The HERPETOLOGICAL BULLETIN

Number 103 – Spring 2008

PUBLISHED BY THE

BRITISH HERPETOLOGICAL SOCIETY

THE HERPETOLOGICAL BULLETIN

The Herpetological Bulletin is produced quarterly and publishes, in English, a range of articles concerned with herpetology. These include full-length papers of mostly a semi-technical nature, book reviews, letters from readers, society news, and other items of general herpetological interest. Emphasis is placed on natural history, conservation, captive breeding and husbandry, veterinary and behavioural aspects. Articles reporting the results of experimental research, descriptions of new taxa, or taxonomic revisions should be submitted to *The Herpetological Journal* (see inside back cover for Editor's address).

ISSN 1473-0928

Printed by: Bruce Clark (Printers), Units 7-8, Marybank Lane, Dundee, DD2 3DY.

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Front cover illustrations. © Anna Perera. *Bufo mauritanicus* from Moussa, northern Morocco. Photographed as found in an agriculture field. See article on page 19.

The eccentric Adder man: a note on the life and works of Albert Franz Theodor Reuss (1879-1958)

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ABSTRACT – The paper gives a short overview of the life and publicist activity of one of the most debated personalities in the history of Viperidae systematics and nomenclature, the amateur German herpetologist Albert Franz Theodor Reuss, who became rather notorious for the unusual names given to the dozens of new, scientifically ungrounded taxa he described during the period 1923–1939. We present a short biography of Reuss, and discuss his entomological activity (both the scientific one especially focused on Lepidoptera, and his activity as a butterfly dealer) and give a short description of his entomological works and other publications on entomological topics published in aquarist and terrarium keeping journals. Reuss's activity in the Group *Lacerta-Gesellschaft für Terrarienkunde*, based in Berlin, is discussed and remarks are made on his habit of presenting live vipers at the group meetings, as well his excentric lifestyle. We comment on the names of Reuss, his strange ideas about systematics in the light of the numerous published critiques, and give an account of papers with herpetological content.

ONE of the most debated personalities in Viperidae systematics and nomenclature is the amateur German herpetologist Albert Franz Theodor Reuss (Fig. 1). He is known for the unusual names given to the dozens of new, scientifically unfounded taxa he described in the period 1923–1939. For a complete list of the names and type specimens by designated by Reuss see Krecsák (2007).

Despite the fact that he published many papers, held several presentations and was actively engaged in terrarium keeping, all that is known about Reuss are the few works, which have been included in lists of synonymy (e.g. Schwarz, 1936) as they contained descriptions of numerous taxa of Viperidae. The recent monographic publication "*Die Geschichte der Herpetologie und Terrarienkunde im deutschsprachigen Raum...*" dealing with the history of German herpetology and terrarium keeping contains only a few sentences about him by Günther (2001).

The purpose of this note is to fulfill this gap, and contribute some further details about the life and activities of Reuss. We also give an account of his papers with herpetological content, together with a short description of his entomological publications and works on entomological topics published in aquarist and terrarium keeping journals.

Biography

Reuss was born on 23rd May 1879 in Munich, as the son of Delphina Garbois from Dublin, and the famous tantric occultist and head of Ordo Templi Orientis Albert Karl Theodor Reuss (1855–1923). His parents married in Ireland in 1876. His father was 21 at that time, and his bigamist mother 31 (Hergemöller, 1998). In 1878 Delphina Garbois settled in München. Their marriage was annulled in the same year by the German court (Hergemöller, 1998), most probably due to the bigamy. Hergemöller (1998) mentioned that their son was born, and named "Franz Albrecht Theodor". Albrecht is most probably a misspelling, as according to tradition the son received the name of the father (i.e. Albert).

Reuss lived and worked in Berlin. It is not known whether he ever had a stable position at an institution or company. All we have been able to ascertain is that he earned money by selling snake venom (Anonymous, 1949; Schnurre, 1948, 1956) and butterflies. Additional income may have perhaps been received from his presentations given at different group meetings dealing with terrarium and aquarium keeping. We should note that Reuss was also a talented painter. Probably his snakes were the subjects of most of his works (Fig.

Figure 1. *"The snake researcher during work. The zoologist Th. Reuss by the study of one of his captive bred snakes (sand viper). "* Cover of nr. 18 of the journal *Die Weite Welt, Verlag Scherl, Berlin* published on 29. April 1928 (source Museum für Naturkunde der Humboldt-Universität zu Berlin Historische Bild- u. Schriftgutsammlungen B I/328).

2). He never attended a university, but was – as he himself declared – "self-educated" (Anonymous, 1949; Schnurre, 1956; Günther, 2001).

Certain details of his life and eccentric habits (see discussion below) are known from two newspaper articles published by Wolf-Dietrich Schnurre, who referrede to him either as "Mr. T." (Schnurre, 1948) or "Mr. Webb" (Schnurre, 1956). Schnurre knew Reuss through his father. From the accounts related by his father, Schnurre found out that Reuss had to change apartments very often, as the landlords always sent him away as soon as they found out that he keeps numerous venomous snakes.

Schnurre (1956) wrote that Reuss committed suicide after the second World War, after his appartment was bombed and his snakes were killed. He was misinformed, as after this incident Reuss built up a new collection with various reptiles (Anonymus 1949). He died on 24th December 1958 in Berlin.

Publications and entomological activity

Reuss was firstly an amateur interested in Lepidoptera (see Fig. 3 showing him with an insect net) and only dealt with vipers afterwards. His first entomological paper was published most probably in 1919, whereas the first paper about Adders was printed in 1923. Reuss published almost as much about different groups of Lepidoptera as about Viperidae, both in German and English. A quick survey of the Zoological Record covering the period 1919–1939 showed that he published 34 papers in various small, German, entomological journals. The number of entomological papers written is most probably much higher as Zoological Record did not contain all printed journals. The general working method with Lepidoptera was similar to the one used on reptiles (or most probably the working method used with Lepidoptera was adapted later to his works on Viperidae), describing as many new genera, species, subspecies and forms as possible. For a small extract from his entomological papers with selected titles see Appendix 1. His works on entomological topics published in terrarium keeping journals are listed in Appendix 2.

We should note that Reuss was a butterfly dealer as well and probably sold butterflies collected in Germany, mostly to museums. The Zoological Museum of the Humboldt University, Berlin houses several butterfly drawers with specimens supplied by him, with purchases documented by letters in the archive of the institution as well (pers. obs.).

At the beginning of the 1900's many small groups dealing with terrarium and aquarium keeping had been established in Germany, with participation of mostly amateur pet keepers (Rieck, 2001a, 2001b). This resulted in an increase in the number of journals that were published, and proved to be a good opportunity for Reuss, who was able to publish all of his doubtful results and long papers containing his strange ideas about systematics and nomenclature (e.g. Reuss, 1937). During his publishing activity he produced at least 121 papers, short notes and reviews on herpetological topics. A complete list of his publications dealing with different herpetological questions can be found in Appendix 3. For an unknown reason he also published using the pseudonym S.A. Sure (e.g. Sure, 1926).

Participation in terrarium keeping

As noted above, in the 1900's the number of German groups dealing with terraria and aquaria was high. Reuss was especially active in the Group *Lacerta-Gesellschaft für Terrarienkunde*, based in Berlin, where he held most of his presentations and also first showed his captive animals, most of which he described later as new. He also visited other Berlin-based groups, such as: *Ludwigia*, *Nymphaea alba*, *Humboldtrose*, *Triton* and *Salamandra*. In addition to presenting the newest specimens of his snake collection at these meetings, he was famous for handling vipers with his bare hands. Due to this strange behaviour he was banned from the group "*Triton*" in Berlin (Rieck, pers. comm.).

However, he became the leader of *Lacerta* in the summer or autumn of 1935. Reuss changed the business address of the group to his home and also its name, to *Lacerta- Interessengemeinschaft für Vivographie* (Reuss, 1935b). The name *Vivographie* (description of the life in words and figures, but especially figures) was promoted by the journal "*Das Aquarium-Eine Zeitschrift mit Bildern für Liebhaber, Schulen und Naturfreunde*" edited by Dr. Ernst Ahl, curator of the herpetological collection in the Museum für Naturkunde Berlin, much appreciated and admired by Reuss. It seems that his enthusiasm for this name did not last long. After one month, in Nr. 37 of the *Nachrichtenblatt für Aquarien- und Terrarien-Vereine*, published on 28th November, he wrote that this imperfect name will be used only until 1st January 1936 (Reuss, 1935c). But in December 1935 the newsletter of the group was published under the name *IFB. (Lacerta)-Interessengemeinschaft für Biographie* (Reuss, 1935d), and from 1936 under a new name *IFB. (Lacerta)-Interessengemeinschaft für Biologie und biologische Berichterstattung* (Reuss, 1936).

Reuss probably remained the leader of the group until it was dissolved in the late 1930's due to the enforced conformity of all groups to the *RDA* (*Reichsbund Deutscher Aquarien- und Terrarienvereine*) which they obviously did not want to be a part of (Rieck, 2001b).

Strange habits

In the following discussion we list certain incidents to illustrate the eccentric lifestyle of Reuss. Generally he seems to have been careless

Figure 2. Aquarelle depicting two adders probably from Serbia (source Ralph Graubaum).

whilst handling snakes. Already in 1929 (Reuss, 1929a) had been bitten 12 times, and probably suffered other accidents after this year. Even these incidents did not stop him from handling very poisonous snakes, like *Daboia russelli*, with bare hands (Fig. 4). According to Schnurre (1948, 1956), he was never seriously injured; the first aid he applied when in the field with no supply of antiserum was to cut the bitten area with a knife and additionally consume huge amounts of alcohol. We also know from Schnurre's (1956) description that he used to carry his captured vipers in paper bags. These careless behaviours lead to long documented denunciations, summons, arrests and delinquency procedures.

One of the well known incidents involving an Adder was on 1st July 1928, in the Restaurant

Figure 3. Postcard showing Reuss in the field, in the area of Munich (source Deutsches Entomologisches Institut Pslg. 3330).

Figure 4. Picture made in the post war years, showing Reuss posing with a *Daboia russelli* (source Werner Rieck).

"Rotkäppchen" in Heiligensee, Berlin, when a fourteen year-old girl was bitten and severly injured (Schnurre, 1948; Anonymous, 2002). Reuss carried two Serbian Adders (*Vipera berus*) with him in a paper bag, and put one of the snakes on the girl's lap to photograph her (Fig. 5), which later lead to the accident.

Reuss spent three months in jail after another incident, similar to the previous, in another restaurant in Berlin. At this time he had a Black mamba (*Dendroaspis polylepis*) with him, which escaped from the paper bag in which Reuss left it together with his coat in the cloakroom (Schnurre, 1948, 1956). Luckily no-one was bitten.

Schnurre (1948) reports, that during a visit to Reuss' appartment, he was told that snakes often escape from the insecure terraria. One morning Reuss woke up with a Sand viper (*Vipera ammodytes*) under his stomach, and he had to lie motionless for hours until the snake crawled away. Interestingly, he did not repair the doors of the terraria, but learned to sleep on one side and motionless.

His captive venomous snakes did not only escape in the apartment, but some managed to find their way outside into the streets. In 1949 one of the local newspapers (*Berliner Zeitung*) reports of a Adder bite (Anonymous, 1949): a child got bitten by an individual that escaped from Reuss' home. After the incident all of his snakes were taken away by a film company. The letter featured in Figure 6 was issued by the local police department 25 days after the incident. The police warn Reuss that for the keeping of venomous snakes he needs approval from the police, which he did not have, and is expected from his to keep away from such troubles, or he will be arrested.

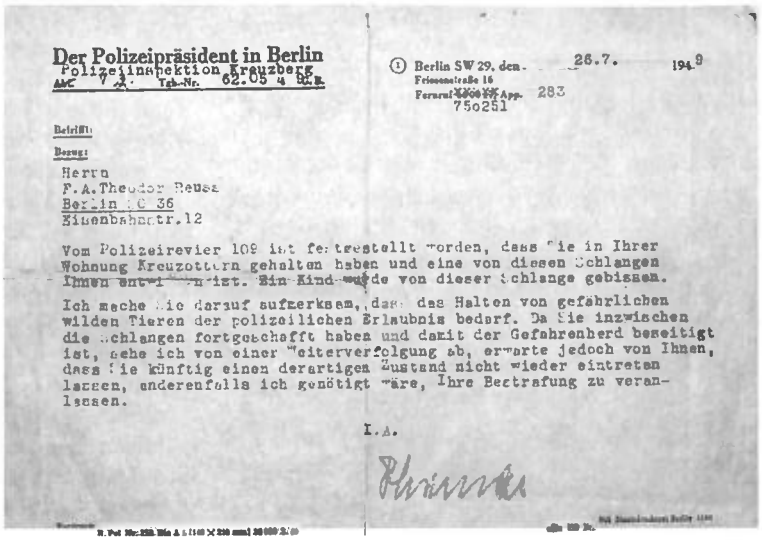
Figure 5. The girl who suffered the accident. Photograph taken before the bite (source Ralph Graubaum).

The Reuss names and his ideas about systematics

Reuss, who was named (or named himself) the well known viper (or snake) researcher and specialist (e.g. Randow, 1924; Reuss, 1935a; Reuss, 1937), had some really strange ideas about systematics and nomenclature. He was especially interested in the local variation of the Adder (*Vipera berus*) and dealt with "elementary species" (Reuss, 1925). We can define his species concept as the individual species concept, according to which each individual is a new taxon. A good example represents the nine forms (*Vipera* (*Pelias*) *berus brunneomarcata* Reuss, 1923 (nomen corrigendum Krecsák, 2007), *Vipera* (*Pelias*) *berus ochraceaasymmetrica* Reuss, 1923 (nomen corrigendum Krecsák, 2007), *Vipera* (*Pelias*) *berus luteoalba* Reuss, 1923 (nomen corrigendum Krecsák, 2007), *Vipera* (*Pelias*) *berus luteachersea* Reuss, 1923 (nomen corrigendum Krecsák, 2007), *Vipera* (*Pelias*) *berus rudolphimarchica* Reuss, 1924 (nomen corrigendum Krecsák, 2007), *Vipera* (*Pelias*) *berus cherseasplendens* Reuss, 1925 (nomen corrigendum Krecsák, 2007), *Vipera* (*Pelias*) *berus rutila* Reuss, 1925 (nomen corrigendum Krecsák, 2007), *Pelias marchici* Reuss, 1930, *Pelias flavescens* Reuss, 1938), all in the synonymy of *Vipera berus*, he described just from the area of Berlin (Krecsák, 2007).

We can state without any doubt that his system was really chaotic. Being 'self-educated' from Berlin (Günther, 2001) he did not care about the general rules of nomenclature, thus he used names from works unvalidated by the *International Commission on Zoological Nomenclature*, or did not follow binominal nomenclature when naming new taxa.

His names are also one of a kind. Reuss was actually a pet keeper and probably named all of his animals, names that he later used when describing these individuals as new taxa. A good example of it can be found in Reuss (1924): "Reddish ♀, captured in Mark Brandenburg IV.1923, Name: "Ruthela"...., Reddish ♀ captured in Mark Brandenburg VIII.1923, Name: "Chersea splendens....". The two specimens were described by Reuss as *Vipera* (*Pelias*) *berus rutila* Reuss, 1925 (nomen corrigendum Krecsák, 2007) respectively *Vipera* (*Pelias*) *berus cherseasplendens* Reuss, 1925 (nomen corrigendum Krecsák, 2007).



Der Polizeipräsident in Berlin
Polizeiinspektion Kreuzberg

① Berlin SW 29, den 26.7. 194.9
Friesenstraße 16
Fernruf [illegible] App. 283
750251

Betrifft:

Bezug:

Herrn
F.A.Theodor Reuss
Berlin [illegible] 36
Eisenbahnstr.12

Vom Polizeirevier 109 ist festgestellt worden, dass Sie in Ihrer Wohnung Kreuzotttern gehalten haben und eine von diesen Schlangen Ihnen entwichen ist. Ein Kind wurde von dieser Schlange gebissen.

Ich mache Sie darauf aufmerksam, dass das Halten von gefährlichen wilden Tieren der polizeilichen Erlaubnis bedarf. Da Sie inzwischen die Schlangen fortgeschafft haben und damit der Gefahrenherd beseitigt ist, sehe ich von einer Weiterverfolgung ab, erwarte jedoch von Ihnen, dass Sie künftig einen derartigen Zustand nicht wieder eintreten lassen, andernfalls ich genötigt wäre, Ihre Bestrafung zu veranlassen.

I.A.

Figure 6. Summons issued by the Berlin police department following the accident from 1949 (source Ralph Graubaum).

The unusual working methods and strange names were criticized ever since his first papers were published (Anonymous, 1925; Lankes, 1925a, 1925b). One of his most criticized papers was "*Canis familiaris* var. *catus* Linné" (Reuss, 1929b) (Müller, 1929a, 1929b, 1930a, 1930b, 1930c; Werner, 1930), especially because he used the well known, old name *Vipera berus bosniensis* Boettger, 1889 (in the text *Mesocoronis bosniensis*) with the indication to the descriptor "(Boettger, 1888) Werner & T. Reuss", and additionally for the criticism written of Schreiber's *Herpetologia europaea* (Schreiber 1912). In 1929 Müller (1929a: 355) wrote: "Such a venture is almost childish and we believe that neither a scientist nor another serious amateur will contradict us, if we give expression to the conviction that the name Schreiber will still be mentioned for a long time with reverence, when Mr. Reuss will long be forgotten.". It seems that Müller was wrong; the name Reuss is still known but mainly for the chaos and introduction of new names leading to page-long lists of synonyms (eg. Schwarz, 1936; McDiarmid *et al.*, 1999; Krecsák, 2007). Another paper, "*Europäische Giftschlangen...*" (Reuss, 1935a), raised severe criticism as well (Stucken, 1935; Werner, 1937), especially for the *Vipera berus bosniensis* name as mentioned above. Stuchen (1935) even pointed out that an editor of journals of the Third Reich has the duty to publish true and correct information and thus not to accept papers like this one by Reuss.

Only three names by Reuss have been resurrected, *Macrovipera* Reuss, 1927, *Acridophaga* Reuss, 1927 and *Vipera eriwanensis* Reuss, 1933. Krecsák (2007) pointed at, that most of his names are taxonomically unfounded and thus should be used with caution. However, the true identity of some names were to be ascertained with confidence; these are available and have a nomenclatural existence (Krecsák, 2007).

Probably Reuss could have been a talented and perhaps even appreciated zoologist if he had followed the rules of nomenclature and adopted a different attitude towards the publications of other researchers. He was well informed, and read probably most of the papers published, but for an unknown reason, he never or very rarely accepted their results.

ACKNOWLEDGEMENTS

We are indebted to many people who provided literature or additional information about Reuss. They are: Åhlander E., Dr. Böhme W., Dr. Cabela A., Dr. Glaw F., Dr. Günther R., Dr. Hallermann J., Dr. Kullander S., Dr. Tiedemann F., Franzen M., Gemel R., Graubaum R., Hill J., Himmel T., Kotrošan D., Kroniger M., Otte N., Rieck W., Schleip W., Stöckli E., Winkler R. The photographs have been provided by Dr. Landsberg H., Dr. Groll E., Kutzscher C., Grauboum R. and Rieck W. Most of the papers by Reuss have been found during research visits by LK to the Natural History Museum in Vienna, Swedish Museum of Natural History, Stockholm and Zoological Museum of the Humboldt University, Berlin. Visits were financially supported through SYNTHESYS funding, which was made available by the European Community-Research Infrastructure Action under the FP6 "Structuring the European Research Area" Programme (projects AT-TAF 566, SE-TAF-462 and DE-TAF-1014). Published material was also obtained from the Berlin State Library. The comment of David Bird (Dorset, UK) highly improved the manuscript.

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Stucken (1935). No title (Rundschau des Vereinslebens-München. "Isis", Gesellschaft für biologische Aquarien- und Terrarienkunde). *Bl. Aqu.-Terr. Kd.* **6**, 141–142.

Sure, S.A. (1926). Neue Giftschlangen. *Scherl's Mag. Berlin* **2**(5), 447–451.

Werner, F. (1930). Über *Vipera* (*Mesocoronis*) *bosnensis* Wern. u. T.Reuss. *Zool. Anz.* **88**(1/4), 89–92.

Werner, R. M. (1937). No title (Vereinsberichte-Kreisleitung Sachsen im BDV.). *Nachr. Bl. Aqu. Terr:-Ver.* **4**, 46–47.

Appendix 1. Selected titles from entomological papers by Theodor Reuss.

Reuss, T. (1922). Eine Androconialform von *Argynnis niobe* L., f.n., und durch entsprechende gekennzeichnete ostasiatische Formen oder Arten, die bisher zu *adippe* L. (rect. *cydippe* L.) gerechnet wurden, sich aber nunmehr durch Art und Verteilung der Androconien abtrennen lassen. Mit einer Revision des Genus *Argynnis* F. *Arch. Naturgesch.*, Berlin, A, **87**(11), 180–230.

Reuss, T. (1922). *Fabriciana* (*Argynnis* part.) taliana *stoetzneri* m. nov. subspez. *Int. ent. Z.* **16**, 110–111.

Reuss, T. (1928). Die *Argyreidae* T.Rss., fam. nov. *Int. ent. Z.* **14**, 145–146.

Reuss, F.A.T. (1936). Einige Aufzeichnungen über die Biologie von *Colias rhammi* (Linné) in der Mark Brandenburg. Mit eine vergleichenden Neubeschreibung der Raupen von *C. rhammi* und *Anthocharis cardamines* (L.) im fünften Stadium und anderen kritischen Vergleichen. *Ent. Z.* **50**, 325–329.

Reuss, F.A.T. (1936). Zwei Prioritätsnamen bei Arten der *Argyreidae* (=*Argynnis*, *Brenthis*, etc., auctorum) und Revision von 4 Gattungsnamen derselben Familie (vgl. I.E.Z. Guben, 22 Jg. 1928, Nr. 14, S. 145). *Ent. Z.* **50**, 373–375.

Appendix 2. Papers on entomological topics published in terrarium keeping journals (*NATV* = *Nachrichtenblatt für Aquarien- und Terrarien-Vereine, Berlin*).

Reuss, T. (1934). Originalbericht. (Vereinsnberichte-"Lacerta", Berlin.). *NATV* **4**, 40–41.

Reuss, F.A.T. (1935). No title (Vereinsberichte-"Lacerta", Berlin.) *NATV* **34**, 434–435.

Reuss, F.A.T. (1935). No title (Vereinsberichte-"Lacerta", Berlin.) *NATV* **36**, 463.

Appendix 3. Herpetological works by Reuss. (Abbreviations: *BATK = Blätter für Aquarien- und Terrarienkunde, Winnenden-Stuttgart, DA = Das Aquarium, Die Fachzeitschrift des Naturfreundes, Berlin, DAAT = Deutscher Almanach für Aquarien- und Terrarienfreunde, Verlag "Das Aquarium", Berlin, DK = Die Koralle. Magazin für alle Freunde von Natur und Technik, Berlin, DN = Der Naturforscher, Berlin-Lichterfelde, LZV = Lacerta. Zeitschrift für Vivarienkunde, Berlin, NATV = Nachrichtenblatt für Aquarien- und Terrarien-Vereine, Berlin, WATK = Wochenschrift für Aquarien- und Terrarienkunde, Braunschweig, ZATV = Zeitschrift für Aquarien- und Terrarien- Vereine, Berlin*).

Reuss, T. (1923). Systematische Beobachtungen an *Vipera* (*Pelias*) *berus* L. in Gefangenschaft. I. Paarung und Zucht; Vererbung asymmetrischer Kopfzeichnung. II. Kämpfe der Ottern, Tänze und Liebeswerbungen. Das Signum der Weibchen. *WATK* 19, 295–296.

Reuss, T. (1924). No titel (Rundschau des Vereinslebens-Die Gesellschaft für Biologie in Berlin). *BATK* **5**, 124–125.

Reuss, T. (1924). Notizen über *Psammophis sibilians* L. (Männchen) in Gefangenschaft. *WATK* **12**, 278–279.

Reuss, T. (1924). No titel (Rundschau des Vereinslebens-Die Gesellschaft für Biologie in Berlin). *WATK* **7**, 187.

Reuss, T. (1924). Systematische Beobachtungen an *Vipera* (*Pelias*) *berus* L. II. Eine neue Mutation der Kreuzotter aus der Mark Brandenburg. *WATK* **25**, 545–547.

Reuss, T. (1924). No title – presentation (Vereinsnachrichten-Berlin. "Lacerta".). *WATK* **25**, 553–554.

Reuss, T. (1924). No title (Vereinsnachrichten-Berlin. "Lacerta".). *WATK* **30**, 652.

Reuss, T. (1924). Systematische Beobachtungen an *Vipera* (*Pelias*) *berus* L. IIa. Eine neue gestreifte Abberation von *Vipera* (*Pelias*) *berus* L. III. "Temperaturformen" der Kreuzotter. *WATK* **31**, 665–666.

Reuss, T. (1924). No title (Rundschau des Vereinslebens-Berlin. "Lacerta".). *BATK* **11**, 313.

Reuss, T. (1924). Announcement of the presentation "*Einheimische Giftschlangen*". (Vereinsnachrichten-Berlin. "Nymphaea alba"). *WATK* **34**, 722.

Reuss, T. (1924). Presentation-*Vorführen verschiedener Giftschlangen* (Vereinsnachrichten-Berlin. "Lacerta"). *WATK* **35**, 747.

Reuss, T. (1924). Presentation-*Etwas über Giftschlangen* (Vereinsnachrichten-Berlin. "Ludwigia"). *WATK* **35**, 747–748.

Reuss, T. (1924). Presentation-*Einheimische Giftschlangen*. (Vereinsnachrichten-Berlin. "Nymphaea alba"). *WATK* **36**, 762.

Reuss, T. (1924). No title – presentation (Vereinsnachrichten-Berlin. "Lacerta".). *WATK* **39**, 820–821.

Reuss, T. (1925). No title (Vereinsnachrichten-Berlin. "Lacerta".). *WATK* **3**, 44–45.

Reuss, T. (1925). Presentation-*Die Biologie im allgemeinen und Giftschlangen im besonderen*. (Vereinsnachrichten-Berlin. "Lacerta".). *WATK* 7, 123.

Reuss, T. (1925). Ergebnisse der Pflege von *Crotalus horridus* L. *WATK* **11**, 193.

Reuss, T. (1925). Zahme Giftschlangen. *Der Stein des Weisen, Ill. Z Verbr. volkstüml. Wiss. Berlin* **2**(9), 201–203.

Reuss, Th. (1925). Systematische Beobachtungen an *Vipera* (*Pelias*) *berus* L. IV. Ergänzungen zu den früheren Abschnitten II und II a, Berichtigungen und Erwiderungen. *WATK* **19**, 341–342.

Reuss, T. (1925). Vergleichende Beobachtungen an einigen Giftschlangen. *BATK* **8**, 211–215.

Reuss, T. (1925). V. Systematische Beobachtungen an *Vipera* (*Pelias*) *berus* L. II b. Eine neue Varietät der Kreuzotter aus Sachsen. *WATK* **26**, 455.

Reuss, T. (1925). No title (Vereinsnachrichten-Berlin. "Lacerta".). *WATK* **26**, 459–460.

Reuss, T. (1925). No title (Vereinsnachrichten-Berlin. "Lacerta".). *WATK* **28**, 495.

Reuss, T. (1925). No title-presentation (Vereinsnachrichten-Berlin. "Lacerta".). *WATK* **36**, 615.

Reuss, T. (1925). No title (Vereinsnachrichten-Berlin. "Gesellschaft für Biologie"). *WATK* **41**, 691.

Reuss, T. (1925). Presentation-*Lautäußerungen bei Schlangen* (Vereinsnachrichten-Berlin. "Lacerta".). *WATK* **43**, 720–721.

Reuss, T. (1925). Die Coronis-Viper. Eine neue Giftschlangen Südost-Europas. *DK* **7**, 80–84.

Reuss, T. (1925). No title – presentation (Vereinsnachrichten-Berlin. "Humboldtrose"). *WATK* **44**, 738.

Reuss, T. (1925). No title (Rundschau des Vereinslebens-Berlin. "Lacerta".). *BATK* 18 , 498–499.

Reuss, T. (1925). No title (Vereinsnachrichten-Berlin. "Lacerta"). *WATK* **46**, 767–768.

Reuss, T. (1925). No title (Vereinsnachrichten-Berlin. "Triton"). *WATK* **46**, 768–769.

Reuss, T. (1925). No title (Vereinsnachrichten-Berlin. "Lacerta"). *WATK* **51**, 84–85.

Reuss, Th. (1925). Die Halsbandkreuzotter. Ein Beitrag zur Widerlegung alter Vorurteile und zur Aufklärung über Ottern und Nattern. *LZV* **3**, 11–12.

Reuss, Th. (1925). Vorläufige Notizen über eine interessante Dämmerungsschlange. *LZV* **4**, 14–15.

Reuss, T. (1925). V. systematische Beobachtungen an *Vipera berus* L. II c. Ueber die Abtrennung der *Vipera* (*Pelias*) *coronis* T. Rss., sp. nov. *LZV* **7**, 26–28.

Reuss, T. (1925). Über Kreuzottern oder Berusvipern. *DN* (1925/1926) 9, 469–471 + Pl. 67–68.

Reuss, T. (1926). No titel (Rundschau des Vereinslebens- "Lacerta", Berlin). *BATK* **1**, 26.

Reuss, T. (1926). Balzkämpfe der Kreuzottern. *DK* 1(12), 42–49.

Reuss, T. (1926). No title (Vereinsnachrichten-Berlin. "Lacerta"). *WATK* **17**, 257–258.

Sure, S.A. (1926). Neue Giftschlangen. *Scherl's Mag. Berlin* **2**(5), 447–451.

Reuss, T. (1926). No title (Vereinsnachrichten-Berlin. "Lacerta"). *WATK* **23**, 344–345.

Reuss, T. (1926). No titel (Rundschau des Vereinslebens-Berlin. Triton E.V.). *BATK* **13**, 336.

Reuss, T. (1926). No title (Vereinsnachrichten-Berlin. Triton E.V.). *WATK* **25**, 392.

Reuss, T. (1926). No title (Vereinsnachrichten-Berlin. "Lacerta"). *WATK* **36**, 541–544.

Reuss, T. (1927). Über vermutliche Stammformen der europäischen Vipern in Südosteuropa. *DN* **3**, 639–642 + Pls. 89–90.

Reuss, T. (1927). Beschreibung neuer Vipern aus Jugoslawien. *Zool. Anz.* 71(9/10),215–223.

Reuss, T. (1927). Sechs europäische Giftschlangengattungen. *Zool. Anz.* 73(5/8), 124–129.

Reuss, T. (1927). Vergleichende Bilder alter und neuer europäischer Giftschlangen. *DN* 4, 127–129+Pls. 20–21.

Reuss, T. (1928). Ottern=Speisezettel. *Scherl's Mag. Berlin* September, 1036–1037.

Reuss, T. (1928). Ueber die toxo-serologische Bedeutung der Gattungs- und Artenkunde bei europäischen Viperinen. *WATK* 39, 560–561.

Reuss, T. (1928). No title (Vereinsnachrichten-Berlin. "Lacerta"). *WATK* **40**, 580–581.

Reuss, T. (1928). No title (Vereinsnachrichten-Berlin. "Lacerta"). *WATK* **50**, 723.

Reuss, T. (1929). No title (Vereinsnachrichten-"Lacerta".). *WATK* **5**, 64.

Reuss, T. (1929). No title (Vereinsnberichte-"Lacerta", Berlin). *NATK* **1**, 5.

Reuss, T. (1929). No title (Vereinsnachrichten-"Lacerta"). *WATK* **13**, 192.

Reuss, T. (1929). "*Canis familiaris* var. *catus* Linné". *WATK* **15**, 217–220; **16**, 235–237.

Reuss, T. (1929). Schlangengift-ein Verjüngungsmittel? *Köln. Ill. Z. Köln* 12.I.1929, 2, 37, 43.

Reuss, T. (1929). No title (Vereinsnachrichten-Berlin. "Lacerta"). *WATK* **23**, 349.

Reuss, T. (1930). Ueber die Wirkung des mit "Aspis"- und "Berus"-Toxinen hergestellten Schlangenserums, Marke ER, Paris, bei Otternbissen in Deutschland. *Münch. Med. Wschr.* **77**(20), 845–846.

Reuss, T. (1930). No title (Vereinsnachrichten-Berlin. "Lacerta"). *WATK* **18**, 296–297.

Reuss, T. (1930). No title – presentation (Vereinsnachrichten-Berlin. "Lacerta"). *WATK* **24**, 397–398.

Sure, S. A. (1930). Bisse von Giftschlangen. Gibt e seine Immunität gegen den Biss von Giftschlangen? Unidentified journal *Stuttgart*, Juli, 235–244.

Sure, S. A. (1930). Jagd auf Kreuzottern. *Die Neue Welt* **25**, 6.

Reuss, T. (1930). Über eine neurotoxische Otterngruppe Europas, *Mesocoronis* 1927, und über ihre Stellung unter den Solenoglyphen der Welt. *Glasnik Zemalsk. Mus. Bosn. Hercegov.* **42**, 57–114 + 3 tables, 1 map, 6 plates.

Reuss, T. (1931). Does venom affect plants? *Bull. Antiv. Inst. Am. Philadelphia* 4(4), 109.

Reuss, T. (1931). No title (Vereinsnberichte-"Lacerta", Berlin). *NATV* 21, 3.

Reuss, T. (1932). No title (Vereinsnberichte-"Lacerta", Gesellschaft für Terrarienkunde. Berlin). *NATV* 4, 4–5.

Reuss, T. (1932). No title (Vereinsnberichte-"Lacerta", Berlin). *NATV* **15**, 4–5.

Reuss, F. A. T. (1932). Ueber zoologische und serontoikologische Schwierigkeiten in der modernen Giftschlangenforschung. *NATV* **19**, 3–4.

Reuss, T. (1933). No title (Vereinsnberichte-"Lacerta", Berlin). *NATV* **5**, 47.

Reuss, T. (1933). No title (Vereinsnberichte-"Lacerta", Berlin). *NATV* **8**, 98–99.

Reuss, T. (1933). No title (Vereinsnberichte-"Lacerta", Berlin). *NATV* **14**, 191.

Reuss, T. (1933). Announcement of the presentation "*Die Wissenschaft in unserer neuen Zeit*" (Vereinsnberichte-"Lacerta", Berlin). *NATV* **16**, 229.

Reuss, T. (1933). No title (Vereinsnberichte-Berlin. "Lacerta".). *NATV* **18**, 267–268. (Anonymous (1933). No title (Druckfehlerberichtigung und andere Korecturen zu dem "Lacerta"-Bericht in "Nachrichtenblatt" Nr. 18 und dessen Fortsetzung in Nr. 19, S. 283/84 1933.) (Vereinsnberichte-Berlin. "Lacerta".). *NATV* 20, 296.)

Reuss, T. (1933). No title (Vereinsnberichte-"Lacerta", Berlin.). *NATV* **19**, 283–284. (Anonymous (1933). No title (Druckfehlerberichtigung und andere Korecturen zu dem "Lacerta"-Bericht in "Nachrichtenblatt" Nr. 18 und dessen Fortsetzung in Nr. 19, S. 283/84 1933.) (Vereinsnberichte-Berlin. "Lacerta"). *NATV* **20**, 296.)

Reuss, T. (1933). No title (Vereinsnberichte-"Lacerta", Berlin). *NATV* **22**, 321.

Reuss, T. (1933). Originalberichte. (Vereinsnberichte-"Lacerta", Berlin.). *NATV* **24**, 349. (Anonymous (1933). Druckfehler-Berichtigung zum Lacerta-Bericht in Nr. 24, Seite 349. (under Vereinsnberichte-Berlin. "Lacerta"). *NATV* **25**, 361.)

Reuss, T. (1933). Fortsetzung der Originalberichte. (Vereinsnberichte-"Lacerta", Berlin). *NATV* **25**, 360–361.

Reuss, T. (1933). Fortsetzung und Schluss der Originalberichte. (Vereinsnberichte-"Lacerta", Berlin). *NATV* **26**, 372–373.

Reuss, T. (1934). No title (Vereinsnberichte-"Lacerta", Berlin). *NATV* **3**, 27.

Reuss, T. (1934). No title (Vereinsnberichte-"Lacerta", Berlin). *NATV* **7**, 76–77.

Reuss, T. (1934). No title (Vereinsnberichte-"Lacerta", Berlin). *NATV* **9**, 99–100.

Reuss, T. (1934). Originalbericht. (Vereinsnberichte-"Lacerta", Berlin). *NATV* **13**, 160–161.

Reuss, F. A. T. (1934). Seidarapan-Ein wirkliches Märchen. (Vereinsnberichte-"Lacerta", Berlin). *NATV* **37**, 450–451.

Reuss, T. (1935). No title (Vereinsnberichte-"Lacerta", Berlin.). *NATV* **5**, 57.

Reuss, F. A. T. (1935). Beiträge zur vorgeschichtlichen Erd- und Lebenskunde. 1. Ein Ausflug ins Miocän (Vereinsnberichte-"Lacerta", Berlin). *NATV* **6**, 72–73; **7**, 82–83; **9**, 105–106.

Reuss, F. A. T. (1935). Europäische Giftschlangen. Uebersichtskarte der Giftschlangenzuwanderung in Europa seit der Eiszeit (Quartärzeit). Mit einer Einführung in die entsprechende Aufteilung der europäischen Ottern unter Berücksichtigung von Gift- und Heilserumfragen. *DAAT* pp. 145–166.

Reuss, T. (1935). No title (Vereinsnberichte-"Lacerta", Berlin.). *NATV* 16, 205–206.

Reuss, F. A. T. (1935). Erläuterungen zur Typenfrage in der Zoologie an hand von Bildern europäischer Giftschlangen. *NATV* 16, 215–218.

Reuss, F. A. T. (1935). No title (Vereinsberichte-"Lacerta", Berlin). *NATV* **33**, 426–427.

Reuss, F. A. T. (1935). No title (Vereinsberichte-"Lacerta", Berlin). *NATV* **37**, 478–479.

Reuss, F. A. T. (1935). No title (Vereinsberichte-"Lacerta", Berlin). *NATV* **38**, 493–494.

Reuss, T. F. A. (1935). No title (Vereinsberichte-IFB. ("Lacerta"), Berlin). *NATV* **39**, 504.

Reuss, T. F. A. (1935). No title (Vereinsberichte-IFB. ("Lacerta"), Berlin). *NATV* **40**, 513.

Reuss, T. F. A. (1936). No title (Vereinsberichte-IFB. (Lacerta), Berlin). *NATV* **1**, 6–7.

Reuss, T. F. A. (1936). No title (Vereinsberichte-IFB. (Lacerta), Berlin) *NATV* **4**, 43–44.

Reuss, T. F. A. (1936). No title (Vereinsberichte-IFB. (Lacerta), Berlin). *NATV* **6**, 73–74.

Reuss, T. F. A. (1936). No title (Vereinsberichte-IFB. (Lacerta), Berlin). *NATV* **7**, 82.

Reuss, T. F. A. (1936). No title (Vereinsberichte-IFB. (Lacerta), Berlin). *NATV* **11**, 148.

Reuss, T. F. A. (1936). No title (Vereinsberichte-IFB. (Lacerta). Berlin.. *NATV* **23**, 333.

Reuss, T. F. A. (1936). Der neue Rohstoff, das neue Rauschgift: Ophiotoxin. Eine Ergänzung zu "Europäische Giftschlangen" in diesem "Almanach", Ausgabe 1935. *DAAT* pp. 141–147.

Reuss, F. A. T. (1937). No title (Vereinsberichte-IFB. (Lacerta), Berlin). *NATV* **15**, 217–218, 224.

Reuss, T. (1937). No title (Vereinsberichte). *NATV* **15**, 224.

Reuss, T. (1937). "Nomenclatur-Fragen" Eingesandt von der Alfred-Brehm-Gesellschaft, Dresden. *NATV* **24**, 330.

Reuss, F. A. T. (1937). Observations on four Species of European Toxicophidia. *Compt. R. XII Congr. Int. Zool.-Lisbonne* 1935, pp. 1787–1804.

Reuss, F. A. T. (1938). Zoogeographische Toxicophiologie im Frühjahr 1938. Mit eine Beitrag zur Kunde der Schlangenbisse und zwei Neubeschreibungen, Mesovip. morathi, spec. nov., und leopontica, subsp.nova. *DA* **12**(5), 78–80.

Reuss, F.A.T. (1938). *Mesovipera stemmler morathi*. Eine neue Nasenotter aus Südfrankreich, Norditalien und der Südschweiz. *ZATV* **15**, 166.

Reuss, F. A. T. (1938). Ein Beitrag zur Kunde der Giftschlangenbisse und der zugehörigen Unterscheidung von Giftschlangen (Toxophidia). *DA* **12**(6), 95–99.

Reuss, F. A. T. (1938). Die Amphibien und Reptilien Griechenlands. *DA* **12**(8), 122–123.

Reuss, T. (1938). *Vipera nasicornis* (Shaw), Nashornotter. *DA* **12**(9), cover page, including one photograh.

Reuss, T. (1938). *Vipera gabonica* (Dumeril & Bibron), Gabunotter. *DA* **12**(10), cover page, including one photograph.

Reuss, F.A.T. (1939). Berichtigungen und Ergänzungen zu meinen Arbeiten über Toxicophidier, 1938. *ZATV* 1,13–14.

Reuss, T.F.A. (1941). Die Ophiotoxine oder Schlangengifte. Ein bericht uber neue Entwicklungen und neue heimische Rohstoffe in der Medizin. *Rhein.-westf. Z.* 25.07.1941. 1 pp.

Reuss, T.F.A. (1941). Die Ophiotoxine oder Schlangengifte. Neue heimische Rohstoffe in der Medizin. *Brüssel. Z.* 30.07.1941. 1 S.

Reuss, T. (1943). Eingesandt. *DA* 4, 45.

Reuss, T. (1943). Ueber die Aufzucht einer neugeborenen Nashornotter aus Kamerun. *DA* 6, 66–70.

Reuss, T. (1944). Herpetologische Rundschau. *DA* **1**. **17**–18; **2**, 33–34; **3**, 49–50.

Reuss, T. (1944). Die Balzkämpfe der Kreuzottern. Stürmischer Hochzeitstag in einem märkischen Waldmoor. *Brüssel. Z.* 23.04.1944. 1 S.

Reuss, T. (1944). Beiträge zur Klärung ophiobiologische Fragen. *DA* **3**, 42–47.

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Prey excavation by *Psammophylax rhombeatus rhombeatus* (Colubridae: Psammophiinae) from South Africa

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PSAMMOPHIINES represent a well-defined monophyletic radiation of African, west Asian, and Mediterranean snakes comprising eight genera and approximately 45 species (Branch, 1998; Kelly *et al.*, 2003; Kelly, 2005; Shine *et al.*, 2006). Most snakes of this clade exemplify the classic convergent "whipsnake" morphology and behaviour (Shine *et al.*, 2006). They are alert, fast-moving, diurnal predators that are able to exploit a diverse array of prey classes (Baha el Din, 1998; Akani *et al.*, 2003; Shine *et al.*, 2006). Despite their ubiquity and ecological importance throughout their range, there have been few field studies investigating the ecology of psammophiines.

It is widely believed that visual stimulation is among the most important cues for predation in diurnal terrestrial snakes, especially whipsnakes (Shine, 1980; Ota, 1986; Mori *et al.*, 1992; Luiselli, 2006). However, complex chemosensory behaviour exhibited by species in the Psammophiinae (De Haan, 2003; De Haan & Cluchier, 2006) suggests that members of this clade may rely on chemical cues in foraging more heavily than previously presumed. Here we report on the excavation of a visually-concealed prey species by the southern African psammophiine, *Psammophylax rhombeatus rhombeatus* (Rhombic Skaapsteker). Despite its wide range (most of South Africa, Lesotho, and Swaziland and disjunct populations in Namibia; Branch, 1998) and local abundance, surprisingly little is known about its diet and foraging strategies. Two previous museum-based studies (Van Wyk, 1988; Flemming & Douglas, 1997) investigated the ecology of the Rhombic skaapsteker, but there have been no published field studies of the species. The following account documents a foraging strategy previously unknown in the psammophiine clade.

METHODS

Observations took place on 2nd November 2006 (South African spring) on Farm Steenboksfontein Nature Reserve (32°10'S, 18°18'E), approximately 7 km south of Lambert's Bay on the semi-arid coast of the Western Cape Province of South Africa, during a radiotelemetric study of *Psammophylax r. rhombeatus*. Annual rainfall in this region ranges from 50–300 mm, with approximately 80% of the precipitation occurring between April and September (Lovegrove, 2003). This Mediterranean-type climate provides the conditions for strandveld (open scrubland) vegetation characterized by woody species that occur on sandy, calcareous soil on low lying coastal plains (Manning & Goldblatt, 2000).

Implantation of radiotransmitters (Holohil, SB-2) followed the procedures of Reinert and Cundall (1982). Snakes were relocated using a hand-held, 3-element Yagi antenna and CE-12 receiver (Custom Electronics, Urbana, Illinois). Photo documentation and short video clips of the excavation behaviour were taken using a MVC-CD1000 Sony Digital Still Camera.

RESULTS

The focal skaapsteker (adult male, weight: 59.2 g, SVL: 49.2 cm, TL: 15.7 cm) was located at 13:32 h on 2nd November 2006 (ambient temperature: 25.4°C; soil temperature: 23°C; humidity: 56%) by radiotelemetry on open sand where it was observed using its head and neck to dig sand out of a deep burrow (Fig. 1A). The dimensions of the hole (approximately 10 cm in diameter) suggest it had been originally excavated by a mammal; moreover, the amount of sand the snake was able to displace with each scooping action was minimal (less than 5 cm^3) and could not have created the resulting burrow in any short period of time.

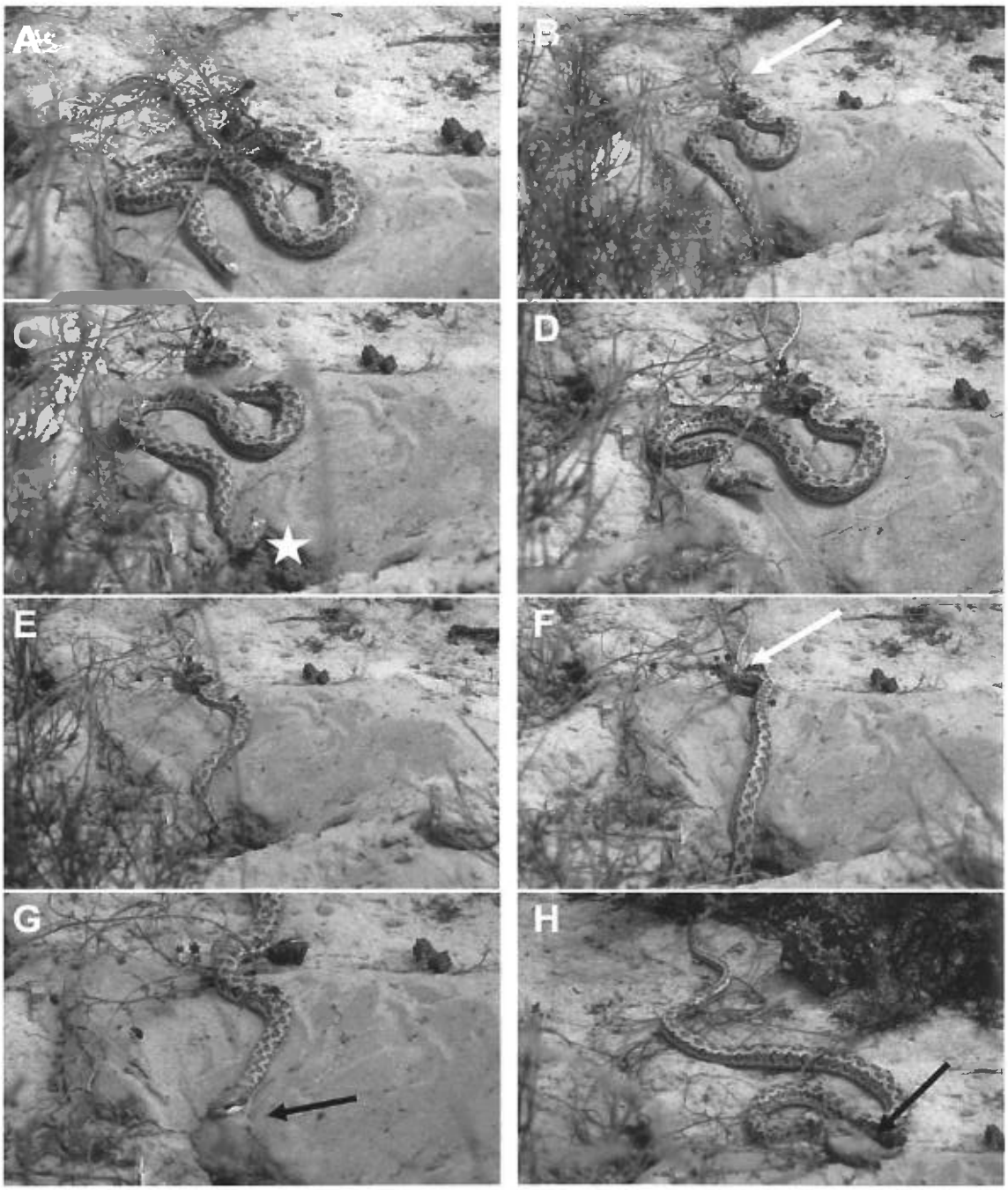

Figure 1. *Psammophylax r. rhombeatus* excavating *Breviceps namaquensis*. (A) Snake when first located at 13:32 h. (B) Snake descending into the burrow head-first. White arrow shows the anchorage point used by the snake when descending into burrow. (C) Snake emerging from burrow and using the bent neck to scoop out sand (white star). (D) Snake emergent during period of rapid excavation (3–5 scoops per 15 sec interval). The displaced whorls of sand around the snake are indicative of body movements made during excavation. (E) Forebody extended into burrow during period of slow excavation prior to prey prehension. (F) Furthest subterranean extension of forebody facilitated by tail anchorage (white arrow) to achieve this. (G) Snake reversing out of burrow at 13:45 h dragging a large *Breviceps namaquensis* (black arrow). (H) Snake pausing to manipulate prey (black arrow) while reversing away from burrow.

The posterior part of the body and tail were anchored around a bush as the snake entered and exited the steep entrance to the burrow (Fig. 1A–F). The snake adjusted its grip around the vegetation as it cycled in and out of the burrow (see progression of Fig. 1A–F). Each time the forebody of the snake descended into the burrow it emerged using the crook of its neck to scoop sand from the burrow entrance (Fig. 1C). It switched between right and left flexures frequently and did not appear to favor one side over the other. It continued digging rigorously (3–5 scoops every 15 s) for approximately 7 min, pausing only occasionally.

The skaapsteker then changed its digging rate; spending longer time intervals (5–15 s) with its forebody beneath the surface (Fig. 1E–F). During these extended periods, the visible portion of its body began swaying from side to side, emerging occasionally to displace sand (although more sporadically and at a slower pace than previously). After a prolonged period (25 consecutive seconds) of having the anterior half of its body below ground, the snake slowly began to reverse out of the hole, still using its tail as anchorage. At 13:45h it emerged with a Namaqua rain frog (*Breviceps namaquensis*) head-first in its mouth (Fig. 1G–H). Based on known measurements of the focal snake, the frog was approximately 5 cm in length and at least 3 cm in width.

The skaapsteker reversed entirely out of the steep burrow but paused four times to advance the frog further into its mouth. Once completely out of the burrow the snake continued to reverse over an additional ~20 cm of level surface (Fig. 1H). It then traveled forward to a bush less than a meter from the hole, where it began a series of lateral head and neck undulations until the entire body of the frog had been ingested. After the bulge had progressed to the stomach, the snake briefly remained laid out straight and motionless and finally moved to another bush about 2 m west of the excavated burrow (14:01 h). Throughout excavation and ingestion the skaapsteker appeared unaffected by observer proximity (~ 1.5 m) and movement.

DISCUSSION

Van Wyk (1988) investigated feeding habits of *Psammophylax r. rhombeatus* using preserved museum specimens and found that small mammals comprised 82% of the identifiable prey items. However, his study was geographically limited to a small area of the species' range and its results may not be representative of the species as a whole, as other sources list frogs as a dominant prey category (Broadley, 1977; Jacobsen, 2005). Our more comprehensive dietary data show that nocturnal and/or diurnally subterranean prey comprise a considerable proportion of the diet of *P. r. rhombeatus* (Cottone & Bauer, unpublished data). Other information concerning the diet of this species is based on anecdotal dietary notes (Broadley, 1983; Branch & Bauer, 1995) and in all of these cases foraging strategy can only be inferred from prey type.

Breviceps namaquensis is a nocturnal, burrowing frog that only emerges from its burrow during rainy periods (Passmore & Carruthers, 1995). Because a night of rain preceded the described predation event, it is likely that the skaapsteker detected the prey the next day using chemical cues. Presumably the snake had only to dig out an entrance plug in order to access the frog, since the burrow itself appeared to have been originally excavated by a mammal. Based on previously published records, as well as 19 identifiable anurans extracted from the stomachs of preserved skaapstekers in our broader study, this is the only *Breviceps* dietary record for *P. r. rhombeatus*.

Digging behaviour similar to that documented here has been reported in colubrid snakes of other lineages. For example, *Pituophis catenifer sayi*, *P. c. affinis*, and *P. melanoleucas mugitus* have been recorded digging through loose sand using neck scooping actions similar to that of *P. r. rhombeatus* in order to retrieve subterranean pocket gophers (*Geomys*) (Carpenter, 1982; O'Brien *et al.*, 2001). Carpenter (1982) also used laboratory data to suggest that *Pituophis* uses chemoreception to actively detect such buried prey.

Other terrestrial colubrid snakes also exploit subterranean prey through probable chemical detection and subsequent extraction. *Dinodon semicarinatum* has been recorded digging and feeding on sea turtle eggs and unemerged hatchlings (*Chelonia mydas* and *Caretta caretta*) (Mori *et al.*, 1999). The Australian whipsnake, *Demansia vestigiata*, has also been reported

extracting a buried *Limnodynastes ornatus* (Trembath & Rowley, 2005). However, both these snakes excavated prey by pushing their snouts through the soil, a different technique than the shoveling motions used by *Pituophis* and *Psammophylax r. rhombeatus*. *Lampropeltis getula holbrooki* has likewise been documented excavating and eating turtle eggs (Brauman & Fiorillo, 1995), although details of the digging technique were not discussed.

In cases where the digging technique is known, the time spent excavating exposes the snake to prolonged predator vulnerability; however, subterranean prey are very unlikely to escape (Trembath & Rowley, 2005). So despite the high risk, either the pay-off of a guaranteed meal or a particularly rich food source may be sufficient for the strategy to be maintained. This could be advantageous for a wide foraging snake by decreasing its overall energy expenditure and exposure to predators.

Additionally, excavation can be beneficial for reasons other than prey capture. A second skaapsteker being tracked was observed for six minutes digging a depression in the sand using the same neck scooping behaviour noted above before it abandoned the excavation (perhaps disturbed by observer presence). This particular snake was observed basking in depressions similar in dimensions to the one it was witnessed excavating throughout the two month period it was being tracked, suggesting that skaapstekers also dig in order to thermoregulate and/or more effectively avoid detection while basking. This behaviour appears analogous to the "cratering" behaviour observed in *Crotalus cerastes cerastes* and other viperids (Brown & Lillywhite, 1992), although the depressions are formed through different body movements.

Our observations suggest that excavation behaviours in skaapstekers may be useful in multiple ecological contexts. Existing data suggest that *Breviceps* species are not crucial, or even common, components in skaapsteker diets, although excavation may also be required to obtain certain mammalian prey, as consumed by *Psammophylax* in the Free State province of South Africa (Van Wyk, 1988). Mechanical specializations, if any, for excavation, as well as the role of chemosensation in the location of subterranean prey have yet to be investigated in skaapstekers but may ultimately provide a functional context for the ecology of African psammophiines which, until now, has been investigated almost exclusively through museum-based dietary studies (Shine *et al.*, 2006).

ACKNOWLEDGEMENTS

We thank the Western Cape Conservation Board for supplying the permits to conduct research and Villanova University for funding the research. We would also like to thank Gerrit Burger for providing the accommodation and permission to conduct the study on his farm. Special thanks to Le Fras Mouton, Mandi Ablas, Hannes Van Wyk, Dahné DuToit, and Jeannie Hayward from Stellenbosch University for logistical help throughout the field season. Finally, thanks to Awesome Tony Gamble for providing the camera with which photo documentation during this study was taken. All snakes in this study were handled in accordance with IACUC standards (05–06) issued through Villanova University.

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Reproduction in the False fer-de-Lance, *Xenodon rabdocephalus* (Serpentes: Colubridae) from Costa Rica

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THE False fer-de-lance, *Xenodon rabdocephalus* (Wied) is a moderate-sized snake that occurs in the lowlands of tropical Mexico south through Central America to Ecuador and the upper portions of Brazil, Peru and Bolivia where it ranges from 1–1200 m; it feeds almost exclusively on toads (Savage, 2002). There is little information known regarding the reproductive biology of *X. rabdocephalus*. Clutches of 9 to 10 eggs are laid in the rainy season (Campbell, 1998; Savage, 2002) and Solórazano (2004) reported clutches of up to 15 eggs. The purpose of this paper is to provide additional information on the ovarian cycle and to report the first information on the testicular cycle from a histological examination. Comparisons are made with the testicular cycles of other snakes from Costa Rica.

Thirty four *X. rabdocephalus* from Costa Rica in the Natural History Museum of Los Angeles County (LACM), Los Angeles, California, USA were examined (Appendix). Samples consisted of 21 males: mean snout-vent length (SVL) = 473 mm ± 87 SD, range: 294-614 mm; 13 females, SVL = 701 mm ± 99 SD, range: 545–840 mm. Snakes were collected 1959–1983. An unpaired *t* test was used to compare male and female mean body sizes (SVL) (Instat vers. 3.0b, Graphpad Software, San Diego, CA).

Counts were made of enlarged ovarian follicles (> 8 mm length) or oviductal eggs. The left testis, and vas deferens were removed from males and the left ovary was removed from females for histological examination. Tissues were embedded in paraffin, sectioned at 5 µm and stained with hematoxylin followed by eosion counterstain. Testes slides were examined to determine the stage of the testicular cycle and ovary slides were examined for the presence of yolk deposition (secondary vitellogenesis *sensu* Aldridge, 1979).

Testicular histology was similar to that reported by Goldberg & Parker (1975) for two colubrid snakes, *Masticophis taeniatus* and *Pituophis catenifer*. All testes examined were undergoing spermiogenesis with metamorphosing spermatids and sperm present. Vasa deferentia also contained sperm. The following monthly samples of *X. rabdocephalus* exhibited spermiogenesis: January (2), February (2), April (1), June (3), July (1), August (7), September (1), November (2), December (2). The smallest spermiogenic male measured 294 mm SVL (LACM 154459) and was collected in June.

Females were larger than males (unpaired *t*-test, $t = 7.0$, $df = 32$, $P < 0.0001$). Monthly distribution of stages in the ovarian cycle of *X. rabdocephalus* are in Table 1. Reproductively active females were found in all months except March. Most of the females (12/13) 92% were reproductively active. Females in early yolk deposition included those that commenced vitellogenesis as indicated by vitellogenic granules = secondary vitellogenesis (*sensu* Aldridge, 1979) to those with yolking follicles reaching 5 mm diameter. Because it was not possible to know if all follicles of 5 mm diameter would have completed yolk deposition they were not considered as the number of eggs in an egg clutch. However, the likelihood is that some of these yolking follicles would have culminated in a clutch of unknown number later in the year. One August female in Table 1 contained enlarged follicles (>12 mm) that were fused (presumably a preservation artifact) and could not be reliably counted. Mean clutch size for five females with enlarged ovarian follicles (>12 mm diamater) or oviductal eggs was 13.0 ± 5.5 SD, range 6–19. Clutch sizes of 18 (LACM 154498) collected 21st November and 19 (LACM 154479) collected 2nd October are new maximum clutch sizes for *X. rabdocephalus*. The smallest

Month	*n*	No yolk deposition	Early yolk deposition	Enlarged follicles > 12 mm length	Oviductal eggs
February	1		1		
March	1	1			
May	1		1		
July	1				1
August	1			1*	
September	1	1			
October	5	1	2	1	1
November	2			1	

Table 1. Monthly distribution of stages in the ovarian cycle of *Xenodon rabdocephalus* from Costa Rica. Values shown are the numbers of females exhibiting each of the four conditions.*Enlarged follicles > 12 mm length are fused (preservation artifact) and cannot be counted.

reproductively active female measured 545 mm SVL (LACM 154481) and was collected 27th October. It contained 6 oviductal eggs. There was no vitellogenesis in the ovaries of the two females with oviductal eggs which would have suggested more than one egg clutch in the same year.

My data suggest *X. rabdocephalus* males produce sperm throughout the year. Extended testicular cycles have been reported in other snakes from Costa Rica: *Drymobius margaritiferus* (Goldberg, 2003a); *Dendrophidion* sp. (Goldberg, 2003b); *Ninia maculata* (Goldberg, 2004a); *Erythrolamprus bizona* and *E. mimus* (Goldberg, 2004b); *Micrurus nigrocinctus* (Goldberg, 2004c); *Hydromorphus concolor* (Goldberg, 2006a); *Mastigodryas melanolomus* (Goldberg, 2006b); *Geophis godmani* (Goldberg, 2007a); *Coniophanes fissidens* (Goldberg, 2007b). It will be necessary to conduct histological examination of the testicular cycles of additional snakes before one can ascertain if year-round sperm production is typical of snakes from Costa Rica. Moreover, since Solórzano (2004) reports there are 137 species of snakes in Costa Rica, the snakes I have examined represent less than 10% of the Costa Rican snake fauna.

Although the two females with oviductal eggs were not undergoing vitellogenesis for a subsequent clutch, in view of the extended period in which reproductively active females were collected (Table 1), it appears plausible that some females may produce multiple egg clutches in the same year. Goldberg (2003b) reported one *Dendrophidion paucicarinatum* from Costa Rica with oviductal eggs that was concurrently depositing yolk in ovarian follicles for a subsequent clutch. Stafford (2003) indicated that *Dendrophidion pericarinatum* and *D. vinitor* females likely produced multiple clutches. Based on his observations of *X. rabdocephalus* neonates appearing from March to December, Solórzano (2004) suggested *X. rabdocephalus* followed a continuous reproductive pattern throughout the year. The reproductive cycle of *X. rabdocephalus* appears to fit the "polyestrous with continued reproduction" category of Saint Girons (1982).

ACKNOWLEDGEMENTS

I thank Christine Thacker (LACM) for permission to examine specimens and Jessica Carlson for assistance with histology. Snakes are part of the CRE collection donated to LACM by Jay Savage in 1998.

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Appendix. *Xenodon rabdocephalus* examined by Costa Rica province from LACM.

Alajuela 154458, 154459, 154475, 154484, 154487, 154492, 154493, 154502; Cartago 154478, 154479, 154481, 154482, 154490; Guanacaste 154486, 154491, 154503; Heredia 154474; Limón 131132–131134, 154473, 154477, 154489, 154501; Puntarenas 154480, 154483, 154497, 154500 ; San José 154472, 154494–154496, 154498, 154499.

Data on the distribution of the terrestrial herpetofauna of Morocco: records from 2001–2006

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MOROCCO is situated in the Northeast point of Africa, with an area of just over 400,000 km^2 (excluding Western Sahara). Together with Algeria and Tunisia it forms the Maghreb, a well defined geographic region within North Africa. Morocco has a great diversity of habitats, ranging from Mediterranean to Sahara, which are essentially separated by the Atlas Mountains range that traverses the country from Northeast to Southwest. Morocco has the highest diversity of herpetofauna of North Africa and of the Western Mediterranean region. Bons & Geniez (1996) accepted 104 species, with 23 endemic to Morocco, and several new taxa have been formally recognised since (e.g. Wade, 2001). Additionally analyses of genetic variation suggest several widespread forms may actually be species complexes.

Here we report on the findings of six years of field work carried out in Morocco, from 2001 to 2006, totalling approximately 70 person/weeks of observations. Field trips were in most cases carried out during spring, and a total of 427 observations of amphibian and reptile species were recorded. When a species was observed, the coordinates of the location were it was found were marked with a GPS. A total of 159 localities were sampled (Map 1, Appendix 1), resulting in the observation of nine species of amphibians and 57 species of reptiles, representing more than two thirds of the known species. Specimens are classified at the species level, but subspecific comments are supplied when relevant. Since the taxonomy of several Moroccan taxa is still unresolved, we implement some of the more stable nomenclatural changes since Bons & Geniez (1996), but also discuss recently suggested alternatives.

AMPHIBIA

URODELA, **Family Salamandridae**

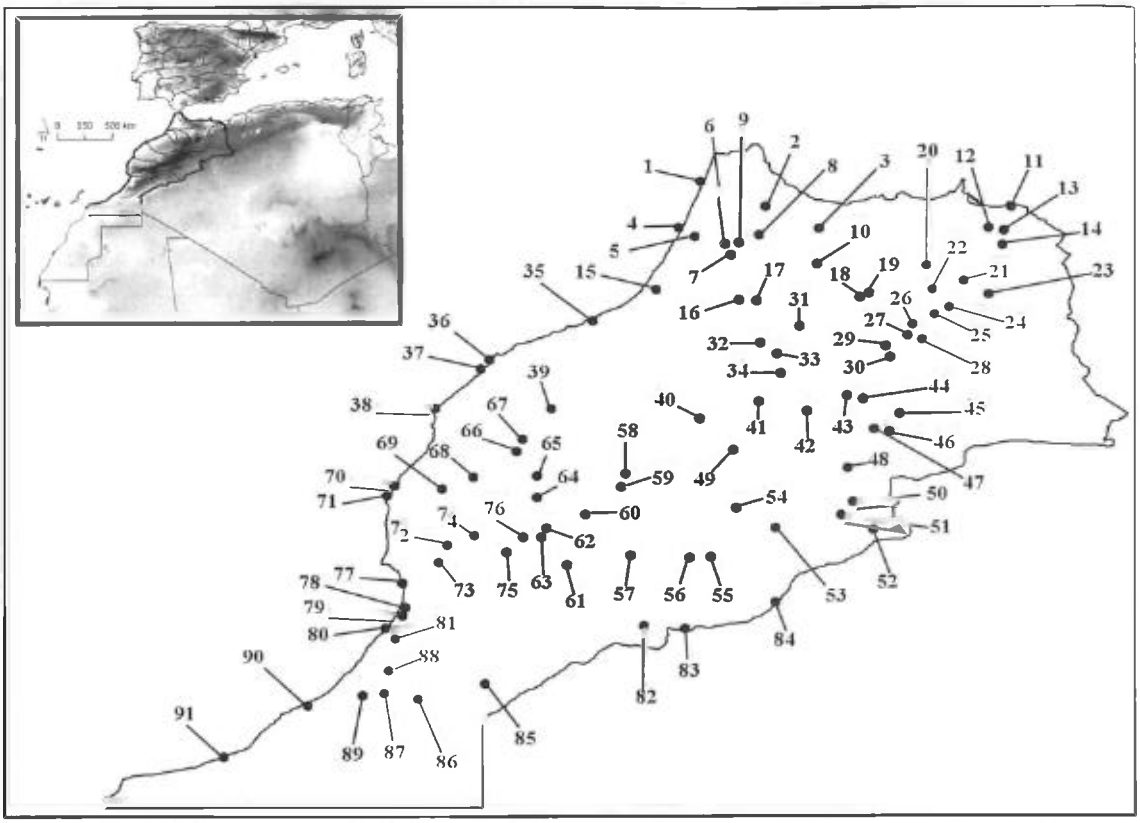
Pleurodeles waltl Michahelles, 1830; localities 5 and 36.

Locality 36, El Jadida (square S11 in Bons & Geniez, 1996): between the northern (main) distribution area and the southern localities were the species was observed, namely Safi [Q15] and Essaouira island [N19], for which Bons & Geniez (1996) suggested the need for confirmation. Adults were found under stones during wet weather (locality 36, reported in detail in Carretero *et al.* (2004)), juveniles in large, shallow temporary ponds (locality 5).

ANURA

Family Discoglossidae

Alytes obstetricans (Laurenti, 1768); only found in locality 19d. Currently referred to *Alytes maurus* (Fromhage *et al.*, 2004, Gonçalves *et al.*, 2007). Adult specimens were found under stones on a well-grazed, steeply sloping hillside.



Map 1. Map of the study area and the principal localities sampled (see Table 1).

Discoglossus pictus Otth, 1837; localities 2a, 18, 19d, 32, 35, 47a and 61. Currently referred to *Discoglossus scovazzi* (Fromhage *et al.*, 2004, Zangari *et al.*, 2006).
Locality 47a: Gourrama. Previously unreported from east of the Atlas Mountains, this extends the distribution into the drier region to the east (Fig. 1A). Found in a variety of ponds, roadside ditches and marshy mountain meadows.

Family Bufonidae

Bufo bufo (L., 1758); localities 31b, 61, 61b, 62a and 73.

Bufo mauritanicus Schlegel 1841, localities 1, 3, 18, 19a, 19d, 24, 29, 31b, 34a, 38, 45a, 46, 50, 57, 61, 69 and 73.

Bufo viridis Laurenti, 1768; localities 24, 28b, 36, 45a, 58 and 68. *Bufo viridis* appears to be a species complex (Stöck *et al.*, 2006). Some of these new localities fill gaps in the known range of this widespread species.

Bufo brongersmai Hoogmoed, 1972; only found in localities 58 and 74a. These connect the locations of Souss basin and south of High Atlas with the isolated observations in the Marrakech plain (Fig. 1B).

Mature adult *Bufo* sp. were generally found under stones. Huge numbers of recent metamorphosed *B. mauritanicus* were observed in various regions of the Rif mountains.

Family Hylidae

Hyla meridionalis Boettger, 1874; localities 19d, 61, 61b and 62. Typically found in reeds near more permanent streams and rivers. Unusual silver coloured individuals were seen at Jebel Sirwah (locality 61).

Family Ranidae

Rana saharica Boulenger, 1913; localities 3, 17, 19, 19a, 28b, 31b, 32, 43, 45a, 46, 47a, 61 and 73. Proposed as a possible species complex by Bons and Geniez (1996), but analysis of mtDNA shows minimal variation across Morocco (Harris *et al.*, 2003a). Common in a variety of water bodies throughout its range.

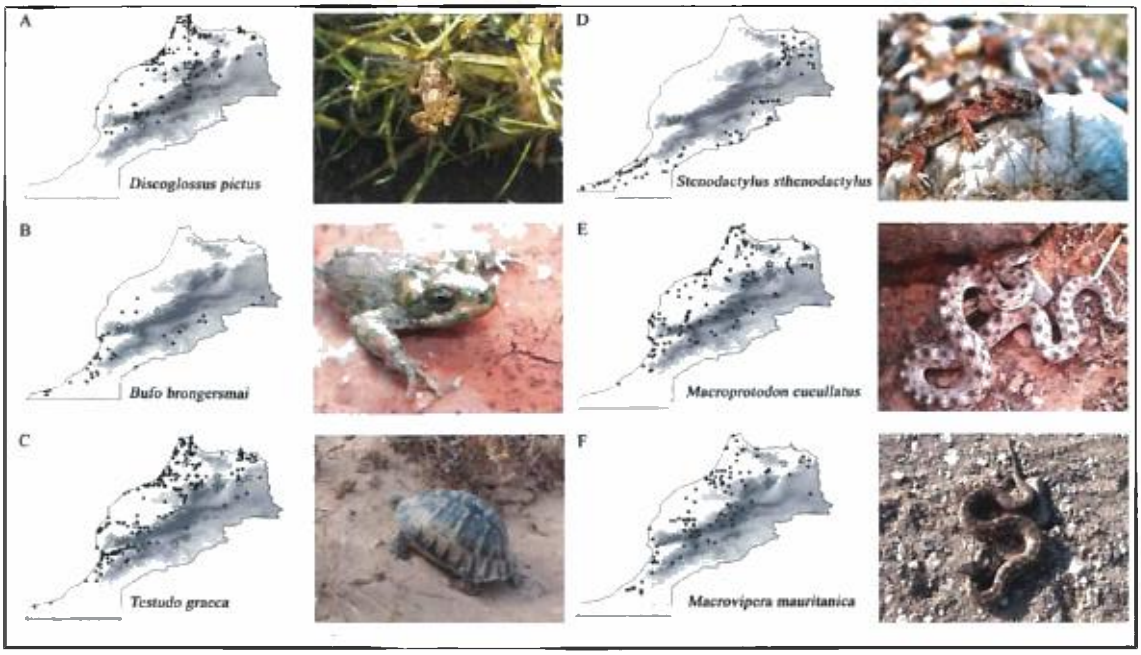


Figure 1. Distribution maps of some of the species observed. Black dots represent known distributions of the species (extracted from Bons & Geniez, 1996) and stars represent new records reported in this study.

REPTILIA

CHELONIA

Family Testudinidae: *Testudo graeca* L., 1758; localities 7, 8c, 13a, 19d, 23, 24b, 32, 38, 40, 56, 59 and 65.

Locality 56: There are few citations of *T. graeca* from the East of the Atlas Mountains. Extensive anthropogenic effects make it difficult to rule out artificial introductions, although this new locality is a long way from any large human settlements (Fig. 1C).

Family Bataguridae: *Mauremys leprosa* (Schweigger, 1812); localities 1a, 8b, 8d, 35, 59 and 87. Although most specimens were found near large mountain streams and rivers, many were clearly of a temporal nature that were likely to be dry for much of the year.

SAURIA

Family Agamidae

Agama bibroni Dúmeril & Dúmeril, 1851; localities 2a, 2b, 3, 5, 8c, 10, 13a, 18, 19d, 20, 30, 31, 32, 37, 44, 47, 47a, 54b, 59, 63b, 74, 75b, 79, 86c and 88b. One of the most commonly seen species in Morocco, found in a wide variety of habitats but typically associated with rocks.

Trapelus mutabilis (Merrem, 1820); localities 45d, 50a, 54a and 59a.

Uromastyx acanthinurus Bell, 1825; localities 20, 44, 47, 54, 54c and 85. Mitochondrial DNA analysis indicates all the Moroccan specimens form a clade within this species, although this includes a relatively high level of genetic variation (Harris *et al.*, 2007). Although still quite common in the rocky desert areas, many specimens were roadkills, and individuals were often observed sold in markets, indicating the dual threats to this species.

Family Anguidae: *Ophisaurus koellikeri* (Günther, 1873); only found in locality 32, under stones in a broad-leaf forest. Currently referred to *Hyalosaurus koellikeri* (Macey *et al.*, 1999).

Family Chamaeleonidae: *Chamaeleo chamaeleon* (L., 1758); localities 20, 54a and 91. One specimen (locality 20) was found in a surprisingly open and arid area, walking along the ground.

Famiily Gekkonidae

Geckonia chazaliae Mocquard, 1895; only found in locality 91a. Currently referred to *Tarentola chazaliae* (Carranza *et al.*, 2002).

Hemidactylus turcicus (L., 1758); only found in locality 11, within a ruined building. Analysis of mtDNA sequence variation indicates *H. turcicus* is probably introduced in Morocco (Carranza & Arnold 2006).

Ptyodactylus oudrii Lataste, 1880; localities 43 and 45a.
Locality 43 (Tamdafelt bridge): This record extends the distribution area of the species further north into the Moulouya river valley. All specimens were found on large boulders. In locality 43 the specimen was on the underside of a rock above an irrigation channel.

Quedenfeldtia moerens (Chabanaud, 1916); localities 63, 72, 75 and 75b.

Quedenfeldtia trachyblepharus (Boettger, 1874); localities 61 and 62.
Locality 61 (El Azib n-Iriri, Jbel Siroua) regarding forms: Most citations from this area are of *Quedenfeldtia* sp. only. This confirms the presence of *Q. trachyblepharus* from this area. *Quedenfeldtia* were active even when the sky was extremely overcast, and were usually found in very high densities when present.

Stenodactylus sthenodactylus (Liechtenstein, 1823); localities 20, 21, 22, 30, 44 and 89.
Localities 22 and 30: these lie between the northern and southern areas of distribution, making it more continuous through the Moulouya river (Fig. 1D). A few specimens were found under rocks, but many more by digging out the small holes beneath thorn bushes, often also occupied by *Acanthodactylus* sp.

Saurodactylus mauritanicus (Dúmeril & Bibron, 1836); localities 12, 13, 13a, 14 and 23.
Saurodactylus brosseti Bons & Pasteur 1957, localities 36, 58, 64, 65, 65a, 68, 71, 72, 74, 77, 78, 81, 88a.

Saurodactylus fasciaticus Werner, 1931; localities 8a, 9a and 39. Locality 39 adds another southerly locality to the few isolated points known, and increases the range of sympatry between *S. fasciatus* and *S. brosseti*. Recent analyses suggest that *Saurodactylus* is paraphyletic (Rato & Harris, 2008), in which case future taxonomic changes to this group are likely.

Tarentola mauritanica (L., 1758); localities 1, 2b, 3, 4, 7, 8c, 11, 17, 19, 19b, 19e, 25, 29, 31, 31b, 32, 32a, 33, 36, 39, 40, 42, 59, 61, 63b, 65, 65a, 67, 73, 75a and 76. *Tarentola mauritanica* appears to be a species complex, although the two accepted subspecies in Morocco do not seem to correspond to genetic lineages (Harris *et al.*, 2004a, b). *Tarentola mauritanica* is extremely widespread in both natural habitats but especially in buildings.

Tarentola deserti Boulenger 1891, localities 50b and 50d. Found on clusters of large boulders. Superficially very similar to *Tarentola mauritanica*, but with a notably ochre-yellow iris.
Tropiocolotes tripolitanus Peters, 1880; found only in locality 89, under rubbish in a small open area within the town of Gourrama.

Family Lacertidae

Acanthodactylus erythrurus (Schinz, 1833); localities 2b, 3, 19b, 24, 32, 32a, 33, 41, 41a, 61, 65, 65a and 72.

Acanthodactylus lineomaculatus Dúmeril & Bibron, 1839; localities 4, 4a, 15, 15a, 38, 70 and 71a. Evidence based on mtDNA do not support the distinction of this species from *A. erythrurus* (Harris *et al.*, 2004).

Acanthodactylus maculatus (Gray, 1838); localities 14, 30a and 53a.

Acanthodactylus busacki Salvador, 1982; localities 79, 81 and 90.
The morphological distinction of *A. busacki* has not always been accepted (see Harris & Arnold 2000). Mitochondrial DNA sequence variation indicates considerable variation within an "*A. pardalis* species complex", including *A. pardalis*, *A. maculatus*, *A. busacki* and *A. mechriguensis* (Fonseca *et al.*, 2008). However, exact delimitation of species remains equivocal. Members of this species complex are extremely difficult to separate in the field. All, like the other Moroccan *Acanthodactylus* sp. are typically seen running over open areas between bushes where the animals take refuge in holes around the roots.

Acanthodactylus boskianus (Daudin, 1802); localities 11, 20, 27, 28, 28a, 28b, 30, 45c, 46, 47a, 48a, 48b, 53, 55, 82, 86, 86a and 86b.

Acanthodactylus dumerili (Milne Edwards, 1829); localities 50c, 50d, 82a, 83a and 84.

Acanthodactylus longipes Boulenger, 1921; localities 52 and 83.

Acanthodactylus aureus Günther, 1903; localities 80 and 90a.

Lacerta tangitana Lataste, 1880; localities 3, 6, 18, 19a, 19d, 24, 32, 32a, 34, 34a, 40a, 40b, 45a, 45b, 61, 63a, 63b and 75. Currently referred to *Timon tangitanus* (Arnold *et al.*, 2007), and may represent a species complex in Morocco (Paulo, 2001). While Debdou (locality 24) is within the range typically assigned to *Lacerta pater*, specimens from here are still *L. tangitana*.

Lacerta andreanszkyi Werner, 1929; localities 62 and 63. Currently referred to *Atlantolacerta andreanszkyi* (Arnold *et al.*, 2007). Found under rocks in the open high mountain meadow of Oukaimeden, with *Podarcis hispanica* and *Scelarcis perspicillata* on the larger rocks and walls surrounding the meadow.

Mesalina guttulata (Lichtenstein, 1823); localities 25, 45a, 48, 54a, 54b and 86c. These new citations fill some gaps in the widespread distribution of this species.

Mesalina olivieri (Audouin, 1829); localities 20, 24, 47 and 65a. The specimen from the last locality (10km NE of Marrakesh) corresponds to the subspecies *M. o. simoni*. All Moroccan *Mesalina* are small, shy species found in dry open areas running between small bushes used as refugia.

Ophisops occidentalis Boulenger, 1887; found only in locality 23.

Podarcis hispanica (Steindachner, 1870); localities 1, 2, 2b, 3, 8, 8c, 8d, 18, 19a, 19b, 19d, 24, 32, 32a, 33, 34, 34a, 42, 61, 61a, 63b and 75. Locality 61 (El Azib n-Iriri, Jbel Siroua): Most Moroccan and Southern Spanish populations are now referred to *Podarcis vaucheri* (Busack & Lawson, 2005). Pinho *et al.* (2006, 2007) show that the populations from locality 61 are not related to other Moroccan populations, but rather to a Tunisian form of the *Podarcis hispanica* species complex. Generally Podarcis were found in areas with Mediterranean climate, and especially near water courses such as streams. However some populations, such as that from within the town of Midelt, were on walls in quite dry areas.

Psammodromus algirus (L., 1758); localities 2a, 2b, 3, 4, 7, 9a, 13a, 19, 19a, 19b, 19d, 19e, 25, 31, 32, 32a, 33, 34, 40, 41a, 45b, 59, 59a and 61. Locality 45b (25km W of Talsinnt): Two other Mediterranean species (*P. vaucheri* and *S. perspicillata*) have isolated records from this region. This adds another Mediterranean species to this isolated group. *Scelarcis perspicillata* was confirmed at the same place, although *P. vaucheri* was not observed. The two accepted subspecies in Morocco do not appear to be genetically distinct based on analysis of mtDNA sequences (Carranza *et al.*, 2006).

Scelarcis perspicillata (Dúmeril & Bibron, 1839); localities 17, 19, 19a, 19b, 19e, 24, 31, 32, 32a, 33, 40a, 45, 59, 61, 63b and 75.

Scelarcis perspicillata has three distinct morphological forms in Morocco. Considerable mtDNA variation was reported (Harris *et al.*, 2003b), and a 100% coincidence of morphotypes and mtDNA lineages was observed at a contact zone of two forms near Taza (Perera *et al.*, 2007), indicating a probable species complex with forms separated by perhaps 5.5 million years (Arnold *et al.*, 2007). However, there are only two distinct genetic lineages, and in other areas populations with similar colour morphs do not coincide with these. Specimens were found predominantly on high cliffs and large rocks, often near running water, where their flattened morphology allows them to take refuge in very narrow crevices. Occasionally also seen climbing on trees.

Family Scincidae

Chalcides colosii Lanza, 1957; only found in locality 2b.

Chalcides minutus (Caputo, 1993); only found in locality 24a.

Chalcides mionecton (Boettger, 1874); localities 15, 15a, 68 and 89.

Chalcides ocellatus (Forsskål, 1775); localities 13a, 14, 20, 22 and 24.

Chalcides polylepis Boulenger, 1890; localities 19b and 36.

Chalcides pseudostriatus (Caputo, 1993); only found in locality 2a. All *Chalcides* specimens were found turning rocks. Recently an extensive review suggests that future taxonomic changes for some species are likely (Carranza *et al.*, 2008).

Eumeces algeriensis Peters, 1864; localities 9a, 16, 19e, 28, 30, 36, 39, 59, 65a, 68 and 79. Eastern localities fall within an area where the form *Eumeces (algeriensis) meridionalis* could have been expected, but all samples corresponded to *E. a. algeriensis*.

Sphenops boulengeri (Anderson, 1896), only found in locality 82.

AMPHISBAENIA

Family Amphisbaenidae (currently Blanidae following Kearney & Stuart, 2004).

Blanus mettetali Bons, 1963; found only in locality 40.

Blanus tingitanus Busack, 1988; localities 8c, 19a and 19b.
Currently two species of *Blanus* are recognised in Morocco, *B. mettetali* and *B. tingitanus*, and one in Iberia, *B. cinereus*. Vasconcelos *et al.* (2006) indicate that *B. cinereus* is a species complex, and that one individual was found in Taza (locality 19). The existence of this form in North Africa needs further investigation.

Family Trogonophidae: *Trogonophis wiegmanni* Kaup, 1830; localities 1, 9a, 19e, 23, 35, 36, 38 and 59. Mendonça & Harris (2007) reported the two localities for *T. w. wiegmanni* in the Moulouya river valley region, that link the northern and southern populations of this form in Morocco. They indicate that three genetic lineages exist in North Africa, corresponding to the accepted subspecies in Morocco plus an additional lineage in Tunisia. All the amphisbaenians observed were found under rocks or litter.

SERPENTES

Family Colubridae (s.l.)

Hemorrhois hippocrepis L., 1758; Localities 7, 9, 9a, 17, 19b, 19c, 24a, 31a, 32, 66 and 67. As with all the following colubrid snakes, many specimens were roadkills.

Hemorrhois algirus (Jan, 1863); found only in locality 54.

Coronella girondica (Daudin, 1803); localities 19d, 24, 49 and 63.

Macroprotodon cucullatus (Geoffroy Saint-Hilaire, 1827); localities 3, 9a, 19b, 19d, 26, 30, 32 and 33. In a recent morphological analysis Wade (2001) recognized four species of *Macroprotodon*, with three, *M. cucullatus*, *M. mauritanicus* and *M. abubakeri* in North Africa and *M. brevis* in North Africa and the Iberian Peninsula. Assessment of mtDNA variation indicates considerable variation in North Africa and a recent colonization of the Iberian Peninsula (Carranza *et al.*, 2004; Vasconcelos & Harris, 2006). However exact delimitation of genetic units in North Africa requires further analyses (Fig. 1E).

Malpolon moilensis (Reuss, 1834); found only in locality 85a.

Malpolon monspessulanus (Hermann, 1804); localities 1a, 2c, 8c, 17, 18, 19d, 33, 61 and 65.
Natrix maura (L., 1758); localities 3, 5a, 8d, 10, 11, 46, 59 and 61. Several specimens were caught swimming in small ponds, streams or irrigation channels. All were collected very close to such water bodies.

Psammophis schokari (Forsskål, 1775); localities 20, 45, 54b and 60. Although three colour morphs have been described for Morocco (Bons & Geniez, 1996), all three form part of the same mtDNA genetic lineage (Rato *et al.*, 2007).

Psammophis and *Malpolon* are the only non-viperid Moroccan snakes belonging to the Subfamily Psammophiinae. Since the recognition of Atractaspididae and Elapidae make traditional Colubridae paraphyletic according to the last molecular phylogenies (Lawson *et al.*, 2005), this well defined group probably merits Family status.
Spalerosophis dolichospilus (Werner, 1923), only found in locality 47a, currently the easternmost report in Morocco.

Family Viperidae

Cerastes cerastes (L., 1758); found only in locality 57a. A roadkilled specimen, without the typical horns.

Macrovipera mauritanica (Gray, 1849); localities 14, 73a and 20. Currently referred to *Daboia mauritanica* (Lenk *et al.*, 2001). These new localities fill gaps in the range of this widespread species, particularly in the low Moulouya basin (Fig. 1F).

ACKNOWLEDGEMENTS

Fieldwork in Morocco was partially funded by grants from FCT, POCTI/1999/BSE/34547, POCTI/2001/BSE/41912, POCTI/BIA-BDE/55596/2004 and POCTI/BIA-BDE/61946/2004, and from the National Geographic Society NGS7629-04. The authors acknowledge Bert Toxopeus and the

International Institute for Geo-Information Science and Earth Observation (ITC, The Netherlands) for georeferenced information on the distribution of Moroccan amphibians and reptiles.

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Appendix 1: Localities sampled (coordinates in WGS1984; LAT D: Latitude, Degrees, LAT M: Latitude, Minutes, LONG D: Longitude, Degrees, LONG M: Longitude, Minutes). Codes in bold letter indicate the localities represented in Map 1. Due to the big number of localities sampled, localities that are close together are grouped together.

1: ASSILAH; N 35° 28.264'; W 6° 1.873'; **1a: Road Larache-Tetouan;** N 35° 23.245'; W 5° 55.788'; **2: CHEFCHAOUENE;** N 35° 10.023'; W 5° 15.145'; **2a: 3km S of Derdara crossroad;** N 35° 5.543'; W 5° 18.445'; **2b: Bab Taza;** N 35° 3.98'; W 5° 12.08'; **2c: After Bab Taza;** N 35° 3.669'; W 5° 6.965'; **3: KETAMA;** N 34° 52.694'; W 4° 36.652'; **4: MOULAY BOUSSELHAIM BEACH;** N 34°

53.761'; W 6° 17.266'; **4a: 1km before Moulay Bousselhaim;** N 34° 53.27'; W 6° 15.5'; **5: ROAD TO MOULAY BOUSSELHAIM 1;** N 34° 46.24'; W 6° 5.195'; **5a: Road to Moulay Bousselhaim 2;** N 34° 41.799'; W 6° 1.552'; **6: CLOSE TO BASRA;** N 34° 47.483'; W 5° 43.533'; **7: 5KM AFTER HAD KOURT;** N 34° 39.059'; W 5° 39.628'; **8: ZOUMI;** N 34° 48.026'; W 5° 20.416'; **8a: Road to Zoumi;** N 34° 46.102'; W 5° 30.971'; **8b: 5km before Zoumi;** N 34° 44.759'; W 5° 25.369'; **8c: 15km before Zoumi;** N 34° 46.102'; W 5° 30.971'; **8d: 4,5km SE of Zoumi;** N 34° 47.361'; W 5° 18.201'; **9: 2KM BEFORE OUAZZANE;** N 34° 47.759'; W 5° 33.543'; **9a: Close to Ouazzane;** N 34° 37.814'; W 5° 32.283'; **10: TAOUNATE;** N 34° 31.797'; W 4° 38.085'; **11: MOUTH OF OUED MOULOUYA; 9KM W OF SAIDA;** N 35° 7.243'; W 2° 19.981'; **12: 3 KM E OF MOULOUYA RIVER BRIDGE;** N 34° 52'; W 2° 36'; **13: ROAD TO TAFORALT;** N 34° 50'; W 2° 25'; **13a: 11km S of Berkane;** N 34° 51.435'; W 2° 25.525'; **14: 10KM N OF EL AIOUN;** N 34° 38.666'; W 2° 26.471'; **15: FORET DE LA MAMORA;** N 34° 6.279'; W 6° 33.73'; **15a: Kenitra (highway);** N 34° 12.264'; W 6° 33.715'; **16: VOLUBILIS (ROMAN RUINS);** N 34° 4.532'; W 5° 33.445'; **17: NEAR MOULAY IDRISS;** N 34° 3.867'; W 5° 21.337'; **18: HALOUANE;** N 34° 6.791'; W 4° 7.283'; **19: RAS-EL-OUED, TAZZEKA;** N 34° 9.249'; W 4° 0.556'; **19a: 10km S of Taza;** N 34° 7.829'; W 4° 1.751'; **19b: 15km S of Taza - Taza Caves;** N 34° 6.257'; W 4° 4.349'; **19c: 30km S of Taza - P.N. Tazekka;** N 34° 5.55'; W 4° 6.188'; **19d: 35km S of Taza - P.N. Tazekka;** N 34° 5.021'; W 4° 6.849'; **19e: Canyons between Sidi Abdallah and Taza;** N 34° 11.573'; W 4° 11.391'; **20: 15KM S OF SAKA;** N 34° 29.801'; W 3° 19.564'; **21: FROM TAOURIRT TO DEBDOU;** N 34° 18.154'; W 2° 53.14'; **22: 5KM S OF CROSSROAD TO MISSOUR;** N 34° 11.629'; W 3° 15.13'; **23: 60KM NW OF AIN BENIMATHAR;** N 34° 1.502'; W 2° 36.34'; **24: GAADA DE DEBDOU;** N 33° 57.7'; W 3° 2.868'; **24a: Gaada de Debdou 1;** N 33° 58.476'; W 3° 1.876'; **24b: Gaada de Debdou (Plateau du Rekkam) 1;** N 33° 47.018'; W 3° 2.518'; **25: RCHIDA;** N 33° 52.472'; W 3° 13.644'; **26: ZERZAIA ROAD S329;** N 33° 45.765'; W 3° 29.688'; **27: FRITISSA;** N 33° 37.288'; W 3° 32.945'; **28: 24KM E OF CROSSROAD TO AIN BENIMATHAR;** N 33° 33.761'; W 3° 22.456'; **28a: 10km E of crossroad to Ain Benimathar;** N 33° 30.446'; W 3° 32.244'; **28b: 2km E of crossroad to Ain Benimathar;** N 33° 20.214'; W 3° 34.962'; **29: TIRNEST;** N 33° 29.268'; W 3° 48.658'; **30: OUTAT-OULAD-EL-HAJ;** N 33° 21.198'; W 3° 45.63'; **30a: 30km N of Missouri;** N 33° 15.927'; W 3° 48.243'; **31: MIDELT TO TAZA 1;** N 33° 44.549'; W 4° 49.911'; **31a: Midelt to Taza 2;** N 33° 29.666'; W 4° 51.754'; **31b: Midelt to Taza 3;** N 33° 15.043'; W 4° 41.229'; **32: 15KM N OF AZROU (BALCON D' ITO);** N 33° 32.562'; W 5° 19.014'; **32a: 5km S of Azrou;** N 33° 26.11'; W 5° 10.913'; **33: MISCHLIFFEN;** N 33° 24.326'; W 5° 6.199'; **34: 10KM S OF TIMAHDITE;** N 33° 9.313'; W 5° 4.096'; **34a: 15km S of Timahdite;** N 33° 6.788'; W 5° 1.652'; **35: N - CASABLANCA (HIGHWAY);** N 33° 42.675'; W 7° 18.922'; **36: EL JADIDA;** N 33° 12.725'; W 8° 33.058'; **37: JORF LASFAR;** N 33° 5.282'; W 8° 39.192'; **38: MOUSSA;** N 32° 36.182'; W 9° 11.5'; **39: MECHRA BEN ABHOU; 110KM NW OF MARRAKECH;** N 32° 36.099'; W 7° 48.66'; **40: EL KSIBA;** N 32° 34.511'; W 6° 2.109'; **40a: El Ksiba Area;** N 32° 33.599'; W 6° 4.135'; **40b: Titt-n-Tazzart;** N 32° 29.281'; W 6° 0.852'; **41: KERROUCHEN;** N 32° 48.106'; W 5° 19.386'; **41a: Tizi-n' Rechou;** N 32° 47.062'; W 5° 13.508'; **42: MIDELT;** N 32° 40.972'; W 4° 44.568'; **43: TAMDAFELT BRIDGE;** N 32° 52.471'; W 4° 15.916'; **44: 25KM S OF MISSOUR;** N 32° 49.87'; W 4° 4.371'; **45: 22KM W OF TALSINNT;** N 32° 38.328'; W 3° 38.489'; **45a: Unnamed village 30km W of Talsinnt;** N 32° 35.158'; W 3° 45.631'; **45b: 25km W of Talsinnt;** N 32° 34.143'; W 3° 42.255'; **45c: 18km S of Talsinnt;** N 32° 22.545'; W 3° 25.897'; **45d: 25km S of Talsinnt;** N 32° 19.321'; W 3° 28.777'; **46: AIT ICHCHOU;** N 32° 25.13'; W 3° 46.232'; **47: 10KM E OF GOURRAMA;** N 32° 21.063'; W 3° 57.967'; **47a: Gourrama;** N 32° 20.094'; W 4° 4.469'; **48: AR-RACHIDIA (CAMPING);** N 31° 51.922'; W 4° 17.17'; **48a: 5km S of Source Blue de Merski;** N 31° 50.935'; W 4° 15.308'; **48b: Aoufouss;** N 31° 47.087'; W 4° 13.525'; **49: LAKE TISLI;** N 32° 11.564'; W 5° 38.054'; **50: ERFOUD;** N 31° 26.215'; W 4° 13.264'; **50a: 5km N of Erfoud;** N 31° 30.012'; W 4° 12.11'; **50b: 10km N - Erfoud;** N 31° 31.098'; W 4° 11.56'; **50c: 15km N - Erfoud;** N 31° 31.205'; W 4° 11.533'; **50d: 12km N of Erfoud;** N 31° 32.343'; W 4° 11.152'; **51: 5KM W OF RISSANI;** N 31° 16.217'; W 4° 21.865'; **52: ERG CHEBBI;** N 31° 4.356'; W 3° 58.173'; **53: 2KM E OF ALNIF;** N 31° 7.117'; W 5° 8.577'; **53a: 10km E of Alnif;** N 31° 9.609'; W 5° 2.237'; **54: MERZOUGA TO OUARZAZATE DESERT ROAD 1;** N 31° 27.708'; W 5° 35.661'; **54a: Merzouga to Ouarzazate desert road 2;** N 31° 22.414'; W 5° 52.564'; **54b:**

Merzouga to Ouarzazate desert road 3; N 31° 6.796'; W 6° 24.474'; **54c: Merzouga to Ouarzazate desert road 4;** N 31° 4.085'; W 6° 32.096'; **55: 15KM W OF TAZZARINE;** N 30° 51.35'; W 5° 54.173'; **56: 20KM NW OF SOUK EL ARBA;** N 30° 50.344'; W 6° 8.735'; **57: 5KM S OF OUARZAZATTE;** N 30° 51.719'; W 6° 50.85'; **57a: 10km S of Ouarzazatte;** N 30° 49.302'; W 6° 46.161'; **58: 3.5KM NE OF TANANNT;** N 31° 53.201'; W 6° 54.85'; **59: IMINIFRI;** N 31° 43.454'; W 6° 58.314'; **59a: After Iminifri;** N 31° 42.428'; W 6° 57.376'; **60: ROAD OUARZAZATTE – MARRAKECH ;** N 31° 22.017'; W 7° 23.53'; **61: EL AZIB N-IRIRI (JBEL SIROUA);** N 30° 44.818'; W 7° 36.557'; **61a: Amzdour;** N 30° 46.617'; W 7° 37.229'; **61b: W of Tachakoucht;** N 30° 48.337'; W 7° 32.627'; **62: OUKAIMEDEN;** N 31° 12.058'; W 7° 51.322'; **62a: 1km S of Oukaimeden;** N 31° 12.757'; W 7° 50.874'; **63: HIGH RERAIA RIVER: 2KM S OF SIDI CHAMHAROUCH;** N 31° 5.254'; W 7° 55.148'; **63a: High Reraia river: Sidi Chamharouch;** N 31° 6.314'; W 7° 54.844'; **63b: Reraia river;** N 31° 6.041'; W 7° 54.867'; **64: 15KM S OF MARRAKESH (S501 TO TAHANNAOUT);** N 31° 29.172'; W 7° 59.022'; **65: MARRAKECH-OULAD SALAS;** N 31° 45.434'; W 7° 58.47'; **65a: 10km NE of Marrakesh;** N 31° 44.335'; W 7° 58.698'; **66: OADDOUR;** N 32° 4.014'; W 8° 13.158'; **67: OULAD BRANIM;** N 32° 13.496'; W 8° 9.89'; **68: OULAD BRAHIM (OUED TENSIFT);** N 31° 45.148'; W 8° 44.06'; **69: AN NZALA;** N 31° 35.43'; W 9° 6.283'; **70: MOULAY BOUZERTOUN BEACH;** N 31° 38.161'; W 9° 40.432'; **71: ESSAOUIRA;** N 31° 30'; W 9° 46'; **71a: 7km S of Essaouira;** N 31° 27.821'; W 9° 45.38'; **72: GRAN PLATEAU DES IDA-OU-BOUZIA;** N 30° 59.567'; W 9° 1.8867'; **73: ARGANA;** N 30° 46.597'; W 9° 7.7717'; **73a: 13km N of Bigoudine;** N 30° 48.713'; W 9° 8.044'; **74: LALA AZIZA;** N 31° 6.223'; W 8° 42.523'; **74a: Temporary pond by the track;** N 31° 10.512'; W 8° 45.217'; **75: 15 KM S-HAZAR ROAD KM 93;** N 30° 54.028'; W 8° 19.888'; **75a: Hazar;** N 30° 56.928'; W 8° 15.853'; **75b: Tizi-n-Test;** N 30° 52.455'; W 8° 22.02'; **76: 31KM S - ASNI;** N 31° 5.413'; W 8° 7.765'; **77: AGADIR, TIZNIT ROAD;** N 30° 25'; W 9° 35'; **78: 49KM TIZNIT;** N 30° 6'; W 9° 33'; **79: TAROUDANT (OUED MASSA);** N 29° 59.828'; W 9° 35.272'; **80: BOU SOUN;** N 29° 51.071'; W 9° 46.238'; **81: OUED MASSA;** N 29° 48.369'; W 9° 38.85'; **82: 30KM E OF FOUM ZGUID;** N 29° 52.81'; W 6° 42.714'; **82a: 40km E of Foum Zguid;** N 29° 51.042'; W 6° 37.318'; **83: ERG MHAZIL - 80KM E OF FOUM ZGUID;** N 29° 51.274'; W 6° 13.535'; **83a: 112km E of Foum Zguid;** N 29° 52.091'; W 6° 0.636'; **84: 60KM E OF TAGOUNITE;** N 30° 11.096'; W 5° 8.796'; **85: 60KM W OF AKKA;** N 29° 9.326'; W 8° 35.596'; **85a: 80km SW of Akka;** N 29° 5.1'; W 8° 41.391'; **86: 3KM E OF TAGGIT;** N 29° 3.177'; W 9° 22.431'; **86a: 4km E of Taggit;** N 29° 3.148'; W 9° 20.753'; **86b: 6km E of Taggit;** N 29° 3.362'; W 9° 20.093'; **86c: 6km W of Taggit;** N 29° 6.052'; W 9° 28.002'; **87: TAGANT;** N 29° 7.48'; W 9° 46.68'; **88: TIZI MIGHERT;** N 29° 24.516'; W 9° 43.634'; **88a: Morght;** N 29° 24'; W 9° 43'; **88b: km.49 Tiznit-Guelmine;** N 29° 23.71'; W 9° 44.065'; **89: GUELMINE;** N 28° 59.87'; W 10° 3.164'; **90: 15KM E OF AOREORA - PLAGE BLANCHE;** N 28° 52.39'; W 10° 42.164'; **90a: 25km S of Aoreora;** N 28° 44.684'; W 10° 44.631'; **91: 50KM S OF TAN-TAN PLAGE;** N 28° 13.847'; W 11° 42.099'; **91a: 60km S of Tan-Tan Plage;** N 28° 11.514'; W 11° 49.47'.

Winding to and fro: constriction in the snake *Anilius scytale*

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SNAKES from different phylogenetic lineages use constriction to subjugate and handle prey, an apparently ancient behaviour (Greene & Burghardt, 1978). This feeding strategy is widespread in alethinophidian snakes from many clades, including both non-caenophidians such as *Cylindrophis*, *Loxocemus*, and Boidae, and caenophidians including *Acrochordus* and several species of Colubridae and a few Elapidae (Willard 1977; Greene & Burghardt, 1978; Shine 1985). The aniliids and cylindrophids are possible sister taxa comprising a clade that is sister to all other alethinopdians (e.g. Scanlon & Lee, 2000, but also e.g. Vidal et al., 2007 for alternative phylogeny), and their feeding biology is thus relevant to understanding the origins and evolution of constriction. Aniliids and cylindrophids both feed on elongate vertebrates. Constriction is known for at least one cylindrophid but has not been reported for the only aniliid, the Neotropical *Anilius scytale* (Greene, 1983). The scarce data on feeding behaviour of *A. scytale* would indicate that this is a non-constricting species (see Savitzky, 1980). However, the only available record on prey subjugation by *A. scytale* is based on an observation with a very small prey item and these often induce no constricting behaviour in snakes known to otherwise constrict (see Greene, 1983). *Anilius scytale* is recorded as occurring in water and both waterlogged and drier soil , but very little is known about its habits (Martins & Oliveira, 1998), although it is known to feed on elongate prey such as eels and caecilians (Beebe, 1946; Cunha & Nascimento, 1978; Martins & Oliveira, 1998).

A specimen of *A. scytale* caught in a hydroelectric rescue at Palmas, Tocantins, central Brazil (11°S, 48°W) (40 cm SVL) was placed in a plastic container and offered a small elongate fish, the cobitid *Misgurnus* sp. The snake grasped the fish and began a coil (Figure 1) but did not proceed and released the prey. This observation gave us the clue that the snake might constrict larger, elongate prey such as amphisbaenians. Thus, we housed another specimen of *A. scytale* (52 cm SVL, collected from the same locality) in a 50 x 25 x 30 cm terrarium with soil and water at room temperature (24–30°C) and offered an *Amphisbaena* sp. individual (22 cm TL) as a potential prey. The whole feeding sequence was video-taped, and some stills were selected to make the pictures used here to illustrate four phases of the constriction behaviour. The complete video-taped sequence is on a DVD housed at Laboratório de Ecologia e Evolução of Instituto Butantan.

The whole feeding sequence occurred on the soil surface. After set free in the terrarium the amphisbaenian was bitten by the snake on the anterior part of its body, the snake keeping its grip for 25 sec. After this, the snake held the prey with anterior, horizontal coils with its right body side in contact with the prey (Figure 2A). As the prey twisted around its long axis (a habitual defensive movement) the snake loosened its coil hold on the prey and immediately constricted the prey again,

Figure 1. The snake *Anilius scytale* (SVL = 40 cm) bites and begins a potential constriction movement on a cobitid fish, *Misgurnus* sp.

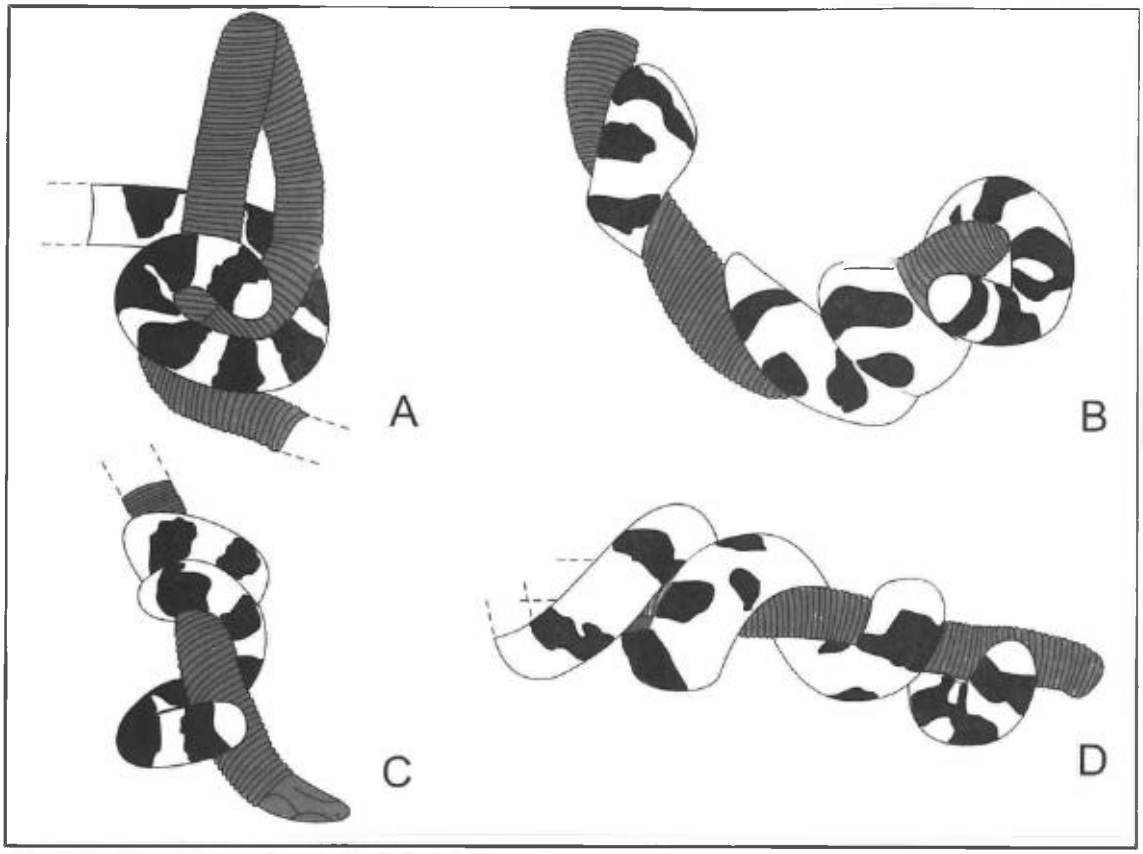

Figure 2. Constriction sequence on an amphisbaenian, *Amphisbaena* sp. (TL = 52 cm) by the snake *Anilius scytale* (SVL = 22 cm). A – After the initial bite, use of anterior, horizontal coils, with the right side of the snake in contact with the prey; B – posterior and horizontal coils with right side in contact with prey; C – anterior and horizontal coil with left side in contact with prey; D – anterior and horizontal coils with left side in contact with prey. Only the head end of the snake is shown. Based on still frames of a video-tape.

this time with posterior, horizontal coils, keeping its right side in contact with the prey (Figure 2B). After a second coil loosening, the snake constricted the prey again with anterior, horizontal coils, but this time with its left side in contact with the prey (Figure 2C). In the fourth and last constricting action (again after loosening the coil grip) the snake constricted the prey with mixed (anterior and posterior) horizontal coils, again using its left side to contact the prey (Figure 2D). The snake sometimes wrapped its lower body around the prey's posterior body, with irregular and overlapping coils. The snake proceeded to bite and constrict the amphisbaenian for about 30 min, in which time the prey died. Thereafter the snake released its bite and coils around the prey, and swallowed it head-first.

The constriction employed by *A. scytale* varied both in the coil composition (anterior-posterior) and laterality (right-left). The coil composition is usually invariable for a given taxon (Greene & Burghardt, 1978), whereas the body side wrapped around the prey is variable both at the specific and individual level, but the coil is applied only once during a predatory event and thus remains invariable till the end of the ingestion (Lopes *et al.*, 1991). Constriction modes vary from lineage to lineage, but there seems to be a pattern within these. For instance, non-caenophidians (*Cylindrophis*, *Loxocemus*, and boids) generally constrict with anterior, horizontal coils (Greene & Burghardt, 1978), while colubrid and elapid constriction is more variable but generally consistent within a given genus (Shine & Schwaner, 1985). Our data indicate that *A. scytale* has no fixed constriction pattern, but more episodes and more individuals need to be

observed. If confirmed, absence of a consistent pattern might represent an ancestral condition that would indicate that constriction in snakes originated as a more or less irregular behaviour, and eventually evolved to a more stable pattern (such as the presently seen in *Cylindrophis*, *Loxocemus*, and boids). The absence of a well defined constriction pattern in *Anilius* might be considered supporting evidence for the hypothesis that Cylindrophiidae is more closely related to Caenophidia than Aniliidae (e.g. Slowinsky & Lawson, 2002; Lawson *et al.*, 2004; Vidal *et al.*, 2007). On the other hand, the changes recorded during the observed feeding episode might not be considered to be a fully developed constriction but simply behavioural adjustments of the predator to a vigorous and constantly twisting prey. Even if this is the case, this would not invalidate the possible phylogenetic conclusion. Our observations are based on a single individual and a single predation event, and additional records would test our interpretations.

The behaviour we recorded for *Anilius* suggests that some form of constriction is widespread in non-caenophidian alethinophidians. The apparent exceptions include Uropeltidae and Xenopeltidae (no data are available for Anomochilidae). The former feed on earthworms (Greene, 1997) and constriction is probably not needed to subjugate such prey. Thus, constriction may be a trait that vanished in some non-caenophidian groups as well as in some caenophidians.

ACKOWLEDGEMENTS

We thank Harry Greene for expert advice on the manuscript. David Gower for considerably improving the manuscript. Fabiana dos Santos Toledo for the video-recording of the constricting sequence. Antonio COR da Costa for rendering the drawings based on the video-records and help with the photograph. Both authors are grantees of the CNPq.

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Changes in the phenology of the Adder, *Vipera berus*, over four decades: a comparison with Prestt (1971)

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ABSTRACT – In 1971 Ian Prestt published his pioneering study of the Adder, *Vipera berus*, in the Purbeck and Wareham area of southern Dorset. Most of this work was completed during 1959–1961, but further observations continued until 1965. The author met with Ian Prestt in 1970 and walked his study sites, and in 1971 two sites, Furzebrook and Wareham Forest, were adopted as potential study areas with regard to continuing research on the Adder, and also the Smooth snake, *Coronella austriaca*. Since that time many aspects of the Adder's lifestyle and behaviour have been recorded. During the latter part of the study period results have shown that there have been significant changes in activity cycles, particularly with regard to an increase in active days, and a more erratic ecdysis regime. To date, these changes do not appear to have had a negative impact, and populations have remained stable throughout the term of the study. In addition, there does not appear to be any notable change with regard to reproductive cycles of either males or females.

THERE is now a consensus that climate change is affecting a wide range of animal and plant species throughout Britain (Sparks, *et al.*, 1998; Collinson & Sparks, 2003; Collinson & Sparks, 2004; Thomas *et al.*, 2004). Changes in the timing of naturally occurring events is most obvious in the annual cycles of plant growth, and the arrival and nesting dates of migrant birds. Herpetologically, the Common frog, *Rana temporaria*, has been shown to be an excellent indicator of phenological change with regard to spawning dates and tadpole development (Beebee, 2002; Cummins, 2003; Collinson & Sparks, 2004). Information with regard to the affect on reptiles in Britain is virtually non-existent, although Phelps (2000) has shown that the Sand lizard, *Lacerta agilis*, in southern Dorset breeds earlier than in previous years, and that there has been a significant increase in fecundity in that currently around 25% of females produce two clutches each year.

Changes in the annual cycle of the Adder, *Vipera berus*, were not apparent in the current study until comparatively recently, and from 1971–1989 very much mirrored the results from 1960 (Prestt, 1971). The date of emergence from hibernation was probably the most obvious clue to any change in annual activity. However, emergence dates have always been variable, Prestt in 1959 gives emergence dates for males from March 4th–10th, and for 1960 February 27th–29th. Phelps (in prep) also recorded similar variables in emergence dates between 1971 and 1989, and although commonly observed, solitary Adders recorded as early as January were not included in the results. The aim of the study was to determine the potential influence of increased activity days on such aspects as feeding periods and female reproductive cycles.

MATERIALS AND METHODS

Study Area: The study area was situated in the Isle of Purbeck, Dorset, three miles south of Wareham and formed part of Ian Prestt's original study area. The area covered approximately 75 ha, and habitat consisted of large expanses of lowland heath mosaic, (*Calluna, Erica* spp.), with good stands of common gorse, (*Ulex europa*), and significant carpets of dwarf gorse (*Ulex minor*). Tree cover was minimal with some scattered young Corsican pine, (*Pinus* sp.) and small copses of birch (*Betula* sp.). About 35 ha to the south and west of the study area consisted of wet heath and bog. *Molinia* and *Erica* formed the dominant vegetation with the occasional small willow carr. This latter area formed the summer feeding ground for the majority of the Adder population.

Identifying Individual Adders: Until 1989 individual Adders were marked by clipping a series of ventral scales to a preconceived code (See Prestt, 1971 for details). From 1989 each Adder was also given a photographic identification with particular attention given to the head and anterior part of the body. More recently photographs have been scanned, or method replaced directly with digital photography. This allowed a snake to be examined more easily in greater detail.

Study Period: The study took place from 1972 until 1980 and then continued from 1985 until 2003. The most intensive study took place during the spring and late summer/Autumn months, i.e. emergence and ingress. During these periods the study area was visited a minimum of twice weekly.

RESULTS

A range of differences were observed in Adder phenology between Prestt's (1971) study and the current study (Figures 1–3). For spring emergence, marked differences were observed between males and females in both 1960 and 2003 (Figure 1) with females emerging 20.6 days later than males on average across the two years. There was no evidence of a change of emergence date between the two study years for either male or female (Figure 1). In contrast, the date of the last sighting (ingress) showed evidence of substantial difference between 1960 and 2003 (Figure 2). Both sexes ingressed later in 2003 than 1960 with a similar mean day of 275.7 in males and 283.3 in females (30 days later for males; 26.4 days later for females). Based on a comparison of data from 1978 and 2003, this was statistically significant (males: paired samples t test = -144.649, df 11, P = 0.000; females: t = -6.869, df 12, P = 0.000). As

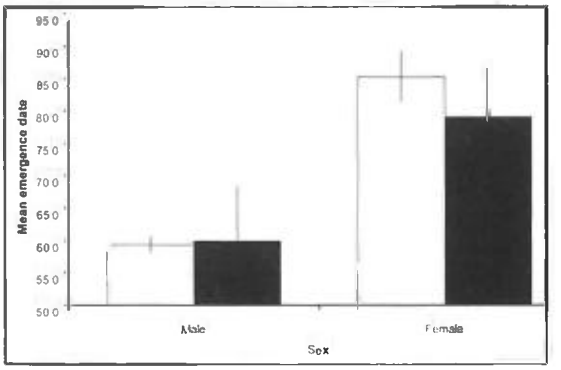


Figure 1. The mean emergence date (± standard deviation) for male and female Adders in the years 1960 (open bars) and 2003 (filled bars). Females emerged significantly later than males, with no evidence of differences between years for either sex (two–way ANOVA: Sex $F_{1, 34}$= 48.88, P < 0.001; Year $F_{1, 34}$= 0.49, P = 0.49; Sex x Year $F_{1, 34}$= 0.75, P = 0.39).

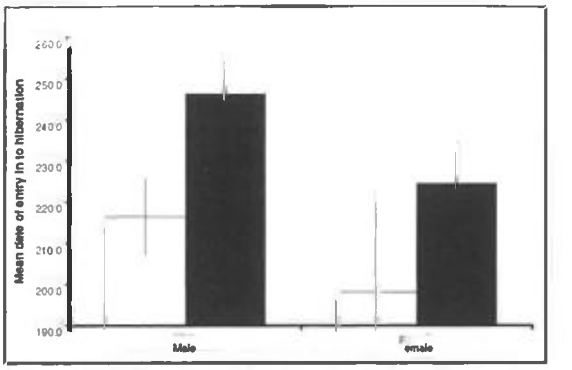
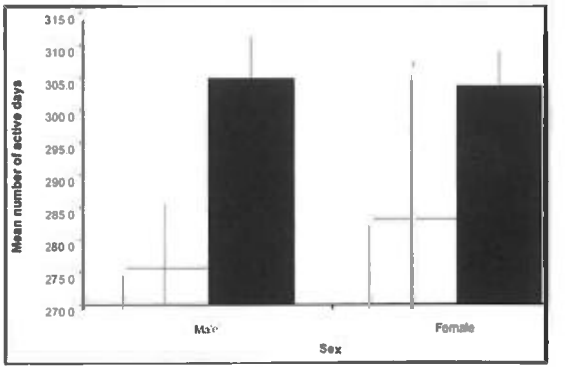


Figure 2. The mean date of last sighting (± standard deviation) for male and female Adders in the years 1960 (open bars) and 2003 (filled bars). There was no significant difference between the sexes, but ingress was significantly different later in 2003 than 1960. Interaction between year and sex was not significant (two–way ANOVA: Sex $F_{1, 24}$= 1.23, P = 0.28; Year $F_{1, 24}$=11.89, P = 0.002; Sex x Year $F_{1, 24}$= 1.65, P = 0.21).

Figure 3. The mean number of active days (± standard deviation) for male and female Adders in the years 1960 (open bars) and 2003 (filled bars). Males were active for a significantly longer period during the year than females, with both sexes being active for significantly longer in 2003 than 1960 (two –way ANOVA: Sex $F_{1, 24}$= 15.56, P = 0.001; Year $F_{1, 24}$= 22.92, P < 0.001; Sex x Year $F_{1, 24}$= 0.01, P = 0.94).



a consequence of the last sighting dates, the combined number of active days was greater in 2003 than in 1960 (Figure 3), and the earlier emergence of males in both years was reflected in a greater number of active days than females (Figure 3). Both males and females showed the same pattern of change in activity in 1960 to 2003 (Figure 3).

Prestt's mean figure for active days for 1960 was males = 219 (range 210–237, n=3) and females = 197.75 (range 170–228, n=4). Data for intervening years did not differ too significantly from Prestt's 1960 results. The most recent data for 2003, number of active days, males, mean = 248.08 (range 230–265, n=12); for females, mean = 228.33 (range 207–244, n=9).

The very significant increase in the number of active days influenced behaviour in other important ways. Firstly, this has presented the opportunity for a higher feeding regime, and one positive indication was that around 50% of both adults within a population moulting more frequently (pers. obs).

It was thought that an increased feeding regime would affect the average size of adults within a population. Data for the general adult population for 1978 showed a mean total length of 470.41mm (range 340–610mm, n=60), and for 2003, a mean total length of 478.42mm (range 345–650mm, n=54). Although this appears insignificant, more meaningful results were obtained by comparing a sample of males of the same age, in the sixth season of growth for the same two periods: 1978 – mean (mm) = 438 (range 410–480, n=5); 2003 – mean (mm) = 485 (range 470–510, n=5); a mean increase of 47mm for this male age group (t = -4.799, df = 5, P = 0.005).

Although respective emergence dates for both males and females were similar, there appear to have been notable changes to the phasing of the male spring moult, and the timing of the mating period. Prestt (1971) shows a peak of the first male moult in mid-April across the adult male population (n=56).

The current study showed a similar peak between the years 1971–1989, and also that the male spring moult was fairly synchronised, with all males within a population moulting over a period of two to five days. Since 1989 there are indications that the male spring moult is becoming more erratic, and phased over several weeks rather than days. However, results so far are inconclusive, in so far as how this may affect mating strategies. Phelps (2008) states that the highest number of mating pairs in 2002 occurred during the first week in April, which is earlier than as stated in Prestt (1971).

DISCUSSION

The number of active days for females slightly exceeding that of males was unexpected, as traditionally the active season of females was around 20 days shorter. It may be that a larger sample will be required to confirm this phenomenon, but currently it is of interest to note that in recent years the latest sightings of Adders at ingress have always been females (pers obs).

It is well known that the male spring moult is the trigger for the mating season (Prestt, 1971; Andren *et al.*, 1997; Phelps, 2004a). The combined phenomena of a less synchronised male spring moult, and that of earlier mating, had the potential of impacting on behaviour. One possible effect was the influence on the male hierarchic structure, an important component of male strategy during the mating period (in press). However, observations in recent years have shown that male behaviour appears so far to be unaffected.

The mean increase in total length of a specific male age group for 1978 and 2003 was significant, and a subtle indication of change. Unless a detailed history of a particular population was known, then such data would remain hidden.

Since 1995 there has been a definite increase in the feeding rate for both males and females, and also the Smooth snake, which occurs in the same area (in prep). It was thought that a higher feeding rate for post-parturition females would influence breeding cycles; but so far this has not been the case. However, since 1995 there are significantly more females with a total length in excess of 650 mm, with the potential of increased fecundity expressed by larger litters (>14). It is appreciated that with an extended foraging opportunity there was a trade-off with increased exposure to

predators, although results to date show that this has been minimal.

There is also a trade-off between the number of potential active days and inactive days because of extended periods of extreme warm weather. Adders reacted in several ways to hot weather, firstly, it was known that some engage in crepuscular and nocturnal activity (Wareham, 1998; Phelps, 2003). A more recent phenomenon was that at Furzebrook, during the summer of 2003, when a number of Adders underwent a period of aestivation for periods of up to 28 days (Phelps, 2003). Adult males actually returned from the summer grounds to the hibernation bank during this period, and the longest period of aestivation was for two non-breeding females that remained in the area throughout the season.

It is almost impossible to forecast how further climate change will affect Adder, and other reptile populations in southern Britain. Results from this study strongly indicate that Adders within specific age groups are larger than their counterparts of 30 years ago. Lourdais *et al.* (2004) in a recent study of *Vipera aspis,* have shown that thermal conditions during pregnancy influence gestation length, embryo viability and offspring phenotypes. It was stated that extended periods of hot weather hastened gestation and reduced the incidence of stillborn. Hot weather early in gestation produced offspring with increased ventral scale counts. This last result is most interesting with regard to the Adder. Lindell *et al.* (1993), in a study of ventral scale counts and body size in the Adder, have shown that there is a probable link between high number of ventral scales, increased growth, body size and survival.

Although the Adder has the widest known range of any snake (Mallow *et al.*, 2003) it is found largely in areas within a moist temperate climate, and in the southern parts of it's range occupies montane habitat (Luiselli, 1995). No part of the Adder's range is characterized by a Mediterranean climate (Capula *et al.*, 1992) and such typical dryer habitats are occupied by other members of the genus, *Vipera aspis, Vipera ammodytes*, and *Vipera latastei* (Arnold, 2002). In some areas the range of the Adder appears to overlap with at least two of the above mentioned species, however they are almost always locally allopatric. Monney (1996) has shown that the Adder and *Vipera aspis*, which appear to have an overlapping range in Switzerland, are actually largely separated by altitude, and also exhibit significant differences in habitat choice.

Results clearly show that so far, the changes in activity cycles have not produced any negative effect, and that population numbers have remained remarkably stable for more than three decades (Phelps, 2004b). However, the present study shows that populations in Britain, and elsewhere in Europe, need careful and consistent monitoring, because the causes, and consequent effects will probably be slow and subtle, and may easily go unnoticed.

ACKNOWLEDGEMENTS

I am indebted to the late Ian Prestt for his help and guidance during the early part of this research. My grateful appreciation to all those who have assisted me in the field over the years. Finally my thanks to Richard Griffiths, Peter Stafford, Rhys Jones, and an anonymous reviewer, for their assistance in the preparation of this paper.

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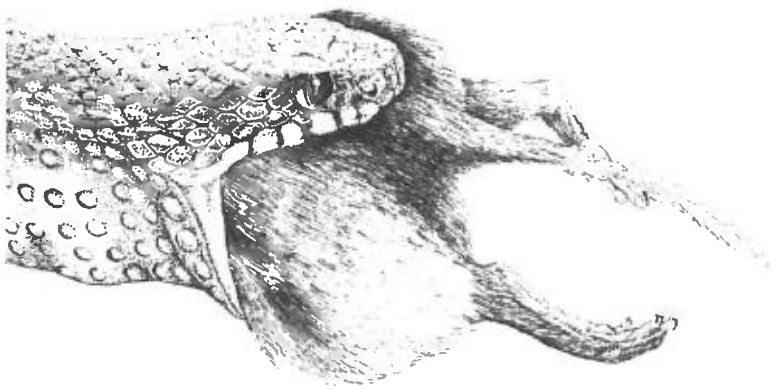

Vipera berus. P. Stafford.

An incidence of *Natrix natrix helvetica* observed in arboreal mating

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THE observation herein described only came about because a study that had been undertaken in Epping Forest since 1994 had to be halted due to 'external influences'. Unfortunately, in an effort to restore the open spaces to Epping Forest and also to encourage growth of Heather (*Calluna vulgaris*), the introduction of Long Horn cattle has meant considerable disturbance to the "traditional haunts" of *Natrix natrix* within the forest and which in turn has interrupted the study situation with fewer and fewer incidents of regular groupings etc. A decision was therefore taken by the author to suspend the study in the interim (or at least until the Long Horn experiment has ended) and relocate to a lake on the Hertfordshire / Essex border that was known locally for the frequency of *Natrix natrix* sightings, so that a continued log of snake activity could be maintained.

Female remaining motionless after having retreated from the males (above) and before, again, being located within the tree branches (below).

The lake is surrounded for much of the perimeter by various shrubs and trees and for the most part is fringed with shallow banks which are covered with mosses and grasses, but, to the southern end, the weir takes the outfall to the Lee Relief Channel.

On 6th April 2007 the author visited the lake, arriving at 08:45 h. At 09:30 h, with the shade temperature at 14°C and rising (considerably warmer in the sun), a "mating ball" of around eight *Natrix natrix* were observed in a sunlit avenue between several trees. The writhing and knotting gradually increased in intensity for at least fifteen minutes before the largest of the group (female) broke free, but, it was quickly followed across the grass, then into and out of the (still chill) water and up another steeper bank. At the ridge of the bank several trees (including willow) push out and overhang the lake at regular intervals with many branches intertwining to form a long running tangle of about 50 metres in length and 10–15 m in height.

On reaching the ridge, the female entered into the lower branches of the trees and began to climb higher and higher, not stopping until her pursuers had lost her 'scent'. There she remained motionless between twigs at a high level (at least 5–6 metres) for around half an hour (see photographs on preceding page), in which time, roughly half of the group of males had dispersed on a wider search of the lake fringes, apparently unaware that the female was above them, all the while. Gradually however, the males that remained at the scene appeared to gain an appreciation of the position and they too began to climb through the tangle, periodically stopping, retracing their movements and retracing again, while all the time, checking the whereabouts of the other males. After twenty minutes or so more (and with the female still remaining motionless) they located her and again began to entwine tails in order to force her to mate. She did not make any further attempt at retreat and the group were still in tree when the author decided to withdraw.

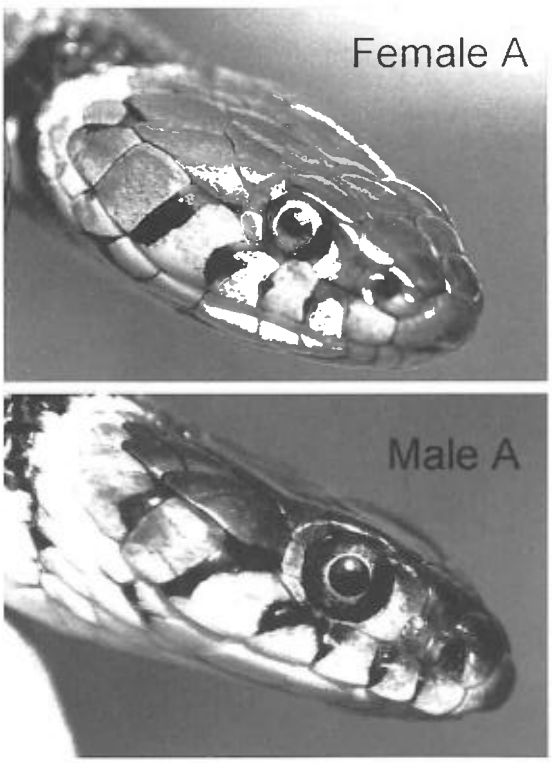
It is not known to the author if this action is a standard diversionary tactic used by individual females on a regular basis, as it seems that this is the first time that such an event had been witnessed in *Natrix natrix* and despite the years of study previously, such behaviour had never been noted (let alone photographed) in Epping Forest.

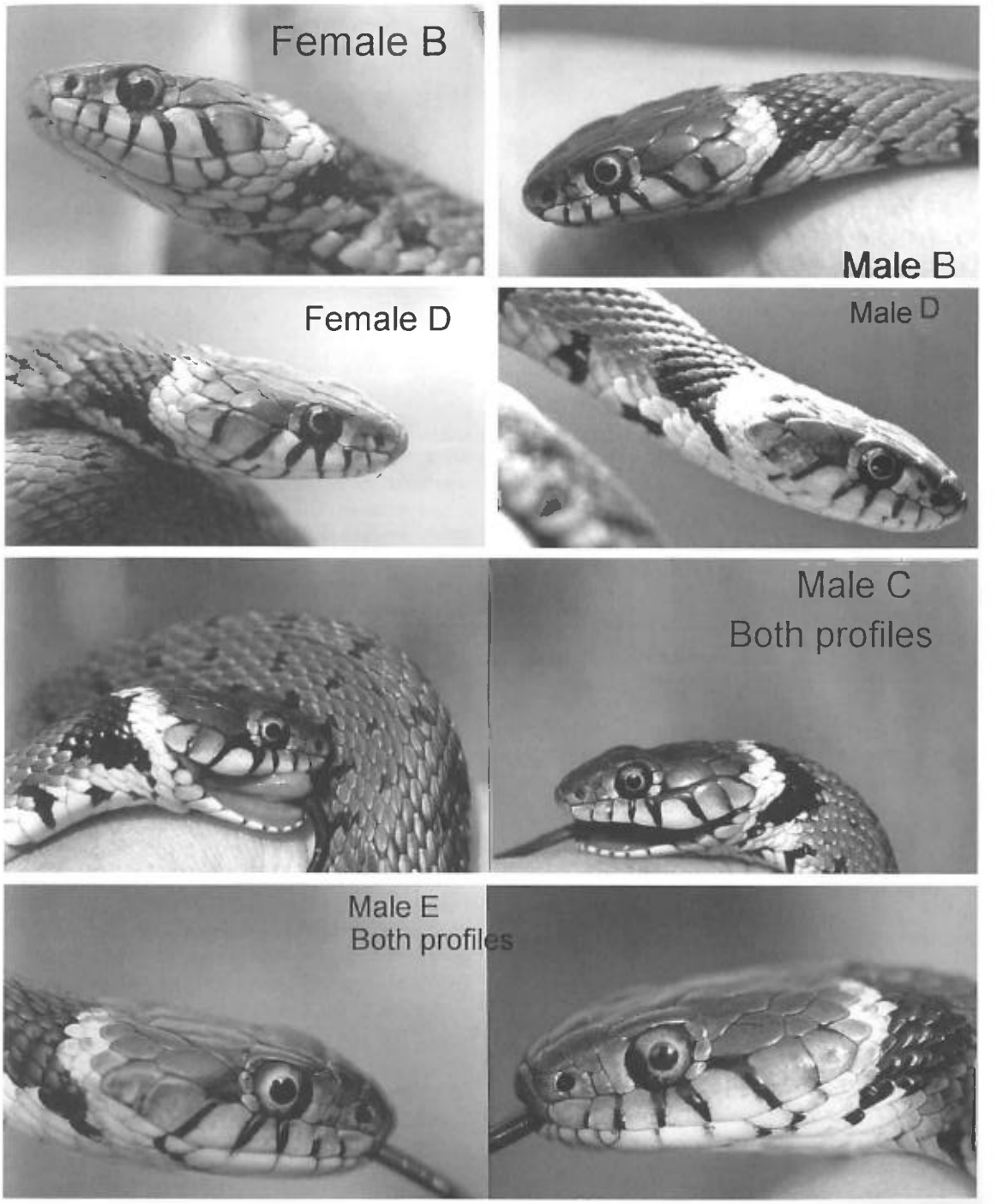
Further notes on individual facial identification of *Natrix natrix* and sexual dimorphism in the incidence of different postocular scale arrangements

WITH reference to an earlier submission (Vaughan, 1999), this study continued until the Spring of 2007. During its course, which spanned between 1994 and 2006 (work in 2007 being suspended due to poor results and too few sightings), several aspects of facial identification had proved to be a success, not least, because it was possible to monitor the movements of a study group within a given area without too much interruption to natural behaviour or pattern-altering interference. Using only the facial patterns and collar / neck colour arrangement it was possible to follow a group in as near-natural behaviour as is possible while still being within study distance.

By using telephoto zoom lenses, many subject individuals were repeatedly noted and identified over the years and from using this technique a log was able to be built showing preferred routes and movements for the group. Obviously, it required considerably more patience than a repeated 'capture-and-identify' approach, and many 'tail shots' simply didn't add up to much and sometimes proved inconclusive in identifying an escaping member of the group, however, the methodology still allowed close detail to be kept and even led to the positive identification of an adult female that had died due to suspected dog attack as well as incidental notes of a breeding male with confirmed copulation with three different females in three consecutive years.

One unexpected aspect of the study which came to light raised an interesting question that cannot immediately be answered, in that the apparent high incidence of distinct scale patterns as a difference between the sexes was so pronounced as to warrant further investigation. It was noted (see photographic examples shown) that a high incidence of two





postocular scales occurred in females and three postocular scales occurred in males.

Of the 111 individuals captured over the period, 53 were photographed in such a way as to portray head and facial patterns (the use of inferior photographic equipment during 1994 to 2000 meant that insufficient facial detailing existed in some shots) and there were 11 confirmed pairs actively involved in the mating process and subsequently recorded by means of a photograph. This did not

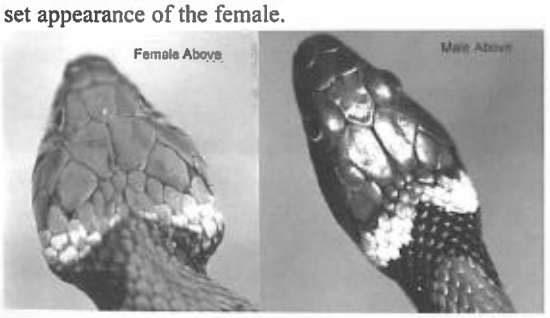
Female H. The only individual positively identified as female (*helvetica*) and with the possibility of three post ocular scales (the lower scale though may be kinked and not separate).

take into account the nine occurrences of "mating balls" observed during the period and which involved many individuals (up to eight) at one gathering and these were not disturbed in any way or counted as a 'pair'.

By taking account of confirmed 'partners' only, this ensured that even where some doubt existed over an individual's sex (it is known that young adult males and females can have a similar head shape and which only becomes more clearly defined when full adulthood /maturity is reached) (see photographs), the results would not be in doubt, as they had been involved in the actual mating process.

In the 11 confirmed pairs of male and female 'partners', only two examples existed where the female appeared to have three post ocular scales rather than two. However, one of those examples, was not thought to be *natrix helvetica*, but, due to the lack of yellow collar and distinct green stripe in evidence, rather suggest a random appearance of *natrix astreptophorus* (its overall influence on future populations cannot be forecast) to have entered the group. The second example had several scale defects apparent on the face and it

Sexual dimorphism in head shape of adult *Natirx natrix*. The male adult head (right) is more slender and has an elongated appearance. It lacks the triangular and thick-set appearance of the female.



Suspected *Natrix n. astreptophorus* also with three postocular scales and confirmed as female.

was therefore difficult to determine if the lower scale was broken or merely 'kinked'.

No explanation is offered by the author for this apparent anomaly between the scale patterns and between the sexes, for as the study originally set out merely to prove that identification of individuals could be achieved solely through photographic means and at distance, the sexing of the study group was not refined so as to include definitive numbers of males and females at the outset and so the actual and precise incidence of "two's" and "three's" cannot be confirmed at numbers higher than the 11 pairs mentioned. It seems reasonable to assume however that such an observation might be more than just coincidence, as twenty individuals from the twenty two confirmed, means that over 90% of females followed the suggested pattern; ie, two post ocular scales and 100% followed the pattern of three post ocular scales for males. If this proves to be the rule generally (countrywide), whether the scale patterns are so formed so as to take account of the difference in head shape between male and female is one suggestion (see photographs) and it is one that would provide the most likely explanation.

ACKNOWLEDGEMENTS

Special thanks also to Gemma Fairchild RAUK for continued endeavours in the maintaining of a web site dedicated to our (UK) native herps, and where the voice of the amateur still rates a mention.

***BUFO BUFO* (European common toad: JUVENILE BASKING BEHAVIOUR.** Fieldwork on the ecology of *B. bufo* on the British Channel Island of Jersey was conducted during 2005–2007. During summer 2006, several daytime visits were made to one of the study sites (Grosnez pond in the Les Landes maritime heath in the NW) to assess pond desiccation. This particular pond was created by stone quarrying in past centuries and is fed by water draining through a cliff face, below which it is situated. It is heavily shaded by the cliff and other large rocks except when the sun is very high in the sky.

On several occasions in May and June 2006, 30 to 40 yearling (20–35 mm) toads (Fig. 1) were seen active along one side of the pond during the early afternoon and in full sun. On at least one occasion the air temperature at this location was in excess of 30°C. Small insects (particularly immature grasshoppers) were abundant there and shelter was available in the form of nearby vegetation and several rocks (Fig. 2). The toads were actively foraging or (apparently) basking, some being very dark in colour (Fig. 1), and "ran" away to hide when I approached. Several at least remained in this area of the pond perimeter until mid-August (C. Lenoir, *pers. comm.*).

Basking behaviour is known in other juvenile toads (reviewed by Carey, 1978) and specifically described for *B. americanus* (Taigen, 1981), as well as high altitude species such as the Andean *B. spinulosus* (Sinsch, 1989) and arid-landscape dwellers like *B. debilis* (Seymour, 1972) and *B. granulosus* (Navas *et al.*, 2007). In European *Bufo*, this type of behaviour is more typical of juvenile green toads (*B. viridis*; *pers. obs.*) and natterjacks (*B. calamita*; T. Beebee, *pers. comm.*) but has not, to my knowledge, previously been described in *B. bufo* (R. Oldham, T. Beebee, *pers. comms.*). Meek & Jolley (2006), however, recorded diurnal sentinel/basking behaviour of adults in their study on *B. bufo* in France and daytime migration has been observed (e.g. Harrison, 1985).

For other *Bufo* spp., juvenile basking behaviour is attributed to the need to raise metabolism and therefore allow increased energy allocation to development (Taigen, 1981; discussed by Navas *et al.*, 2007). I suggest that this is also the case with the juvenile toads at Grosnez pond due to its heavy shading and the (often harsh) conditions on the surrounding heathland.

ACKNOWLEDGEMENTS

I thank Trevor Beebee, Rob Oldham and Richard Griffiths for their comments and Caroline Lenoir for additional field observations.

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Figure 1. Some of the juvenile toads seen active in full sun at Grosnez pond, Jersey, summer 2006. © J. Wilkinson.

Figure 2. Grosnez pond photographed from the adjacent cliff top. The area enclosed by the white line (NW side) is where the juvenile toads were seen. © J. Wilkinson.

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***TRACHYLEPIS SECHELLENSIS* (Seychelles skink): REPRODUCTION.** *Trachylepis* (previously *Mabuya*) *sechellensis* is an abundant lizard species in the Seychelles. It is endemic and occurs on virtually all granitic islands, but it has also been introduced to several coral islands (Cheke, 1984; Gerlach, 2006). It is particularly common near human settlements, but quite rare in densely populated parts of the capital Victoria. Nevertheless, its biology, including reproduction, has been poorly studied.

During a visit to the Seychelles in 2006 a clutch of eggs of *T. sechellensis* was found at Anse Royale on the east coast of Mahé on 7th

Figure 1. Three eggs of *Trachylepis sechellensis* found on the soil under a rock on the east coast of Mahé on 7th April 2006. © H. Bringsøe.

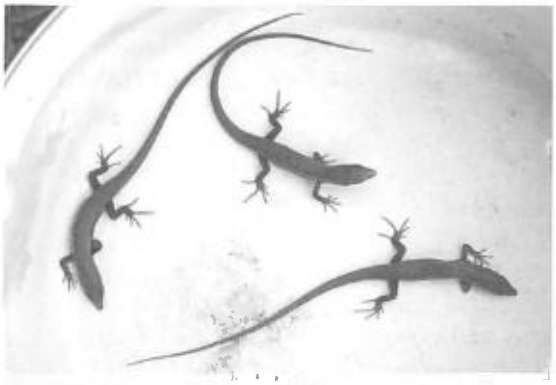

Figure 2. Three hatchlings of *Trachylepis sechellensis*, hatched and photographed on 10th April 2006. © H. Bringsøe.

Figure 3. Ventral surface of hatchling *Trachylepis sechellensis*. Notice the mark after the yolk sac. © H. Bringsøe.

April. The habitat was along the road side about 1 m from a private garden. The clutch consisted of three eggs which were situated in a slight cavity of approximately 3–6 mm on the soil under a rock (Figure 1). Their measurements were as follows: 23.2 x 16.9 mm, 23.6 x 16.7 mm, 23.7 x 17.5 mm.

The three eggs were kept temporarily in a small cloth bag. They hatched three days later, i.e. on 10th April 2006. The measurements of the hatchlings were: SVL 35 mm + tail 72 mm = total length 107 mm; SVL 36 mm + tail 74 mm = total length 110 mm; SVL 36 mm + tail 74 mm = total length 110 mm. They were released after they had been photographed (Figures 2–3).

Trachylepis sechellensis breeds throughout the year, August–October being the peak months (Brooke & Houston, 1983; Cheke, 1984). According to Brooke & Houston (1983) the clutch size of *T. sechellensis* consists of 4–6 eggs whereas Cheke (1984) mentions 2–4 eggs per clutch. It is impossible to say whether the clutch which I found, might have been bigger as it was laid. However, no remains of egg shells were found under the rock and there was no obvious trace of predators. Most probably the eggs were considerably smaller as they were newly deposited. Hatchling size of *T. sechellensis* has so far not been documented and photographs of hatchlings have to my knowledge never been published.

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BOOK REVIEWS

Homalopsid Snakes, Evolution in the Mud

By John C. Murphy

Krieger Publishing Company,
Malabar, Florida

Publication Date: 2007

The subjects of this book, snakes of the family Homalopsidae, are aquatic to semi-aquatic serpents that despite fascinating adaptations to marine, brackish and fresh water and some unusual dietary habits, have received only scant and scattered attention from scientists, and except for some commercial exploitation, even less from the public. Dr. Murphy's book does an admirable job of bringing together the information that is available and presenting it in a stimulating and attractive fashion. Although containing technical information designed for the professional biologist and naturalist, it has much to offer amateur herpetologists and interested laymen willing to learn from it. In general, the illustrations are good, many in colour.

The first section deals with the general biology of these fascinating snakes. It begins by placing the family within the framework of ophidian taxonomy and proceeds to a discussion of the adaptations of these snakes generally to an aquatic lifestyle. The section then gives a succinct, eminently readable account of the rather convoluted history of the nomenclature of what is now the family Homalopsidae, followed by an assessment of the relationship of the homalopsids to other taxa of snakes and of genera within the family, based on modern biochemical taxonomic approaches.

A section on biogeography then follows and outlines the distribution of the group as a whole and provides a map. Reversing of east and west in the text is a somewhat confusing distraction. This section is enhanced by an appendix listing the species by country.

Sections on size and shape and ecology deal with a wider range of subjects on the natural history of these snakes than the sectional titles indicate. The treatment of abiotic factors affecting these snakes include salt, acidity, temperature, tidal cycles and stream gradients supplements the strictly ecological material with discussions of physiological adaptations and the histology of the salt gland. Considerable attention is devoted to feeding behaviour and includes mention of the habit of Gerard's water snake of dismembering its crustacean prey and eating it piecemeal, a most usual feeding pattern for a snake. Most species feed on fish and/or crustaceans. The opposite side of the trophic coin was examined by indicating the known predators of homalopsid snakes. The anatomy of Duvernoy's (venom) gland and the grooved rear fangs is portrayed and the nature of the venom discussed; the symptoms of envenomation of humans are mentioned. It was concluded that snakes of the family usually are not a threat to human health. The brevity of the section on reproduction attests to the paucity of information currently available on that topic.

The treatment of conservation included an inserted section written by Sharon Brooks, John Reynolds, Edward Allison and Touch Bunthang on the exploitation of homalopsids at Tonlé Sap Lake in Cambodia, the site of a truly spectacular snake "fishing" industry where prodigious numbers of snakes are harvested for meat and skins and especially for feeding to crocodiles in farms.

Of especial use to persons not versed in ophidian taxonomy, is a methods section in which characters used in identification are described and illustrated. The key that follows is also richly illustrated by line drawings showing the characters of importance in distinguishing species. These are generally excellent, but one couplet is marred by a labeling line that gives the impression there is a loreal scale in a snake that lacks one.

The major part of the book deals with a species-by-species account including the synonymy, etymology, distribution (with coloured distribution maps), diagnosis, common names, size, external morphology, and then such topics on natural history as habitat, diet and feeding, reproduction and relationships to other species in the family, finally ending with a list of the specimens that were examined. For species with more extensive information available, supplementary topics such as diving and breathing, venom, population dynamics, locomotion, or growth were included – in short, whatever information was available, making the book a valuable reference. Line drawings were used to illustrate salient features and supplemented, when available, by photographs, many in colour. A charming feature of the book is that several species are illustrated by magnificent wood cuts from the literature of the 19th century.

One hopes this book will serve as a model stimulating production of similar treatises for other ophidian families.

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