and how this is related to function.

Full investigation is necessary. The taking of a clinical history is always important and in view of the frequent role of the environment in oral diseases

should, if possible, be coupled with inspection of the management. The patient should be carefully observed before handling: subtle clinical signs, such as a tendency to yawn or to rub the side of the head on the substrate, may assist in diagnosis. More apparent signs may include salivation and the appearance of bubbles around the mouth and nares. Clinical examination must be thorough and may be facilitated by the use of an auriscope or rigid endoscope.

The taking of samples - for example, swabs and biopsies - for laboratory examination is advisable at an early stage and may play a key role in diagnosis. Likewise, *post-mortem* examination of reptiles with oral disease should include submission of specimens for bacteriology, histopathology and other investigations. It is most important to preserve material for subsequent examination: the authors recommend that whenever possible one portion is retained in buffered formol-saline and another in a deep freeze (-20°C).

Treatment has not been discussed in this paper: excellent papers are to be found amongst the references. Treatment of oral diseases will often include attention to management as well as (on their own or in combination) chemotherapy, surgery and supportive care.

Oral diseases of captive reptiles are best prevented by good management, the maintenance of hygiene and prompt attention to minor abrasions and other lesions. The veterinary surgeon can do much to promote this approach amongst those who keep and breed these animals.

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CLIMATIC FACTORS AFFECTING THE ACTIVITY OF NATTERJACKS (*BUFO CALAMITA*) AND COMMON TOADS (*BUFO BUFO*) OUTSIDE THE BREEDING SEASON: MATHIAS REVISITED

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A multivariate analysis was performed on a set of data which contained records on the capture rates outside the breeding season, under varying environmental conditions of the two native British toads, *Bufo bufo* and *Bufo calamita*. The data were taken from a study by Mathias (1971). Although statistical relationships within the data set were generally weak, results of the analysis suggest that activity outside the breeding season of *Bufo bufo* showed the stronger dependence on the recorded environmental parameters. In particular, a striking correlation was found to exist between capture rates of *Bufo bufo* and temperatures recorded at 30 cm below ground earlier the same day.

INTRODUCTION

Relatively few studies on European amphibians have concentrated on their activity outside the breeding season. Any study which attempts to assess the effects of the environment during this terrestrial phase is likely to face great difficulty in obtaining adequate data from the field. Apart from the problem of actually finding individuals in the first place, there is the obstacle of adequately taking into account the extremely variable nature of most terrestrial environments. This is particularly true where continually changing parameters such as climatic conditions are also to be included in the assessment. In this context, previous studies which include environmental parameters have largely tended to focus on the influence of habitat as opposed to that of climate (Strijbosch, 1980; Beebee, 1985; Pavignano, Giacomini & Castellano, 1990). It is nevertheless clear that the effect of climate is of great importance in determining amphibian activity and so must be taken into account if knowledge of terrestrial amphibian ecology is to be improved. This was clearly indicated in a recent study on natterjack activity during the terrestrial phase in which greater than 81% of the variance in sightings at a particular site could be accounted for simply by using multilinear regression of temperature and rainfall readings (Denton & Beebee, 1992).

In fact, before the above recent study took place, a similar one was performed as part of a thesis by Mathias (1971) although no multivariate analysis of the data collected was carried out then. This classic comparative amphibian study of common toads, *Bufo bufo* and natterjack toads *Bufo calamita*, actually contains several data sets collected over a three year period. The data, which are generally both meticulous and extensive, were collected in one of the few British natural habitats where both species are to be found in coexist-

ence. The study location, situated on the Merseyside coast, is today one of only a few remaining areas where the natterjack toad is still to be found in reasonable abundance within Britain (Beebee, 1983). Results of a multivariate analysis on the data set relating to the above-mentioned Mathias study are now presented for the first time. The objective of this analysis was primarily to test for the possible existence of a relationship between individual toad movements and climatic conditions, outside the breeding season.

METHODS

DATA COLLECTION

Mathias assessed toad movements by carrying out night observations at two study sites termed the North and South site, respectively. Observations were carried out at night because this was found to be the most effective time at which to locate toads. Denton & Beebee (1992) also found night searching to be the best time for finding adults of both species outside the breeding season.

Regular night field trips to the sites were carried out by Mathias for the entire duration of the active part of the annual life cycle of each species during the period April 1968 to June 1970. The 'sampling method', by which the degree of toad night activity was assessed, consisted simply of noting the total number of captures made of each species on a predefined route within the field trip. After capture, each toad was marked and then released at the same point where it was caught. In addition to capture numbers, the values of ten environmental variables were obtained for the locality (Southport) for every field trip (Mathias 1971: Table 3.14, p. 204). Efforts were continually made to ensure that possible sampling bias, such as variation of route within the field trip, were kept to a minimum.

	North Site (19 trips)			South Site (20 trips)			Both Sites (39 trips)		
	Bb	Bc	total	Bb	Bc	total	Bb	Bc	total
No. of captures	9	226	235	204	159	363	213	385	598
less: recaptures	(1)	(26)	(27)	(30)	(38)	(68)	(31)	(64)	(95)
= individuals captured	8	200	208	174	121	295	182	321	503
% of total captures	2	38	40	34	26	60	36	64	100
Recapture rate %	11	12	11	15	24	19	15	17	16

TABLE 1. Summary of captures and recaptures occurring in the extracted non-breeding data set, 1968-1970. Bb - *Bufo bufo*, Bc - *Bufo calamita*.

The field sites were located at opposite ends of a nature reserve, approximately 3 km apart, and each was a few thousand square metres in area. They were selected so as to be representative of two different types of dune habitat. The North site was more exposed to wind and had little tree cover whereas the South site was less exposed because of protection afforded by the close proximity of nearby woodland. The data collected for field trips made outside of the breeding seasons of each species (39 out of a total of 55 trips) are referred to as ‘non-breeding’ data. It is this data set which has been extracted for analysis.

A summary of the total number of captures of each species recorded at each site, for the 39 extracted field trips is shown in Table 1. Mathias did not record the number of *individuals* captured on each trip but did, however, record those individuals that were captured more than once. This additional information enables recaptures to be individually identified and then subtracted from the captures presented in his Table 3.14., so that the total number of individuals included within the extracted data set can also be deduced. Since the recapture rate turned out to be low (16%), the number of captures (598) reasonably equates with the number of individuals that were captured (503). Either of these latter two parameters could therefore be taken as a measure of general toad movements, with negligible difference to analytic results. Capture numbers per field trip were selected as these were already presented in Table 3.14, thereby avoiding any further need for reconciliation. The respective capture variable is denoted by the following abbreviation for each species: *Bbcaught* - number of common toad (*Bufo bufo*) captures on a night field trip; and *Bccaught* - number of natterjack toad (*Bufo calamita*) captures on a night field trip.

DATA ANALYSIS

Data were analysed for dependence of capture rates on climatic conditions and also for interdependence. Abbreviations and respective definitions of each of the

ten environmental variables recorded, the lower eight (i.e. *maxtemp* down to *windspeed*) of which can be classed as strictly climatic, are: *date* - day of year (numbered 1 to 365); *site* - capture locality, North Site or South Site (numbered 1 and 2, respectively); *maxtemp* - maximum recorded day temperature; *mintemp* - minimum recorded day temperature; *grasstemp* - temperature recorded in grass (time of day not recorded); *g30temp* - temperature 30 cm below ground at 09.00 hr; *rainfall* - rainfall recorded (1/100 in); *sunshine* - sunshine recorded (1/10 hr); *winddir* - mean recorded wind direction (degrees); and *windspeed* - mean recorded wind speed (knots).

All of the above climatic recordings were made on the day prior to the night field trip. The curious variable *grasstemp* is, unfortunately, also vague since no information was given on either how or at what time of day temperature recordings in grass were made.

It can be seen from Table 1 that very few common toad captures were made at the North Site (% of total captures: 2% North, 34% South) whereas the natterjack toad captures were more evenly distributed between each site (% of total captures: 38% North, 26% South). Discriminant analysis of data collected for the field trips on the basis of *site* was therefore, unsurprisingly, found to be highly significant (null hypothesis rejected at $P = 0.001$). Hence data were also categorised as ‘North Site’ and ‘South Site’ according to the site visited in all of the subsequent analysis.

The possible interdependence between variables was investigated in two parts. Firstly, a correlation analysis was performed to generally identify the stronger and weaker relationships between all variables. Secondly, any interdependence between the eight climatic variables themselves was analysed by a principal component analysis, to assess whether the broad effects of climate could be more concisely described in terms of a few key factors.

Following the encouraging multilinear regression results obtained by Denton & Beebee (1992) between natterjack sightings vs. climatic readings, the depend-

ence of capture rates on recorded climatic conditions was assessed by a similar regression analysis on the Mathias captures of each species vs. recorded climatic data. For all of the defined data categories, *Bbcaught* and *Bccaught* were each taken as the dependent variable within the regression, initially with all climatic variables included as independent variables. A stepwise sequential selection procedure was then used to identify the key named climatic variables behind the relationships within these regressions. This technique calculates an ‘optimal subset’ of variables to describe any dependence, using the criterion of maximization of the R^2 -adjusted value, out of the variables defined in the original regression model (e.g. see Draper & Smith 1981). Principal component analysis would also have served to achieve a reduction in the number of variables here, but a meaningful interpretation of the main components would have been difficult.

RESULTS

CORRELATION ANALYSIS

When data for both sites were analysed collectively, the strongest general correlations were found, unsurprisingly, between the temperature-dependent climatic variables such as, for example, *g30temp* vs. *maxtemp* ($r = 0.70$, $P = 0.0001$). For some unknown reason, perhaps related to the way in which grass temperature recordings were made, the mysterious variable *grasstemp* correlated strongly with *mintemp* ($r = 0.89$, $P = 0.0001$).

The correlations of *Bbcaught* or *Bccaught* with all environmental variables, for the collective data are shown in columns 1 and 3 of Table 2. Toad captures in general can be seen to show significant correlations ($P < 0.05$) with only two climatic variables, namely *g30temp* for the common toad ($r = 0.43$, $P = 0.01$) and *maxtemp* for the natterjack ($r = 0.35$, $P = 0.03$). The number of common toad captures *Bbcaught* showed greatest correlation with *site* ($r = 0.66$, $P = 0.0001$) mainly as a result of the great disparity of capture numbers of this species with respect to the two study sites.

Table 2 also shows the correlations of *Bbcaught* or *Bccaught* with environmental variables for the separate data sets North Site and South Site. For these localized data sets, captures now showed significant correlations with a total of four climatic variables, namely *maxtemp*, *sunshine*, *g30temp* and *mintemp*. Common toad captures correlated significantly with all of these variables in turn, at one or other of the sites, but natterjack captures still only correlated significantly with *maxtemp*, at the North Site.

For the North Site, common toad captures were found to correlate significantly with *maxtemp* ($r = 0.50$, $P = 0.03$), and *sunshine* ($r = 0.48$, $P = 0.04$). No inference can be made from this though, since the actual number of common toad captures at this site were too few. For the same reason, no real significance can be attached to the apparently significant correlation between captures of the two species themselves, *Bbcaught* vs. *Bccaught* ($r = 0.60$, $P = 0.007$). However,

	Both Sites <i>n</i> = 39				North Site <i>n</i> = 19				South Site <i>n</i> = 20			
	<i>Bbcaught</i>		<i>Bccaught</i>		<i>Bbcaught</i>		<i>Bccaught</i>		<i>Bbcaught</i>		<i>Bccaught</i>	
	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>
<i>Bbcaught</i>	*	*	0.03	NS	*	*	0.60	0.00	*	*	0.30	NS
<i>Bccaught</i>	0.03	NS	*	*	0.60	0.00	*	*	0.30	NS	*	*
<i>site</i>	0.66	0.00	-0.18	NS	*	*	*	*	*	*	*	*
<i>date</i>	-0.20	NS	-0.12	NS	-0.36	NS	-0.26	NS	-0.40	NS	0.10	NS
<i>maxtemp</i>	0.29	NS	0.35	0.03	0.50	0.03	0.53	0.02	0.52	0.02	0.11	NS
<i>mintemp</i>	0.19	NS	-0.12	NS	-0.18	NS	-0.23	NS	0.46	0.04	0.00	NS
<i>grasstemp</i>	0.14	NS	-0.12	NS	-0.20	NS	-0.23	NS	0.32	NS	0.04	NS
<i>g30temp</i>	0.43	0.01	0.06	NS	0.28	NS	0.12	NS	0.77	0.00	-0.04	NS
<i>rainfall</i>	-0.15	NS	0.14	NS	0.08	NS	0.10	NS	-0.21	NS	0.19	NS
<i>sunshine</i>	0.19	NS	0.09	NS	0.48	0.04	0.17	NS	0.53	0.02	-0.13	NS
<i>winddir</i>	0.08	NS	-0.18	NS	-0.02	NS	-0.16	NS	0.21	NS	-0.26	NS
<i>windspeed</i>	-0.20	NS	-0.13	NS	-0.07	NS	-0.03	NS	-0.17	NS	-0.42	NS

TABLE 2. Correlations of the number of toad captures outside of the breeding season with recorded environmental variables, 1968 to 1970. NS not significant, ($P > 0.05$).

Climatic variable	PC1	PC2	PC3
<i>maxtemp</i>	-0.43	-0.40	-0.10
<i>mintemp</i>	-0.51	0.37	-0.08
<i>grasstemp</i>	-0.43	0.45	-0.01
<i>g30temp</i>	-0.55	-0.20	-0.03
<i>rainfall</i>	-0.03	0.41	-0.06
<i>sunshine</i>	-0.23	-0.51	0.35
<i>winddir</i>	-0.10	0.15	0.67
<i>windspeed</i>	-0.01	0.14	0.64
Eigenvalue	2.51	2.02	1.56
%Explained variance	32	25	19
%Cumulative variance	31	57	76

TABLE 3. Weightings of first three principal components (PC) in principal component analysis of climatic variables ($n = 39$).

for the natterjack captures at this site, which were numerous, the significant correlation found with *maxtemp* was therefore also important ($r = 0.53$, $P = 0.02$).

For the South Site, stronger correlations between toad captures vs. environmental variables were found to exist. Since the capture numbers at this site were more evenly distributed between the two species, these data are more likely to demonstrate any comparative differences in the behaviour of each species. Common toad captures were again found to show stronger and more numerous correlations. Significant correlations for this species were with: *g30temp* ($r = 0.77$, $P = 0.0001$), *maxtemp* ($r = 0.52$, $P = 0.02$), *sunshine* ($r = 0.53$, $P = 0.02$), and *mintemp* ($r = 0.46$, $P = 0.04$). The number of

natterjack captures showed no significant correlations at $P < 0.05$ although a noteworthy negative correlation was seen with *windspeed* ($r = -0.42$, $P = 0.07$).

PRINCIPAL COMPONENT ANALYSIS OF CLIMATIC VARIABLES

Table 3 shows the weightings for the first three principal components obtained from a principal component analysis in which all the climatic data was utilised ($n = 39$). These three components accounted for 76% of the variance in the climatic data (by Kaiser's criterion the other five principal components may be discarded since their eigenvalues are less than 1). There was no significant difference between the average climatic conditions recorded for the visits to each site. The weightings for component 1 are dominated by all of the temperature variables *maxtemp*, *mintemp*, *grasstemp*, and *g30temp*. This component therefore strongly reflects 'temperature'. Component 2 is more difficult to interpret, but the opposite sign of the variable pairs *maxtemp* and *mintemp*, *grasstemp* and *g30temp*, and *rainfall* and *sunshine* suggests that this component may be loosely described as 'contrast between hot and cold'. Component 3 largely reflects 'wind' because of the heavy weightings with *winddir* and *windspeed*. Thus overall, the recorded climate can be roughly described in terms of the three key factors, temperature, contrast between hot and cold, and wind. Component 1 also further demonstrates the existence of interdependence between the temperature variables, observed in the correlation analysis.

REGRESSION ANALYSIS

It was found, as in the correlation analysis, that common toad captures showed the stronger relationship with the recorded environmental conditions. This

Dependent variable	Both Sites $n = 39$		North Site $n = 19$		South Site $n = 20$	
	<i>Bbcaught</i>	<i>Bccaught</i>	<i>Bbcaught</i>	<i>Bccaught</i>	<i>Bbcaught</i>	<i>Bccaught</i>
Independent variables						
All 8 climatic variables	8	9	2	3	38	0
Optimal subset*	16	16	23	27	56	17
*Optimal subsets of climatic variables in descending order significance	<i>g30temp</i>	<i>grasstemp</i> <i>mintemp</i> <i>maxtemp</i> <i>sunshine</i> <i>rainfall</i>	<i>sunshine</i> <i>maxtemp</i>	<i>maxtemp</i> <i>mintemp</i> <i>sunshine</i> <i>grasstemp</i>	<i>g30temp</i>	<i>windspeed</i> <i>rainfall</i>

TABLE 4. Comparison of R^2 -adjusted values (in %) obtained in linear regressions using climatic variables.

was most clearly seen in the regressions performed on the South Site data, by the value of the R^2 -adjusted multiple regression coefficient. The coefficient gives a measure of the extent of the variance in the number of captures which can be explained by the regression, simultaneously taking into account the number of variables used (hence the term 'adjusted'). This adjustment for the number of variables used is an important one, since the R^2 value alone will always "artificially" increase with an inclusion of more variables, in any regression model. Clearly then, the R^2 -adjusted value will always be more appropriate for making comparisons between any regression models which have different numbers of variables, such as those that we shall now come across.

Table 4 compares the R^2 -adjusted values found for regressions performed with the inclusion of all climatic variables against the respective figure found for regressions with the optimal set. Whereas the R^2 -adjusted value was improved in each data category by a reduction to the optimal set, the values for the South Site common toad captures are markedly better than for captures in any other category. This particular optimal variable set, which turned out only to contain the single variable *g30temp*, gave the highest R^2 -adjusted value out of all the regressions, at 56%. Thus, it turns out that the majority of the variance in common toad captures can be accounted for solely in terms of the temperature readings made at 30 cm below ground earlier in the same day as the field trip. It would be dangerous to attach too much importance to the other named sets of optimal variables since the respective R^2 -adjusted values are much too low.

DISCUSSION

The multivariate analysis demonstrates the existence of some, hitherto unnoticed, correlations within the non-breeding data. These correlations of capture numbers *vs.* recorded environmental conditions, were found to be more significant for the common toad. For this species, it was also possible to obtain a 'best fit' multilinear regression model to the data which gave a 56% R^2 -adjusted value for the South Site captures. In the case of the natterjack toad, the respective best fit only gave a 27% R^2 -adjusted value for captures, this time from the North Site. The extent to which these best fit models differ between the two species is one of the most interesting comparative aspects uncovered by this analysis.

What do the actual significant correlations between capture numbers *vs.* recorded environmental variables imply? These observed correlations only serve to *suggest* possible causes of true underlying relationships. It must be remembered that any statistical relationship, no matter how strong, can never establish causal connection. For the common toad, the extent of significant correlation with temperature-dependent variables was clear. It was apparent that the observed movement of individuals, presumably for foraging and so on, in-

creased detectably with higher temperatures. In particular, the striking correlations with recorded ground temperatures suggest that temperature below ground has a great influence in determining its night activity. The fact that interdependence existed between all of the recorded temperature variables, further accentuates the significance of the observed relationship with the *g30temp* variable alone. Are common toads, therefore, particularly sensitive to subterranean temperatures?

Why are such strong relationships absent for the natterjack toad? Could the absence of correlation with ground temperature for this species perhaps be associated with the greater depth below ground of the preferred abode, namely that of burrows in sand dunes? Or alternatively, does this absence of correlation suggest an intrinsic difference between the two species in behavioural response to either ground temperature or some other related factor?

Captures of natterjacks were only found to correlate significantly with recorded maximum temperatures. For a poikilothermic animal, such a correlation is of course, not that surprising. However, the nearly significant negative correlation observed between South Site natterjack captures and wind speed, completely absent for common toad captures made at the same site, supports the premise made by Mathias that natterjacks are more susceptible to dehydration by exposure to the wind (p. 150). It is curious then, that no support to this premise is to be found in the larger number of natterjack captures made at the more exposed North Site. How much of this discrepancy can be attributed to the actual place of capture within the site itself? A natural extension to the current analysis would be to define two new variables which combine the variables *windspeed* and *winddir*, in terms of two vector components. This would then both eliminate the awkward and discontinuous *winddir* variable and at the same time also enhance interpretation of the overall influence of the wind on captures of both species. (The variable *winddir* contributes little useful information in most statistical calculations because of a discontinuity in the scale of measurement. For example, wind directions of 2° and 359° are virtually the same but would be assigned misleadingly different calculative values.)

Further inferences beyond this are not possible, because of the lack of detail in the climatic records. These records serve only as a rough guide to prevailing conditions since they were not actually obtained at the exact time (night) or place (study site) of the field trip in question. This is a frequently encountered limitation in studies of this type (Andren & Nilson, 1985; Iverson, 1992). Even so, the recorded local conditions must still have had a strong bearing on the night 'micro-climate' of the site visited. In this respect, the correlations with ground temperature are potentially more significant because temperatures below ground are usually subject to much less daily variation, depending on the soil type and its moisture content (e.g. van Wijk & de Vries, 1963). Data on both of these unrecorded soil param-

eters would also have served to clarify the importance of the observed absence of any significant correlation of natterjack captures with *g30temp*. It is therefore a pity that no such precise information is available in respect of the soil in which the *g30temp* readings were actually recorded. Clearly, there is still scope for future practical research into this important point.

It must be stressed that only the possible existence of linear relationships is addressed in this kind of a statistical analysis. In nature, most things are not linear. Thus, it is quite possible that significant nonlinear relationships still remain hidden so that, for example, a multivariate loglinear regression analysis may help to reveal these. The comparative lack of correlation of natterjack captures with environmental variables is nevertheless surprising, especially given that a greater proportion of this species were captured (64% total captures). Also surprising for its absence, is the lack of support to the frequently held contention that 'rain brings out toads'. Denton & Beebee (1992) found in their study that natterjack sightings generally correlated with rainfall ($r = 0.6$, $P < 0.01$). Mathias commented on the absence of such anticipated correlations but then went on, overhastily, to conclude that (p. 171) 'there is no apparent correlation between the numbers of animals caught per trip and the temperature, rainfall, and wind speed recordings'. The data obtained in this unique past study may shed still greater future light on the individual movement behaviour of the two native British toads.

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THE 'SURVEY' POSTURE IN WALL LIZARDS, *PODARCIS MURALIS*

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Male, female and juvenile wall lizards (*Podarcis muralis*) observed living on a high, south-facing brick wall in April and August were sometimes (4% of total observation time in adult males) seen immobile, facing downwards in an orientation equivalent to the 'survey' posture of *Anolis* and other Iguanidae. Some aspects of the temporal dynamics of the behaviour were investigated. It was most commonly seen in adult males during August, when there were significant trends for the frequency of the posture to increase towards the base of the wall and for the mean time spent immobile in the posture to be greater than the mean times immobile at other orientations. The 'survey' posture at the middle and higher levels of the wall appeared to be associated with topographical features such as small tufts of vegetation or bricks which stood proud from the remainder. This association could not be tested directly, but fixing a small strip of wood to the wall increased the duration of locomotor pauses and the frequency of 'survey' postures of lizards when they were immediately above it.

INTRODUCTION

Many species of arboreal lizards which have a 'sit-and-wait' foraging strategy, perch on vertical or near-vertical surfaces, such as the trunks of trees, with the longitudinal axis of the body vertical and the head facing downwards. The behaviour is seen particularly commonly in *Anolis* species (Iguanidae), in which it has been called the 'survey' posture (Stamps, 1977).

During a study of the thermoregulatory behaviour of wall lizards (*Podarcis muralis*; Lacertidae) in Italy, it was noticed that the behaviour was sometimes displayed by individuals of this species living on the walls of the city of Lucca. The behaviour has not previously been recorded in Lacertidae, except for a passing reference "... there is scarcely a wall on which these active lizards (*P. muralis*) do not bask or run up and down, often head downwards, in search of insects" (Gadow, 1901). The posture is illustrated (but not described as such) incidentally in a photograph of *P. muralis* by Guttner (1988).

This paper describes some observations on the incidence of the behaviour and gives the results of a simple experiment devised to test the association of 'survey' postures with irregularities on vertical surfaces.

MATERIALS AND METHODS

The city of Lucca, in NW Italy, is surrounded by a massive rampart, 4 km in length, the outer sides of which are near-vertical walls approximately 6.5 m high and faced with small bricks. Wall lizards are abundant on these walls. They were studied at a south-facing part of the wall near the Porta San Pietro; the profile and dimensions of the wall at this site are shown at the right hand side of Fig. 1. The lizards could readily be observed when they were moving on the wall, but not of

course, when they disappeared into crevices within it. Sometimes the movements of an individual took it into the grass at the base of the wall. This grass was mown frequently and so provided little cover, but there was a narrow strip of unmown vegetation (mainly annual herbs) immediately adjacent to the wall. Movements off the top of the wall also took place, but these were relatively infrequent. The behaviour of lizards on the wall was recorded using a dictaphone, while individuals were watched through binoculars from distances of 6-10 m, between 1000 and 1600 hr in August 1988 (times are EST, which is about 15 min ahead of solar time at Lucca). Weather conditions were stable, with little cloud; daily maximum shade air temperatures were always greater than 28°C.

The movement pattern of *P. muralis* usually involves an alternation of periods of locomotion with pauses; the latter are of very variable duration (Avery, Mueller, Jones, Smith & Bond, 1987). The orientations of lizards which were stationary for more than 5 s (hereafter referred to simply as 'stationary') were recorded by estimating to the nearest 45° the angle with respect to the vertical of an imaginary line between the middle of the shoulder and pelvic girdles; vertical orientation with the head upwards was defined as 0°. The period of 5 s was arbitrary, and dictated by the practicalities of working in the field without video recording equipment (see also Discussion). The height of a lizard on the wall was easily measured by counting bricks. Heights were recorded in six bands 1 m in width beginning at 0.5-1.5 m. The presence of lizards in the band 0-0.5 m was recorded separately, because the animals were often concentrated there. Lizards in the 180° orientation (in reality between about 157.5 and 202.5°) were considered to be in the 'survey' posture. Lizards were initially

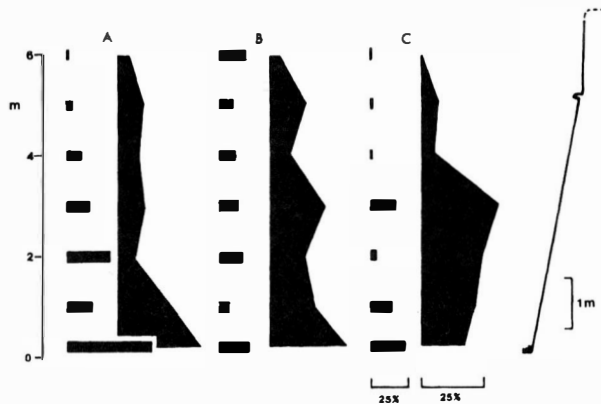


FIG. 1. Kite diagram showing relative frequencies of periods stationary for more than 5 s at different heights on the wall by (A) adult male, (B) adult female and (C) juvenile lizards in August. Horizontal histograms to the left of each kite diagram show the percentage of periods stationary at each height in the 'survey' posture. Note that the width of the lowest sampling band (0-0.5 m) is one half that of the remainder. A profile of the wall is shown at the right hand side of the Figure.

selected at random, and their behaviour (duration of time moving, duration of time stationary when this was >5 s, orientation when stationary, height) recorded until they disappeared from view. Sequences lasting less than 10 min were discarded; the longest continuous sequence of behaviour recorded for any individual was 2.1 hr. After a total of 25.6 hr of observations, attention was concentrated exclusively on adult males.

Observations of lizards on the wall were also carried out in April 1989, when the weather was varied and shade air temperatures at mid-day never exceed 21°C. They commenced on the first occasion after 1100 hr on any day ($n = 9$ days) when the sun reappeared after being obscured by cloud ('start time'). The numbers of lizards which could be counted while stationary along a 200 m length of wall were recorded within the periods 2-5, 7-10 and 20-30 min following each start time; height and orientation of each lizard were also noted.

The impression was gained that 'survey' postures at the middle and near the top of the wall were particularly associated with irregularities on the surface, due either to vegetation (mostly *Callaris spinosa* or small annual weeds) or to bricks which stood slightly proud of their surroundings. In order to test this association, a flat unvegetated area at a height of 3 m, and measuring 60 x 60 cm, was delineated. This was within the area of overlap of the home ranges of two identifiable juvenile lizards. The frequency of periods for which these two lizards were stationary for >5 s within nine subareas measuring 20 x 20 cm (all areas were delineated by marking bricks with a spot of paint) during the period 1000-1200 hr for four days were recorded. A piece of wood measuring 20 x 1 x 1 cm was then glued along the base of the central cell. No observations were made for 7 days to allow the lizards to adapt to the strip of wood. The observations were repeated, for a further four days.

RESULTS

AUGUST

Lizards were active over the whole wall for the entire period 1000-1600 hr every day although there was a reduction in the amount of movement observed from 1200-1500 hr. Adult males were recorded as stationary for 86.5% of a total observation period of 33 hr. The frequencies of recorded stationary periods at different heights on the wall were not equal; 56% of stationary periods (irrespective of their duration) were within 1.5 m of the base of the wall (left hand kite diagram in Fig. 1; $\chi^2_{(5)} = 76$ calculated with frequencies at 0-0.5 and 0.5-1.5 m combined and with expected values adjusted for differences in sampling width, $n=296$, $P<0.001$). The frequency of the 'survey' posture as a fraction of all periods stationary decreased progressively with increasing height (histograms on the left hand side of Fig. 1; $Z=4.5$, $df=294$, $P<0.001$) and exceeded random expectation of 12.5% i.e. 100/8, since there are eight possible orientations when measured at 45° intervals, at all heights up to 2.5-3.5 m (binomial tests: $P<0.001$ for 0-0.5 m and 0.5-1.5 m; $0.01<P<0.05$ for 2.5-3.5 m). The lizards on average spent longer periods stationary when in the 'survey' posture than at other orientations (Table 1; one-way ANOVA calculated on log-transformed data, $F_{2,294}=7.4$, $P<0.001$).

Adult females were stationary for 76.5% of a total observation time of 7.5 hr. They showed significant excess of stationary periods within 1.5 m of the base of the wall (44%; middle kite diagram in Fig. 1; $\chi^2_{(5)}=39$, $n=61$, $P<0.001$, calculated as above). Apparent peaks near the middle and the top of the wall were not significant (binomial tests, $P>0.05$). There was no apparent trend in the frequency of the 'survey' posture with height, although the frequency at 0-0.5 m exceeded random expectation (middle histogram in Fig. 1; binomial test, $0.01<P<0.05$).

Juveniles were stationary for only 61.4% of a total observation time of 8.3 hr. Stationary periods were

Orientation	n	Frequency (%)		Mean duration (s)	CV (%)
		observed	expected		
180° ('survey')	108	36.5	12.5	293.9	67.3
135° and 225°	68	23.0	25.0	175.2	76.4
other	120	40.5	62.5	137.9	54.3

TABLE 1. Orientation of adult male lizards while stationary for more than 5 s on the wall in August.

concentrated at the middle of the wall; 36.5% were within the band 2.5-3.5 m (right hand kite diagram of Fig. 1; $\chi^2_{(4)}=63$, $n=82$, $P<0.001$, calculated as above except that frequencies for the top two bands were combined because of small sample sizes). Frequency of 'survey' postures exceeded random expectation at 0-0.5, 0.5-1.5 and 2.5-3.5 m (histograms on the right hand side of Fig. 1; binomial tests, $0.05<P<0.1$, $0.01<P<0.05$ and $P<0.1$ respectively). 'Survey' postures were significantly lower than random expectation at the remaining four heights (binomial tests, $P<0.05$ in all cases).

APRIL

The activity patterns of lizards during April were very different from those in August, since the amount of movement depended on weather conditions. The entire height of the wall was utilised during long periods of continuous sunshine, as in August. Activity ceased when the sun was obscured by thick cloud. When overcast periods occurred after earlier sunshine, many lizards retreated into the vegetation at the base of the wall, re-emerging to bask if the sun reappeared. The kite diagram in Fig. 2 shows the distribution of lizards recorded as stationary when they were first observed at periods from 2-5, 7-10 and 20-30 min after the sun had begun to shine following a cloudy period between 1100-1200 hr. Individual frequency distributions for adult males, adult females or juveniles within any of the three sampling periods did not differ significantly (χ^2 tests) and so the data for all lizards were pooled. There were significant concentrations of lizards in the lowest 1.5 m of the wall 2-5 and 7-10 min after the sun had begun shining (left hand and middle

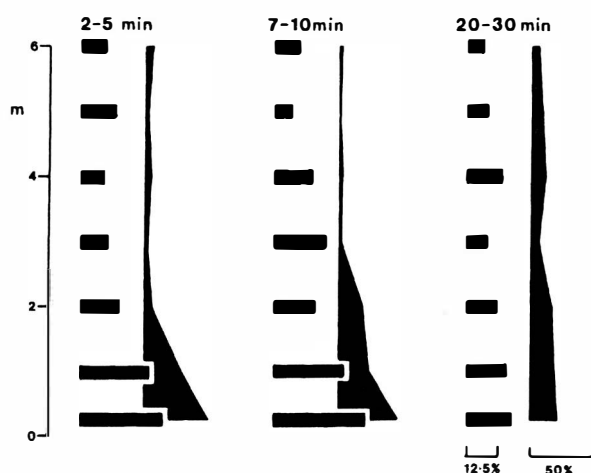


FIG. 2. Kite diagrams showing relative frequencies of periods stationary for more than 5 s at different heights on the wall by all lizards in April, 2-5 min (left hand kite), 7-10 min (middle kite) and 20-30 min (right hand kite) after the end of a cloudy interval. Horizontal histograms to the left of each kite as in Fig. 1.

kite diagrams in Fig 2; $\chi^2_{(5)}=123$ and 95, $n=345$ and 298, $P<0.001$, calculated as in the previous section), but this had disappeared by the 20-30 min period, when distribution with height was homogeneous (right hand kite diagram in Fig. 2; $\chi^2_{(5)}=8.3$, $n=406$, $P>0.1$). 'Survey' postures exceeded random expectation of 12.5% at 0-0.5 and 0.5-1.5 m in the first two sampling periods (left hand and middle histograms in Fig. 2; binomial tests, $P<0.05$) but did not differ significantly from random expectation at other heights (binomial tests, $P>0.5$). None of the frequencies of 'survey' postures in the third sampling period differed significantly from random expectation (right hand histogram in Fig. 2; binomial tests, $P>0.05$).

THE RELATIONSHIP OF 'SURVEY' POSTURES TO SURFACE IRREGULARITIES: A SIMPLE EXPERIMENT

The distribution of stationary periods by two juvenile lizards within nine equal sub-areas ('cells') of the study space was homogeneous (left hand box in Fig. 3, bold numbers; $\chi^2_{(8)}=5.5$, $n=181$, $P>0.1$). None of the frequencies of 'survey' orientations differed from random expectation of 12.5% (left hand box in Fig. 3, small numbers; binomial tests, $P>0.05$ in all cases). The durations of periods stationary did not vary between cells (overall mean=104.3 s; one-way ANOVA calculated on log-transformed data, $F_{8,103}=1.22$, $P>0.1$). Placing a wooden strip along the lower edge of the central cell, however, resulted in a significant excess in the number of periods stationary within this cell compared with the remainder (right hand box in Fig. 3, bold numbers; $\chi^2_{(8)}=25.9$, $n=180$, $P<0.01$). Frequencies of orientations did not differ from random expectation (right hand box in Fig. 3, small numbers; binomial tests, $P>0.05$) except in the cell immediately above the wooden strip (31.6%; binomial test, $0.01<P<0.05$). The mean duration of stationary periods was significantly greater in the central cell (142.5 s; one-way ANOVA calculated on log-transformed data and S-N-K test, $P<0.05$); values in the remaining cells were homogeneous ($F_{7,135}=1.03$, $P>0.1$) and did not differ

10 20	8 25	18 17
17 25	11 23	4 18
19 16	21 15	16 22

17 21	16 24	18 24
6 14	32 38	20 17
8 14	17 12	6 16

FIG. 3. Large numbers: stationary periods observed over four days between 1000-1200 hr by two juvenile lizards in nine equal cells measuring 20 x 20 cm. Smaller numbers: frequency (%) of 'survey' postures in each cell. The two boxes show data obtained before (left) and after (right) a strip of wood was glued to the wall along the base of the central cell.

significantly from those recorded when the wooden strip was not present (Mann Whitney *U*-test, $P > 0.1$).

DISCUSSION

One of the major problems which arises in a study of this kind is semantic. Any functional label assigned to a specific behaviour may at best be misleading, at worst subsequently shown to be incorrect. This problem has been of long-standing concern in ethology (e.g. Tinbergen, 1951; see DeCourcy & Jenssen (1994) for a recent discussion in relation to lizard social interactions). 'Survey posture' is a case in point: it has been used as a label here because of the obvious analogy with the well-known similar behaviour of *Anolis*. In many instances, the function of the behaviour in *P. muralis* may be at least as much concerned with thermoregulation as with detection of prey, predators or conspecifics. Operationally, these individual functions would be very difficult to separate.

All the circumstantial evidence points to the 'survey' posture in *P. muralis* as being partly a means to scan horizontal surfaces for potential prey, as in *Anolis* (Stamps, 1977). There is not an equivalent posture in which the lizards look upwards; no increase in either the frequency or duration of 0° orientations was seen in lizards beneath the experimental wooden strip (Fig. 3). Nor were such postures seen beneath the ledge at the top of the wall (although wall lizards tended to avoid this because many geckos, *Tarentola mauritanica*, spent the day there). The 'survey' posture is clearly equivalent to the 'scan' posture which *P. muralis* adopt at the edges of horizontal surfaces (Avery, Basker & Corti, 1993), but is less frequent. Individuals in many populations do not appear to adopt 'survey' postures at all, for example those living in scrub environments in the vicinity of Lucca (unpublished observations) or on the walls of Mont Orgueil Castle in Jersey (unpublished observations), which is near the northern limit of the distribution of the species (Perkins & Avery, 1989) and so may have comparatively low densities of potential invertebrate prey.

The 'survey' posture as described here was not a major component of the behaviour of *P. muralis* on the wall at Lucca. Even in the situation in which it was recorded most frequently - in adult males in August - a simple calculation from the data shown at the left hand side of Fig. 1 and in Table 1 shows that it accounted for only 4% of the total time between 1000 and 1600 hr during which observations were made. In this respect it contrasts with 'survey' behaviour in *Anolis* and other Iguanidae, which may occupy a high fraction of an individual's time. *Anolis conspersus*, for example, spent 70% of the period for which they were observed in the 'survey' posture (Avery, 1988).

The methods by which the data have been recorded and analysed probably slightly underestimate the total time in the 'survey' posture, because only orientations between about 155 and 205° were included within the category. Lizards with other head-down orientations,

or even with the axis of the body horizontal, can turn their heads and look directly downwards. The incidence of these orientations was not recorded because their interpretation would depend on a more detailed knowledge of the visual field and require methods for measuring and recording the orientation of the head relative to the body.

There are a number of questions raised by these data which remain unanswered. One of the most important is the significance of the differences in vertical distribution of adult males, adult females and juveniles in summer (Fig. 1). It can be hypothesized that the base of the wall represents the most favourable environment, because it provides opportunities for finding food, both on the wall and in the vegetation at its base, and that males are most abundant there because they are dominant. This hypothesis has yet to be tested.

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**CONTRIBUTION TO THE SNAKE FAUNA OF THE SULU ARCHIPELAGO,
WITH THE DESCRIPTION OF A NEW SUBSPECIES OF
DENDRELAPHIS CAUDOLINEATUS (GRAY, 1834)**

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On the islands of Bongao, Sanga Sanga, Siasi, Sibutu, and Tawitawi (all in the Sulu Archipelago) a total of 18 species/subspecies of land snakes were recorded. The observations on the different islands resulted in many new distribution records, 19 of which are published here for the first time: five for Bongao, four for Sanga Sanga, four for Siasi, and six for Tawitawi. One of the snakes (*Boiga drapiezii drapiezii* Boie, 1827) was not known before from the Philippines and the endemic subspecies *Dendrelaphis caudolineatus flavescens* nov. subsp. is described. The Sulu Archipelago shelters several endemic species/subspecies (e.g. *Maticora intestinalis suluensis* [Steindachner, 1891], *Oligodon meyerinkii* [Steindachner, 1891]). Other members of its land snake fauna are widely distributed on Borneo but occur nowhere else in the Philippines (*B. d. drapiezii*, *Sibynophis geminatus geminatus* Boie, 1827), while some are only known from the Philippines (*Elaphe erythrura erythrura* [Duméril, Bibron & Duméril, 1854], *Chrysopelea paradisi paradisi* Boie, 1826).

INTRODUCTION

Knowledge of the fauna of the Sulu Archipelago, one of the most remote areas of the Philippines, is still fragmentary. The herpetological records are based mainly on the investigations of E.H. Taylor, who obtained small collections of reptiles from several of the Sulu Islands some 70 years ago. This material resulted in range extensions for several species, and the description of other new species and subspecies (Taylor, 1918a,b, 1919, 1922a,b,c, 1923). "Reptiles of Sulu Archipelago" (Taylor, 1918a), lists 13 species of snakes for the Sulu Archipelago, with the highest number of records from the Bubuan/Tapaan group (five species, including the sea snake *Laticauda colubrina*). Only on Jolo, the largest island of the Archipelago (345 square miles), was a significant increase in the snake fauna inventory made. While Taylor (1918a) recorded only *Python reticulatus* for Jolo, he found several more species in the following years (Taylor, 1918b, 1919, 1922a,b,c, 1923). Leviton (1963) lists 13 land snake species for this island. On the other islands none or very few further records have been made. Even for Tawitawi, the second largest island (229 square miles), only two species of land snakes are listed in Leviton (1963).

Recent observations on the distribution of land snakes on some islands of the Sulu Archipelago are given here, contributing considerably to their fragmentary snake lists. A new endemic subspecies of *Dendrelaphis caudolineatus* (Gray, 1834) is described. The dispersal routes of the listed snakes are discussed, emphasizing the special position which this island group holds as a transitional zone between Borneo and the Philippines.

MATERIAL AND METHODS

During three excursions to the Sulu Archipelago in 1990, 1991, and 1992 the following islands were visited: Bongao, Sanga Sanga, Siasi, Sibutu, and Tawitawi (Fig. 1). The time spent on each of these islands varied between almost three weeks on Sibutu, and less than a week on Siasi. Therefore the number of species which were detected on each island is correlated to the observation time, not the actual number of species present. Records are mainly based on sightings. If possible, specimens were caught for closer examination and photographic records. A few specimens were preserved, including dead or badly injured ones brought by inhabitants, and those which could not be identified in the field. Observations on habitat, relative abundance, and behaviour were recorded. The field investigations were supplemented by examination of material from the herpetological collection of the "Forschungsinstitut und Naturmuseum Senckenberg" (SMF). Additional material for Tawitawi, collected by the Noona-Dan expedition from Denmark, which visited the island in 1961, was examined in the Zoological Museum in Copenhagen, Denmark (ZMUC).

RESULTS

The species recorded are listed below, and their previously known and newly determined distribution within the Philippines is given. New island records are marked with an asterisk, and all the Sulu Islands are italicised. A species' occurrence on Borneo is mentioned, but its distribution elsewhere in Asia is not given since this is of little importance for the discussion of the direct zoogeographical relation of the Sulu Archipelago.

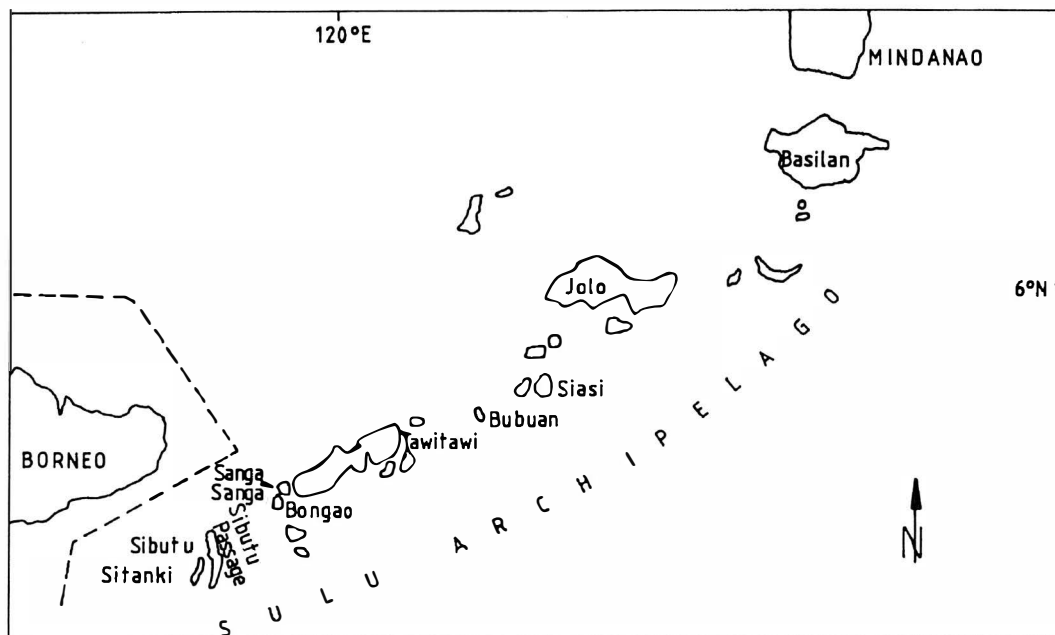


FIG. 1. Sulu Archipelago, generalized map of the study area.

A list of the visited islands and their known land snake fauna, determined from the previous and new records, is added as Appendix I.

SPECIES LIST:

Python reticulatus (Schneider, 1801).

Range: Basilan, Bohol, Bongao*, Cebu, Jolo, Leyte, Luzon, Mindanao, Mindoro, Negros, Palawan, Panay, Polillo, Samar, Siasi*, Sibutu, Tawitawi. Borneo.

Remarks: The reticulated python is widespread in the Sulu Archipelago, and will certainly be found on several more islands. It is not restricted to a special habitat. On Sibutu an adult specimen was observed in a cave at the coastline, and on Tawitawi a juvenile was seen in secondary forest. On Bongao and Siasi pythons were kept as pets by villagers, who had caught them near their homes. However, I was informed by inhabitants that the populations are decreasing because of continued hunting for its skin.

Ahaetulla prasina suluensis Gaulke, 1994.

Range: Bongao, Sanga Sanga, Siasi, Sibutu, Tawitawi.
Material: SMF 74298-9, 74844-5, 74870-2, 75059-60, 75231.

Remarks: This recently described subspecies of the Malaysian vine snake is one of the most common snakes on all of the visited islands. Like the other subspecies, this diurnal, arboreal snake inhabits primary and secondary forest, bushland and bamboo forest. It was observed several times at night sleeping on river-side trees. It was seldom found on the ground, e.g. if crossing a trail.

Malaysian vine snakes were reported from the Sulu Archipelago previously, including the nominate race

A. p. prasina (Boie, 1827) from Sibutu (in Gaulke, 1994, transferred to *A. p. suluensis*), and the Philippine subspecies *A. p. preocularis* (Taylor, 1922) from Jolo (in Leviton 1963).

Boiga cynodon (Boie, 1827).

Range: Basilan, Culion, Dinagat, Leyte, Luzon, Mindanao, Palawan, Polillo, Sibutu, Tawitawi*. Borneo.

Material: SMF 74304, ZMUC R63877.

Remarks: This large, nocturnal and aboreal cat snake is reported from Sibutu (Gaulke, in press). Examination of the Noona-Dan expedition material has also revealed a specimen from Tawitawi (ZMUC R63877). In spite of its wide distribution in Southeast Asia, the poorly known dog-toothed cat snake, seems to be confined to primary forest. Since deforestation is almost complete on the islands of the Sulu Archipelago, it must be considered as endangered in the region.

Boiga drapiezii drapiezii (Boie, 1827).

Range: Tawitawi*. Borneo.

Material: ZMUC R631170.

Remarks: The Noona-Dan expedition material contains a juvenile *Boiga* from Tawitawi (ZMUC R631170), whose head and neck are unfortunately badly battered. The determinable features are as follows: About 255 ventrals, 140 subcaudals, and 19 midbody scale rows. Dorsal colour light brown with 67 dark transverse bars across the back, not extending onto the belly. Inconspicuous lighter blotches on border between dorsals and ventrals. Tail lighter than back, without dark bands, but 20 whitish blotches both sides along border of ventrals. Belly slightly lighter than

back, heavily powdered with darker speckles, dark stripes along the edges.

The closely related forms *Boiga angulata* (Peters, 1861), *Boiga d. drapiezii* and *B. d. schultzei* Taylor, 1923 are distinguished from each other by head scalation, and therefore the identity of the Tawitawi specimen cannot be determined by this feature. Mindanao is the nearest locality from which the rare *B. angulata* is known, while on Borneo, which is much closer to Tawitawi, *B. d. drapiezii* occurs. On Palawan, which like the Tawitawi group is geographically and zoogeographically very close to Borneo, but geographically separated from the Sulu Archipelago, another subspecies of *B. drapiezii* occurs (*B. d. schultzei*). The relations between the three forms, especially the specific status of Philippine *B. angulata*, are still under discussion (see Leviton, 1970). Because of the close faunistic relation between Tawitawi and Borneo, the complete geographic separation from Palawan, and the wide separation between Tawitawi and Mindanao, the snake from Tawitawi almost certainly belongs to the nominate form, which is the most widespread and common of the three forms. This determination is strongly supported by an unpublished determination key (pers. com. J. B. Rasmussen/Copenhagen, 1993; key system based on Kroon). *B. angulata* and *B. d. schultzei* have unstriped bellies, while *B. d. drapiezii* has a pair of dark stripes on the belly. These stripes are present in the specimen under discussion.

This record adds another species to the Philippine herpetofauna.

Chrysopelea paradisi paradisi Boie 1826.

Range: Sibutu. Borneo.

Material: 74300-3.

Remarks: Although in most publications they are just named as *C. paradisi*, all other known records of the paradise tree snake from the Philippines, refer to the Philippine subspecies *C. p. variabilis* Mertens, 1960. The nominate form was only recently detected on Sibutu (Gaulke, in press). This diurnal, arboreal snake is rather common in the forest and coconut plantations on Sibutu.

Chrysopelea paradisi variabilis Mertens 1960.

Range: Balabac, Bantayan, Banton, Basilan, *Bongao**, *Bubuan*, Camiguin, Cebu, Dinagat, *Jolo*, Kalotkot, Leyte, Luzon, Marongas, Medis, Mindanao, Mindoro, Negros, Palawan, Polillo, Samar, *Sanga Sanga**, Sibuyan, Siquijor, *Tawitawi**.

Material: SMF 74779, 75175, ZMUC R63880.

Remarks: The distribution of this widespread Philippine form was extended to three more islands of the Sulu Archipelago, and it will certainly be found on several more in the future. Like the nominate form, it inhabits forests and coconut plantations. On Sanga Sanga one specimen was found basking on a fence just 1 metre above ground.

Dendrelaphis caudolineatus caudolineatus (Gray, 1834).

Range: Balabac, Busuanga, Candaraman, Palawan, *Sibutu*. Borneo.

Material: SMF 74296-7, 74375.

Remarks: The range of this snake in the Philippines is confined to the Palawan province and the westernmost island group of the Sulu Archipelago, where it was recently discovered (Gaulke, in press). This diurnal snake is relatively common on Sibutu. It was mostly observed climbing on bushes and trees in the forest and shrublands, and seldom seen on the ground.

Dendrelaphis caudolineatus flavescens nov. subsp.

Range: *Bongao**, (*Bubuan*), *Sanga Sanga**, *Tawitawi**. The island in parenthesis is a distribution record for *D. modestus* Boulenger, 1894 (now *D. c. modestus*) given by Taylor (1922a). As the discussion will show, it belongs to the newly described subspecies. *Holotype:* SMF 74846, female, Sanga Sanga, Sulu Archipelago, Philippines.

Paratypes: SMF 75174 (Sanga Sanga), SMF 75173 (Bongao), ZMUC R60763 (Tawitawi).

Diagnosis: *Dendrelaphis caudolineatus flavescens* is characterized as follows: No hint of black stripes on back, sides of head, or underside of tail; a very conspicuous, broad, metallic orange-yellow band extends from both sides of the neck along the anterior part of the body; eyes large; ground dwelling.

Derivatio nominis: *flavescens* because of the yellowish band.

Description of holotype: The elongate head is distinct from body. Rostral wider than high, pointed behind, visible from above. Internasals as broad as long. Large prefrontals, wider than deep, longer than internasals. Frontal as long as its distance from end of snout, widening anteriorly. Supraoculars as long as frontal, widening posteriorly. Parietals longer than frontal, longer than wide. Nasal completely divided into a smaller anterior and a larger posterior part. One loreal, much longer than high. One big preocular and two postoculars, the superior larger and the inferior in contact with anterior temporals. Temporals on right side 1+2+2, left 2+2+2, increasing in size posteriorly. Nine upper labials, numbers 5 and 6 entering orbit. The seventh upper labial is positioned below the orbit, but is excluded from it because the 6th is much prolonged posteriorly at its upper part (Fig. 2). Nine lower labials right, 10 left, the first 5 touching anterior chin shields. Diameter of eye greater than its distance from nostril, pupil round. 15 scale rows around neck, 13 around midbody, and 11 before tail. The median scale row is slightly enlarged. There are 178 ventrals, a divided anal, and 103 paired subcaudals. Snout-vent length 930 mm, tail-length 33 mm. Colour in life: Back dark olive brown, head and anterior part of body slightly darker than rest. Dorsal scales with darker edges. Supralabials yellowish, with brown borders between

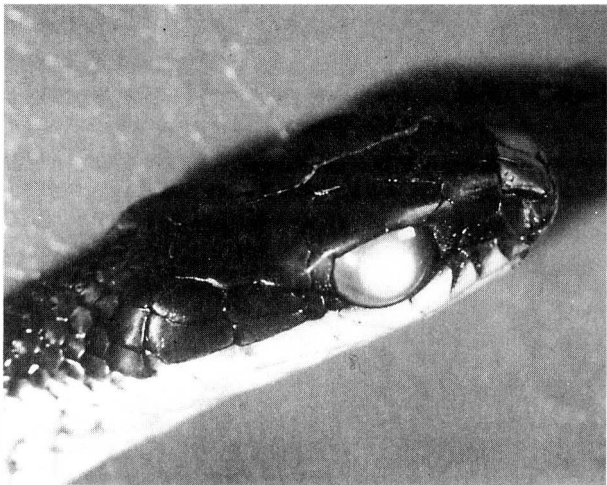


FIG. 2. Portrait of *Dendrelaphis caudolineatus flavescens* nov. ssp. (SMF 74846). Notice the lack of a black ocular stripe and the big eye.

the first four. A broad metallic orange-yellow band extends from behind the head about 9 cm backwards, to the 32nd ventral. This band covers the lowest three dorsal scale rows anteriorly, and reduces to two scale rows posteriorly. The ventral side is greenish yellow. *Colour in alcohol:* The metallic orange-yellow stripe fades quickly in alcohol; however, it remains visible as a lighter band. The greenish yellow tinge of the ventral side becomes a dirty greyish white.

Variation: There is no significant difference between the four specimens at hand. The juvenile (ZMUC R60763) has the same colouration as the adults, and also lacks completely any dark stripes. For measurements and scale counts see Table 1.

Discussion: Taylor (1922a) assigns an unstriped olive brown form of *Dendrelaphis*, which he detected on Palawan, Mindoro, Negros, and Sulu (Bubuan), to *D. modestus*. He considered it to be sympatric with *D. caudolineatus* on Palawan, and with *D. terrificus* (Peters, 1872) on Mindoro and Negros. Meise & Hennig (1932) regard these three forms as subspecies of *Dendrophis* (= *Dendrelaphis*) *caudolineatus*, therefore excluding a sympatric occurrence. They considered Taylor's (1922a) Philippine *D. modestus* to be only a colour variant of *D. c. terrificus*, especially as they do not have the higher ventral counts typical for *D. c. modestus*. Leviton (1968), who differentiates *D. c. terrificus* into two subspecies (the northern *D. c. luzonensis* Leviton, 1968 and the southern *D. c. terrificus*), agrees with Meise & Hennig (1932) in the evaluation of the unstriped Philippine *Dendrelaphis*. He regarded it as a colour variation of *D. c. terrificus* and, more seldom, of his newly described *D. c. luzonensis*. Leviton (1968) mentions that this colour variety lacks dorsal stripes, but has a well developed black stripe along the middle of the ventral surface of the tail.

The examination of three *D. c. modestus* from the SMF collection (SMF 18637-9, from Batjan) showed that they have a well developed black ocular stripe (as all described subspecies of *D. caudolineatus*), and at least the indication of a stripe along the underside of the tail.

Taylor (1922a) recognized a difference in the unstriped *Dendrelaphis* between the Sulu Archipelago and the rest of its Philippine distribution. He writes (1922a:173): "The greatest variation found in the Philippine specimens of this species (meaning *D. modestus*) occurs in one from Bubuan Island, Sulu Archipelago. An orange stripe is present in life behind the eye, continuing some distance on the neck. This stripe is formed by a wash colour over the greenish ground colour and disappears largely in alcohol. The eye is larger, its diameter greater than distance from eye to nostril.....". This stripe should not be confused with the yellowish lateral band considered by Meise & Hennig (1932) as a distinguishing feature for *D. caudolineatus* in general. This is a small, non-metallic stripe, sharply bordered by two black stripes, which runs the entire body length, and does not occur in the new subspecies.

	SMF 74846	SMF 75174	SMF 75173	ZMUC R60763
SVL(mm)	93.0	72.0	80.0	31.6
TL(mm)	33.0	26.5	26.3	11.7
Ventrals	178	171	172	171
Subcaudals	103	108	95 (Tm)	104
Supralabials	9/9	9/9	9/9	9/9
Supralabials entering eye	56	56	56	56
Sublabials	9/10	10/10	10/10	10/10
Preoculars	1	1	1	1
Postoculars	2	2	3	2
Loreals	1	1	1	1
Temporals	122/222	222/222	222/222	222/222
Scale rows:				
neck	15	17	17	15
midbody	13	13	13	13
tail	11	11	13	11

TABLE 1. Measurements and scale counts of *Dendrelaphis caudolineatus flavescens* nov. ssp. (Tm, tip missing.)

The broad metallic orange band, and the complete lack of black stripes not only on the back but also on the underside of the tail and the headsides, clearly separates the new subspecies from all other forms of *D. caudolineatus*, including the unstriped varieties of *D. c. terrificus* and *D. c. luzonensis*. It does not occur sympatrically with other forms of *D. caudolineatus*.

Differences from closest forms: From *D. c. modestus* the new form differs in having larger eyes, no hint of a black stripe under the tail, no ocular stripe, and lower ventral and subcaudal counts. From *D. c. terrificus* it differs in the lack of black stripes on the body, head and underside of tail, and it is bulkier in appearance.

Range: The new subspecies is only known from the western part of the Sulu Archipelago (Bongao, Bubuan, Sanga Sanga, Tawitawi). Its range is separated by the Sibutu Passage from the nominate form, which is widespread on Sibutu. Since no *D. caudolineatus* is known yet from the Jolo group, its exact range to the northeast remains open. The Philippine *D. c. terrificus* occurs on Basilan and Mindanao. The occurrence of *D. c. terrificus* on Sitanki (Sibutu group) (a juvenile snake, Leviton, 1963) must seriously be doubted. Either it is an accidentally introduced specimen, as assumed by Leviton (1963), or it is a not yet completely marked, or abnormally marked specimen of the nominate form, which is abundant on the nearby island of Sibutu.

Observations: It is not a rare snake. In all, 10 specimens were sighted, but as it is a very fast snake, few were caught. All sighted snakes agreed in their colouration, showing no hint of black stripes on their back or head, but having a conspicuous yellowish band on the sides. Besides the difference in colouration, there is presumably an ecological difference from other subspecies. While all other forms are mainly arboreal, climbing in trees and bushes, all sighted specimens of *D. c. flavescens* were observed on the floor of primary and secondary forest. One snake was basking on a small trail leading up to Bongao Peak. When disturbed, it reared like a cobra, displaying its beautiful orangish neck sides. It is assumed that these markings may have a warning function.

One specimen on Tawitawi was observed hunting for locusts between stones and rotten logs in the forest. It caught several grasshoppers before being disturbed, and then quickly disappeared into the undergrowth. Another specimen was seen crawling over leaf litter, and SMF 75173 was found run over by a car on the street in front of Bongao Hill. It was the only one seen outside the forest.

SMF 75174 was kept alive in a terrarium for about 12 months. It behaved very calmly, feeding on live geckos. Locusts and mice were not taken. One morning it was found dead; the reason is unknown.

Dendrelaphis pictus pictus (Gmelin, 1789).

Range: Bohol, Bongao*, Busuanga, Cagayan Sulu, Cebu, Culion, Guimaras, Jolo, Lapac, Luzon,

Mindanao, Mindoro, Negros, Palawan, Panay, Polillo, Samar, Siargao. Borneo.

Material: SMF 74780-3.

Remarks: Considering the wide distribution of this snake and its high abundance on many Philippine Islands, it is surprising that it is known from comparatively few of the Sulu Islands. This climbing and ground dwelling snake is found in cultivated areas, and along forest edges and riversides.

Elaphe erythrura erythrura (Duméril, Bibron & Duméril, 1854).

Range: Bohol, Camiguin, Dinagat, Jolo, Mindanao, Pacijan, Polillo, Ponson, Poro, Samar, Siasi*.

Remarks: Only one specimen of this large, diurnal, ground dwelling snake was sighted on Siasi. However, it normally is not a rare snake, inhabiting forested as well as cultivated areas.

Elaphe erythrura philippina Griffin, 1909.

Range: Balabac, Bongao, Busuanga, Culion, Palawan, Sanga Sanga*, Sibutu, Tawitawi*.

Material: SMF 74305-6, 74784, 74847.

Remarks: This subspecies is confined to the westernmost islands of the Philippines (Palawan Province and Tawitawi group), close to Borneo. Therefore it can be expected that it will be detected on Sabah in future, from where it most probably originated, as already assumed by Leviton (1963). It occupies the same habitats as the nominate form, and is relatively common.

Gonyosoma oxycephala (Boie, 1827).

Range: Balabac, Bohol, Bongao*, Dinagat, Lubang, Luzon, Mindoro, Negros, Palawan. Borneo.

Material: One snake from Bongao, kept alive at the "Forschungsinstitut Senckenberg."

Remarks: This snake was not previously recorded from the Sulu Archipelago, not even from the Mindanao region. However, it can be expected on several more of the islands. Even though this arboreal snake is very large, and looks very conspicuous in captivity, it is seldom found in the Philippines. This is probably due to its habitat in the tree canopies, where it is well camouflaged with its bright green colouration.

Oligodon meyerinkii (Steindachner, 1891).

Range: Bongao, Jolo, Papahag, Sibutu, Tawitawi.

Material: SMF 19213, 74281-2, 74791, 75057-8.

Remarks: This kukri snake is one of the few snake species confined to the Sulu Archipelago, being distributed on the Tawitawi and Jolo groups. No range extension was recorded, but its presence on Bongao, Sibutu, and Tawitawi was confirmed. The specimens from Sibutu show no external morphological differences to the striped kukri snake (*O. octolineatus* [Schneider, 1801]), which is widely distributed in Malaysia and Indonesia, including Borneo. For discussion see Leviton (1962) and Gaulke (1993b).

These small, ground dwelling and burrowing snakes are not rare in their habitat. However, since they are confined to the forest floor, they must be considered as endangered, together with the rapidly vanishing forest.

Sibynophis geminatus geminatus Boie, 1827.

Range: Tawitawi. Borneo.

Material: SMF 74249.

Remarks: Only one specimen of this species was found in the Philippines previously (Gaulke, 1993a). It came from a still undisturbed forest in the vicinity of Languyan/Tawitawi, where it was found at a river bank. Not much is known about this small, obviously rare and secretive snake, and it is not surprising that it has escaped detection on the Philippines for so long. However, as other regions of the Philippines are explored much more intensively, it can be assumed that it is confined to the Sulu Archipelago, or even the Tawitawi group in the Philippines. Its relation to the polyodont snake found on Palawan province (*S. bivittatus* [Boulenger, 1894]) is discussed in Gaulke (1993).

Xenopeltis unicolor Reinwardt, 1827.

Range: Balabac, Bongao, Jolo, Palawan, Sanga Sanga*. Borneo.

Material: SMF 75222.

Remarks: On Sanga Sanga a burned specimen was found in a dried and burned mangrove swamp near the coastline. On Bongao Peak a sunbeam snake was observed swallowing an *O. meyerinkii*, lying half-buried under the leaf litter of the forest floor.

Observations in other regions show that they also live under coconut debris and in village gardens.

Maticora intestinalis suluensis (Steindachner, 1891).

Range: Jolo, Siasi*.

Material: SMF 74873.

Remarks: According to present knowledge this subspecies of the banded Malaysian coral snake is confined to the Jolo and Tapul group in the Sulu Archipelago. It seems to be a very rare snake. On Siasi, from where it was not known before, one specimen was found under leaf litter at the forest edge. This small, burrowing snake is one of two dangerously poisonous snakes known from the Sulu Archipelago.

Tropidolaemus wagleri (Boie, 1827).

Range: Balabac, Basilan, Calamianes, Dinagat, Jolo, Leyte, Luzon, Mindanao, Negros, Palawan, Samar, Siasi*, Sibutu, Tawitawi*. Borneo.

Material: SMF 74283-5, 74307-8, 74874-6, 74901.

Remarks: Until recently (Gaulke, in press), Wagler's pit viper was unknown from the Tawitawi group, but is now found to be a rather common snake on Sibutu and Tawitawi. It will certainly be found on other islands as well. The highest abundance of this nocturnal and ar-

boreal snake was observed on Siasi (Tapul group), where it appeared to be the most common snake. It inhabits forests as well as fruit (e.g. mango trees) plantations and bamboo forest. During the daytime it rests motionless on a branch, and therefore is easily overlooked. The stomach of one big specimen from Siasi contained two large rats. These poisonous but not aggressive snakes are beneficial to men.

Rhamphotyphlops suluensis (Taylor, 1918).

Range: Basilan, Bubuan, Sibutu.

Remarks: The recent record of this poorly known blind snake from Sibutu (Gaulke, in press) extends its range from Basilan throughout the Sulu Archipelago. However, it remains known from very few places. It is a relatively large, arboreal blind snake. During the night it was observed actively climbing across branches. It was not rare on Sibutu. However, like all species which are confined to forests, its continued existence is highly endangered by deforestation.

DISCUSSION OF DISPERSAL ROUTES

The islands of the Sulu Archipelago lie on a high submarine shelf (that is about 50 m below sea level), extending from Zamboanga province (western Mindanao) southwards. Between Bongao and Sibutu there is an abrupt drop to a depth of about 300 m. This Sibutu Passage (see Fig. 1) seems to be geologically young, having formed after the mid-Pleistocene (Voss, 1974). This island chain has probably formed a continuous land connection between Borneo and the Philippines during the height of the Pleistocene glaciations (Brown & Alcala, 1970; Dickerson, 1928; Inger, 1954; Leviton, 1963; Wang & Wang, 1990). Of the two former land connections between Borneo and the Philippines, Palawan in the north and the Sulu Archipelago in the south, the latter is generally considered as the more important entryway for herptiles (e.g. Brown & Alcala, 1970; Inger, 1954; Leviton, 1963).

Leviton (1963) divides the land snakes of the Philippines into five districts. The Sulu Islands (district four) are a transitional region between Borneo and the Philippines, with elements of the Philippine fauna migrating southwest towards Borneo, and Bornean elements migrating northeast towards the Philippines. According to him, the small size of the Sulu Islands and the periodic inundation of many of them is responsible for the scarcity of snakes. As the new investigations show, these islands shelter a richer snake fauna than expected by Leviton (1963). Therefore we now have better evidence to demonstrate the role which this island group holds as a former entryway to the Philippines, and as a present transitional zone between both regions.

Fig. 3 shows the recent distribution of the listed snakes. Even though no new investigations took place on Jolo, this island is included, because it is the biggest

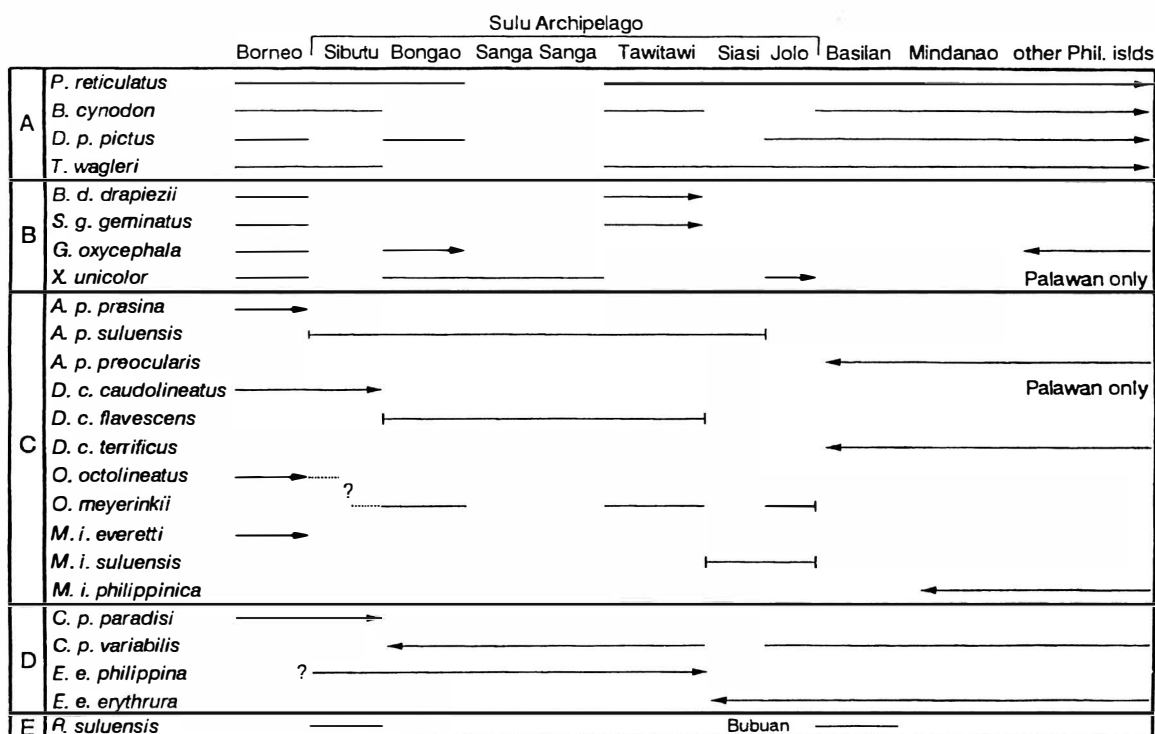


FIG. 3. Distribution and dispersal routes of the observed snakes. Lines indicate the known range, arrows the direction of migration.

A: This group includes species/subspecies which are widespread on Borneo and the Philippines, and occur on the Sulu Archipelago. None of these snakes originate in the Philippines. Therefore it can be concluded that the Sulu Islands functioned as a migration route from Borneo to the Philippines.

B: This group includes Bornean species/subspecies, which are found on the Sulu Archipelago, but to our present knowledge neither on Basilan nor on Mindanao. *Sibynophis* and *Xenopeltis* have presumably never dispersed to the more eastern islands of the Philippines, since they are known only from the Sulu Archipelago and Palawan. A close relative of *B. drapiezii*, *B. angulata*, inhabits several Philippine Islands. It can be assumed that its progenitor reached the Philippines via the Sulu bridge, and the recent population of *B. drapiezii* on Tawitawi attributes to a more recent immigration from Borneo. As long as *G. oxycephala* is not recorded on Mindanao, it is more likely that it has occupied the Philippines via Palawan.

C: This group includes snakes which are endemic to the Sulu Archipelago. The nearest Bornean and Philippine relatives are also figured.

D: This group includes two species, which are represented on the Sulu Archipelago by two different subspecies. One subspecies came from Borneo, the other from the Philippines.

E: *R. suluensis* has a scattered distribution on the Sulu Archipelago and Basilan. It's closest relative, *R. olivacea* (Gray, 1845) is known from Borneo and the Philippines. It is possible that the dispersal of this blind snake took place via the Sulu route, and the population of this area became isolated later on, developing into a new species.

island of the Sulu Archipelago, and it's snake fauna is fairly well known. The arrows indicate the direction from which the represented species presumably occupied the Sulu Islands.

As shown in Fig. 3, the Sulu Archipelago cannot be considered as a closed faunistic unit at present. In general the Bornean influence is stronger than the Philippine one, with two Bornean forms being known from nowhere else within the Philippines (*B. d. drapiezii* and *S. g. geminatus*). However, there are several gradations. While the snake fauna of Sibutu is closest to Borneo (*C. p. paradisi* and *D. c. caudolineatus*), the Philippine influence becomes stronger on the rest of the Tawitawi group (*C. p.*

variabilis), and adds another Philippine element on Siasi (Tapul group, *E. e. erythrura*). However, even on Sibutu a typical Sulu element (*A. p. suluensis*) can be found, with more endemic forms on the rest of the islands (*D. c. flavescens*, *O. meyerinkii* and *M. i. suluensis*). At present, with even the few remaining forests on these small islands quickly vanishing, a change in the snake fauna will take place. While some of the specialized forest dwellers (e.g. *O. meyerinkii*, *R. suluensis*, *D. c. flavescens* and *M. i. suluensis*), including most of the endemic forms, will have little chance of survival, other more opportunistic ones like *D. p. pictus*, *E. erythrura*, or *T. wagleri* will continue their dispersal.

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APPENDIX I

ISLAND LISTS (COMPILED FROM NEW AND PREVIOUS RECORDS)

BONGAO ISLAND

Bongao is a small island in the south of the Tawitawi group. Only little forest remains on the upper part of Bongao Peak (330 m). Observations took place on Bongao Peak, and in the shrub and bushlands around the city of Bongao.

Python reticulatus
Ahaetulla prasina suluensis
Chrysopelea paradisi variabilis
Dendrelaphis caudolineatus flavescens
Dendrelaphis pictus pictus
Elaphe erythrura philippina
Gonyosoma oxycephala
Oligodon meyerinkii
Psammodynastes pulverulentus
Xenopeltis unicolor
Rhamphotyphlops braminus

Two of the snakes listed, *P. pulverulentus* and *R. braminus*, were not observed during the recent expeditions.

SANGA SANGA ISLAND

This island is situated between Bongao and Tawitawi. Observations were made in the partly forested area near Boloboc, and along the trail from the airport to the forest (through agricultural areas and bushlands).

Ahaetulla prasina suluensis
Dendrelaphis caudolineatus flavescens
Chrysopelea paradisi variabilis
Elaphe erythrura philippina
Xenopeltis unicolor

No snakes were reported from here previously.

SIASI ISLAND

This small island belongs to the Tapul group, situated between the Tawitawi and Jolo groups. The last tiny forest can be found on Siasi summit. Observations were made around this area.

Python reticulatus

Ahaetulla prasina suluensis

Elaphe erythrura erythrura

Maticora intestinalis suluensis

Tropidolaemus wagleri

No snakes were reported from here previously.

SIBUTU ISLAND

This small island is separated from the Tawitawi group by the Sibutu Passage. It lies 29 km off the coast of Sabah/Borneo. Observations were made in the forest around Kaban Kaban, and on the small Sibutu Peak (165 m).

Python reticulatus

Ahaetulla prasina suluensis

Boiga cynodon

Chrysopelea paradisi paradisi

Dendrelaphis caudolineatus caudolineatus

Elaphe erythrura philippina

Oligodon meyerinkii

Tropidolaemus wagleri

Rhamphotyphlops suluensis

The herpetofauna of Sibutu, including the snakes listed above, is published in Gaulke (in press).

TAWITAWI ISLAND

This is the second largest island of the Sulu-Archipelago (229 square miles), and still holds several forested areas. Observations were made in the forest of Languyan, Magsaggaw, and Tarawakan.

Python reticulatus

Ahaetulla prasina suluensis

Boiga cynodon

Boiga drapiezii drapiezii

Chrysopelea paradisi variabilis

Dendrelaphis caudolineatus flavescens

Elaphe erythrura philippina

Oligodon meyerinkii

Sibynophis geminatus geminatus

Tropidolaemus wagleri

Only two species are reported in Leviton (1963), both of which could be observed in the recent investigations.

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EFFECTS OF BODY TEMPERATURE ON THE PREDATORY BEHAVIOUR OF THE LIZARD *PSAMMODROMUS ALGIRUS* HUNTING WINGED AND WINGLESS PREY

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The thermal dependence of predation success in the Mediterranean lacertid lizard *Psammodromus algirus* was studied using two types of prey (winged and wingless flies) that differed in their ability to escape predation at all T_b s (body temperatures) tested (25-27°C, 29-32°C, and 34-37°C). Both number of failures and handling time decreased significantly at higher T_b s, and capture success was much higher for wingless flies; in fact, low T_b s were associated with a significant increase in capture success only in the case of winged flies. At low T_b s, winged flies could be efficiently seized by lizards only if pursued from a short distance. The attack distance was therefore larger for the less mobile (and less detectable) wingless flies at low T_b s, which suggests a trade-off between attack distance and capture success under conditions of impaired locomotor performance. Results of this study show that the escape abilities of prey are crucial to evaluate the effects of temperature on the performance of reptiles as predators.

INTRODUCTION

The body temperature (T_b) of reptiles affects their behaviour by influencing biochemical and physiological mechanisms (Dawson, 1975), but the ecological and evolutionary implications of such thermal dependence are best revealed at the level of organismal performance (Huey & Stevenson, 1979; Huey, 1982, 1991). The increased efficiency of muscular contraction and neuromuscular coordination at higher temperatures (Putnam & Bennett, 1982; Marsh & Bennett, 1985), for instance, leads to higher sprint speeds (Bennett, 1980) that improve the ability to capture prey and the ability to escape predation (Christian & Tracy, 1981; Avery, Bedford & Newcombe, 1982; Van Damme, Bauwens & Verheyen, 1991). These abilities, in turn, directly affect Darwinian fitness (Huey, 1991). It is therefore not surprising that diurnal lizards use behavioural means to achieve relatively high and constant body temperatures (Cowles & Bogert, 1944), even if such thermoregulatory behaviour entails costs in time, energy or predation risk (Huey, 1974; Huey & Slatkin, 1976).

Within this context, one central aspect of the thermal biology of lizards that has received relatively little attention is the thermal dependence of predation success (though see Greenwald, 1974; Avery *et al.*, 1982; Avery & Mynott, 1990; Van Damme *et al.*, 1991). Most of the work on this subject has been carried out using experimental (and often clumsy) prey whose behaviour bears little resemblance with the predator avoidance tactics of arthropods under more natural field conditions (Edmunds, 1974; Curio, 1976; Endler, 1986). Without using fast-fleeing prey, it is difficult to

evaluate the role of predatory efficiency as a selective force leading the evolution of behavioural thermoregulation in reptiles (Avery *et al.*, 1982). The experiments reported here were designed to analyse to what extent the escape abilities of prey influence the thermal dependence of predation success in a Mediterranean diurnal basker. For this purpose, I employed two types of prey (winged and wingless flies) and offered them to lizards whose T_b had been previously fixed. The particular issues addressed were: (1) Do the escape abilities of prey influence the effects of lizard T_b on predation success?; (2) What aspects of the feeding system (e.g. handling time or attack distance) have larger sensitivities to T_b and/or prey fleeing abilities?; and (3) Considering the data available about T_b s of active lizards, how good are the performance levels of lizard predation expected under field conditions?

METHODS

The predator of choice was *Psammodromus algirus*, a medium-sized lacertid lizard (adult snout-vent length: 60-85 mm; mass: 6-14 g) that actively searches for a variety of arthropod prey (Díaz & Carrascal, 1990, 1993) and most frequently inhabits broad-leaved (both deciduous and evergreen) forests with a well developed undergrowth of shrubs (Díaz & Carrascal, 1991). It is a shuttling heliotherm (Díaz, 1991) whose microhabitat selection is strongly related to thermoregulatory behaviour (Díaz, 1992).

Animals used in the experiments reported here were nine adult lizards (mean [\pm SD] snout vent length of 74.3 \pm 5.02 mm, and mean [\pm SD] body mass of 9.9 \pm 2.26 g) collected in an open forest of *Quercus*

pyrenaica oaks at the northern slope of the Sierra de la Morcuera (40°35'N, 3°53'W, province of Madrid, Central Spain). Upon arrival at the laboratory, lizards were housed in leaf-litter filled terraria (100 x 50 x 30 cm) with a 60-W bulb providing heat for 8 hr per day and allowing lizards to maintain temperatures within previously reported field activity ranges (20–38°C; Carrascal & Díaz, 1989; Díaz, 1992). Food (mealworms, blowflies and wasp larvae) and water were supplied *ad libitum*.

The experiments on predatory behaviour were carried out in a 90 x 50 x 40 cm wooden cage with a transparent wall allowing direct observation of lizards, and whose floor had been ruled with a 10 x 10 cm grid to facilitate recording attack distances. A few dead branches were used to provide environmental complexity. Illumination was natural daylight complemented with an additional bulb inside the cage. I took advantage of natural fluctuations in temperature, together with the effects of varying the power of the bulb used (40, 60, or 100 W) and its distance from the substrate (15–30 cm), to manipulate the thermal environment in such a way that the operative temperatures monitored using copper models (Bakken & Gates, 1975; Bakken, 1992) fell within one of three distinct temperature ranges, hereafter referred to as low (25–27°C), moderate (29–32°C), and high (34–37°C). Models were copper cylinders with a small hole allowing insertion of the sensing tip of an electronic digital thermometer (precision of $\pm 0.1^\circ\text{C}$) that were placed under the bulb to mimic the location of “basking” lizards. Model verification was obtained by comparing equilibration temperatures of models against those taken from anesthetized *P. algirus* under varying conditions of radiant heating. In addition, cloacal temperatures measured after each trial (see below) confirmed the accuracy of operative temperature copper thermometers (mean $T_b \pm \text{SD}$ in $^\circ\text{C}$, n , range; low temperature: 26.1 ± 0.47 , 17, 25.4–27.0; moderate: 31.0 ± 0.97 , 17, 29.4–32.5; high: 35.9 ± 0.79 , 20, 34.4–37.2). These ranges were realistic considering available data about body temperatures in the field (Carrascal & Díaz, 1989; Díaz, 1992) and preferred body temperatures, that is, temperatures lizards would attempt to achieve in the absence of physical and biotic restrictions (Licht, Dawson, Schoemaker & Main, 1966); in *P. algirus*, mean selected T_b is about 35.2°C (unpublished data).

Experimental prey were commercially supplied blowflies (*Calliphora* sp.) with an average body length of 10.4 mm and an average head width of 3.1 mm. All flies were offered to the lizards within two days after their emergence from pupae, thus eliminating differences in escape ability that could have been acquired in previous encounters with predators. Flies were kept in refrigerated chambers at 4°C until the moment they were taken out, in groups of four, for lizard feeding. Immediately after extraction, two randomly chosen

flies had their wings removed by cutting their base. The dichotomy between these two types of prey seemed an appropriate one under the experimental conditions employed, because even winged flies could eventually be captured (after several trials, if necessary) due to the limited distance they could fly in the feeding enclosures. In addition, defence against predators is assumed to be a basic function of insect flight, and dipterans, that are among the more efficient insect fliers, make a small but evenly distributed contribution to the diets of more than 90 species of desert lizards (Pianka, 1986). This probably reflects the fact that rapid movements not only favour predator avoidance, but also elicit the attack response of visually-guided predators such as insectivorous amphibians and reptiles (Freed, 1988; Díaz & Carrascal, 1993). In addition, dipterans have been shown to make a major contribution to the diet of at least some populations of *P. algirus* (Carretero & Llorente, 1993).

The four prey (two winged and two wingless flies) were subsequently introduced into a matchbox that was allowed to warm up for a few minutes under a 60-W bulb. At the same time, an individual lizard was placed in the experimental cage and given 5 min to habituate to the feeding environment and have its T_b equilibrated within the range selected (low, moderate, or high); the lizards were allowed to sit under the bulb and warm up before the experiment was started. The sequence of temperatures for each individual was deliberately non-systematic to prevent within-subject order effects. Following this interval, the matchbox containing the flies was simultaneously opened and thrown into the experimental cage, as far from the predator as possible. An obvious problem of this experimental protocol, but one which is impossible to solve in a study involving ectotherms, is that fly temperatures in the terrarium cannot be controlled, so that results could reflect in part the physiology of the flies, not just of the lizards. Anyway, results (see below) showed that temperature effects on the escape behaviour of flies did not compensate for the reduced predation success of lizards at low temperatures.

Lizard behaviour was observed for the next five minutes or, alternatively, until all prey had been captured. A stop watch (± 0.1 s precision) was used for measuring handling times, defined as the time elapsed between the first seizure of a prey by a lizard, and the first complete closure of the jaws after it had been swallowed. All observations were dictated to a tape recorder, so that the following variables could be noted when transcribing the tapes: (1) thermal regime (low, moderate or high temperature); (2) type of prey (winged or wingless) being attacked; (3) number of attacks, i.e. chases and jaw closures in an obvious attempt to catch a prey; (4) number of captures (ranging between one and four); (5) number of failures (attacks minus captures); and (6), when attack was successful (that is, when it led to prey capture), attack distance (± 1

cm), defined as the distance between the lizard's snout and the location of the fly when the lizard started moving towards the prey before seizing it. In addition, the behaviour of both prey types (percentage of time immobile vs. percentage of time walking or flying) was monitored in a series of two minutes observations of randomly selected flies (10 winged and 10 wingless) that were released two at a time into the empty experimental cage.

After ending a trial, the lizard was taken out from the experimental cage and its T_b was immediately measured ($\pm 0.1^\circ\text{C}$) with a Miller-Weber cloacal quick-reading mercury thermometer. All lizards were successfully tested (a trial was successful when it led to the capture and consumption of at least one prey) at each temperature range at least twice, always in different days. Individual data were averaged for each trial, and, in order to avoid pseudoreplication (Hurlbert, 1984), trial means were averaged over experimental subjects within temperature ranges. Mean (\pm SD) number of replicates per lizard was 3.00 ± 0.62 at each temperature interval (range 2-4, $n = 27$). Data on capture efficiency, handling times, and attack distances were analysed using repeated measures two-way (temperature by type of fly) analyses of variance, after having checked their conformity with the assumptions of ANOVA.

RESULTS

Wingless flies spent significantly less time moving ($t = 2.42$, $n = 10$ for both series of data, $P < 0.05$) than did winged flies (mean \pm SD: $28 \pm 22\%$ vs. $53 \pm 25\%$, respectively). The body temperature of lizards influenced both capture efficiency and handling time (Figs. 1a & 1b), since warmer lizards had higher capture success (number of failures: $F_{2,16} = 4.23$, $P < 0.05$) and shorter handling times ($F_{2,16} = 3.67$, $P < 0.05$). The winged-wingless condition had no significant effect on handling time ($F_{1,8} = 2.85$, $P > 0.1$), but lizards were clearly more successful in capturing winged flies ($F_{1,8} = 183.79$, $P < 0.001$). No interaction was found between the effects of prey type and T_b on capture success or handling time ($P > 0.1$ in both cases), though the effect of T_b on number of failures was significant for winged flies ($F_{2,16} = 3.68$, $P < 0.05$) but not for wingless ones ($F_{2,16} = 2.64$, $P > 0.1$). The attack distance, that was smaller for winged flies ($F_{1,8} = 9.08$, $P < 0.05$), varied significantly with T_b ($F_{2,16} = 6.48$, $P < 0.01$) because at low temperatures attack distances were much reduced for winged flies; there was a marginally significant interaction ($F_{2,16} = 3.49$, $P = 0.055$) between the effects of T_b and type of prey on attack distance (Fig. 1c).

The proportion of trials in which first capture was a winged fly (ranging between 0/2 and 4/4 for each experimental subject at each T_b range) tended to increase at higher T_b s (Fig. 2; repeated measures ANOVA model with linear contrast: $F_{1,8} = 5.12$, $P = 0.053$). At low T_b s, lizards captured wingless flies in first place

more frequently than expected by chance (equal proportions of 0.5 for each prey type: $t_8 = 2.38$, $P < 0.05$), whereas no significant deviations from random were found at moderate and high T_b s ($t_8 = 1.06$ and $t_8 = 0.78$, respectively; $P > 0.1$ in both cases).

DISCUSSION

Perhaps the most remarkable finding of this study is that the effects of body temperature on the predatory efficiency of lizards were more clear-cut for winged prey than for wingless ones (Fig. 1). A number of previous studies have shown that reptilian handling times increase as T_b decreases (Avery *et al.*, 1982; Avery & Mynott, 1990; Van Damme *et al.*, 1991). These increases are probably due to a reduction in neuromuscular coordination at tissue or lower levels (Putnam & Bennett, 1982; Marsh & Bennett, 1985) that would also affect sprint performance and hence ability to chase fast-moving prey (Huey & Stevenson, 1979; Huey, 1982).

The unsuccessful attempts to feed at low temperatures are similar to Greenwald's (1974) observations on strike efficiency in gopher snakes and to the results reported by Avery *et al.* (1982) and Van Damme *et al.* (1991) with *Lacerta vivipara*. These later authors, however, could not demonstrate a decrease in capture

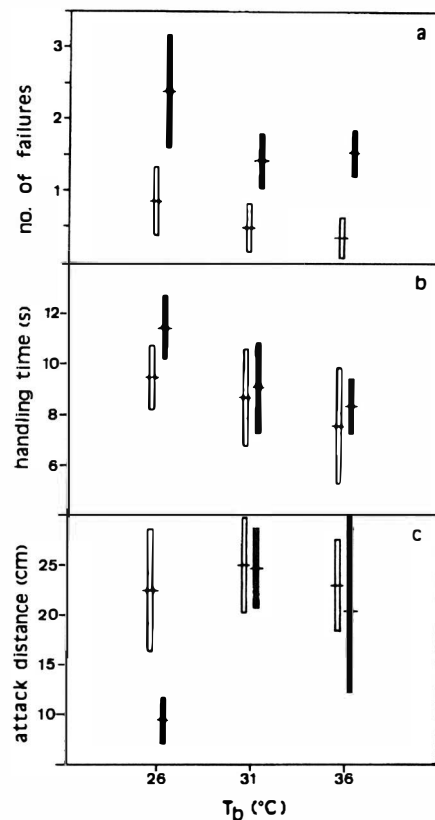


FIG. 1. Mean ($\pm 2\text{SE}$) number of (a) unsuccessful capture attempts, (b) handling time (in s), and (c) attack distance (in cm), according to body temperature and type of prey (winged vs. wingless flies). Solid and white bars represent winged and wingless prey, respectively. $n = 9$ data (means of two to four replicates per individual lizard) for each prey type - T_b combination.

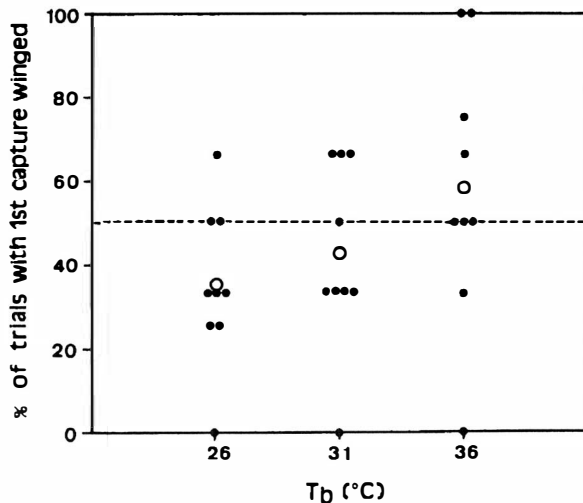


FIG. 2. Proportion of trials in which first successful capture was a winged fly for each of the nine lizards tested at each temperature range. The dashed line indicates the null hypothesis of equal number of first captures for both prey types, and the circles show the mean values at each temperature range.

success at low T_b , probably because they employed crickets with their hind legs removed to prevent escape from the terrarium. Results of the present study show that the escape abilities of prey are crucial to evaluate the effects of temperature on the performance of reptiles as predators.

The physical condition and vulnerability to predation experienced by prey (e.g. wingless flies) may determine what defence tactics should be adopted (Endler, 1991), for instance whether to freeze or flee (Bauwens & Thoen, 1981). Alternatively, wingless flies could move less than winged ones as a consequence of recent injury. Whatever the reasons for fly behaviour, immobility is useful as an antipredator defence as long as predators rely on sensory modes that detect motion (Edmunds, 1974; Endler, 1986), and lizards (including *P. algirus*; personal observation) often do not detect objects outside their tongue-flicking reach unless such objects are moving. Nevertheless, this antipredator strategy did not seem to be very efficient in the case of wingless flies, as it could not compensate their reduced fleeing speed: wingless flies were in fact captured before winged flies at low T_b s (Fig. 2).

On the other hand, in a series of feeding trials with *P. algirus* similar to the ones reported here, and allowing for the effects of prey size, the attack distance was larger for moving prey than for immobile ones (Díaz & Carrascal, 1993). One should therefore expect attack distance to be larger in the case of the more mobile winged flies. However, no difference was found at moderate or high T_b s, and the reverse was true at low T_b s: the attack distance decreased only in the case of the more difficult and mobile prey, suggesting a trade-

off between attack distance and capture success under conditions of impaired locomotor performance. Though I did not compare distances for attacks that did and did not result in prey capture, lizards did in fact attempt to make long distance attacks on winged flies at low temperatures; these long distance attacks were at least partially responsible for the high number of failures on winged flies at low T_b s shown in Fig. 1. In lizards, sprint speed exhibits a high thermal dependence, with slower and clumsier movements at lower T_b s (Bennett, 1980; Hertz, Huey & Nevo, 1983; Avery & Bond, 1989; Van Damme, Bauwens, Castilla & Verheyen, 1989; Van Damme *et al.*, 1991). Reduced locomotor performance at low T_b would have enhanced the escape abilities of winged flies by increasing the time available for detecting lizards. This would have reduced the mean distance of successful attacks to winged prey at low temperatures, and would have increased the mean number of unsuccessful, long distance attacks to such prey.

To what extent can the results obtained in this study be used to predict performance by field-active lizards under more natural conditions? According to a sample of 302 field T_b readings in a nearby area (part of which have been reported elsewhere, see e.g. Carrascal & Díaz, 1989; Díaz, 1992), most active lizards had T_b s within the moderate and high ranges defined above (47.7 % of the readings between 28.6 and 33.5 °C, and 33.1 % higher than 33.5 °C, respectively). However, 19.2 % of the T_b readings were at or below 28.5 °C, so that a relatively large number of active lizards would be expected to show a diminished efficiency when trying to capture flying prey. Although some of these low T_b s probably correspond to lizards within the period of morning warm-up, when reduced capture abilities might not be relevant, a high proportion of the winged prey (assuming similar thermal sensitivities for most winged insects) would have effectively avoided lizard predation in the field. In fact, casual observations of this and other lacertid species (e.g. wall lizards, *Podarcis*) suggest that attacks to diptera are likely to succeed only when launched from a very short distance.

One final speculation is that improved ability to capture fast-fleeing, winged prey is likely to evolve if such "difficult" prey become more common than "not-so-difficult" ones, which is the expected result of stronger selection for prey defences than for predator counter-defences (Dawkins & Krebs, 1979; Endler, 1991). This suggests that reduced ability to capture fast-fleeing prey at low T_b may have been a major selective force leading to the evolution of behavioural thermoregulation in reptiles (Avery *et al.*, 1982). Results of this study indicate that high T_b s (that were close to the value of mean preferred T_b) not only improve predatory efficiency, but also widen the range of prey that is actually available for lizards, because only at high T_b s can lizards counterbalance the escape abilities of their more difficult and faster fleeing prey.

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PAEDOMORPHOSIS AND DIFFERENCES IN LIFE-HISTORY TRAITS OF TWO NEIGHBOURING CRESTED NEWT (*TRITURUS CARNIFEX*) POPULATIONS

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Two neighbouring crested newt populations (Ceklin and Lokanj) from Montenegro differ in several important life-history traits. Females from Ceklin laid significantly larger eggs. Larval size at hatching did not differ between Ceklin and Lokanj, but larvae from larger eggs survived better under laboratory conditions. Newts from Lokanj had a higher overall larval growth rate and a longer larval period. Consequently, they metamorphosed at larger size than Ceklin individuals. They also attained sexual maturity at smaller size than newts from Ceklin. It is shown that male newts with larval morphology may be sexually mature. Individuals from Lokanj population had a more plastic life-history, including facultative paedomorphosis, than individuals from Ceklin population. Out of five ontogenetic stages, juveniles and adult males showed significant interpopulation difference in size-shape trajectories. This might be the consequence of different ontogenetic pathways followed by crested newts from these populations.

INTRODUCTION

The life-history of urodeles is generally characterized by an aquatic larval stage and an adult stage adapted to diverse terrestrial habitats. The transition between these two ecologically distinct phases occurs during the period of metamorphosis. The timing of metamorphosis can influence associated traits such as body size at metamorphosis, one of the most important life-history features in this group (e.g. Smith-Gill & Berven, 1979; Werner, 1986), which potentially may affect adult survival, body size and age at first reproduction, and fecundity. In other words, a direct relationship exists between phenotypic variation generated in the larval stage and adult traits closely associated with fitness (Semlitsch, Scott & Pechmann, 1988). Timing of metamorphosis in urodeles is further complicated if some individuals in the population follow other ontogenetic trajectories, excluding metamorphosis in extreme cases.

The genus *Triturus* is of interest in this respect because some species are facultatively paedomorphic; i.e. some sexually mature individuals are characterized by adult morphology while others reproduce in the larval form. Among these species the alpine newt (*Triturus alpestris*) and the smooth newt (*Triturus vulgaris*) show a high incidence of paedomorphosis, especially in the Balkan area (Dzukic, Kalezic, Tvrtkovic & Djorovic, 1990).

In the crested newt (*Triturus cristatus* superspecies), however, the reproductive strategy of facultative paedomorphosis seems to be very rare. Occasionally 'giant overwintering larvae' have been found, or the in-

cidence of paedomorphosis has been reported but without firm evidence that specimens were sexually mature (for recent reports see Frazer, 1983; Kalezic & Dzukic, 1990; Fasola & Canova, 1992). In the course of our intensive study of the crested newt populations from former Yugoslavia, out of more than 1500 specimens examined (unpubl.), only a few males from a Montenegrin population had well developed gills and were sexually mature.

Variation in life-history traits on a large geographic scale has been the subject of considerable attention in urodeles, but differences on a smaller scale have received little study. This paper compares some of the life-history traits of *Triturus carnifex* in two neighbouring breeding sites in Montenegro. In one of these sites clear evidence of a nontransforming life-history path has been observed. The traits measured in this study included: (1) egg size and embryo survival; (2) larval survival and growth rate; (3) duration of larval stage; (4) time and size at metamorphosis; (5) size at onset of sexual maturation; and (6) characteristics of ontogenetic size-shape trajectories.

MATERIALS AND METHODS

STUDY SITES

Population localities are situated in the Montenegrin part of the Dinaric Alps, a limestone area of exposed karst. The climate is Mediterranean with hot and dry summers and rainy, mild autumns and winters. In spite of very high precipitation (3500 mm yearly on average), highly porous limestone base causes extreme aridity during summer. Such environ-

ment is rarely occupied by the crested newt elsewhere (Kalezic & Dzukic, 1990).

The study populations inhabit water bodies in sinkholes with impermeable bottoms. During summer months the water level in these ponds decreases considerably. Physical characteristics of the newt breeding sites are similar in many respects. The first pond (Ceklin) is a transformed sinkhole, 21 m wide and 56 m long with the maximum depth of about 1.8 m. The other pond, Lokanj, is 16 m wide and 19 m long basin with the maximum depth of about 2 m. The distance between the ponds is about 5 km. Both ponds are rain fed and hence show wide fluctuations of water level, especially Ceklin pond.

FIELD AND LABORATORY PROCEDURES

The crested newt larvae, juveniles and adults from both ponds were collected in September 1991, brought into the laboratory and anaesthetized by immersion in a 2:1000 MS 222 Sandoz solution before being measured. Shortly after measuring, juveniles and adults were put into hibernation in the cold room at 7.5°C.

Characteristics of the Lokanj and Ceklin populations, from oviposition to metamorphosis, were studied under laboratory conditions. Three males and nine females of each population sample were put to breed in separate aquaria in February 1992 to provide eggs and larvae. To exclude possible effects of larval density, food level and aquaria drying regime on life-history pathways (see Semlitsch, 1987), these variables were kept constant. Water in aquaria was continually recycled and filtered. Aquaria with the breeding individuals, and thereafter eggs and larvae, were exposed to natural photoperiod and daily changes in room temperature (10°C - 25°C).

Courtship, insemination, and oviposition occurred during February, March and April. As the first egg appeared, aquaria were checked twice a day, so that no eggs older than 12 hours were measured. Eggs were measured to the nearest 0.01 mm using a dissecting microscope fitted with an ocular micrometer. After measuring, embryos were cultured in aerated tap water until hatching.

Larvae were fed *ad libitum* with a concentrated mixture of zooplankton, phytoplankton and other micro-organisms collected from natural ponds. Total body length (L) was measured at hatching and each subsequent 15 days. From day 60 onward larvae were measured for total length, head width and tail height. The length of the larval period was defined as the number of days from hatching to metamorphosis. Metamorphosis was considered as completed upon loss of the gills and the closure of the gill slits. Body mass was determined by blotting individuals dry and weighing them to the nearest 0.01 g.

The reproductive organs of specimens thought to be sexually mature were examined by dissection. Maturity in females was determined by the presence of enlarged,

yolk-filled ovarian follicles and/or enlarged oviducts. Maturity in males was determined by the presence of enlarged and/or pigmented testes and vasa deferentia.

MORPHOMETRIC VARIABLES

In 461 hatchlings only body length was measured. Three linear measurements were taken from 44 specimens of 60-day old larvae (larvae I), 75 larvae about the time of metamorphosis (larvae II), 133 juveniles, 50 adult females and 39 adult males. Total body length (L) was measured from the snout to the tail tip, head width (Ltc) was taken at the angle of the jaw, and the maximum fin height (Lh) was measured at the base of the tail from dorsal to ventral edges. These three characters were chosen to document a difference in shape between paedomorphs and metamorphs, as suggested by Shaffer (1984) and Harris (1989). Larval measurements were taken under a dissecting microscope fitted with an ocular micrometer. Older larvae, juveniles and adults were measured with dial calipers with 0.1 mm precision.

TESTICULAR HISTOLOGY

A testis, removed from an adult male with well developed gills (Lokanj pond), was embedded in paraffin wax and longitudinal sections 5 µm thick were cut. Sections were stained with Alcian Blue Pas Orange G.

AGE DETERMINATION

Age was estimated by the technique used initially for fish otolith preparation (Mosegaard, Svedang & Taberman 1988). Humeri were removed from individuals, rinsed in water, air-dried, and mounted in thermoplastic resin. The surface of the bone was then ground and polished in aluminosilicate paste to enhance visibility and to achieve maximal contrast and high transparency. The age appeared to be accurately reflected by the number of the growth lines with a precision of ± 1 year. The results were checked using the standard skeletochronological technique on the same humerus bones (for detailed description see Francillon, 1979).

STATISTICAL ANALYSIS

Data were examined using various univariate and bivariate analyses, and the multivariate procedure of principal-component analysis (PCA). PCA was used to derive multivariate measures of newts, size and shape (e.g. Bookstein, Chernoff, Elder, Humphries, Smith, & Strauss, 1985). The analysis was performed on the variance-covariance matrix of log-transformed variables L, Ltc and Lh. The use of variance-covariance matrix rather than correlation matrix is recommended when dealing with morphometric data. The original variables were log-transformed in order to meet the assumption of homoscedascity (Zar, 1974). Ontogenetic trajectories were obtained for each group (larvae I, larvae II, juveniles and adults) by linear regression analysis of PC2 scores (an aspect of shape) on PC1

scores (a general size aspect). Rate of change in shape relative to size was estimated by the slope of the regression lines.

RESULTS

Females from Ceklin laid larger eggs than females from Lokanj. Differences in all corresponding egg measures appeared to be highly significant (Table 1). Muroid capsules in Ceklin eggs were thicker, relative to ova, than those of Lokanj eggs, the difference being highly significant as well.

Eggs from Ceklin, with more yolk and thicker muroid capsules, survived incubation in our laboratory better than those from Lokanj; survival was 0.413 and 0.227, respectively.

Ceklin eggs produced hatchlings with mean total length of 9.90 ± 0.09 mm ($n = 165$), while those of Lokanj were somewhat smaller (9.81 ± 0.07 mm, $n = 296$). The difference was insignificant (χ^2 NOVA, $P > 0.05$). In both cases the range of total length of newly hatched larvae appeared to be the same (7.1 - 14.0 mm; Fig. 1a).

Larval survival was low during the period from 15-45 days after hatching (0.47 for Ceklin and 0.25 for Lokanj larvae). After this critical period, larval survival stabilized at high level (about 0.90) in both groups until metamorphosis. Apparently, larvae from larger eggs (Ceklin) survived better during the first 45 days of larval life than larvae from smaller eggs (Lokanj).

Larval growth, from hatching to metamorphosis, was estimated as the change in mean body length between measuring dates (each 15 days). Linear

Measure		Ceklin $n=124$	Lokanj $n=133$
Ovum	length	2.68 ± 0.02	2.59 ± 0.02
	width	2.49 ± 0.02	2.39 ± 0.02
Total egg	length	5.50 ± 0.04	4.73 ± 0.04
	width	3.40 ± 0.02	3.10 ± 0.03
Ovum/total egg	length	0.49 ± 0.00	0.55 ± 0.00
	width	0.73 ± 0.00	0.78 ± 0.00

TABLE 1. Mean values (\pm SE) of egg size (in mm) and of ovum/total egg ratio for two crested newt populations. n = sample size. All corresponding egg measures between populations are highly significant (ANOVA, $P < 0.001$).

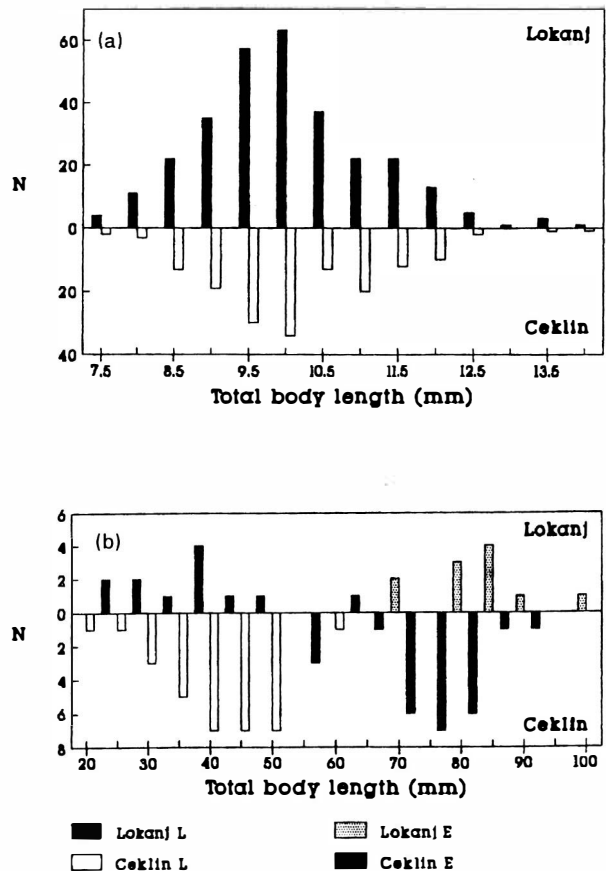


FIG. 1. (a) Distribution of total body length (in mm) of hatchlings from Lokanj and Ceklin populations. n = number of individuals. (b) Distribution of total body length (in mm) of 60-day old larvae (L) and efts (E) from Lokanj and Ceklin populations. n = number of individuals.

regressions of total length on age are presented in Fig. 2. Growth appeared to be faster in larvae from Lokanj; the difference between the two slopes was significant (t -test, $P < 0.01$).

The mean duration of larval development was 176.9 ± 8.2 days (range 122-211; $n = 11$) in the Lokanj sample, and 158.8 ± 6.3 days (range 89-200; $n = 25$) in the Ceklin sample. A non-significant difference between mean time of metamorphosing of Ceklin and Lokanj larvae was found in this study (ANOVA, $P > 0.05$). Probably the number of surviving larvae was insufficient to detect subtle difference in this obviously variable life-history trait.

Total body length at which Ceklin larvae metamorphosed ranged from 52.3 mm to 87.0 mm, with the mean value of 70.39 ± 1.62 , while larvae from Lokanj sample transformed at larger size (range 65.4 - 95.6; mean \pm SE = 79.43 ± 2.39); the difference being highly significant (ANOVA, $P < 0.005$). Putting this in terms of weights, at metamorphosis the crested newt reached 19.7% (Ceklin) and 33.6% (Lokanj) of its mean adult weight.

Sample	<i>n</i>	Body length	Head width	Fin height
<i>Lokanj</i>				
Larvae I	12	36.53 ± 11.57	5.33 ± 1.65	6.23 ± 1.66
Larvae II	35	83.89 ± 3.53	9.19 ± 0.53	8.35 ± 0.83
Juveniles	43	89.67 ± 6.16	8.77 ± 0.53	7.22 ± 0.62
Adults (female)	21	130.81 ± 9.31	12.84 ± 1.13	9.57 ± 1.14
Adults (male)	19	123.89 ± 8.16	12.46 ± 0.96	9.68 ± 1.36
<i>Ceklin</i>				
Larvae I	32	38.80 ± 8.20	5.75 ± 1.23	7.25 ± 1.59
Larvae II	40	64.18 ± 5.50	7.39 ± 0.47	6.74 ± 0.79
Juveniles	90	73.93 ± 5.86	7.34 ± 0.56	5.70 ± 0.70
Adults (female)	29	142.50 ± 12.48	14.00 ± 1.31	11.28 ± 1.80
Adults (male)	20	122.80 ± 10.44	12.49 ± 0.75	10.18 ± 1.14
<i>F values</i>				
Larvae I		0.53	0.84	3.53
Larvae II		330.61***	239.43***	74.10***
Juveniles		203.25***	193.82***	144.08***
Adults (female)		13.07***	10.68**	14.75***
Adults (male)		0.13	0.01	1.53

TABLE 2. Means and standard errors of morphometric characters (in mm) for five forms (*n* = sample size). Differences between two populations were tested by means of ANOVA. ** $P < 0.01$, *** $P < 0.001$.

Sixty-day-old larvae (larvae I) from both populations showed statistically non-significant differences in body size (Table 2). Being longer in larval stage was associated with larger size at metamorphosis: larvae II were much larger in the Lokanj sample for all measured traits. Also, a little overlap in total length of Lokanj and Ceklin efts (Fig. 1b) was even less in postmetamorphic juveniles (Fig. 3).

Frequency distribution of body length of adults is shown in Fig. 3. Adult males from Lokanj and Ceklin were of about the same size and weight (ANOVA, $P > 0.05$ in both cases). Females from Ceklin appeared to be much larger and heavier than those from Lokanj (ANOVA, $P < 0.001$). Morphological differences between sexes were apparent in both populations (Table 2). Adult females were larger than adult males; the difference was more pronounced in the Ceklin sample. Comparing body weights, females and males from the Lokanj population did not differ significantly (ANOVA, $P > 0.05$), in contrast with Ceklin adults (ANOVA, $P < 0.001$).

Out of 40 sampled branchiate males from Lokanj, four specimens had secondary sexual characteristics, including a well developed dorsal crest, a prominent cloaca, and a whitish streak along the side of the tail.

The size of the smallest one ($L = 92.0$ mm, $L_{sv} = 52.9$ mm) was assumed to be the size of the first reproduction of Lokanj males. The testes of this male were lobulated. The largest branchiate male ($L = 116.0$ mm, $L_{sv} = 66.1$ mm) had one-lobe testes. The breeding capability of this male was confirmed by the presence of spermatozoa in the spermatid ductus and ampullae with spermatids (April 1992). The estimated age of this male, 5 years, was in the range shown by breeding males from Ceklin and Lokanj (4-11; $n = 38$; unpubl. data). It is also in concordance with data on the age of sexual maturation in crested newt in France (Francillon-Vieillot, Arntzen & Geraudie, 1990). Sexually mature branchiate females were not found. The size of the smallest mature female from Lokanj ($L = 97.0$ mm, $L_{sv} = 55.9$ mm) was taken to be the size of the first reproduction of this sex.

In the Ceklin population only non-branchiate mature specimens were found; the smallest male had 100 mm body length ($L_{sv} = 67.1$ mm) and female 114 mm ($L_{sv} = 65.6$ mm). These figures were taken to represent the size of the first reproduction in Ceklin. This size happened to be very close to those established for the crested newt (*Triturus cristatus*) from England (Bell, 1979).

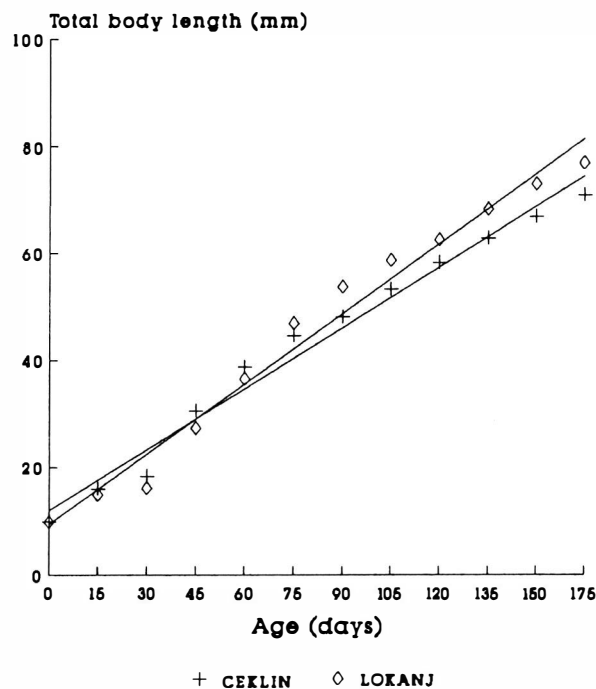


FIG. 2. Regressions of total length on age for larvae from two populations.

Principal component one (PC1) is highly positively correlated with the original morphological variables and it was taken as a latent size variable (in the sense of Bookstein *et al.*, 1985). This component explained almost 90% of the total variation in trivariate sample space (Table 3). Total body length, head width and fin height loaded positively and significantly on the first component in decreasing contributions. Principal com-

Variance-covariance matrix				Eigenvectors		
	Lsv	Ltc	Lh	PC1	PC2	PC3
Lsv	0.031	0.022	0.014	0.72	-0.51	-0.47
Ltc		0.018	0.013	0.56	0.04	0.83
Lh			0.014	0.40	0.86	-0.32
Eigenvalues				0.0561	0.0061	0.0004
Percent of variance				89.58	9.65	0.77

TABLE 3. The PCA of variance-covariance matrix derived from pooled data (larvae I, larvae II, juveniles and adults) of two populations. The variables are the logarithms of body length (L), head width (Ltc) and fin height (Lh).

ponent two (PC2), contrasted original measures with each other. Thus, eigenvector of total body length had negative value, while fin height was positively correlated to PC2. Ltc showed a negligible correlation with PC2. Therefore, PC2 summarizes aspects of newts' shape, explaining about 10% of the remaining variation. PC3 explained a negligible amount of variation (< 1%), and was not considered further.

Means and standard errors of PC1 and PC2 scores for different life stages are presented in Table 4. The ontogenetic trajectories, represented by separate regressions of PC2 on PC1 scores for five corresponding

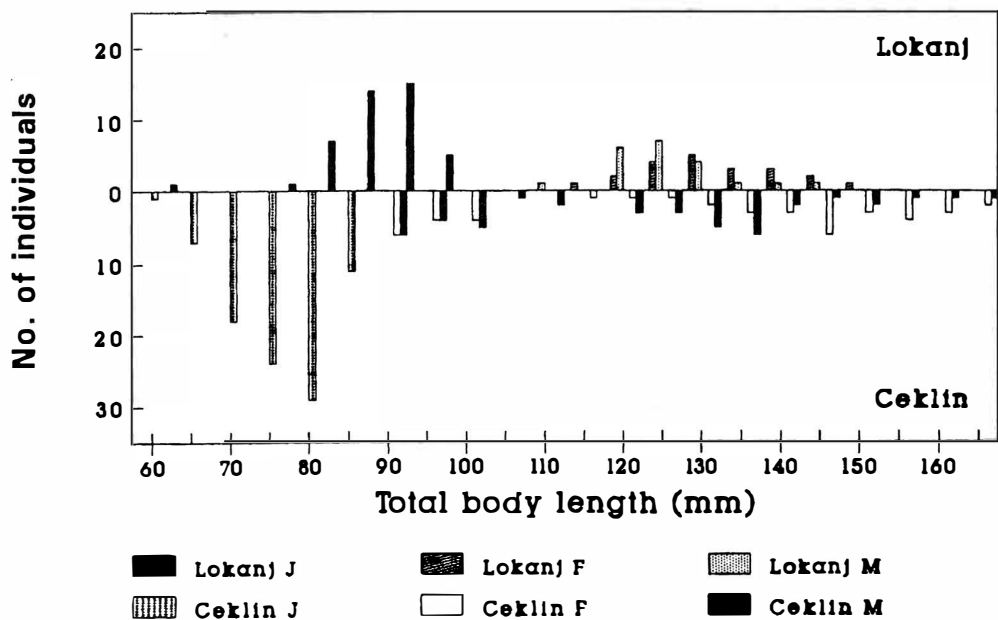


FIG. 3. Distribution of total body length (in mm) of juveniles (J), males (M) and females (F) from two populations.

	<i>Lokanj</i>		<i>Ceklin</i>		<i>t</i>
	PC1	PC2	PC1	PC2	
Larvae 1	1.83±0.22	-0.09±0.05	1.90±0.18	-0.05±0.05	1.37
Larvae 2	2.30±0.04	-0.16±0.03	2.13±0.05	-0.18±0.04	1.53
Juveniles	2.28±0.04	-0.22±0.03	2.14±0.06	-0.28±0.04	2.38**
Females	2.54±0.05	-0.20±0.04	2.62±0.07	-0.16±0.05	0.51
Males	2.52±0.06	-0.18±0.04	2.53±0.06	-0.16±0.03	1.97*

TABLE 4. Means and standard errors of PC1 and PC2 scores. *t*-values obtained from testing for difference between regression coefficients of PC2/PC1 scores between five corresponding forms from two populations. * $P < 0.05$, ** $P < 0.01$.

forms of two populations, estimate changes of shape relative to size. Regression coefficients were compared by means of *t*-test. Adult females appear to be most similar, followed by younger larvae and older larvae, respectively. Juveniles and adult males showed significant interpopulation differences in the ontogeny of size and shape changes.

DISCUSSION

This study deals with differences in life-history traits of two neighbouring populations of the crested newt. Females from Ceklin laid significantly larger eggs (with more yolk for larval development) than those from Lokanj. The size of mucoid capsule is also relevant for the future of the developing embryo; it gives protection from injury and fungal infestation and improves fastening to an object (Duellman & Trueb, 1986).

We found that larvae from larger eggs survived better under laboratory conditions than larvae from smaller eggs. That egg size was related to larval success, was found previously for *Ambystoma talpoideum* (Semlitsch & Gibbons, 1990). However, in contrast with the above study, larval size at hatching did not differ between Ceklin and Lokanj; egg size did not significantly affect body size of larvae at hatching.

Newts from Lokanj had higher overall larval growth rate and a longer larval period; consequently, they transformed at larger size than Ceklin individuals. They also attained sexual maturity at smaller size. This study confirms that at least some males matured while possessing a larval morphology. To the best of our knowledge, this is the first report of fully sexually mature crested newts with well developed gills that can therefore be considered paedomorphic.

The most common life-history pathway in newts leads to obligate metamorphosis. This path is followed by newts from Ceklin. However, juveniles are more

aquatic than elsewhere; it appears that the surrounding terrestrial environment, which is arid and unproductive, does not support juvenile growth sufficiently.

Individuals from Lokanj have a plastic life-history including facultative paedomorphosis. The Lokanj larvae have three possible fates during ontogeny: (1) some larvae transform in the same year they were hatched; (2) a considerable number of larvae have a prolonged period of growth, overwintering in the pond and then metamorphosing to immature juveniles; (3) in some larvae a prolonged period of growth is followed by attaining sexual maturity and then metamorphosing into adults. Larvae with an initial growth advantage are more likely to take this life-history pathway. Body size advantage, at a time when larvae are most vulnerable, may account for increased survival through size-specific mechanisms. This increased growth results in earlier sexual maturation of aquatic larvae, in comparison to terrestrial or aquatic juveniles of the same year class.

Moreover, there is evidence that paedomorphs breed earlier within a season, providing their larvae with an early growth advantage over the offspring of metamorphs (Semlitsch, Harris & Wilbur, 1990). Apart from an increase in potential survivorship, other advantages gained through a fully aquatic life cycle, such as elimination of energetic costs of metamorphosis and terrestrial migration, play an important role in the maintenance of paedomorphosis. Males are prime candidates to follow this ontogenetic pathway since they reach sexual maturity earlier than females (e.g. Duellman & Trueb, 1986: 169).

A prerequisite for a polymorphic life-history in newts, is an extended residence in water. It is strongly supported by our data: in both ponds adults as well as subadults are abundant out of the breeding season and numerous juveniles are found in water during autumn. That the juveniles returned to water shortly after the

terrestrial phase, as was found for the crested newt in England (Verrell, 1985), is less likely. Metamorphic individuals would be exposed to stress of heat, desiccation and starvation in dry karst habitat. Moreover, in xeric environment there is a critical surface/volume ratio for metamorphosis above which terrestrial activity is disadvantageous (Bruce, 1976).

In newts, growth in the aquatic environment is greater than in the surrounding terrestrial environment (Verrell & Halliday, 1985). Larger size in amphibians may also be advantageous in terms of fecundity (Kaplan & Salthe, 1979; Verrell & Francillon, 1986). However, though several newt species, such as *Notophthalmus viridescens* (Healy, 1973, 1974) and *Triturus vulgaris* (Bell, 1977), show higher growth rates in aquatic habitat, they have lower mortality rates in terrestrial habitat. It is possible that the above trade-off contributes to the maintenance of both life strategies.

Variation in life-history traits may arise from both genetic and non-genetic sources (e.g. Stearns, 1977; Berven & Gill, 1983; Semlitsch & Gibbons, 1985; and references therein). Non-genetic differences may result from plastic phenotypic responses to local environmental conditions or may be due to non-genetic maternal effects (e.g. Falconer, 1981), as stated for egg quality in some anuran species (Travis, 1980; Berven, 1982).

Though the option for paedomorphosis is under genetic control, it is also highly susceptible to environmental conditions (Harris, 1987; Semlitsch 1987; Semlitsch & Wilbur, 1989; Semlitsch *et al.*, 1990). The agent of selection could be the desiccation history of a pond (Semlitsch *et al.*, 1990). According to local inhabitants, Ceklin pond undergoes more drastic changes of water level, though it never dries completely. Thus, it is possible that the Lokanj population has been subject to long term natural selection for overwintering larvae and for paedomorphosis. In Ceklin pond selection for metamorphosis predominates since falling water level, concomitant deterioration of the water quality and increased larval density, would accelerate metamorphosis.

Significant differences in size-shape trajectories for juveniles and adult males might be the consequence of different ontogenetic pathways followed by Lokanj and Ceklin individuals. The more similar size-shape trajectories for females may be due to absence of paedomorphosis in this sex.

Another consequence of different ontogenetic pathways is a reduced size difference in Lokanj females and males. Rapid larval growth, prolonged time of metamorphosis, earlier sexual maturation of males (more time for growth) and the incidence of paedomorphosis apparently reduced sexual size difference in the Lokanj population. Facultative paedomorphosis has the same effect in the alpine newt (*Triturus alpestris*) and to a lesser degree in the smooth newt (*Triturus vulgaris*) (Kalezic, Crnobrnja, Djorovic & Dzukic, 1992).

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PLEISTOCENE AMPHIBIANS AND REPTILES FROM EMIRKAYA-2, TURKEY

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The Middle Pleistocene fissure-filling deposits of Emirkaya-2 in central Turkey yielded numerous bones of amphibians and reptiles, belonging to at least 11 taxa: *Bufo viridis*, *Lacerta* sp., *Pseudopus* cf. *P. apodus*, *Scolecophidia* indet., *Coluber caspius*, *Coluber* sp., *Elaphe* cf. *E. quatuorlineata*; cf. *Telescopus* sp., *Colubridae* indet., *Natrix* cf. *N. natrix* and *Vipera* sp. from the "Oriental vipers" group. The assemblage probably comprised only living forms occurring in the area today. The faunal composition of this locality indicate warm climate and at least a partly forested environment.

INTRODUCTION

The available palaeontological data suggest that most of the modern herpetofauna of Europe is of Asiatic origin (Bailon, 1991). Due to its geographic situation, Asia Minor probably played a significant role in the distribution of amphibians and reptiles during Neogene times, serving as an important route for migrants passing around the Paratethys. However, the fossil herpetofauna of Turkey is as yet poorly known. Our knowledge concerning this group in the area (including Aegean islands) is limited to the fauna described from the early Pliocene of Maritsa, Greece (Szyndlar, 1991a, 1991b), late Pliocene of Çalta, Turkey (Rage & Sen, 1976; Sen & Rage, 1979), early

Pleistocene of Laghada A and B, Greece (Szyndlar, 1991a, 1991b), middle Pleistocene of Latomi-1 (Chios), Greece (Schneider, 1975) and late Pleistocene of Pili B, Greece (Szyndlar, 1991a, 1991b).

The fossiliferous site of Emirkaya-2 is a fissure-filling in the Emirkaya limestone quarry, 1.5 km south of the town of Seydisehir (dept. of Konya) in Central Anatolia (Fig. 1). It was discovered in October 1989 by a French team during prospecting in the area. The bituminous limestones of this quarry are attributed to the late Triassic. The fissure-filling is about 5 m wide, and nearly 10 m in thickness. Well consolidated brecciated sediments contain abundant remains of small and large mammals, amphibians, reptiles and birds. A previous paper (Sen, Bonis, Dalfes, Geraads, Jaeger & Mazin, 1991) presented this locality along with a preliminary study of a mammal assemblage. A short report on the amphibians, reptiles and birds was given by Kessler & Venczel (1993). Based on the large mammals and on the *Miomys-Arvicola* association, Sen *et al.*, (1991) tentatively assigned a Middle Pleistocene age to this fauna. Studying the small mammals, Montuire (1991) and Montuire, Sen & Michaux (in press) deduced its age as Holsteinian, which corresponds to the Mindel-Riss interglacial. The mammal fauna is characterized by its diversity, since it contains 36 species of mammals belonging to 20 families. The vertebrate remains were obtained by dissolving blocks in diluted formic acid and by washing some weathered sediment in the field. The material is stored in the collections of the Laboratoire de Paléontologie, Muséum National d'Histoire Naturelle, in Paris.

The anatomical nomenclature of Anura follows that of Sanchíz & Mlynarski (1979), lizard nomenclature follows Rocek (1984). The anatomical nomenclature of snakes and the methodology of measurements of snake vertebrae follow Szyndlar (1984).

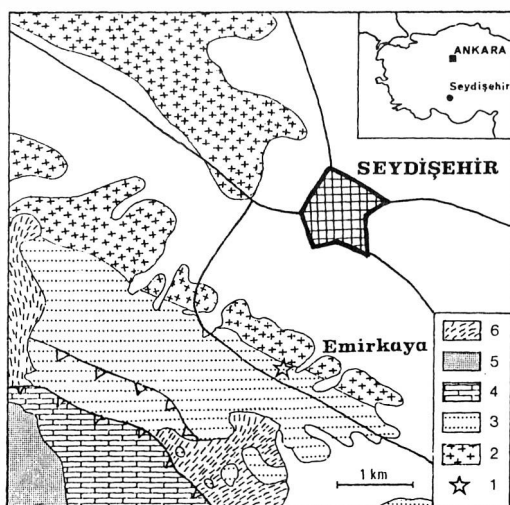


FIG. 1. Location map of the Emirkaya-2 fissure-filling. 1. The locality, 2. Cambrian, 3. Triassic, 4. Jurassic, 5. Cretaceous, 6. Screens.

SYSTEMATIC STUDY

AMPHIBIA

Order Anura Rafinesque, 1815

Family Bufonidae Gray, 1825

Genus *Bufo* Laurenti, 1768*Bufo viridis* Laurenti, 1768

Material. One fragmentary atlas, 15 fragmentary vertebrae, seven fragmentary humeri, six fragmentary scapulae, six radioulnae (proximal fragments), six fragmentary ilia (EM 501 to 544).

The available postcranial fragments are distinctive enough to provide the basis for the specific identification.

The atlas, with the condyle broken off, displays morphological features of the recent *Bufo viridis*. The mode of articulation is of type II (Lynch, 1971). The neural canal is round, the postzygapophyses are moderately developed. The subzygapophyseal spine (sensu Bailon, 1986) is present, this structure being slightly expressed in *Bufo calamita* and lacking in *Bufo bufo* (Sanchíz, 1977; Bailon & Hossini, 1990). The trunk vertebrae are procoelous (generally badly preserved). The transverse process in the second vertebra (preserved only in the left side) is flattened dorsoventrally and slightly directed anteriorly. The sacral vertebrae are procoelous. In all the specimens, the diapophyses are broken off distally. A shallow groove at the base of the sacral processes is directed laterally, somewhat similarly to that of *Bufo* aff. *viridis* from Latomi-1, in Chios (Schneider, 1975: Fig. 9). The dorsal crest of the urostyle is moderately high, the cotyles are well separated from each other and are flattened dorsoventrally.

The tuber superius of ilium (Fig. 2a and 2b) is prominent, and usually divided in two protuberances, the posterior one being smaller. The preacetabular fossa is deep. In *Bufo raddei* this fossa is similarly developed (Hodrova, 1986: Figs. 5 & 6), shallow in *Bufo calamita* and lacking in *Bufo bufo* (Sanchíz, 1977).

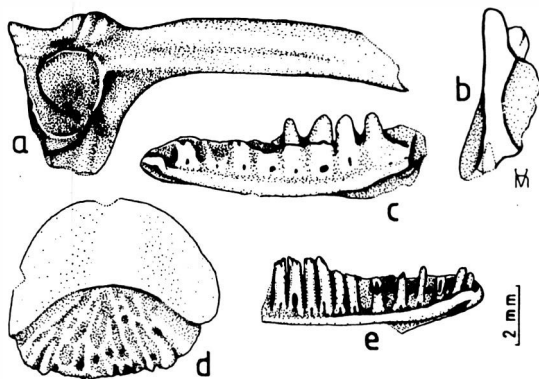


FIG. 2. Anuran and lizard remains from Emirkaya-2. a, b: right ilium of *Bufo viridis* (EM 501); c: right dentary of *Pseudopus* cf. *P. apodus* (EM 546); d: osteoderm of *Pseudopus* cf. *P. apodus* (EM 547); e: left dentary of *Lacerta* sp. (EM 545).

The pars cylindriformis lacks the 'calamit lamina', present in *Bufo calamita* and *Bufo raddei* (Sanchíz, 1977; Bailon 1986; Hodrova, 1986).

The remaining specimens are fragmentary (scapulae, humeri and radioulnae) and provide limited taxonomic information.

In the Aegean area, fossil remains assigned to this species as *Bufo* aff. *viridis* are already known from the late Pliocene of Çalta (Rage & Sen, 1976; Sen & Rage, 1979) and from the middle Pleistocene of Latomi-1 (Schneider, 1975). These localities lie within the present range of distribution of this species.

REPTILIA

Order Sauria McCartney, 1802

Family Lacertidae Bonaparte, 1831

Genus *Lacerta* Linnaeus, 1758*Lacerta* sp.

Material. One fragmentary dentary (EM 545).

The dentary fragment preserves 18 tooth positions and corresponds in size and shape with the living *Lacerta viridis* - *Lacerta trilineata* (Fig. 2e). The dentition is of pleurodont type, the teeth are provided with bicuspid or tricuspid tips.

Family Anguidae Gray, 1825

Genus *Pseudopus* Merrem, 1820*Pseudopus* cf. *P. apodus* (Pallas, 1775)

Material. One fragmentary dentary, nine osteoderms (eight of them fragmentary), two fragmentary caudal vertebrae (EM 546 to 557).

The medium-sized dentary preserves 12 tooth positions (Fig. 1c). The Meckelian groove opens ventrally, being visible medially only in its anterior portion (below the symphysis). The crista splenialis is ended anteriorly in the moderately developed spina splenialis. The teeth are conical, with a fine striation near the crown tips. The two caudal vertebrae, although fragmentary, can be assigned to this genus by their size and morphology. The posterior part of the osteoderms is covered with vermicular-shaped tubercles, while the anterior part is smooth and devoid of tubercles (Fig. 2d).

The observable features of the above described skeletal fragments are consistent with those of living *P. apodus*. In Turkey, fossil remains belonging to *Pseudopus* (= *Ophisaurus*) were also reported from the late Pliocene of Çalta by Rage & Sen (1976).

It should be noted that the genus *Pseudopus* has been revalidated by Klembara (1979). This author, using the rich fossil material from Dolnice (MN4), described *Ophisaurus fejfari* and *O. spinari*, and came to the conclusion that *Ophisaurus* (including fossil and living forms) and *Pseudopus* (*P. moguntinus*, *P. pannonicus* and *P. apodus*) were two distinct phylogenetic lineages. In contrast, Sullivan (1987)

pointed out that the genus *Ophisaurus* comprises only New World forms, and the Old World '*Ophisaurus*' may be assigned to the *Ophisauriscus-Anguis* lineage.

The fossil relatives of the living *Pseudopus apodus* (i.e. *P. moguntinus* and *P. pannonicus*) inhabited a large part of Europe from the Upper Oligocene up to the Middle Pleistocene (Fejérváry-Láng, 1923; Bachmayer & Mlynarski, 1977; Klembara, 1979, 1981, 1986; Rocek, 1984; Bailon, 1989, 1991). The youngest of them, *P. pannonicus*, progressively retreated from the north during the late Neogene, to become extinct during the early Pleistocene. On the other hand, it should be mentioned that *P. pannonicus*, by its morphology, was rather similar to the living *P. apodus*, differing mainly from the latter by its larger dimensions.

Although in Europe the extinct *P. pannonicus* survived up to the Middle Pleistocene (i.e. in the Vaalian of Betfia, Romania, pers. obs.), at the same time in Anatolia, the genus was already represented by the living species.

Order Serpentes Linnaeus, 1758
Scoleophidia indet.

Material. Four trunk vertebrae (EM 558 to 561).

The vertebrae are well preserved and of minute size. The centrum length in three measured vertebrae ranges between 0.8-1.05 mm, while the centrum width between 0.61-0.75 mm. All the vertebrae are depressed dorsoventrally, lacking the neural spine and paracotylar foramina. The haemal keel is imperceptible, the synapophyses are undivided, the cotyle and condyle are strongly flattened dorsoventrally (Fig. 3).

The above morphological features, shared by the members of the families Typhlopidae, Anomalepididae and Leptotyphlopidae, make it impossible to identify these fossils below the subordinal level (Szyndlar, 1987, 1991a; Szyndlar & Zerova, 1992). Fossil remains of Scoleophidia, coming from the area, are known from the early Pliocene of Maritsa (Szyndlar, 1991a) and from the late Pliocene of Çalta (Rage & Sen, 1976). Presently, Anatolia is inhabited by members of both the Typhlopidae and the Leptotyphlopidae (Baran, 1976, 1978).

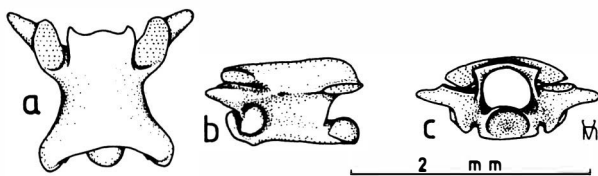


FIG. 3. Trunk vertebra (EM 558) of *Scoleophidia* indet. in dorsal (a), lateral (b) and anterior views (c).

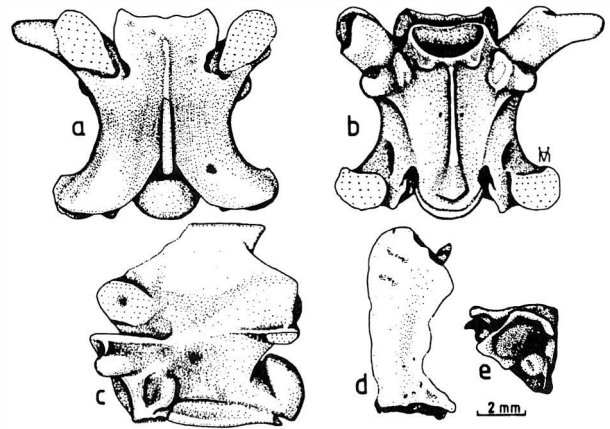


FIG. 4. *Coluber caspius*. Trunk vertebra (a-c: EM 563) and frontal (d, e: EM 562). a, d: dorsal; b: ventral; c: lateral; e: anterior views.

Suborder Alethinophidia Nopcsa, 1923
Family Colubridae Oppel, 1811
Genus *Coluber* Linnaeus, 1758
Coluber caspius Gmelin, 1789

Material. One right frontal, 44 vertebrae (EM 562 to 606).

The frontal resembles closely that of the living *Coluber caspius* because of its internal prefrontal process projecting anteriorly (Fig. 4d, 4e). The vertebrae are vaulted, the neural spine is high, overhanging posteriorly and slightly anteriorly. The epizygapophyseal spine is absent, the zygosphenes are concave. Prezygapophyseal processes are equal in length to the prezygapophyseal articular facets and are blunt on their edge. Below the cotyle rim a pair of tubercles can be observed. The subcentral ridge is better defined posteriorly to the paradiapophyses. The haemal keel is sharp and prominent, in lateral view it is slightly curved ventrally, its depth diminishing posteriorly, where it becomes wider. The para- and diapophyseal portions of the paradiapophyses are equal in height. The diapophyses are slightly shifted posteriorly (Fig. 4b, 4c). The centrum length of the largest vertebra is 6.84 mm, while the centrum width is 5.56 mm (centrum length/centrum width ratio: 1.23).

For comparison of these remains, it was not possible to see comparative material of all living colubrids, but only some species from Eastern Europe and Anatolia. However, some key characters of vertebrae and frontal bones are sufficiently characteristic for species allocation. As indicated by Szyndlar (1991a), the trunk vertebrae of *C. caspius* can be well differentiated from the other large-sized European colubrids by their distinctly elongated centra, concave zygosphenes, prominent and sharp haemal keel, and long prezygapophyseal process. Moreover, the prefrontal

process of the Emirkaya-2 specimen has a similar shape to that of *C. caspius*. These diagnostic features, as well as the geographical distribution of this species, allow us to assign this material to *C. caspius*.

Surprisingly, a species, *C. caspioides*, very similar to the living *C. caspius* was recently described from the late Lower Miocene (MN4) of Petersbuch 2 in Germany (Szyndlar & Schleich, 1993). The fossil record from Emirkaya-2 lies within the present range of distribution of the living species.

Coluber sp.

Material. One frontal, 15 vertebrae (EM 607 to 622).

The frontal somewhat resembles those of the living *Coluber najadum*-*C. rubriceps* group (Fig. 5c, 5d), but the internal prefrontal process of the above group is comparatively larger and slightly projecting anteriorly. The vertebrae are moderately vaulted, with long and low neural spine. The centrum length of the largest vertebra (Fig. 5a, 5b) is 3.74 mm, while the centrum width is 2.29 mm (centrum length/width ratio: 1.63). The zygosphenal roof is slightly convex, the zygosphenon is provided with three lobes. The prezygapophyseal articular facets are ovaloid, the prezygapophyseal processes are slightly longer than the prezygapophyseal articular facets with pointed tips. The haemal keel is prominent, its depth slightly diminishing posteriorly. The parapophyses are minute, divided into para- and diapophyseal portions. The diapophyses are not shifted posteriorly and are equal in height with the parapophyses.

The above features somewhat resemble those of the recent *C. najadum*, *C. rubriceps*, and also *C. gemonensis*. The scantiness of the available material, as well as the overlapping vertebral characters of the above species (see Szyndlar, 1991a) do not permit more precise identification of these fossils.

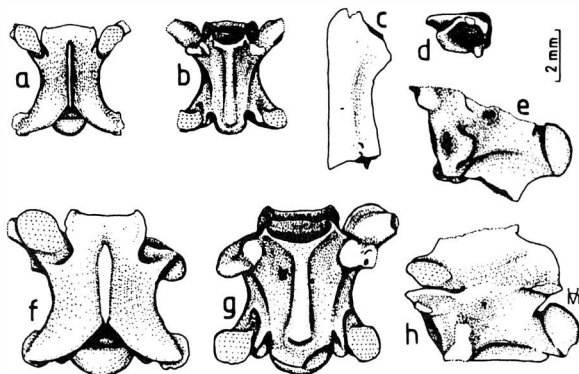


FIG. 5. Fossil remains of *Coluber* sp. and *Elaphe* cf. *E. quatuorlineata*. a, b: trunk vertebra of *Coluber* sp. (EM 607); c, d: frontal of *Coluber* sp. (EM 608); e: cervical vertebra of *Elaphe* cf. *E. quatuorlineata* (EM 623); f, g, h: trunk vertebra of *Elaphe* cf. *E. quatuorlineata* (EM 624). a, c, f: dorsal; b, g: ventral; d: anterior; e, h: lateral views.

Nowadays, the area is inhabited by several members of the genus *Coluber* (Baran, 1976; Schëtti & Agasian, 1985; and others).

Genus *Elaphe* Fitzinger, 1833

Elaphe cf. *E. quatuorlineata* (Lacépède, 1789)

Material. One fragmentary cervical vertebra, four trunk vertebrae (EM 623 to 627).

Only the centrum of the cervical vertebra is preserved (Fig. 5e). The tip of the hypapophysis is broken off, but its base is orientated forward, as observed in the living *Elaphe quatuorlineata* (condition also shared by other members of the genus, e.g. *E. schrenki*). The trunk vertebrae are vaulted, the zygosphenon is concave, the haemal keel is flattened and is not widened before the condyle. The parapophyses are large, projecting laterally. Neither neural spine, nor prezygapophyseal processes are preserved in the material (Fig. 5f, 5g, 5h).

The anteriorly projected hypapophyses of the cervical vertebrae, combined with the strongly flattened haemal keel, concave zygosphenon and very short prezygapophyseal process of the middle trunk vertebrae are considered as key characters of the living *E. quatuorlineata* (Szyndlar, 1991a).

The scarcity of the material from Emirkaya-2 and its poor state of preservation does not allow observation of all the features mentioned above. Thus, the allocation of these remains to the living *Elaphe quatuorlineata* cannot be fully demonstrated.

Genus *Telescopus* Wagler, 1830

Cf. *Telescopus* sp.

Material. Six trunk vertebrae (EM 628 to 633).

The vertebrae are somewhat fragmentary. The neural arch is depressed; the neural spines in all the specimens are lacking. The zygosphenon is crenate, the prezygapophyseal articular facets are oval, the prezygapophyseal processes are very short and obtuse shaped. The haemal keel is flattened and only slightly widened before the condyle. The parapophyses are not preserved in the material (Fig. 6d, 6e).

The lack of the neural spine and the parapophyses, which are extremely important to determine *Telescopus fallax*, makes impossible the specific allocation of these remains. Presently, South Anatolia is inhabited by the living *T. fallax*.

Colubridae indet.

Material. Fourteen trunk vertebrae (EM 634 to 644).

The vertebrae are vaulted, the neural spine is high, the zygosphenon usually is triangle-shaped. The prezygapophyseal processes are slightly longer than or

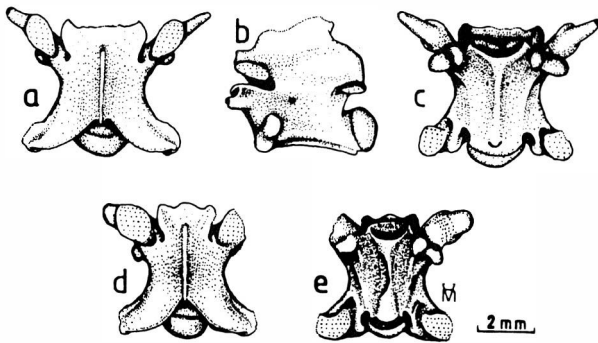


FIG. 6. Trunk vertebrae of Colubridae indet. (a-c: EM 634) and cf. *Telescopus* sp. (d, e: EM 628). a, d: dorsal; b, lateral; c, e: ventral views.

of equal length with the prezygapophyseal articular facets, ending in pointed tips. The haemal keel is poorly developed. The subcentral area is somewhat concave. The paradiapophyses are slightly divided into para- and diapophyseal portions and are equal in height (Fig. 6a, 6b, 6c). The centrum length in three measured vertebrae ranges between 2.90-3.32 mm, while the centrum width is between 2.31-2.70 mm. Some of the above vertebral characters are shared by several small members of the genus *Coluber* (e.g. *C. ravergeri*), but more precise identification of this material is impossible.

Genus *Natrix* Laurenti, 1768

Natrix cf. *N. natrix* (Linnaeus, 1758)

Material. One fragmentary dentary, 150 vertebrae (EM 645 to 648).

The dentary fragment, with its proximal and distal portions broken off, preserves 16 tooth sockets. Its assignment to this form remains doubtful. The vertebrae display all the diagnostic features of the living *Natrix natrix* (Szyndlar, 1991b). The neural arch is moderately vaulted, the neural spine strongly overhangs anteriorly and posteriorly, the hypapophysis is sigmoid-shaped with obtuse tip, the parapophyseal process is obtuse-shaped (Fig. 7a, 7b, 7c). The centrum length in six measured vertebrae ranges between 4.33-5.08 mm, the centrum width between 2.75-3.41 mm. The centrum length/width ratio is between 1.43-1.66.

Fossil remains belonging to the Natricinae were reported from the Middle Pleistocene of Latomi-1, in Chios Island, by Schneider (1975), while remains of *Natrix* sp. from the Lower Pleistocene of Laghada B, Greece, and from the late Quaternary of Pili B, Greece, were reported by Szyndlar (1991b).

In addition, the fossil material comprises 480 fragmentary vertebrae, grouped under the number EM 656, probably belonging to the above taxa of the family Colubridae.

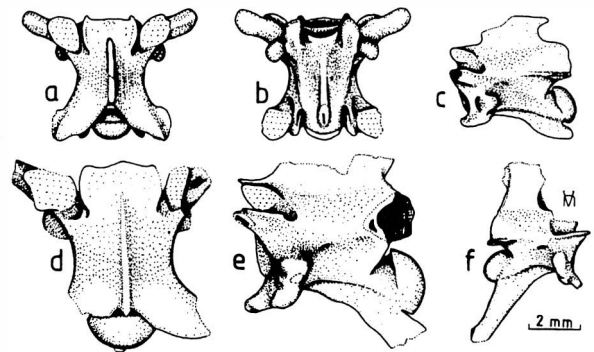


FIG. 7. Vertebrae of *Natrix* cf. *N. natrix* (a-c) and *Vipera* sp. (d-f). a, b and c: trunk vertebrae of *Natrix* cf. *N. natrix* (EM 646 and 647); d, e: trunk vertebra of *Vipera* sp. (EM 649); f: cervical vertebra of *Vipera* sp. (EM 650). a, d: dorsal; b, ventral, c, e, f: lateral views.

Family Viperidae Oppel, 1811

Genus *Vipera* Laurenti, 1768

Vipera sp.

Material. Six fragmentary vertebrae (EM 649 to 655).

The neural spine of the cervical vertebra is lacking, the hypapophysis presumably was longer than the centrum (Fig. 7f). The centrum length of the largest middle trunk vertebra is 6.4 mm, and its width is 4.68 mm. The centrum is 1.36 times longer than wide. The neural arch is flattened. In all specimens, the neural spine and the hypapophyses are lacking. The zygospheneal roof is slightly convex; in dorsal view, the anterior margin of this structure is trilobate. The pre- and postzygapophyseal articular facets are rectangle-shaped, the parapophyseal processes are oriented anteroventrally, having pointed tips (Fig. 7d, 7e).

These remains, despite their fragmentary state, but considering the absolute size of the trunk vertebrae and their relatively low centrum length/centrum width ratio, are consistent with those of the larger members of the genus *Vipera* ('Oriental vipers' group - sensu Szyndlar, 1987, 1988, 1991b).

Fossil remains belonging to this group of vipers were reported from the Middle Pleistocene of Latomi-1, Chios, by Schneider (1975). Today Anatolia is inhabited by members of both the 'lebetina' and 'xanthina' complexes of the 'Oriental vipers' (sensu Groombridge, 1986).

CONCLUSIONS

The previous studies of mammals (Sen *et al.*, 1991; Montuire, 1991; Montuire *et al.*, in press) and the present study of the herpetofauna show that the Emirkaya-2 fissure filling locality has yielded one amphibian, at least ten species of reptiles, several birds and thirty-six species of mammals. Based on the abundance of bears and beavers in this locality (Sen *et al.*,

1991), we can conclude the presence of a forested, or at least woodland, environment. However, some elements among the mammals, such as a dipodid *Allactaga* sp. and a bat *Hipposideros* sp., are indicative of high temperature and open environments (Montuire, 1991; Montuire *et al.*, in press).

The herpetofauna of Emirkaya-2, on the basis of the available fossil remains, was composed exclusively of extant genera and species, the majority of them belonging to thermophilous and xeric- adapted forms (e.g. *Pseudopus* cf. *P. apodus*, *Coluber caspius*, *Elaphe* cf. *E. quatuorlineata*, cf. *Telescopus* sp., etc.). Probably only one form, *Natrix* cf. *N. natrix*, was closely associated with aquatic environments, as are the above mentioned beavers. The anuran *Bufo viridis*, the single amphibian recognized in the fossil assemblage, is a form with a wide ecological tolerance. The herpetofauna of Emirkaya-2 only contains Palaearctic species, and it does not include an African component.

From the available data, it can be concluded that the Emirkaya-2 fauna was living in a temperate period, and its environment was partly forested with permanent water ponds.

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SHORT NOTES

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THE NUMBER OF CERVICAL VERTEBRAE IN LACERTID LIZARDS: SOME UNUSUAL CASES

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The presence, shape and size of the ribs associated with the vertebrae have constituted the most important criteria in delimiting different presacral subregions within the vertebral column of reptiles. Nevertheless, in lizards, the strong morphological variations that occur in the ribs along the first presacral vertebrae have led to the use of different criteria when defining the cervical region (see Estes, de Queiroz & Gauthier, 1988, for a discussion of this subject). Using the most common definition according to which the cervical region includes all vertebrae preceding that bearing the first rib joined to the sternum, most lizards have typically eight cervical vertebrae (Hoffstetter & Gasc, 1969). Until now, this number has been considered unvariable for a number of squamate taxa among which the lacertids are included (Hoffstetter & Gasc, 1969; Barbadillo, 1989). However, here we report two cases of lacertid lizards whose respective cervical regions, according to the definition given above, consist of only seven vertebrae. One of the specimens is a cleared and stained subadult female of *Psammotromus algirus* referred to as UAMPS038 and housed at the Unidad de Paleontología of the Universidad Autónoma de Madrid (Fig. 1). The other one corresponds to a cleared and stained adult female of *Lacerta vivipara* housed at the same collection and referred to as UAMLV057. As is the most common pattern observed in lacertids, the fourth, fifth and sixth vertebrae of both specimens bear short, relatively broad, free ribs whose size progressively increases in the caudal direction. Each of these ribs has associated distal, forked cartilages. A pair of long, free ribs with distal, single cartilages is connected to the seventh vertebra. However, the eighth vertebra bears a pair of long, thin ribs joined via cartilaginous elements to the sternum; in this way, the thoracic (=sternal) subregion extends in this specimen from the eighth to the twelfth vertebra. This means a general 'forward displacement' of the thoracic subregion with respect to the usual pattern seen in lacertids in which the thoracic subregion begins at the ninth vertebra (Hoffstetter & Gasc, 1969; Barbadillo, 1989). Although UAMPS038 and UAMLV057 represent less than the 3% of the whole

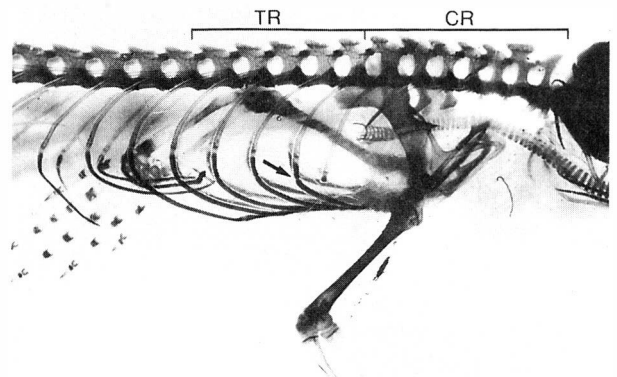


FIG. 1. Lateral view of the specimen UAMPS038 described in the text. CR: Cervical subregion; TR: Thoracic subregion. The arrow indicates the first rib joined to the sternum (see text for explanation).

sample examined for both species (*L. vivipara*: $n = 32$; *P. algirus*: $n = 36$), the interest of these kinds of phenotypic variants should not be underestimated. In lizards, similar individual deviations from the common cervical formula have been described for some geckonids and scincids (Hoffstetter & Gasc, 1969). On the other hand, in lacertids, considerable individual variability has been recorded for many other osteological traits (Barbadillo, 1989). There is clearly a need to quantify the extent of these individual variations before assigning character states to species. Moreover, a detailed study of the morphological variants shown by a given phenotypic trait, even if they represent true teratologies, can be useful in order to interpret the nature of some morphogenetic processes (Alberch, 1980).

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BOOK REVIEWS

Lacertids of the Mediterranean Region. A Biological Approach. (1993). E. D. Valakos, W. Böhme, V. Pérez-Mellado & P. Maragou (Eds.). 281 pp. Hellenic Zoological Society, Athens, Bonn, Alicante (paper).

This book is the outcome of a congress held on the Greek island of Lesbos in April 1992. Proceedings of scientific meetings typically suffer from a lack of coherence and synthesis. They offer snapshots of prevailing topics within a field, but do not present a comprehensive overall picture. Consequently, proceedings books are generally appreciated more by specialists (who attended the meeting anyway) than by laymen.

In the preface to *Lacertids of the Mediterranean Region*, the editors promise their readers a volume 'more fully integrated than a typical proceedings book'. To achieve this estimable goal, they have urged all authors to make cross-references where possible and had all contributions refereed by respected and independent herpetologists. In addition, the editors have grouped the contributed papers in three sections, each with an introductory chapter that was intended to set the stage for the chapters that follow.

The start is very promising. The first chapter, by E. N. Arnold, beautifully illustrates the revival of interest in phylogeny reconstruction, and its current uses in non-systematic areas of biology. Drawing from a rich variety of examples on lacertid features such as tail autotomy, mite pockets, hemipenis structure and sand diving, Arnold shows how estimates of phylogeny are essential to our understanding of present ecological and behavioural patterns. In a second part, he reviews classic and new methods of determining phylogenies and the difficulties encountered within the lacertid family. He concludes that, in spite of remaining uncertainties, enough is known about lacertid relationships to allow a cautious use of the comparative approach in ecomorphology, ethology and physiology; but he also stresses the need for other (non-morphological) character sources to construct a more reliable phylogenetic tree.

In four subsequent chapters, Laforgia *et al.* (comparative morphology of the adrenal gland), Odierna *et al.* (chromosome G-banding), Putti *et al.* (immunocytochemistry of the pancreas) and Olmo *et al.* (karyology) try to fulfill Arnold's call for such new character sources. The first three contributions are sequels to other papers published by these Italian research groups, presenting similar data on additional species. The fourth chapter, by E. Olmo and co-authors, offers a thorough and easy-reading review of chromosome numbers, chromosome morphology and sex chromosomes in more than 50 species of lacertids, and discusses the use of these karyological traits in the phylogeny and taxonomy of these lizards.

Pérez-Mellado and co-authors exemplify the unfinished state of lacertid taxonomy with a study on the colour pattern, body dimensions, scalation and osteology of the Iberian Rock lizard (*Lacerta monticola*). They consider the Pyrenean population to be a separate species, renaming it '*Lacerta bonnali*'.

In their chapter on zoogeography, W. Böhme and C. Corti try to correlate the phylogeny of west-Mediterranean lacertid lizards to paleogeographic events in that area, but run into strong inconsistencies and contradictions between the two data-sets.

The Lanza *et al.* chapter on geographical variation in numbers of scales and femoral pores in *Podarcis sicula* has few affinities with the other chapters of part I. However, it includes the important message that, because of the smooth clinal character of the variation, these meristic characters do not seem suitable for taxonomical purposes. The origins of the intriguing relations between the traits and latitude and temperature remain undiscussed.

The second section of the book starts with a general picture of lizard ecology by E. R. Pianka, treating such wide and extensive research topics as microhabitat use, temporal patterns of activity, thermoregulation, diet, reproductive tactics and predator escape tactics. The chapter offers little new. Most of the data and ideas presented here have been put forward a long time ago, and in a few cases can hardly be called up-to-date. In one of the last paragraphs, Pianka recognizes the power of the comparative approach in ecological studies, but then leaves the reader with the tantalizing remark that 'he plans to undertake such an analysis in the genus *Ctenotus*'. I also found it disturbing to see that many recent studies on lacertid ecology were not cited. I agree that lizard ecology has its roots in American and Australian deserts, but it would have been interesting to see how Mediterranean lizards fit into the general picture presented here.

A population of *Ophisops elegans* on Lesbos was the subject of a four-day study by Pérez-Mellado *et al.*, a study that covered the habitat, thermal, reproductive and trophic niche dimensions of this animal. The authors discovered a strong morphological and ecological similarity between this species and *Psammodromus hispanicus*, and attribute this resemblance to convergent evolution.

Three other chapters in this section focus on the trophic niche of lacertid lizards. Carretero & Llorente provide us with yet another study of the feeding habits of *Psammodromus algirus* and *Acanthodactylus erythrurus*; Chondropoulos *et al.* report on the diet of *Podarcis taurica*. These are archetypal descriptive diet studies, with numerous indices of diet breadth, overlap, dominance etc. However, since prey availability was not measured, the biological significance of all these parameters is difficult to evaluate. One might ask whether the limited insights obtained through such studies validate the enormous efforts and the killing of

so many animals. The paper by Gil *et al.* on seasonal shifts in diet composition in *A. erythrurus* illustrates how, by measuring food availability and consumption simultaneously, one can succeed in linking diet with food search strategies. The authors conclude that phylogenetic constraints in foraging behaviour strongly influence the diet of *A. erythrurus*, thus providing one of the few cross-links in this section with Arnold's chapter.

The ecology section of the book also includes two chapters by the Spanish researchers Desfilis, Font and Gomez on the behaviour of *Podarcis hispanica*. The first is an ethogram of feeding in this lizard, meticulously describing over 20 separate behavioural acts and their sequential occurrence. The second is a carefully designed experimental analysis of the role of chemoreception in exploration and the recognition of conspecifics and syntopic heterospecifics.

A note by J. Moravec on the captive breeding of two pairs of *Podarcis filfolensis* concludes this section of the book.

If the first two sections are not entirely coherent, the third is a real melting pot, with papers on thermal biology, parasitology and conservation.

In a short prospectus, R. A. Avery advocates a more 'fine-grained' approach to thermal biology, arguing that detailed observation of individual lizards will lead to a better understanding of the ecological, behavioural and physiological correlates of thermoregulation. Although I agree that such observations will generate insights into the mechanism of thermoregulation, I feel that an understanding of the evolution of thermal biology is more likely to arise from comparative studies on carefully selected species or populations. Sadly, links between Avery's and Arnold's chapter, although obviously of great potential interest, are missing completely. The effects of incubation temperature on embryo and hatchling development is another growing area of interest in thermal biology that is ignored in the prospectus.

The chapter on parasites of Mediterranean lizards by V. Roca does not provide any data. It stresses the need for a sensible selection of study animals, explains why helminth communities in island lizards are likely to be simple, and how parasites can teach us about what lizards eat and what eats them. Nothing is said about the possible role of parasites in the process of sexual selection in these lizards.

The closing chapter by A. Y. Troumbis recapitulates some problems, aims and methods of conservation biology in general and then attempts to apply some of these concepts to the situation of the European and, in specific, the Greek herpetofauna. It also discusses the use of data bases (e.g. CORINE) in reptile and amphibian conservation strategy planning.

In retrospect, I feel that the editors have only partially delivered on their opening promise. With the exception of some parts in the first section, the book

does not offer much synthesis or integration. *Lacertids of the Mediterranean Region* to me is a rather neatly edited proceedings book (although some of the chapters contain a disturbing number of typographic and linguistic errors), with some fascinating and original contributions, but it is not more than that. This is a pity: the convocation of lacertologists with various biological backgrounds seems to be a proper way to obtain a more integrative view of this interesting animal group. It was not to be. Let's wait and see whether the Proceedings of the *Second* International Congress on the Lacertids of the Mediterranean Basin will bear more mature fruits of this attempt at cross-fertilization.

Raoul Van Damme

University of Antwerp

Herpetology of China. Ermi Zhao & Kraig Adler. (1993). 522 pp. Society for the Study of Amphibians and Reptiles, Oxford, Ohio, USA (in cooperation with Chinese Society for the Study of Amphibians and Reptiles). (Contributions to Herpetology No. 10). \$60.00 (cloth).

SSAR have for many years performed a useful service to herpetology by publishing facsimile reprints of important, but otherwise unavailable, books and papers. For a decade and a half they have also produced book-length monographs. The present volume is the tenth such and is arguably the most impressive to date.

China, including Taiwan and Hong Kong, has 661 recognized species of reptile and amphibian, 308 of which are endemic. The biogeographic diversity of its 10 million square kilometres is reflected in the 34 families and 164 genera to be found within the country's borders. Affinities are often to be discerned with species occurring in other parts of Asia, Europe and North America.

Herpetology of China is the first book to comprehensively review all taxa. This is accomplished through a checklist that runs to 188 pages. For each subspecies there is a brief synonymy and an indication of world range, often with helpful additional notes. There are 33 pages of keys to major groups and genera, and 32 pages devoted to distribution within China. With 371 photographs reproduced in 48 colour plates, the size of each is obviously limited. In spite of this, the quality is mostly adequate and often very good. 330 species and all genera are illustrated, as well as representative habitats. There are six pages of maps.

There are no descriptions of species, or details of their biology, as these are beyond the intended scope of the book; one might hope to see a further volume (*Herpetofauna of China?*) at some stage. There is, however, a 49 page appendix on collecting and preserving, by John E. Simmons.

Undoubtedly, many readers will find the extensive bibliography to be the most useful part of the book. This is not intended to be comprehensive, but covers most of the material likely to be fairly readily accessible. Even so, at 106 pages, it gives an indication of the thoroughness that characterizes this book, as does the fact that indices alone take up 51 pages. Chinese Herpetological Journals are listed in an appendix.

The inclusion of a brief history of Chinese herpetology (42 pages) puts the present state of knowledge in context; it is clear that much work still remains to be done. The co-authorship, by figures of international status, emphasizes the importance of collaboration between Chinese workers and those from other countries. Travel to, from and within China is becoming less difficult, but it is sobering to observe that, as commerce also becomes easier, many animals of Chinese origin are appearing in the West via the pet trade, and that some of these seem to be of uncertain taxonomic status.

This, then, is a book for which a real need existed. It successfully provides an introduction to the herpetology of an intriguing part of the world while, at the same time, functioning as a sourcebook for current research. For years to come, it will certainly be indispensable to anyone with an interest in Chinese reptiles and amphibians, and is likely to be immensely useful to many others besides.

Leigh Gillett

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Predation and Defence Amongst Reptiles. J. L. Cloudsley-Thompson. (1993). 138 pp. Boulengerina, Taunton, England. £12.75 (paper).

For anyone with either a general or passing interest in reptiles this book is certainly worth a read. It provides a useful presentation of the physiological and behavioural adaptations which reptiles have evolved in order to secure food and to avoid becoming the food of others. As such, it clearly demonstrates the author's wide-ranging knowledge of the field and provides a useful contribution to the herpetological literature. The subject is addressed systematically and the reader is treated to a highly entertaining exposition which ranges from the predatory and escape techniques which reptiles employ, through reptilian armour and weapons, to the more weird and wonderful methods ex-

hibited by particular species, including mimicry, bluff, death-feigning and tail-shedding (autotomy). The text is profusely illustrated and packed with many interesting facts and thought-provoking observations and I particularly liked the inclusion of dinosaurs in the subject matter. It lent a fresh and attractive air to the publication. I did find myself asking questions about some areas which were not covered in depth, such as the relative advantages of the different predation and defence strategies for specialist and generalist species and the mechanisms of predator/prey population dynamics. However, these subjects are arguably outside the scope of this particular volume and indeed, my interest in them might be regarded as having been an achievement of the author in leading the reader to consider related areas.

Unfortunately, my overall assessment was somewhat clouded by the quality of production. The book seems to have been rather hurriedly put together. There are some typographical errors and a general "cut and paste" feel to the text, which although mostly fluid and accessible, is occasionally unclear or confusing. Perhaps part of the problem lies in identifying which audience the book has been pitched at. We are told that it is a non-technical summary intended for herpetologists and field naturalists and that it will also be of value to university students and research workers. Yet, there are few recent references for those who already know something of the subject and want to be brought up to date, and there is no glossary included for those who might be unfamiliar with herpetological terminology but who want a straightforward reference book.

Perhaps the most disappointing aspect of this publication relates to a number of the illustrations. A few seem rather detached from the text or somewhat superfluous, while a handful, notably some of the photographs, are of such poor quality that I was somewhat surprised to come across them at all.

Notwithstanding these criticisms, I would certainly encourage herpetologists to have a look at *Predation and Defence Amongst Reptiles*, for it is a sound introduction to the topic. However, I would have liked to have seen a rather more substantial and detailed volume on the subject. Perhaps the author will produce one for us in the near future.

Ian Bride

University of Kent

ANNOUNCEMENT

FOURTH EDITION OF THE INTERNATIONAL CODE OF ZOOLOGICAL NOMENCLATURE

The International Commission on Zoological Nomenclature proposes to publish a new edition of the Code, taking into account the large number of possible amendments which have been received. It is planned that the Fourth Edition will be published during 1995 and that on 1 January 1996 its provisions will supersede those in the current (1985) edition.

The Commission's Editorial Committee met in Hamburg from 12-16 October 1993 to prepare a discussion draft for the new edition of the Code. Copies of this draft will be sent without charge to all subscribers to the *Bulletin of Zoological Nomenclature* and to members of the American and European Associations for Zoological Nomenclature. Any other institution or individual may order a copy from the Executive Secretary, I.C.Z.N., c/o The Natural History Museum, Cromwell Road, London SW7 5BD. Bank charges on currency exchange make it uneconomic to charge the cost of printing and postage (£3 or US\$5) except for payment in sterling or US dollars. The draft will therefore be sent free of charge, but those able to pay in sterling or US dollars are asked to enclose a cheque for £3 or US\$5 to cover the cost.

Before completing the definitive text of the Fourth Edition, the Commission will (in accordance with Article 16 of its Constitution) carefully consider all comments and suggestions on the draft. Zoologists and others are asked to send these to the Executive Secretary of the Commission at the above address as soon as convenient, and in any event not later than February 1995.

***The British Herpetological Society,
c/o The Zoological Society of London,
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THE HERPETOLOGICAL JOURNAL

INSTRUCTIONS TO AUTHORS

(revised January 1992)

1. The *Herpetological Journal* publishes a range of features concerned with reptile and amphibian biology. These include: full papers (no length limit); reviews and mini-reviews (generally solicited by a member of the editorial board); short notes; controversies, under 'Forum' (details available from the Editor); and book reviews. Faunistic lists, letters and results of general surveys are not published unless they shed light on herpetological problems of wider significance.
2. Three copies of all submissions, and illustrations, should be sent to the Editor. All papers will be subject to peer review by at least two referees.
3. Authors should consult a recent issue of the Journal regarding style. Papers should be concise with the minimum number of tables and illustrations. They should be written in English and spelling should be that of the *Oxford English Dictionary*. Papers should be typed or produced on a good-quality printer (at least near-letter quality, avoid worn ribbons), and double-spaced with wide margins all round. Typesetting is greatly assisted if accepted manuscripts can be supplied on microcomputer diskettes. Authors are therefore strongly encouraged to produce manuscripts using a wordprocessor (preferably on a PC-compatible microcomputer).
4. For all papers the title page should contain only the following: title of paper; name(s) of the author(s); address of the Institution where the work was done; a running title of 5 words or less. The text of the paper should begin on page 2 and be produced in the following order: Abstract, Text, Acknowledgements, References, Appendices. Full papers and reviews should have the main text divided into sections. Short notes (generally less than six manuscript pages and accompanied by a single data set) should be produced as continuous text. The first subhead will be centred in capitals, the second shouldered in lower case, and the third run on in italics. Footnotes are not permitted.
5. The usual rules of zoological nomenclature apply.
6. Tables are numbered in arabic numerals, e.g. Table 1; they should be typed double spaced on separate sheets with a title/short explanatory paragraph underneath.
7. Line drawings and photographs are numbered in sequence in arabic numerals, e.g. Fig. 1. Colour photographs can

only be included at cost to the author. If an illustration has more than one part each should be identified as (a), (b), etc. The orientation and name of the first author should be indicated on the back. They should be supplied camera-ready for uniform reduction of one-half on A4 size paper. Line drawings should be drawn and fully labelled in Indian ink, dry-print lettering or laser printed. A metric scale must be inserted in micrographs etc. Legends for illustrations should be typed on a separate sheet.

8. References in the text should be given as in the following examples: "Smith (1964) stated —"; "—as observed by Smith & Jones (1963)." "—as previously observed (Smith, 1963; Jones, 1964; Smith & Jones, 1965)". For three or more authors, the complete reference should be given at the first mention, e.g. (Smith, Jones & Brown, 1972), and *et al.* used thereafter (Smith *et al.*, 1972). For the list of references the full title or standard abbreviations of the journal should be given. The following examples will serve to illustrate the style and presentation used by the Journal.

Bellairs, A. d'A. (1957). *Reptiles*. London: Hutchinson.

Boycott, B. B. & Robins, M. W. (1961). The care of young red-eared terrapins (*Pseudemys scripta elegans*) in the laboratory. *British Journal of Herpetology* 2, 206–210.

Dunson, W. A. (1969a). Reptilian salt glands. In *Exocrine glands*, 83–101. Botelho, S. Y., Brooks, F. P. and Shelley, W. B. (Eds). Philadelphia: University of Pennsylvania Press.

Dunson, W. A. (1969b). Electrolyte excretion by the salt gland of the Galapagos marine iguana. *American J. Physiol.* 216, 995–1002.

9. Final acceptance of a paper will depend upon the production by the author of a typescript and illustrations ready for the press. However, every assistance will be given to amateur herpetologists to prepare papers for publication.
10. Proofs should be returned to the Editor by return of post. Alterations should be kept to the correction of errors; more extensive alterations will be charged to the author.
11. Twenty-five offprints and one complimentary copy of the Journal are provided free of charge. Further copies (minimum of twenty-five) may be purchased provided that they are ordered at the time the proofs are returned.
12. All submissions are liable to assessment by the editorial board for ethical considerations, and publication may be refused on the recommendation of this committee. Contributors may therefore need to justify killing or the use of other animal procedures, if these have been involved in the execution of the work.

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