The HERPETOLOGICAL BULLETIN

Number 102 Winter 2007/2008

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. A 28 year-old male Adder, *Vipera berus* (above) and 32 year-old female (below) monitored during long-term studies at Furzebrook, U.K. © Tony Phelps. See article on page 18.

Printing error

In issue number 100 of *Herpetological Bulletin*, an error occurred on page 34 in the printing of an author's surname. The editor would like to apologize to the author concerned (*JAN DVOŘÁK)* for this oversight. The error affects the printed issue only and not the webpage pdf version. *Ed.*

Kenya Reptile Workshop report

A One-Day Workshop on the Care, Health and Welfare of Reptiles was held at the Nairobi Snake Park, National Museums of Kenya, on Wednesday 13th June. Sponsored and supported by the British Herpetological Society (BHS) Council and Captive Breeding Committee, the Workshop was designed primarily for those who keep and exhibit reptiles. It was intended to provide an introduction to the care of snakes, lizards, tortoises and crocodiles in captivity and how best to keep them healthy.

Fifty-five people attended the Workshop and these participants included curators of reptile collections, owners of 'snake parks' and similar exhibits, academics, professional and amateur herpetologists and local naturalists. The event attracted much interest from the national press and media. Several reporters attended and interviewed speakers and participants, two cameramen stayed for the whole event and the Workshop featured prominently on television.

The day started with registration, followed by introductions. Each participants said who s/he was and explained their interest/involvement in herpetology. Questionnaires were distributed in order to obtain more information about the attendees and their expectations from the Workshop. All attendees received copies of Course Notes and literature that was kindly provided by the BHS, the British Chelonia Group (BCG) and the journal *Applied Herpetology*.

The co-ordinator, Mrs Damaris Rotich (Senior Curator, National Museums of Kenya) welcomed all those present and pointed out that participants had travelled from all parts of the country, some overnight by public bus. She then introduced the morning's chairman, Professor John E. Cooper (The University of the West Indies).

The first lecture, "An Introduction to the Class Reptilia", was given by Damaris Rotich. She reminded the audience that there were approximately 7000 extant species of reptile: 1000 of them are found in Africa and Kenya is home to 400. The particular features of the group were emphasised - ectothermy, specialised anatomy and diverse reproductive patterns.

Mrs Margaret Cooper (The University of the West Indies) was the next speaker. Her subject was "Reptile Law and Ethics: an International Perspective". Mrs Cooper explained the different levels of law (International, Regional and National) that may be applicable to the conservation of the Class Reptilia. She pointed out that, while CITES was the International Convention of most relevance to those wanting to export or import reptiles, others were also important - Ramsar, for example, which protects wetlands where certain species such as freshwater terrapins, are likely to be found. There are also a lot of regional (Indian Ocean) provisions for the protection of sea-turtles. Mrs Cooper discussed, with the aid of powerpoint pictures, the legal constraints on sending live animals or their derivatives overseas. She reminded participants that reptiles for export were likely to need not only a CITES permit but also authorisation under the relevant national conservation and animal health legislation.

A paper by Ms Nancy Kabete (Kenya Wildlife Services), given later in the day, was on a similar theme but concentrating specifically on Kenya. Entitled "The Legal Situation in Kenya", the lecture described the role of Kenya Wildlife Services (KWS) in encouraging the sustainable use of wildlife, including the "farming" of reptiles so that their progeny could be sold and exported overseas. KWS was available to advise on such enterprises, with assistance where needed from the National Museums of Kenya (NMK) and others. In order to start such an operation, an official application had to be made to the Director of KWS, together with a management plan and an environmental impact assessment. An inspection of the location was then carried out by KWS and NMK, and if the inspection report was favourable, authority to take and keep the reptiles was granted, subject to certain conditions. There was particular emphasis in the inspection on the design of cages or enclosures, and cleanliness and unequivocal evidence of successful captive-breeding.

The Director-General of the National Museums of Kenya, Dr. Idle Farah, is presented with a set of Course Notes by John Cooper.

Registration. Each participant receives printed Course Notes and herpetological literature.

Professor Titus Kanui, of the University of Nairobi, introduced the next lecture, on "Reptiles in Captivity", which was presented by Dr Stanley Wambugu. The paper focussed on the maintenance of hinged-back tortoises (*Kinixys* spp.) in captivity but led on to discussion of factors that are pertinent to the care and breeding of other species of reptiles. Professor Kanui pointed out that in Kenya, as in many other countries, the keeping of reptiles has become popular. The underlying philosophy is that reptiles are attractive and because "they do not eat much" are good alternatives to dogs and cats! It was important to counter such ideas, to educate the public properly and to generate sound scientific data on the requirements of these often neglected species.

The final formal lecture of the morning, by Professor Cooper, was entitled "Maintenance of Health and Prevention of Disease" and was intended as a prelude to the afternoon's practical session. The speaker pointed out that health was more than just an absence of disease. It was a positive state, that could be measured. The aim when reptiles are kept in captivity should be to promote their health, rather than merely to control or try to treat diseases. When disease did occur, it could be non-infectious (eg due to trauma, burning or electrocution) or infectious (caused by pathogenic organisms such as viruses, bacteria and worms). The ectothermic nature of reptiles meant that immune and other responses were likely to be inadequate if the environmental temperature was too low or too high. Infectious (including parasitic) diseases could often be excluded by instigating strict quarantine measures, coupled with health-monitoring for incoming reptiles. If this failed, containment (control) or elimination (sometimes involving culling of reptiles) became necessary.

The key to preventing disease and promoting the welfare of captive reptiles was health-monitoring (described graphically as an "early warning system") which consisted of:

a) proper record-keeping and retention of relevant samples eg. shed skins.
b) regular observation of all captive specimens.
c) regular examination of all captive specimens.
d) full clinical investigation, when disease was suspected.
e) post-mortem examination of all reptiles that died.

All but d) and e) could, and should, be carried out by the reptile-keeper. Clinical

One participant examines a lesion on a snake using a hand-lens while others discuss the intricacies of keeping and breeding local species in captivity.

Practical work! John Cooper and assistants demonstrate the handling and examination of reptiles, in the central pit of the Nairobi Snake Park.

and post-mortem (necropsy) examination were largely the preserve of the veterinarian but herpetologists could participate and assist in a number of ways.

Before adjourning for lunch the registrants were addressed by the Director-General of the NMK, Dr Idle Farah, who congratulated the organisers on a successful Workshop and the high level of attendance. He reiterated the need to ensure that reptiles continued to be given better publicity and afforded greater protection in Kenya and elsewhere in East Africa.

The afternoon session, led by Professor Cooper, took place in the Snake Park. It was preceded by a short talk on health and safety and risk-assessment by Mrs. Margaret Cooper and on snakebite by Mrs. Sanda Ashe (an experienced local herpetologist). Participants handled chelonians, snakes and lizards and were taught how to measure their health. Sloughed skins were handled and examined using a hand-lens and transillumination. Investigation of sick reptiles was then demonstrated, using clinical cases - two sand snakes (*Psammophis* spp.) which displayed different types of skin disease.

Finally, a dead Boomslang (*Dispholidus typus*) was dissected, under guidance, by one of the registrants, a recently qualified veterinarian from the University of Nairobi. This was an opportunity

The Press were present in large numbers. Here they are interviewing a Kenyan who breeds and sells chameleons.

The old and the new! Mr. Jackson Iha, Curator of the Nairobi Snake Park in the early 1970s, discusses the features of a sand boa (*Eryx* sp.) being handled by a graduate herpetologist, Beryl Bwong, from the National Museum of Kenya

to provide some practical training and, in so doing, demonstrate both the anatomy and pathology of squamate reptiles and to analyse factors that may have contributed to the snake's decline and demise.

The Workshop concluded with refreshments, closing remarks, the distribution of a final questionnaire and the presentation of certificates. It had been an intensive day of study but registrants confirmed that they had learnt a great deal from the lectures and practical sessions - and from one another. The Workshop had been enhanced by the enthusiastic help and preparation by NMK and Snake Park staff and by the support for the venture given by the Director-General.

A recently qualified veterinary surgeon from the University of Nairobi learns how to dissect a dead snake.

This was, arguably, an important landmark in the evolution of East African herpetology, especially the care of reptiles in captivity. It was appropriate that the NMK's Snake Park, which in past years had played such a key role in promoting studies on reptiles and in the development of herpetological medicine, should provide the venue for this Workshop and might well serve as the focus of future training programmes.

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Postscript

Since the Workshop was held Mrs Rotich has reported that several of the participants have contacted her for further information and advice, for example on record-keeping and how best to obtain educational literature. It has become clear that many reptile-keepers in outlying areas work in isolation and are enthusiastic to improve their facilities and management. Mrs Rotich plans to disseminate further literature and we feel that visits to the collections to provide in situ advice and training could be the way forward.

Return to Nilaveli: Edward Harrison Taylor's Sri Lankan herpetofaunal hotspot revisited

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THE American herpetologist Edward Harrison Taylor (1889–1978; Fig. 1) is widely remembered for his contributions to the systematics of selected taxa, such as caecilians and skinks of the genus *Eumeces*, as well as for his important works on the herpetofauna of the Philippines, Thailand, Mexico and Costa Rica (Adler, 1989). Taylor's contributions to the herpetology of Sri Lanka are less widely known, but no less significant. During the latter part of World War II Taylor was involved in intelligence gathering in Asia for the United States. While based in the region he visited Sri Lanka (then Ceylon) during parts of 1944 and 1945 and eventually published five papers on the lizard and snake fauna of the island (Taylor, 1947b, 1950a, 1950b, 1953a, 1953b) as well as a paper on the dating of Kelaart's *Prodromus Faunae Ceylonicae* (1947a), and a review of P.E.P. Deraniyagala's *A Colored Atlas of Some Vertebrates of Ceylon*, which appeared at the same time as Taylor's own major works.

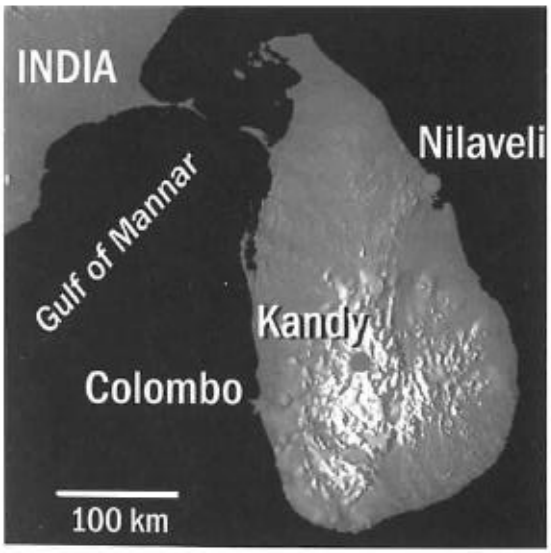
Little is known of Taylor's sojourn in Sri Lanka. His own field notebooks reveal almost nothing. All of Taylor's material from Sri Lanka is listed in Volume 7 of his notebooks and falls in the range of his field series EHT 30165-31260. This run of numbers is interrupted by a smaller number of specimens from Malaysia, India and Singapore. The specimens from Sri Lanka itself total 898 and are in the following series of numbers EHT 30165-232, 30244-46, 30343-67, 30370-89, 30391-495, 30500-18, 30574-672, 305674-755, 30778-31058, 31059-062, 31067-31247, and 31250-31260. Virtually all of these have the locality "12 miles N Trincomalee" (Figure 2) or some variant thereof (e.g., 12-14 miles or 12-16 miles north of Trincomalee). A single specimen of *Python molurus* was collected from a small island 1.5 miles offshore of the same locality and a few specimens were collected 21-23 miles inland of Trincomalee (the holotype of *Sphenomorphus rufogulus* has been incorrectly recorded from "21 mi. E Trincomalee" –a point in the ocean!; Smith *et al.*, 1964). Specimens without specific locality and probably some of those from localities other than Trincomalee were the result of exchanges with European museums and the Colombo Museum (Taylor 1950a). These include lizards from Kandy and Badulla (*Cnemaspis kandiana*), Galle (*Cnemaspis tropidogaster*), and Nuwara Eliya (*Calotes nigrilabris*)

Most of Taylor's Sri Lankan material is today housed in the Illinois Natural History Survey (UIMNH) collection in Champaign, Illinois or in the Field Museum of Natural History (FMNH) in Chicago, Illinois, but Taylor's notes indicate that he made exchanges with other collections, including those in Basel and Amsterdam. The UIMNH collection contains 321 Sri Lankan specimens of amphibians and reptiles, at least 215 of which were collected by Taylor, whereas the Field Museum holds 228 reptiles and 357 amphibians from Taylor's Sri Lankan work. Taylor's herpetofaunal studies were based on these extensive collections, as well as 367 Sri Lankan squamates in the United States National Musuem (USNM) and additional material from the collection of W.W.A. Philips, which was donated to the University of Kansas (Taylor 1950a).

We visited the area that Taylor used as his base during the period 6-8 November 2004 and collected in the vicinity of the Nilaveli Beach Hotel (8°42'22"-8°43'48"N, 81°10'41"-81°11'24"E). By road this hotel is ~18.2 km north of Trincomalee. We searched a number of

Figure 1. Edward H. Taylor circa late 1940s. Photograph courtesy of Kraig Adler.

localities between the hotel and a point approximately 2 km north of the hotel. Although it was not possible to determine exactly where the centre of Taylor's activity had been, this area certainly placed us within 1-2 km of it. The area was near the junction of the area of government control and that of LTTE (Liberation Tigers of Tamil Eelam) at the time of our visit, but as we were in the area during a period of relative calm and rapprochement, our movements were not severely limited. The area consisted of beach front occupied by the hotel and, to the north, by a small fishing village. Just inland from the beach were some isolated patches of native strand vegetation as well as coconut plantations (Figure 3). We conducted our searches by day and night, turning all natural debris as well as trash, peeling bark where possible and scanning trees, shrubs and leaf litter for reptile activity.



Taylor collected material representing 47 species of reptiles north of Trincomalee. In our short stay we collected or observed 14 species of reptiles in the region (Table 1). Ten of these were also collected by Taylor. The four new records include *Varanus salvador* and *Geochelone elegans* (Figure 4), two widespread species that one must assume Taylor encountered, but that may have been passed over because they presented no taxonomic problems and were large and inconvenient to preserve. Another species, *Oligodon arnensis*, may have been missed by Taylor, although it is one of the most common road killed snakes in Sri Lanka and it is odd that none were encountered during Taylor's lengthy stay in the region. We also observed, but did not capture, an unidentified agamid similar to *Calotes liolepis* – a species limited chiefly to the wet zone of southern Sri Lanka (Bahir & Maduwage, 2005).

Not surprisingly, Taylor, in a stay of several months, encountered many more snake species than we did. The most striking snake discoveries made by Taylor relate to typhlopids. He collected 34 typhlopid specimens from the area, all in sandy soil, some only a few feet from the shore of a salt water lagoon in debris left at the high water mark, others under leaves or coconut debris and others in the soil itself, usually under only a few inches of sand (Taylor 1947b). What makes these snakes interesting is that none were assigned by Taylor to

Figure 2. Map of Sri Lanka showing the position of Taylor's site 12 miles north of Trincomalee (Nilaveli) as well as the capitol, Colombo and the highland centre of Kandy. Map from the National Geophysical Data Center GLOBE (Global Land One-kilometer Base Elevation) digital map series.

Taxon	Taylor (1944-45)	Bauer & de Silva (2004)
Testudinidae		
Geochelone elegans		X
Agamidae		
Calotes calotes	X	X
Calotes cf. *liolepis*		X
Calotes versicolor	X	X
Otocryptis nigristigma	X	
Sitana ponticeriana	X	X
Gekkonidae		
Geckoella collegalensis	X	
Hemidactylus brookii parvimaculatus	X	X
Hemidactylus depressus	X	
Hemidactylus frenatus	X	X
Hemidactylus leschenaultii	X	X
Hemidactylus triedrus lankae	X	
Scincidae		
Eutropis beddomii	X	
Eutropis floweri (9/3/44)	X	X
Eutropis carinata	X	
Lygosoma punctata	X	
Lankascincus fallax (23 miles west of Trincomalee) [includes the synonym ***Sphenomorphus rufogulus***, 21 miles E. Trincomalee (sic); 9/44, treated by Taylor as a separate species; synonymy fide Greer (1991)]	X	
Nessia sarasinorum (21 miles west of Trincomalee)	X	
Nessia deraniyagalai (16 mi N Trincomalee; 10/24/44)	X	
Varanidae		
Varanus salvator		X
Typhlopidae		
Typhlops lankaensis (9/13/44)	X	X
Typhlops malcolmi (10/5/44 and 11/44)	X	
Typhlops tenebrarum (10/5/44)	X	
Typhlops veddae (9/29/44)	X	
Typhlops violaceus (10/5/44)	X	
Uropeltidae		
Rhinophis oxyrhynchus	X	X*
Pythonidae		
Python molurus (small islet 1.5 miles offshore, 15 mi. north of Trincomalee)	X	
Colubridae		
Ahaetulla nasutus	X	
Ahaetulla pulverulentus	X	
Amphiesma stolatum	X	
Boiga beddomei	X	
Boiga forsteni	X	
Cerberus rhynchops (in a salt water lagoon)	X	
Chrysopelea taprobanica	X	
Coelognathus helena	X	
Dendrelaphis bifrenalis	X	
Dendrelaphis oliveri (1944)	X	
Dendrelaphis tristis	X	
Lycodon aulicus	X	
Macropisthodon plumbicolor	X	
Oligodon arnensis		X
Oligodon taeniolatus ceylonicus	X	
Ptyas mucosa	X	X
Sibynophis subpunctatus	X	
Xenochrophis piscator	X	
Elapidae		
Lapemis curtis	X	
Microcephalophis gracilis	X	
Naja naja	X	
Pelamis platurus	X	
Viperidae		
Daboia russelii	X	
Hypnale hypnale	X	

Table 1. Reptile species recorded in the vicinity of Trincomalee by Edward H. Taylor (in 1944–45) and the authors (2004). All of Taylor's material was collected "12 miles North of Trincomalee" unless otherwise indicated. Species whose type material was collected near Trincomalee are indicated in bold and their date of collection is indicated. Current names are used for all species. *observed on a subsequent visit to the Nilaveli region.

a known species (contra Mahendra, 1984). In all, Taylor described five new species of typhlopids at this single site – *Typhlops lankaensis*, *T. malcolmi*, *T. tenebrarum*, *T. veddae*, and *T. violaceus*. Mahendra (1984) synonymised all five of Taylor's species with *Ramphotyphlops braminus*, although other workers (e.g. de Silva, 1980) considered them valid or as doubtfully distinct (de Silva, 1990). The status of these taxa has yet to be critically assessed, but at present, all five are considered as good species and all remain known

Figure 3. View of overgrown coconut plantation and beach vegetation (foreground), 2 km north of Nilaveli.

Figure 4. Specimen of *Geochelone elegans* in situ in a tangle of roots, 0.5 km north of Nilaveli Beach Hotel.

Figure 5. Living specimen of *Typhlops lankaensis* from 0.5 km north of Nilaveli Beach Hotel.

Figure 6. Live specimen of *Eutropis floweri* from 1.0 km north of Nilaveli Beach Hotel.

only from the type locality (McDiarmid *et al.*, 1999). Type material for all of these is present in the Field Museum collection, but the holotypes of *Typhlops malcolmi* (EHT 30072) and *T. tenebrarum* (EHT 30063) are apparently lost (Hahn 1980). Despite intensive searching under leaf litter, logs and debris, we collected only a single specimen of one of these species, *T. lankaensis* (Figure 5), in sandy soil at the base of a coconut tree. This species was previously known only from the holotype (FMNH 100066) and numerous FMNH and UIMNH paratypes (Marx, 1976; Philips, 2003).

Interestingly, several lizard species represented by large series in Taylor's collection were not observed by us at all, despite focal searches for these taxa. In particular, the ground-dwelling gecko *Geckoella collegalensis* (Beddome, 1870) reported under "masses of coral and about a plant, *Zanzeveria zeylanica*, growing in sand and coral along the beach" by Taylor (1953a) was not located. Likewise, the agamid *Otocryptis wiegmanni* was found in forest by Taylor in the 1940s. Although we made special checks of the high tide zone to look for *Geckoella* cf. *collegalensis*, no coral rubble of any size was found along the beach and no geckos were located in any of the beach vegetation. Deraniyagala (1945a, 1945b) described *Gymnodactylus* (now *Geckoella*) *yakhuna* from Kalivila and *G. y. zonatus* from Manampitiya. Taylor (1953a) did not examine these specimens but, based on the

published descriptions, assumed that his *G. collegalensis* from the east coast were not the same as Deraniyagala's species. Wickramasinghe and Somaweera (2002) mapped *G. yakahuna* from Trincomalee, possibly on the basis of Taylor's records. We examined some of Taylor's specimens of this gecko (UIMNH 37508-15) and believe that they differ both from *G. yakhuna* from the west coast of Sri Lanka and from *G. collegalensis* from peninsular India, but the resolution of the status of the Trincomalee *Geckoella* awaits a thorough revision of this endemic South Asian genus (Manamendra-Arachchi, 1997).

We also examined Taylor's specimens of *Hemidactylus brookii parvimaculatus* (UIMNH 37553-58), a gecko we also found near Nilaveli, and *H. triedrus lankae* (UIMNH 37560), a species which we did not locate. Two specimens identified by Taylor as the latter species (UIMNH 37559, 37561) were actually *Hemidactylus depressus*, a species that reaches its northeastern limits near Trincomalee (Wickramasinghe and Somaweera 2002). The other *Hemidactylus* found by Taylor, *H. frenatus* and *H. leschenaultii* were common in 2004 and the latter species, which was found to be active both diurnally and nocturnally, was located both on trees and on buildings, including the army and navy guard posts along the road near Nilaveli. Another species reported in large numbers by Taylor near Trincomalee was the agamid *Otocryptis wiegmanni*. Taylor (1953a) noted that there were differences between his coastal specimens and those from highland localities, but recognised no taxonomic distinction between the two. Recently, however, Bahir & Silva (2005) described *Otocryptis nigristigma* from the dry zone (< 2000 mm rain/yr) forests of eastern Sri Lanka, restricting typical *O. wiegmanni* to the southwestern wet zone. Bahir & Silva (2005) mapped a locality for *O. nigristigma* just north of Trincomalee, probably corresponding to Taylor's site, but they did not list specimens from this locality in their material examined. We, therefore, confirmed this specific assignment by examining some of Taylor's original specimens (UIMNH 37530-35). *Otocryptis* spp. are forest dwelling lizards, but we found no suitable habitat in the immediate vicinity of Taylor's locality and observed no *O. nigristigma*. The cases of both *Geckoella* and *Otocryptis* suggest that changing land use in the area may have resulted in the local extirpation of some of the herpetofauna.

Among the lizards, our most exciting find was *Eutropis* (formerly *Mabuya*) *floweri*, otherwise known only from the two types (holotype UIMNH 37565; paratype FMNH 178243) collected by Taylor in September 1944 (Smith *et al.*, 1964; Marx, 1976; Philips, 2003). Our single specimen (Figure 6) was found under the base of a coconut tree stump and was collected only after digging out the space underneath the stump. This same specimen was figured by Das and de Silva (2005). The specimen (AMB 8494, to be deposited in the Department of National Museums, Colombo) is a male of SVL 49 mm and tail length 62 mm. It agrees in all details of scalation with the description provided by Taylor (1950a).

Shortly after our visit to the area, the tsunami of 26th December 2004 hit with full force on this area of coast (Gunatilaka, 2005), completely destroying the Nilaveli Beach Hotel, along with neighboring villages and devastating the coastal zone within 1–2 km of the shore, and with it Taylor's original collecting site. Subsequently, interactions between the Sri Lankan government at the LTTE have deteriorated as well, hindering further field work in the area.

Recent intensive research in Sri Lanka has revealed spectacular diversity in frogs and reptiles (Pethiyagoda & Manamendra-Arachchi, 1998a, 1998b; Meegaskumbura *et al.*, 2002; Bossuyt *et al.*, 2004; Manamendra-Arachchi & Pethayagoda, 2005; Meegaskumbura & Manamendra-Arachchi, 2005; Batuwita & Bahir, 2005) and a continuing stream of descriptions indicates that new taxa remain to be discovered in virtually all major herpetofaunal groups. The majority of this work, however, has been conducted in areas that been under government control for the majority of the period of the Sri Lankan civil war (begun in 1983). Taylor's locality near Trincomalee lies at the northern edge of this area and on the doorstep of Sri Lanka's far north, in which little herpetological work has been conducted. Given the tremendous diversity recorded by Taylor in a very small area, we believe that additional herpetological novelties may be expected from the region.

ACKNOWLEDGEMENTS

Permission to conduct research in Sri Lanka was kindly provided by the Director General, Department of Wildlife Conservation. We also thank the Conservator General of Forests for his approval. We thank Christopher Philips, Center for Biodiversity, Illinois Natural History Survey for the loan of specimens and the microfilm version of Taylor's notebooks and Kalana Maduwage for assistance with the identification of typhlopids. Riyas Ahamed served as our local guide in the Trincomalee area. Ananda Gunatilake kindly provided data about the effects of the tsunami on the Nilaveli coast.

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Precocious reproductive development in a farm-raised and released American alligator, *Alligator mississippiensis*

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ABSTRACT – An alligator trapper from Cameron, Louisiana recently reported harvest of a small "nuisance" alligator (total length = 142.24 cm) which upon internal examination contained 12 hard-shelled eggs within one oviduct. The alligator had been released from a commercial alligator farm as part of Louisiana's alligator egg ranching program 27.75 months prior to being caught. Prior to release, it had been marked with numbered tags attached to the webbing between the toes on the rear feet and by a permanent tail-notch. Based on the size and date of release, the alligator was less than four years old when harvested. To my knowledge this is the smallest female alligator in which reproductive development has been documented..

WILD American alligators (*Alligator mississippiensis*) reach sexual maturity in Louisiana at a minimum estimated total length (TL) of approximately 183 cm (Joanen & McNease, 1980), although a higher percentage of female alligators are reproductively active and nest successfully as TL approaches 213 cm (see review in Elsey *et al.*, 2001a). The age at which wild female alligators reach sexual maturity in Louisiana was estimated to be eight years in estuarine habitats, and thirteen years in paulstrine habitats, where growth rates are slower (Rootes *et al.*, 1991). Wilkinson (1983) reported female alligators in South Carolina do not begin breeding until attaining a TL of 213 cm, at which time they are estimated to be 11.5 years old (Wilkinson & Rhodes, 1997). McIlhenny (1935) reported the smallest female alligator he caught at a nest was 190.5 cm TL, which he estimated to be seven years old. His examination of 175 female alligators killed

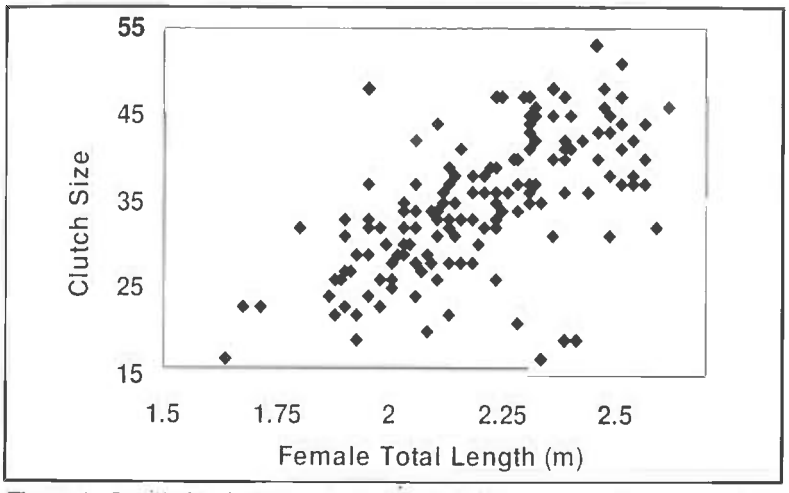

Figure 1. Correlation between clutch size and female total length (m) in *Alligator mississippiensis*.

during the breeding season showed the smallest "with eggs" was 185.42 cm, which led him to conclude female alligators do not breed until they are six or seven years old (McIlhenny, 1935).

In captivity, growth rates of alligators can be markedly accelerated due to animals being fed a high energy diet and maintained in a heated environment, which avoids a winter dormancy seen in wild alligators. These captive-reared alligators grow to a length of approximately 183 cm, and can reach sexual maturity in 5 years, 10 months (70 months total); as compared to wild alligators (from unspecified habitat salinity) that require approximately ten years to attain breeding size (Joanen & McNease, 1987).

In Louisiana, an extensive commercial alligator farming program has been in place since 1986. An alligator egg "ranching" component of this program allows licensed farmers to collect eggs from the wild, and a percentage of the juveniles reared from the hatched eggs are later released back to the wild as part of a "head start" program (Elsey *et al.*, 2001a, 2001b). The superior growth rates of alligators initially raised for one or two years in heated sheds on alligator farms, and subsequently released back to the wild has enabled some farm-released juveniles to reach sexual maturity (based on examination of the reproductive tracts of harvested specimens) and exhibit evidence of nesting in the wild by age 5 years, 10 months (Elsey *et al.*, 2001a).

In many crocodilians, clutch size is strongly correlated with female body size (Thorbjarnarson 1996). Hall (1991) used morphometric models to predict the minimum size (snout-vent length) at reproduction for wild alligators to be 90 cm (approximately 180 cm total length). Joanen (1969) found the smallest female to have nested in his study to be 68.25" TL (173.36 cm) and having a clutch size of 28 eggs; with the average clutch size in that population being 38.9 eggs. A more recent paper (Platt *et al.*, 2004) reviewed the maximum clutch size in American alligators and the relationship between clutch size and female total length, and predicted body length in females based on clutch size (Hall 1991).

OBSERVATIONS

As part of Louisiana's "nuisance" alligator program established to allow for take of alligators causing conflicts or safety concerns for citizens, licensed nuisance trappers are called to relocate or harvest problem alligators. Trappers are mandated to maintain written records of complaints received and the disposition of the alligator in each case for which they are asked to respond.

On approximately 8th August 2006, I received such documents from Mr. Malcolm Savoie from the town of Cameron, Louisiana (Cameron Parish) and upon review noted the written comment "5041170 had 12 eggs hard shell" recorded for an alligator he harvested on 2nd August 2006. I immediately looked at the length of the alligator, which would be of interest as the alligator had been tagged and marked as part of Louisiana's alligator egg ranching program; we have previously documented successful reproduction of farm-released alligators after their release to the wild as part of a "head-start" program (Elsey *et al.*, 2001a). Mr. Savoie listed the alligator's length as 4' 8" (56" TL, or 142.24 cm). As previously mentioned it is generally accepted that female alligators are usually approximately 72" TL (183 cm) when they become sexually mature, although we have documented smaller alligators at successful nests (LDWF unpublished data as detailed below).

The web tag and tail notch on the alligator revealed it had been marked and released from an alligator farm on 12 April 2004, at which time it was 47" TL (119.38 cm). The tail notch reported by Mr. Savoie was the same ("DG") as per our agency's records for the alligator bearing the web tags he reported. The alligator was noted to be female at the time of release, and the growth interval was appropriate (Elsey *et al.*, 2001b). The land company on which the alligator was released was in close proximity to the residential yard from which the nuisance complaint was filed in a rural area of West Creole, Louisiana. It was not noted to be at or near an alligator nest when caught.

I telephoned the trapper and specifically asked if the alligator had any part of the tail missing; he said it did not. I inquired if the term "eggs" was meant to imply an oval, completely formed egg (because he had supplied the term "hard shell" it seemed likely, however I have heard local trappers use the term "egg" in reference to retained follicles/ova present in an ovary). Mr. Savoie had not personally seen the eggs in question, but referred me to the gentleman who processed the carcass for meat after having removed the hide and had reported the finding. He confirmed what he observed were hard-shelled eggs, and supplied me with four he had saved as he realized it was an unusual finding in such a small alligator. When asked, he stated all twelve eggs were found in one oviduct ("channel") and he had examined the contralateral oviduct, which did not contain further eggs.

The mean length, width, and mass of the four eggs were (mean +/- SEM) 66.57 +/- 1.10 mm; 38.25 +/- 0.53 mm; and 56.52 +/- 2.25 g, respectively; somewhat smaller than normal for alligator eggs. The four eggs examined were infertile and several had mild chalky deposits on the outer surface and two had minor cracks on one pole.

The length of the alligator when initially measured by Louisiana Department of Wildlife and Fisheries staff at a commercial alligator farm immediately prior to release to the wild indicated it had been hatched in late August or early September of 2002. Therefore, this female alligator was less than four years of age when she developed the hard-shelled eggs.

I reviewed data previously collected predominantly on Rockefeller Wildlife Refuge, wherein we captured female alligators at nests (n = 163 nests in ten collecting seasons between 1992 and 2006; although only three nests were from 1992, two from 1995, and one in 1996) and collected the entire clutch of eggs, allowing us to examine the relationship between TL of female alligators and clutch size. There was a strong positive linear correlation between female TL and clutch size ($r^2 = 0.62$; $P < 0.0001$, Fig. 1). In three cases a large female had a relatively small clutch (n = 17, 19, and 19); we speculate that these females had one functioning ovary/oviduct as the clutch sizes of 17, 19, and 19 are about half of a normal clutch quantity. Excluding these three outliers improves the fit of the model ($r^2 = 0.69$, $P < 0.0001$, n = 160). The two smallest clutches in past years were a clutch of 17 eggs from a 163.83 cm female (64.5" TL); and a clutch of 23 eggs from a 171.45 cm female (67.5"); all 23 hatched successfully after incubation in our field laboratory. The eggs from the clutch of 17 were sacrificed intermittently throughout incubation for another study, thus hatch rates are unavailable; but the eggs appeared viable when removed from the incubator.

DISCUSSION

The 142.24 cm (TL) female alligator containing hard-shelled eggs in the oviduct is to my knowledge the smallest and youngest alligator to have demonstrated reproductive activity. I was unable to determine if this female actually constructed a nest in 2006. Nest construction usually occurs in June, and females often (but not always) remain in nest attendance until hatching in late August or early September. The alligator was not reported to be at or near a nest upon capture. It is possible that due to the severe drought conditions in southwest Louisiana in 2006 she did not construct or attempt to construct a nest, or she may have aborted nesting efforts and retained eggs in the oviduct. In addition, she also may have been forced to move away from a nest site to seek a den or source of water, again due to severe drought conditions. Moreover, it is also possible that this alligator did expel eggs from one oviduct, and retained the eggs in the other oviduct. However, it is unlikely such a small female would have produced ~ 24 eggs, if she had approximately the same number of eggs in each oviduct.

The alligator described in this account may have experienced accelerated reproductive development, because it was initially reared in a captive setting on a commercial alligator farm under an aggressive heating and feeding regime, which leads to rapid growth (Elsey *et al.* 2001a, 2001b). Still, this is an unusually small alligator to have exhibited reproductive development. The eggs appeared to be infertile owing to the lack of the opaque band on the eggshell, which can be used to determine fertility and age the developing embryo (Ferguson 1982). It is unknown if female alligators must physically mate with a male alligator in order to initiate the development of fully calcified eggshells, or if infertile eggs can develop in the absence of breeding behavior or copulation. Of note, we have previously observed eggs in alligator nests in which the entire clutch is infertile.

According to the equation of Hall (1991) for predicting female body length from clutch size in alligators [TL = 144.41 + 2.1512CS ($r^2 = 0.64$; SE = $\pm$ 12.8 cm)], a clutch size of 12 eggs would be produced by a female of 170.22 cm; substantially larger than the 142.24 cm measured for the female reported herein.

The philosophy of 'sustained use management' in crocodilian egg ranching has been accepted as a sound wildlife management practice, and the rapid onset of sexual maturity and documentation of successful breeding of 'head start' reintroduced specimens can be helpful to resource managers considering similar programs. The case described in this paper is another example of rapid attainment of reproductive activity in reintroduced alligators, at even a younger age and smaller size than those previously described (Elsey *et al.*, 2001a).

ACKNOWLEDGEMENTS

I thank Mr. Malcolm Savoie for his reporting harvest information on the alligator and clutch described herein, and Mr. V. H. Faul for providing additional details and eggs for measurement. I thank Mr. W. Parke Moore III for administrative assistance at the time of the study, and Lisa Morris DeReus of the Department of Experimental Statistics at Louisiana State University for technical advice. I appreciate input from Jon Wiebe, Dr. Steve Platt, Dr. Val Lance, and two anonymous reviewers for helpful comments on an earlier draft of the manuscript.

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An observation of *Calumma tigris* (Squamata: Chamaeleonidae) feeding on White-footed ants, *Technomyrmex albipes* complex, in the Seychelles

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ABSTRACT – A sub-dult *Calumma tigris* was observed eating White-footed ants, *Technomyrmex albipes* complex, in the Vallée de Mai national park on Praslin (Seychelles). It is noteworthy that this species of ant is, as far as can be demonstrated, not eaten by any other predator in the Seychelles. Considering the restricted range and possibly low population densities of *C. tigris*, it will be relevant to investigate its natural diet. It will also be crucial to monitor the role of White-footed ants in Seychellois ecosystems which are fragile and very sensitive to allochthonous species.

THE biology of the Tiger chameleon, *Calumma tigris* (Kuhl, 1820), of the Seychelles is not well known. Merely a little anecdotal information has been published and some scattered reports on reproduction exist. Thus, until proper studies will be carried out, virtually any contribution to the biology of *C. tigris* may prove valuable.

Calumna tigris is a relatively small species which normally attains a total length of approx 16 cm. The SVL is slightly greater than the tail as it has been reported to constitute 51–53% of the total length (Bourgat & Domergue, 1971). Cheke (1984) mentioned an individual of 88 mm SVL which might well have corresponded to a total length of some 16.6–17.3 cm. However, the species may grow much bigger as Nečas (2004a, 2004b) recorded an exceptionally large individual of 23 cm total length. According to Nečas (pers. comm. 2007) it was kept in captivity and he personally measured it. A distinctive feature of *C. tigris* is the pointed projection on the chin which can be up to 3 mm long (resembling a goat's beard!). The head has a low casque without occipital lobes, slightly outgrowing the dorsal crest. The parietal crest is curved and bifurcated at about two thirds into two protrusions that extend up to each orbital crest. The gular crest consists of 9–15 enlarged conical scales. The dorsal crest consists of 14–23 isolated conical scales. The dorsal colouration is variable. It may be nearly uniform, i.e. from quiet light grey or light brown to yellow, yellow-orange, green or dark brown. This base colour may also have conspicuous black spots or some brighter coloured markings. Generally a light coloured vertebral line is present. An interesting observation on colour change has been expressed by van Heygen & van Heygen (2004). They state that the colours of *C. tigris* depend on the environment, i.e. crypsis as the individuals resemble a random sample of the relevant aspects of their environment. That would be unusual for chameleons (Nečas, 2004a, 2004b)!

Calumna tigris is an endemic of the Seychelles and is distributed only on the three islands of Mahé, Praslin and Silhouette (Cheke, 1984). It is unclear how common and widespread the species may be on these three islands though it is generally considered comparatively uncommon, cf. Gardner (1986). This arboreal species is found in primary forest, secondary forest and upland rural gardens.

In April 2006 my wife (Aoi Bringsøe) and I spent two weeks on the granitic islands of the Seychelles. This paper deals with an observation made in the small national park Vallée de Mai on the island of Praslin. The park is a World Heritage Site and is home to the renowned coco-de-mer palm (*Lodoicea maldivica*) which produces the largest seed (a nut) in the plant kingdom. We had three day excursions and two night excursions in the small park. Each of the five excursions lasted for approx. 1½-2 hours.

We found three individuals of *Calumma tigris* in the primary forest of Vallée de Mai, two sleeping at night and one being active during the day. All were observed at least 50 metres away from streams though other observers have regularly

Figure 1. Microhabitat of *Calumma tigris* eating ants in a coco-de-mer palm. © H. Bringsøe.

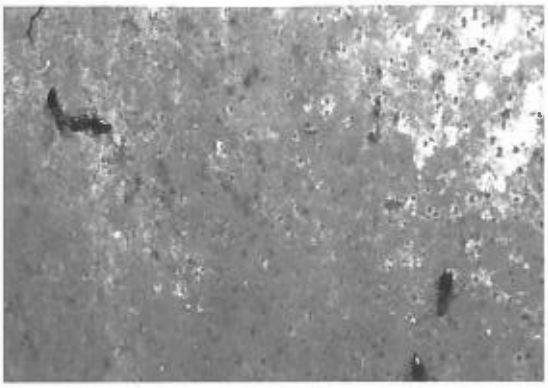

Figure 3. White-footed ants, *Technomyrmex* cf. *albipes*, on a coco-de-mer palm. © H. Bringsøe.

recorded *C. tigris* in close proximity to streams and ponds (Neèas, 2004a, 2004b). Another three chameleons which we found on Mahé during the day, were also living well away from aquatic habitats.

At 11:15–11:30 h on 16th April 2006 we observed one chameleon in a coco-de-mer palm at a height of approximately 1 m (Fig. 1). The coco-de-mer was immature and not fully grown as it had not yet developed a pillar-like trunk. Its total height was estimated to 11–14 m. The microhabitat was shaded in the dense forest. Air temperature was 31°C. The altitude was approximately 350 m.

The individual remained undisturbed and continued its foraging activities. It was actively hunting small black ants, length approx. 2.0–2.5 mm (Figs. 2–3). In two cases we observed the chameleon 'shooting' ants which were swallowed quickly without any sign of distaste.

Afterwards, the sub-adult chameleon was measured (SVL 63 mm + tail 66 mm = total length 129 mm), and then released. Its dorsal and lateral colouration was light brown, nearly uniform with scattered dark brown, greenish and light markings.

Later the ants were identified on basis on the photograph (Fig. 3) by J. Gerlach (pers. comm.) as a member of the *Technomyrmex albipes* complex (White-footed ant). This group is at present being revised and it is expected that several closely related species may be recognised.

The natural diet of *C. tigris* has not been investigated; basically it is only known that *C. tigris* lives on insects (Cheke, 1984), like most other chameleons. Individuals in captivity have accepted a wide variety of insects. Fruit flies (*Drosophila*) were eaten according to Bourgat & Domergue (1971) whereas small grasshoppers were not accepted. Grimm & Grimm (1999) used soft-shelled insects up to a length of 10 mm and presented a photo of an individual shooting a cricket at nymph stage. van Heygen & van Heygen (2004) stated that various smaller insects including house flies are eaten.

Figure 2. *Calumma tigris* hunting ants. © H. Bringsøe.

Technomyrmex cf. *albipes* is a pantropical species of Indo-Pacific origin. It is abundant in all terrestrial habitats in the Seychelles. Dorow (1996) states that *T. albipes* was introduced into the Seychelles in the 18th or early 19th century (with reference to Dupont, 1937). However, according to Gerlach (pers. comm.) it is a tramp species well-adapted to both human-assisted dispersal and natural dispersal, and he considers that it is not clear whether the presence of *T. albipes* was introduced by man or not. This species is considered a pest and an invasive species in USA (Suarez *et al.*, 2005), however, its role in the Seychelles is not fully known. This type of ant possesses a sort of venom gland containing unsaturated secondary amines, and the ant also produces cyclopentanoid monoterpene alkaloids (Brophy *et al.*, 1993). The antipredator effect of these compounds has not been fully documented. This ant is considered relatively unaggressive by Pacinotti (pers. comm.) since it is eaten by Asian toads *Duttaphrynus* (former *Bufo*) *melanostictus* and various birds in the Danish tropical zoo Randers Regnskov where it has established a colony. In the Seychelles the endemic tree frog *Tachycnemis seychellensis* has been recorded preying on *T. albipes* (Gerlach & Rocamora, 2004).

Considering the restricted range and possibly low population densities of *Calumma tigris*, it will be relevant to carry out a detailed investigation of its natural diet. It will also be crucial to monitor the role of White-footed ants in Seychellois ecosystems which are fragile and very sensitive to the presence of allochthonous species.

ACKNOWLEDGEMENTS

I am grateful to Lindsay Chong-Seng (Seychelles Island Foundation) who helped us on our travels. Atterville Cedras and Wenner Anacoura (Seychelles Island Foundation, Vallée de Mai) facilitated our work in Vallée de Mai. Justin Gerlach (Nature Protection Trust of Seychelles) kindly identified the ants. Useful information on White-footed ants was provided by Philip S. Ward (University of California, Davis, California), Wolfgang H.O. Dorow (Projekt Hessische Naturwaldreservate, Forschungsinstitut Senckenberg, Frankfurt am Main) and Sergio Pacinotti (Randers Regnskov Tropical Zoo, Randers, Denmark).

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Reproductive strategies and life history traits of the Adder, *Vipera berus* (Serpentes: Viperidae), in southern England and central Wales

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THIS study of the Adder, *Vipera berus*, was unusual in that it spanned a very long period of time, from 1971 until 2003. The life histories of a significant number of snakes, particularly breeding cycles of females, were made known. This sample included a large number of Adders recorded from birth to old age or death. A total of 2200 males and 1934 females were identified throughout the period of research. Results confirm the findings of other researchers with regard to large male advantage, and furthermore define a clear hierarchic structure within the male population. The length of the study period revealed that a biennial female breeding cycle was the exception, and that a more irregular cycle was the norm with positive benefits relating to survival and longevity.

The life history traits of the Adder, *Vipera berus*, are now well known, and it is arguably the most intensively studied snake in the world (Shine & Madsen, 1994; Phelps, 2004a). During the last three decades or so much has been revealed with regard to reproductive behaviour and seasonal movement, including pioneering work in England and Scandinavia (Viitanen, 1967; Prestt, 1971; Phelps, 1978; Nilson,1980; Andren, 1981; Madsen, 1988; Andren *et al.*,1997).

A fundamental feature of Adder ecology is fidelity to the hibernation site and associated mating areas. There has been some consensus with regard to site fidelity in the short term (Prestt, 1971; Phelps, 1978; Madsen & Shine,1993; Luiselli, 1994). Volkl & Biella (1988) conducted a long term study of the Adder in the German highlands and found that the various mating areas were occupied by the same subpopulations each year, and this was confirmed for the duration of the study. More recently, subpopulations in southern Dorset have been defined as stable autonomous mating and breeding units for a period of more than three decades (Phelps, 2004b).

Although this pattern of distribution could be described as the 'norm' where optimum conditions exist, it is equally likely that more dynamic habitats would exhibit fluctuations with regard to population numbers and site fidelity. Prey resources have a direct impact on population stability. Extreme examples of this have been found in insular populations off the coast of Sweden where numbers can range from ten to two hundred individuals, which can be directly attributed to a narrow adult prey spectrum, namely one species of vole, *Microtus agrestis*, which varies temporally in numbers (Andren, 1982; Andren & Nilson, 1983). Adder populations can also be dramatically affected by excessive predation. Again in the German highlands, Volkl & Thiesmeier (2002) found that a former stable population suffered a decline because of habitat loss and predation by Wild boar, *Sus scrofa*. Wild boars are also known to have a negative effect on snake populations in other areas (Filippi & Luiselli, 2002, 2003).

Climate and topography are also major influences. Kaseweiter *et al.* (2004), in a study of a population in the Lech Valley in southern Bavaria, found no site fidelity and explains that this is caused by the dynamic habitat which changes after each spring flood. Human influences on Adder populations are exemplified by the fragments of heathland within urban areas of southern Dorset where there are high levels of disturbance most often in the form of regular fires, but also from other factors such as motorcycle erosion, persecution, and predation by domestic cats, *Felis catus*.

Recently, high levels of heathland management have introduced a new dynamic which has had a

significant impact on former stable populations with regard to disturbance and mortality (in prep). Habitat dynamics have a direct influence on reproductive output and frequency (Capula *et al.*, 1992). Phelps (2004b) found that in a stable environment, population numbers hardly varied over a thirty year period and adult sex ratios were maintained. The main effect in more disturbed areas is an imbalance of the adult sex ratio, which disrupts the breeding cycle. Heath fires in the early spring can cause high mortality of adult males, which are the first to emerge from hibernation and therefore the most exposed. Such events are often quick surface fires, and females, which emerge later, appear to survive to a higher degree, although much depends on the availability and proximity of adequate cover (in prep.). This study embraces a range of habitats and conditions representative of a variable lifestyle for the Adder in southern England and central Wales

A number of viperids from temperate regions exhibit communal behaviour in that they form aggregations at winter dens, and are most obvious during emergence in the spring and again at ingress in the autumn. Spring aggregations are not necessarily associated with a spring breeding cycle. The North American rattlesnakes *Crotalus horridus* and *Crotalus viridis,* for example mate during summer when dispersed from the winter dens. This mating system is typical for a number of North American pitvipers (Duvall *et al.*, 1992). It has been hypothesized that communal hibernation may be a comparatively recent event and a summer mating system is a relict component that has survived to the present day. Duvall (1992) has suggested that summer mating in North America pitvipers evolved in response to (i) the pattern of the adult shed cycle (King & Duvall, 1990) and (ii) the Type IIFY female reproductive cycle (Rahn, 1942; Klauber, 1972; Aldridge, 1979). Another explanation is that females are not sexually receptive during the spring period (King & Duvall, 1990).

The Adder adheres to a spring breeding cycle, although within the Arctic Circle the mating period begins in June (Anderson, 2004). The mating period is triggered by the spring moult of the adult males which is more or less synchronised within a population. Agonistic behaviour of males following the spring moult is well known (Prestt, 1971; Andren, *et.al.*, 1997; Luiselli, 1995; Hoggren & Tegelstrom, 2002). My study has shown, however, that adult males within a subpopulation form a hierachic group and competitive interaction exists at various levels in accordance with size and also age. This hierarchic structure is founded on first (large) male advantage with the result that as few as 30% of males actually mate successfully (Phelps, 2004a). Hoggren & Tegelstrom (2002) have also provided genetic evidence for first male advantage in the Adder.

Phelps (2004b) has shown that although birth litters consistently exhibit an even sex ratio the adult ratio is male biased. This is explained by the high mortality of young females that breed in the first year of maturity, and a corresponding lower cost of reproduction in males. A biennial breeding cycle has often been quoted to be the 'norm' for female Adders throughout much of its range (Smith, 1951; Saint Girons & Kramer, 1963; Prestt, 1971; Nilson, 1981) and this statistic is also quoted in more recent literature (Beebee & Griffiths, 2000; Arnold, 2002), although it is also noted by several of these authors that in Scandinavia females breed every third year. This study is perhaps unique in that the life histories of individual snakes for a period of over thirty years have been made known. An important consequence of this is the revelation that females do not maintain a biennial breeding cycle throughout life even in areas that contain a consistently high level and wide spectrum prey resource.

Information with regard to survival and longevity has been gathered mainly from Swedish studies where Adders existed as insular populations or occupied a variable environment (Andren, 1982; Madsen, 1988; Madsen & Shine, 1994; Forsman, 1995). These studies have suggested that Adders attain an age of around ten years and are sexually productive just two or three times during a lifetime. My study strongly indicates that Adders in a stable environment have the potential for a much longer lifespan and are not compromised by old age, and that a delayed and irregular female breeding cycle together with a hierarchic male structure suggests a successful strategy for survival and longevity.

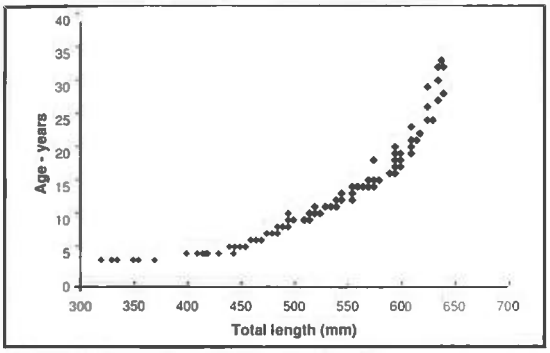


Figure 1. Size and age structure of adult males across six subpopulations at Studland, Dorset.

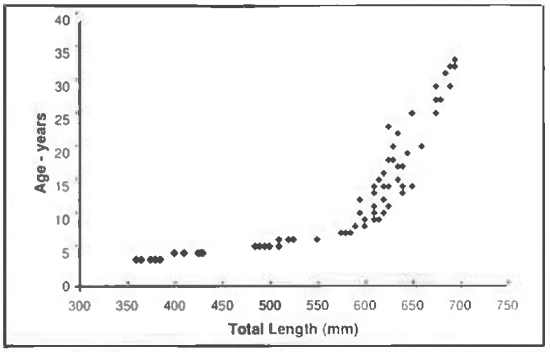


Figure 2. Size and age structure of adult females across six subpopulations at Studland, Dorset.

METHODS

Duration and study areas

The study was first initiated in 1971 and continued through until 1980, and then resumed again in 1986 until 2003. Six key sites in south east Dorset were established during 1971 and 1972, and all but one (Norden), are large areas of protected heathland with two (Furzebrook and Wareham Forest) being part of the original study areas of Prestt's (1971) pioneering work. These areas have been shown to contain the most stable Adder populations, although in recent years there has been a negative impact because of to inappropriate habitat management (in prep.).

Three other sites represent more dynamic habitats subject to disturbance or other negative influences. One area situated in the Mendip Hills, Somerset, consists of a number of clearings with variable heather cover within a pine forest. Another embraces Cors Caron, National Nature Reserve, a raised bog in Ceridigion, central Wales. The third site is a 45 ha fragment of urban heath near Bournemouth, southern Dorset. Although vulnerable, for various reasons these three sites all contain, or have contained, high density Adder populations. Study on these more dynamic sites began in 1989.

Table 1. General population numbers and stability of adult *Vipera berus* throughout the six key study areas in south east Dorset. Also showing a consistently male biased sex ratio.

Site Name	2004		1974 - 2003 maximum		1974 - 2003 minimum		No. of subpopulations
	males	females	males	females	males	females	
Furzebrook	48	35	52	41	42	30	6
East Creech	85	58	91	71	81	52	10
Norden	36	26	41	34	32	24	2
Studland	77	62	81	71	72	54	11
Wareham	59	44	64	52	50	38	8
Hartland	85	62	93	74	85	62	9

Identifying individual Adders

On first capture, individual immature and adult Adders were permanently and uniquely marked by clipping a series of four ventral scales (see Prestt, 1971 for details). Each Adder was also examined for unusual scalation, markings and scarring. Since 1989 each Adder has been photographed for identification of head and dorsal markings (see Sheldon & Bradley, 1989; Benson, 1999). Adders were measured in plastic tubes of appropriate size to an accuracy of ± 5mm and weighed with a fine spring balance. From early on in the study non-invasive techniques were employed as far as possible. When it became possible to identify individual Adders by sight alone much was achieved by passive observation. Most sampling, weighing, measuring, and identification photography took

place shortly after emergence with further recording in the summer grounds and again at ingress in the autumn. It was policy not to disturb any Adders engaged in mating activity, and sampling for this period involved only juveniles, immature and non-breeding females. During the latter part of gestation a number of females, average four to six each season, were held to record brood sizes, identification of neonates and physiological factors pertaining to the female. Most females were held for no more than six days. Females and their broods were returned to their place of origin shortly after parturition.

RESULTS

Population structure and site fidelity

A four year period of intensive mark and recapture at the six key study areas was sufficient to assess accurately adult population numbers. (Phelps, 2004b) gives details for two of these (Furzebrook and Norden). It also became clear that in a general area Adders are split into a variable number of distinctive groups, described here as subpopulations. These subpopulations may be separated by as little as 300 metres but adults have consistently exhibited a 100% fidelity and mating autonomy. In the key study areas the general population numbers have been remarkably stable (Table 1). Immature Adders, both males and females in their second season and older, never constituted more than 15% of the total population and at Furzebrook and Norden this was as low as 10% (Phelps, 2004b). This contrasts markedly with the Smooth snake, *Coronella austriaca*, and Grass snake, *Natrix natrix*, which occurred in the same areas in which immature snakes constituted 30% and 40% respectively of the general population (Phelps, 2004a). Phelps (2004b) also explains how, for a confined autonomous mating group, genetic integrity is maintained by the random dispersal of immature Adders and their final placement as young adults in subpopulations other than their birthplace. In other words, once an Adder, male or female, has been absorbed into a subpopulation then site fidelity is maintained through life.

males	females	breeding females
8	6	2 = 33.33%
9	7	4 = 57.14%
11	8	3 = 37.51%
8	5	1 = 20.00%
10	7	3 = 42.85%
12	9	5 = 55.50%
10	8	4 = 50.00%
8	6	2 = 33.33%

Table 2. Details of adult numbers within subpopulations at Hartland Dorset and breeding status of females at 2002 showing that 38.70% of the total adult female population were breeding (n = 24). This figure was fairly constant for this and the other key study areas in Dorset (range 32-42% n = 287 range 260 - 343).

Reproductive sex ratios

The total number of adults active during the mating period is described as the Operational Sex Ratio (OSR). This usually involved 100% of the adult males, regardless of size, and 32–42% of adult females (Table 2). At subpopulation level Table 2 shows that at Hartland in 2002 throughout the metapopulation, breeding females represented between 20% and 57.14%, which was found to be fairly constant for subpopulations in this and the other key study areas and reflects the irregular breeding pattern of adult females.

Negative influences impacted on the more dynamic areas in a number of ways. In the Mendip Hills, a metapopulation of 72 adults (40 males, 32 females) were divided into four subpopulations, two of which were close to a popular walking and picnic area. The main consequence was habitat degeneration through trampling, but also a fairly high level of persecution, particularly of exposed breeding females during the summer. One subpopulation lost eight females over a two year period (1998 and 1999), which represented 80% of the adult females, and has since shown little sign of recovery, and further degeneration of habitat has probably negated any recruitment from nearby subpopulations.

The Adder metapopulation at Cors Caron was spread over sphagnum bog and along the route of a disused railway and represented a total of 88 adults (52 males, 36 females), divided into five subpopulations. Three of the subpopulations hibernated just a few centimetres above the water

Date	Males	Females	Source	Distance (m)
2000	2	9	-	
2001	3	9	subpopulation 3	400
2002	4	8	subpopulation 2	550
2003	4	8		-
2004	6	8	subpopulation 3 & 6	400 & 300

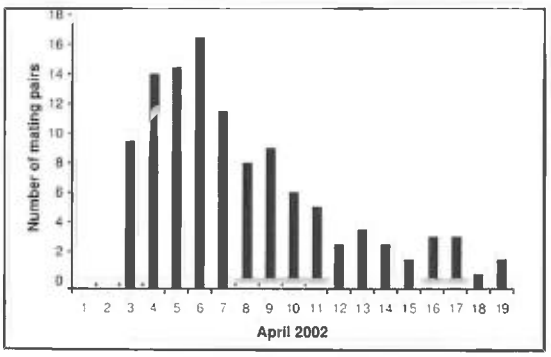
Table 3. The more dynamic habitats of *Vipera berus* often exhibited an extremely skewed adult sex ratio. Turbary Common, an isolated area of urban heathland, shows an example where for one subpopulation the ratio was as low as 2:9 and furthermore how this is being addressed via the recruitment of young males from other subpopulations.

table at the base of heather roots. Erratic seasonal flooding caused some mortality in winter, but also notable population shifts during active months. However, recent management (bunding) has alleviated much of this problem and future work will examine the full effect of this habitat enhancement.

At Turbary Common, spring fires (arson) caused high mortalities and local population shifts, and had a profound effect on the OSR for a number of subpopulations. An extreme case occurred during 1999 when a fire almost annihilated the adult male population. This subpopulation has been closely monitored since that time and Table 3. shows how the adult sex ratio is slowly returning to the former level as a result of ingress by young males from other subpopulations.

Despite the variety of negative influences, Adders in these more vulnerable areas still maintained a population structure virtually identical to that of the key study sites.

Figure 3. Dates and numbers of mating pairs at Hartland in 2002.



Age and size structure within a metapopulation is shown in Figs.1 and 2 for Studland in 2003, which was fairly typical of all the key areas throughout the study period. This structure was maintained at subpopulation level, although numbers of young adults were more variable because of erratic recruitment. Results have shown that age and size could be correlated with mating success in males and mortality and fecundity in females.

The mating period

During the last decade the timing of the male moult and dates of first mating in Dorset were significantly earlier than in previous years In the 1970s the first mating pairs were consistently observed during the third week of April with a peak around early May and then tailing off toward the end of that month. Since 1989 there has been a definite trend for earlier mating activity and Fig 3. shows Hartland as a typical example in 2002 when the highest numbers of mating pairs were observed during the first week of April. The Mendips, which are at a higher altitude, show a similar pattern to that of Dorset in the 1970s with a peak of mating pairs during the first week of May (Fig. 4). The mating period can extend to just over thirty days, however, mating activity for the majority of breeding adults occurred during the first seven to ten days.

Male reproductive behaviour

Close observation during the mating period showed that males formed a definitive hierarchic structure, with behaviour and mating success varying with size and age. All males with a total body size of 350 mm and above were assumed to be sexually mature (see Prestt, 1971), although a small number of males with a body size of around 320 mm were also seen to be active during the mating period. A first male advantage was achieved by larger males finding females very quickly and exhibiting mate-searching behaviour very different from smaller males.

Shortly before the start of the mating period breeding females undertook a local dispersal of distances varying between five and one hundred metres from the hibernation den. The same

locations were used each year by a variable number of females and the furthest positions dictated the outer limits of the mating area within a subpopulation. The fidelity of females to specific mating areas was a constant feature and provided a predictable pattern for searching males.

Mate-searching: Immediately following the spring moult males became alert and excitable and after a short session of basking around mid-morning moved around in earnest. Close observation at this time has revealed that males of various size and age groups exhibited different behaviour patterns. When expressed in terms of reproductive behaviour males could be divided into three distinct groups. This division calculated for all 46 subpopulations across the six key study areas over a ten year period showed small males in the 320 mm to 400 mm range with a mean of 2.65 per subpopulation (range 1–7, n=122). Large males in excess of 550 mm showed a mean of 2.26 per subpopulation (range 0–4, n=104). The majority of males were in the 420 mm to 540 mm size range with a mean of 8.23 per subpopulation (range 6–10, n=379). Male Adders are guided by pheromone trails exuded by the female which are both ground-based and airborne. Typical male searching behaviour was to move slowly over the ground, with much tongue flicking, and occasionally pausing raising the head and foreparts for visual cues. This visual awareness also served to confirm the presence, or otherwise, of other males. Although alert at this time male Adders were seen to be apparently oblivious of danger, often crossing and re-crossing open ground, and even roads. This behaviour was typical for all but the small number of older large males.Mate searching behaviour for large males was quite different and much more direct. Knowing the location of breeding females made it possible to assess the success rate of these large males. During the early part of the mating period males still mainly occupied the same surface dens as in previous weeks, and it was possible to follow the movements of individuals. Large males, after a short period of basking would leave the den and start to move purposefully at a moderate speed. It was relatively easy to track these males and it was noted that there was no pausing or tongue flicking and long distances were covered in a short amount

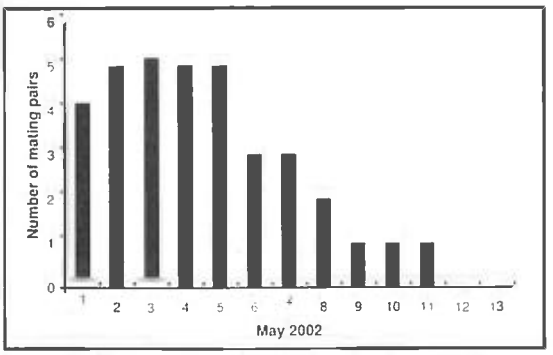


Figure 4. Dates and numbers of mating pairs in the Mendips in 2002.

of time. One male at Hartland in 2002 covered 80 metres finding a female in just fifteen minutes. This was typical for the small number of large old males and showed that this behaviour did not rely on chemical cues and although controversal, suggested imprinting or some kind of learning process. This strategy resulted in a high success rate with regard to first male advantage and for most years was seen to be virtually 100%. Although the remaining two groups each showed similar behaviour when searching, small males travelled longer distances per day and almost always with a negative outcome, and the group containing the majority of males travelled less and were more successful at finding females. Search patterns for the last two groups were partly linear, but became circular on entering a receptive female location. This involved much retracing of movement, and for small males the longest daily distance travelled was 600 metres, but all within a 120 square metre area. The maximum daily distance travelled by the majority of males was around 200 metres. The males at this time were closely observed, often by more than one person, and were seen never to venture outside their respective groups. This was unexpected as it had been predicted that males would disperse more widely in search of females. Andren *et al.* (1997) states that males are attracted by female pheromones at a distance of at least 500 metres. Most subpopulations throughout the study areas are separated by distances within this limit and in theory would have detected chemical cues from females situated outside the subpopulation. Although by no means conclusive, one

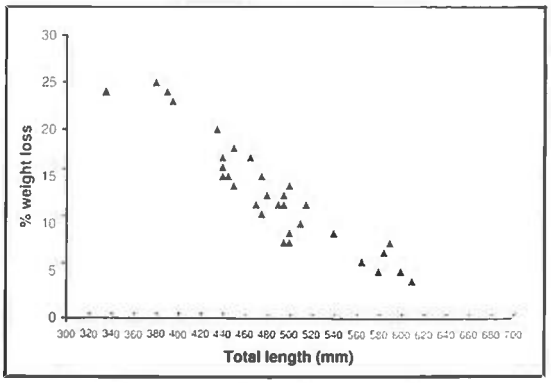


Figure 5. Percentage weight loss of adult males during the mating period, recorded at Norden in 1999, representing energy expenditure for the various size groups.

explanation is that perhaps ground-based pheromones are stronger and therefore over ride airborne chemical cues which may be at the limits of effectiveness. Even at this stage of the study, it would perhaps be not too unexpected if, in the future males were seen to interact with other nearby subpopulations, particularly during a year that exhibited a low number of breeding females within a particular subpopulation. However, the tenacity and familiarity of larger males to their respective subpopulation suggests that this would just involve the smaller males.

Combat and mate-guarding: Agonistic behaviour between rival males was a component part of Adder mating behaviour and this became manifest in spectacular bouts of combat. However, interaction between males was observed to exist at various levels which could be defined as size related. When small males encountered larger males this usually involved brief skirmishes lasting just a few seconds, often followed by a quick short chase by the larger male. Short bouts of combat were common during mate-searching by the majority of males, but increased in duration when in close proximity to a female. The most serious and prolonged bouts occurred when a male in possession of a female was approached by another male. At such times a male in company with a female would become highly agitated and would rush to meet the encroaching male and a long bout of combat would ensue. This often had a negative outcome, for although the defending male almost always won such bouts, the female would move away and another period of mate-searching would be undertaken. In most cases the defending male was successful in finding the female again before another male could intrude. The minority group of large males most often employed a different tactic, and when approached by another male instead of leaving the female would go directly into combat mode, often raising the body to a height of 30 cm, which in most cases was sufficient to ward off other males. Females remained passive during such encounters, and on many occasions such pairs were actually observed to be copulating. Although there were an equal number of males participating during the mating period annually, the levels of combat varied from year to year and was directly in accordance with the number of available females. Although combat defined male superiority, the most effective method of promoting first male advantage were long periods of mate-guarding ranging from one to eight days; the longest sessions being undertaken by the larger males. The exclusion of other males was enhanced when in almost all cases after first mating such pairs would undertake a local dispersal, becoming cryptic and hard to find visually. In addition, after a period of seven to ten days females became unreceptive and did not invite any response from other males. Although such a long attachment by these large males to a single female represented other lost mating opportunities, the efficiency of prolonged mate-guarding probably guaranteed single male paternity for that particular pair.The majority group of males was more erratic with regard to duration of mate-guarding but periods of up to five days were recorded. This resulted in some females mating with more than one male but some males, those that exhibited in excess of three days mate-guarding, successfully maintained a single mating pair showing behaviour comparable to that of the largest males. At Hartland during 2002 in one subpopulation 25% of males (n=2) mated successfully with two females. In another, also at Hartland, 33.33% of males (n=4) mated successfully with five females. First male advantage strongly indicated that the most likely outcome of mating resulted in single male paternity for the smaller subpopulations, but in

subpopulations with larger numbers there probably existed a mix of both single and multiple maternity.

Male reproduction costs: Over a period of twenty five years a total of 2200 males were sampled during the early spring phase when in the premoult condition. Each male was assessed visually for fitness and then weighed and measured. With such a large sample it was ultimately possible to correlate weight and body size against mating fitness potential. As expected, this represented a wide range of weight and body size, (28 g–110 g 318–650 mm [n=2200]). Only a small number failed to meet this criteria (4%, n=88) and these were males that expressed a body weight ± 10% under the expected fitness weight. Males were again sampled at the end of the mating period, although this proved more difficult and over the twenty five year period a total of 1200 males were recaptured at this time. This usually represented a recapture rate of between 40–50% but at Norden in 1999 88.88% of males (n=32) were accounted for at the end of the mating period. The results were almost identical to other study areas and Fig. 5 shows weight loss across the whole male spectrum which reflects the levels of activity for the various size groups in terms of energy expenditure. Other samplings were undertaken in July and August when males were in the summer (feeding) grounds, and again on return to hibernation areas. A total of 1750 males were sampled and 92% (n=1610) were seen to have regained the spring weight with 75% (n=1260) having exceeded this with some showing a maximum of 15% above the spring weight (n=440). However, even for those males that failed to meet the fitness criteria many were seen to survive into the following season and beyond. Results show quite clearly that energy expenditure and mortality are unrelated in male Adders which is proven by the ability to forage successfully during the post-mating period and regain condition rapidly as a consequence. Adult males do not feed during the mating period and Madsen & Shine, (1993) have stated that there is an 'opportunity cost' in that reproductive activities reduce feeding rates. However, it is doubtful if this can be regarded as a cost of reproduction as the

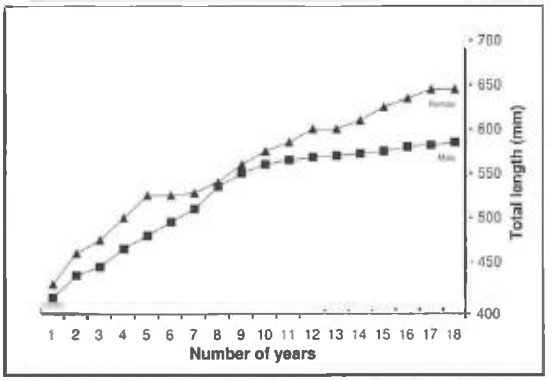


Figure 6. Growth of male and female Adder at Furzebrook from fourth season until 22 years of age. Shows female first breeding age of nine years, years of zero growth represent breeding years.

participation of 100% of adult males during the mating period in an inherent feature of all Adder populations. Mortality of male Adders expressed as a cost of reproduction was difficult to assess as many were found dead both within and outside the mating period. Immediately following the spring moult Adders were uncryptic and vagile and vulnerable to predation, and at both Hartland and Studland road kill was a significant cause of death. Mate-searching and combat had the potential to attract predators and throughout the study period male Adders were seen to be taken by Crows, *Corvus corone*, Magpies, *Pica pica*, and Buzzard, *Buteo buteo*. At Cors Caron the Polecat, *Mustela putorius*, was a significant predator of Adders typically leaving the head and skin. The domestic cat, was also known to take Adders at Turbary. Although a number of corpses were recovered each year, the only way mortality could be determined with any accuracy was to identify the surviving males on emergence the following spring. Although the time and cause of death could not be established in the majority of cases mortality measured across the active season was comparatively low. The situation at Hartland over a ten year period showed an annual mean of 12.94% across the general population (n=11). Studland showed an annual mean of 15.78% (n=12) and Furzebrook an annual mean of 9.72% (n=7). The significantly lower figure for Furzebrook can be explained by the consistent number of male road kills for the other two areas.

Location	TL (mm)	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	TL (mm)
Furzebrook	520		x			x		x		x		x			620
Furzebrook	550			x				x			x			x	680
Furzebrook	410						x		- presumed dead -						
East Creech	595				x			x				x			695
East Creech	490						x			x			x		610
East Creech	500	x		x			x		x				x		620
Norden	520	x			x		x			x			x		685
Norden	600		x		x			x		x			x		710
Norden	390					x			- presumed dead -						
Studland	650		x			x				x					720
Studland	500		x			x		x			x			x	620
Studland	400							x	- presumed dead -						
Wareham	520		x		x				x		x			x	630
Wareham	500	x		x			x				x			x	650
Wareham	390						x		- presumed dead -						
Hartland	600			x			x				x			x	680
Hartland	510				x			x			x			x	610
Hartland	490					x		x		x				x	600

Table 4. Breeding history of individual *Vipera berus* females in south east Dorset also showing increase in body length since first recorded. x = breeding years.

Female reproductive behaviour

In contrast to males, breeding females were passive and sedentary and once located in the respective mating areas daily movements were minimal. The daily movements for a number of breeding females were measured over a ten year period at Hartland, Studland and Furzebrook, irrespective of male influence, and showed a mean daily movement of >7.08 metres (range 1–15.5, *n*=44). Intense behaviour exemplified by mate-searching, combat and mate-guarding indicated that mate selection was purely male orientated. Close observation however, has shown that females responded to males of various sizes in different ways, which although controversial (see Duvall *et al*., 1992; Andren *et al*., 1997) suggests some form of mate choice. This was particularly noticeable with regard to the larger and older females. When a male with a total length of around 450 mm and above initiated courtship the female remained passive and positively responsive. Smaller males invited a very different reaction in that the female would move off, and even repeated attempts by such males resulted in the same outcome. This was a constant feature throughout the study period, and it was concluded that this was mate choice by rejection, and in combination with combat success reinforced the concept of large male advantage. Smaller males often mated with young females, some of which were in their first year of maturity and more responsive and not usually the target for the larger males. These young females usually mated later than older females with a consequence of late parturition.

Female breeding cycle: The breeding history for eighteen females across the six Dorset study areas for a thirteen year period is shown in Table 4. and for thirteen females in the Mendips and Cors Caron for a ten year period in Table 5. The breeding histories of a further 68 females were recorded throughout the entire study period and results clearly show that only a small number of females maintained a biennial reproductive cycle for up to seven consecutive years of life (*n*= 4) which represented 12.90% of those sampled in Tables 4 and 5. and 15.15% of the total recorded during the study (*n*=15). The total number of females sampled with regard to life histories were those that were recorded from birth (*n*=28) or as immatures and sub-adults (*n*=71). The majority of females were first recorded as mature adults (*n*=1835) and although some were in the 480–500 mm size range (*n*=485) it was not possible to state

age with a great degree of accuracy, although results have consequently indicated that many must have been virgin females. Of the 99 recorded life histories of females 18.18% (n=18) bred during the first year of maturity exhibiting a size range of between 390 mm and 420 mm. A further 235 females with a similar size range were recorded as first time breeders across the Dorset study areas. None of these females were recorded again after parturition and it was concluded that females that bred in the first year of maturity did not survive and represented 100% mortality. Although a high number of females with a size range of around 500mm strongly indicated that first time breeding occurred in later years following maturity, only the females with a complete known life history were included in the results. This showed a mean age of first time breeding of 8.25 years (range 6–11, n=71). Figure 6 shows growth of male and female from fourth season and indicates that the female bred for the first time in the ninth season and a further two times in a period of eighteen years. Result clearly show that a biennial cycle represents the absolute maximum periodic reproductive output for females and that two, three or even longer periods of non-reproductive years conclusively reveals a more typical breeding cycle, and this was at least consistent across all nine study areas. A similar breeding cycle for female Adders has been recorded in other parts of Britain (S. Sheldon, pers. comm.).

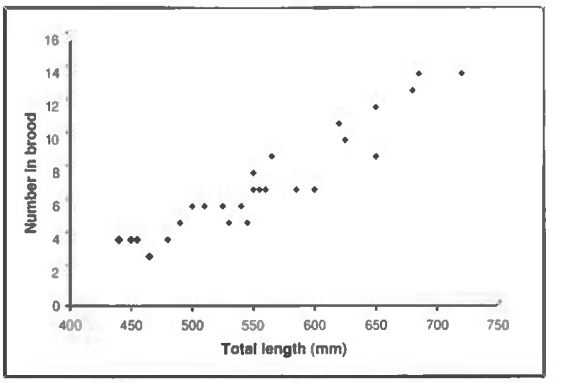


Figure 7. Litter sizes recorded across all age groups showing that this is correlated with body length.

Female reproduction costs: Energy expenditure and mortality was explicitly linked in females, and was manifest in the total non-survival of first time breeders in the early years of maturity. Adult females could be defined as three groups. Those that were of fitness weight and condition, and would breed that year, those that were of fitness weight and condition, and would not breed that year, and those that had bred the previous year. Females were examined on each spring emergence, and as with males the large sample

Table 5. Breeding history of individual *Vipera berus* females in the Mendips, Somerset, and Cors Caron, Ceredigion, also showing increase in body length since first recorded. x = breeding years.

Location	TL (mm)	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	TL (mm)
Mendips	480		x			-presumed dead-						
Mendips	550	x			x		x			x		590
Mendips	610		x				x				x	625
Mendips	520	x			x			x				580
Mendips	575		x		x					x		630
Mendips	650	x			x					x		685
Mendips	670		x				x				x	690
Mendips	420				x	-presumed dead-						
Cors Caron	450		x			-presumed dead-						
Cors Caron	550	x			x			x			x	610
Cors Caron	490		x		x	-presumed dead-						
Cors Caron	620		x		x						x	690
Cors Caron	600		x									650

Figure 8. Reproductive output, less two live young, of 430 mm female from Furzebrook.

made it possible to assess for fitness as expressed by body weight mass to body length. Excluding females that had bred the previous season, this represented optimum bodily condition for females and it was ultimately possible to predict body weight against length with only a small margin of error when assessing fitness. For example, a female with a total length (TL) of 550 mm would have a body mass of around 120 g, and it was this fitness weight minus the immediate post-parturition weight that was used to calculate reproduction costs expressed against body condition. Just prior to giving birth females were emaciated, and the general outward appearance of good condition was entirely due to the litter mass. This became apparent immediately at post-birth when the reduction in fat body was obvious. Reproduction costs were independent of litter mass, and litter sizes were in accordance with the TL of females (Fig. 7). Females between the 550–600 range with an average litter size of seven showed the same percentage weight loss as a 650mm female with a litter size of twelve. Over the study period females were sampled from spring emergence until post-birth. Just prior to birth litter mass represented between 42–52% of the spring fitness weight, (mean = 46.48%, n = 120). However, reproduction cost was calculated as a reduction in body condition (fat reserve), as illustrated in the example below, a breeding female from Hartland in 2002.

TL 550mm – Spring weight 120g – Pre-parturition weight 172g – Post-birth weight – 82g
Litter mass wet weight – 52g Actual fitness mass loss (weight = 38g) = 31.66%

This figure was fairly constant across the whole sample with a mean of 34.88% (range 29.56% –39.44%, n=120).

Because of the similar outward appearance of many females on emergence it was impossible to predict which would breed that particular year. However, during late March or early April close observation showed those females that would breed moved to the traditional mating areas, while non-breeding females left the hibernation areas, and many were seen foraging from early April onwards some significant distance away.

Although all first-time breeding females died as a result of breeding effort and consequent trauma, it was more difficult to attribute this cause when related to older females. Shortly after giving birth females began an intensive feeding regime which involved movement, often travelling distances of several hundred metres, and consequent exposure to predators. It was impossible to evaluate mortality as a cause of predation, but over the entire study period only fifteen females were know to have been killed by predators. During the gestation period females were sedentary, and as such did not attract natural predators. However, a number of mortalities were a direct cause of human persecution and predation by domestic cats. As with males, the number of survivors was established when recorded on emergence the following spring, or in some cases, later that same season.

Fecundity: The recording of birth litters over a long period of time showed quite clearly that the number of young per litter can be correlated with female body size and length. Figure 7 shows a sample of litter sizes for females from Hartland and Studland across the entire size spectrum, (440–730 mm), revealing a mean litter size of 7.42 (range 3–14, n=26). These results do not include stillborn or infertile eggs, however, the largest females produced just 4% of all stillborn recorded. Small litters and a large proportion of stillborn was consistent for females breeding in early years of maturity, Fig.8 shows a part litter, less two small live young, for a 430 mm female from Furzebrook. Litters from these young females accounted for 86.04% of all stillborn recorded during the study period (n=148). The significant number of non-reproductive years for a large number of females

may have suggested a low fecundity across the population as a whole. In fact this was not the case, firstly it was obvious that population numbers were maintained and remained stable for a long period of time. The duration of the study allowed life histories for a significant number of females to be examined. Four females at Norden, and five from Furzebrook, bred for the first time when between 520–555 mm and bred a further four times over a 15 year period producing a total of 485 young. This expressed as an annual fecundity rate produced a mean of 3.60 young, expressed as a biennial rate, a mean of 7.19, which is reasonably close to the mean litter size (7.42), as the sample shown in Fig. 7.

DISCUSSION

The study clearly shows that Adders exist as autonomous mating units at subpopulation level within a wider metapopulation. This was unexpected as other studies have shown that Adders, both males and females, can move long distances to mating areas (Forsman, 1997; Volkl & Thiesmeier, 2002). Although it is possible to overlook a wider dispersal of searching males, it seems fairly conclusive that over a thirty year period this has not thus far been recorded. The only long linear distances recorded was dispersal to summer grounds which involved all but the breeding females.

The hierarchic structure of adult males was a consistent feature at all sites and could be defined by size and age. Small males, many in the first year of maturity, engaged in long periods of negative mate-searching and were excluded from most females by the larger males. Some did mate late with small females and this may account for low fecundity and mortality of these females. The majority group, males those with a size range of 500–600 mm were successful at finding mates but exhibited high levels of combat. The minority of superior males in excess of 600 mm were 100% successful in finding mates because mate-searching techniques transcended conspecific trailing and strongly suggested a learning process which gave quick access to female breeding areas. This success was further enhanced by extended periods of mate-guarding. Females consistently rejected the advances of small males and it raises the question how do they recognize 'inferior' males? Although not conclusive, it may be the weight difference between a 340 mm male at 30 g and a 550 mm male at 70 g. Once a small male mounted a female in preliminary courtship the female may just simply detect the substantial difference in weight. However, it also raises the question, is this really mate selection or choice by females?

Reproductive costs were significantly higher for females than in males, although the majority of mortalities largely affected young females, and explains the male bias with regard sex ratio throughout all areas. During the early years of the study it was expected that most females would show a biennial breeding cycle. The long duration of the study has revealed a very different pattern with most females breeding for the first time well beyond the year of maturity. This was unexpected, but not unique in temperate viperids, Martin (2002) in a study of timber rattlesnakes, *Crotalus horridus*, in West Virginia, states that females, breed for the first time between the ages of 9–14 years, although it is also stated that these females do not mature until eight years of age. This shows that although in good bodily condition, females are not obliged to breed during any one season and a choice is made with regard to energy expenditure. A biennial breeding cycle demands a high feeding regime during the following season, whereas long gap years provide flexibility with regard to negative influences, such as bad weather or fluctuation in prey resources. It is not known what triggers a female's choice to breed, but it is known that the ovarian cycle begins in the season prior to breeding (Nilson, 1981).

This study has shown clearly that female Adders have a reproductive strategy that is explicitly linked to survival and longevity. Males with lower reproduction costs have shown an equal degree of survival and longevity and there is no bias between the achievement of an upper age limit between males and females. In the spring of 2004, across all six study sites 34 males and 37 females were known to be in excess of 25 years of age with twelve now beyond the thirtieth season. This has dictated a low level of recruitment which is reflected in the low number of immature and subadults, the result of a high mortality, (92%),

during the first three years of life (Phelps, 2004b). In the absence of any other known literature this study may represent records for the oldest known wild snakes to date.

ACKNOWLEDGEMENTS

For access to study areas and their cooperation over the years I would like to thank, English Nature (Natural England), Dorset Team, National Trust, Studland, Countryside Council for Wales, Ceredigion, RSPB, Arne, Forestry Enterprises, Wareham and Miss J. Barnard at Blue Pool, Furzebrook. I am grateful to Stuart Clarke and Mark Miller, at Bournemouth Council, for help and funding my Adder research at Turbary Common. My thanks to Sylvia Sheldon with regard to the useful data regarding Adders in the Wyre Forest. My gratitude to the British Herpetological Society Conservation Committee, without who, in those pioneering years, I would never have established any study sites. I must also acknowledge my debt to the late Ian Prestt for his help and guidance during those early years. Lastly, but certainly not least, my thanks and appreciation to all those friends and colleagues who have assisted me in the field over the years.

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The masked newt: variation of body coloration in a Great crested newt, *Triturus cristatus*

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THIS note describes a Great crested newt with unusual colour patterns encountered at a pond in East Kent in April 2007. The belly pattern of the species is unique to each individual (Hagström, 1973), although it does tend to show variation over time (Arntzen & Teunis, 1993). Variation in colour in the upper parts of the body is, however, uniformly described (Smith, 1951; Griffiths, 1996; Beebee & Griffiths, 2000) as varying between dark brown and black with black spots. None of these authors lists any further variation in the coloration of the upper parts of the species.

The unusual animal was obtained by bottle trapping (Griffiths, 1985), carried out as part of a scientific programme in support of the National Amphibian and Reptile Recording Scheme. Bottle traps were set at night and recovered the following morning. Over the course of five surveys in 2007 this was the only unusually marked animal encountered, either at this or adjacent ponds. No strangely patterned animals were encountered by torching or netting, other methods used as part of the survey.

There were no lesions or any other signs on the body to suggest that the coloration was a result of some pollutant entering the pond, and it was therefore assumed that the cause of the unusual markings was genetic rather than a result of contamination.

The animal was an adult male in full breeding condition (Figure 1). The head and throat were predominately yellow-orange, with a small area of normal coloration surrounding both eyes, resembling a mask. The crest was well developed but contained areas of pale pigment. The flanks were mainly normal but with some yellow patches.

The tail (Figure 2) shows an abrupt change from normal coloration to yellow with a few small brown patches. The tail stripe is especially interesting, as the tail plays an important part in courtship. Normally described as white to silver, in this case a definite pinkish hue is visible.

Courtship patterns amongst European newts, including Great crested newts, are amongst the best understood of all amphibian species and were reviewed by Halliday (1977, 1990) and Arntzen & Sparreboom (1989), and are also described in Griffiths (1996). In the case of the Great crested newt, courtship includes the waving of the tail combined with a more violent tail movement over the head of the female, referred to as the whiplash. The male may then stand in a "handstand" position, rocking from side to side, which enables the female to see the size of the male's crest.

Several colour variations within the species have been reported to Natural England in recent years (Jim Foster, pers. comm.), but appear to be very rare. Nowhere have the gene mutations that produce variations become established in local populations. It therefore seems unlikely that brightly coloured Great crested newts will become a regular feature in UK populations.

ACKNOWLEDGEMENTS

The trapping programme described was a part of a project funded by the Esmée Fairbairn Foundation. Also my thanks to Asuman Aydin, my field assistant on the day, who opened the trap and decided the unusually marked animal was worth drawing to my attention! I would also like to thank Richard Griffiths and John Wilkinson for their helpful comments on an earlier draft.

Figure 1. © D. Sewell.

Figure 2. © D. Sewell.

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Adult male *Triturus cristatus* (normal colour variant). © D. Sewell.

A report on male *Anolis sagrei* saurophagy in Chiayi County, Taiwan

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ABSTRACT – Five hundred and two Brown anoles (*Anolis sagrei*) were collected for stomach content analysis from an area surrounding a plant nursery (23°25'51"N, 120°28'30"E) in Santzepu, Sheishan District, Chiayi County, as part of an ongoing study on this invasive species in Taiwan. The stomachs of five *A. sagrei* males contained vertebrate prey, which were isolated for identification to establish a basis upon which future studies can be based. These prey were identified as three hatchlings of *A. sagrei*, a *Hemidactylus frenatus* hatchling, and a skink hatchling – most likely that of *Sphenomorphus indicus*. The results of this study seems to indicate that male *A. sagrei* saurophagy is more likely in cleared open habitats, with no ground cover, than in habitats with ground covering.

As a whole, lizards exhbit a wide range of variation in what they eat; some have a catholic diet, while others are specialists that prey only on specific types of prey (Mattison, 1997). Only a few lizard species, such as *Lialis burtonis* (Pygopodidae), specialize in preying on other lizards (Pianka & Vitt, 2003). Some intermediate sized species like the Western collared lizard (*Crotaphytus insularis*) and the Leopard lizard (*Gambelia wislizeni*) prey on smaller lizards (Pianka & Vitt, 2003; Smith, 2003), although their diet is not restricted to them (Mattison, 1997). A few species such as the Virgin Islands crested anole (*Anolis cristatellus wileyae*) (Owen & Perry, 2005), Northern curly-tailed lizard (*Leiocephalus carinatus*) (Schoener *et al.*, 2002), and Rainbow skink (*Mabuya margaritifer*) (Spawls *et al.*, 2002) will occasionally prey on smaller lizards. It is thus clear that although not all lizard species prey on lizards (saurophagy), it is not that out of the ordinary that some lizards will prey on smaller lizards.

The Brown anole (*A. sagrei*), also known as *Norops sagrei* (Köhler, 2000; Lee, 2000), is a recently recorded invasive lizard species in Taiwan (Norval *et al.*, 2002). In an attempt to gain a better understanding of the food resource utilization of *A. sagrei* in Santzepu, Sheisan District, Chiayi County, a stomach content analysis was done on 502 individuals, consisting of males (n=255) and females (n=247), that were killed with ether. Since the identification of the prey items that were taken from the stomachs of these lizards were usually only extended to the class or order levels, it was decided to isolate all the vertebrate prey from the other prey items for a more in-depth examination to establish a basis upon which future studies on predation on vertebrates by this species in Taiwan can be based.

METHODS

Study site

The Brown anoles were collected along the road; from agricultural fields; along a creek; and from a cemetery in the area surrounding a plant nursery (23°25'51"N, 120°28'30"E) in Santzepu, Sheishan District, Chiayi County.

Field methods and data analysis

Meteorological data, reported for Chiayi City which is located about 5 km from the study area, was obtained from the Taiwanese Central Weather Bureau website.

Between January 10th 2002 and March 28th 2003, a sample of about 30 Brown anoles (*A. sagrei*), consisting of both males and females, were collected monthly by hand or with a fine meshed fishing scoop net. At the point of capture, the GPS location was recorded with a GARMINI 2 PLUS handheld reader (datum: WGS84), the specimen was allocated a field number, and the date and time was recorded.

Upon returning from the study area, each lizard was killed with ether; the SVL and TL were measured to the nearest mm with a transparent plastic ruler; the tail was scored as complete or

Specimen Field No.	Collection date and time	SVL(mm)	TL (mm)	BM (g)	GPS location
GN0010	2002-01-11; 12:30 h	47	86	2.3	23°25'43"N, 120°29'02"E
GN0180	2002-06-06; 10:03 h	50	93	4.1	23°25'43"N, 120°28'54"E
GN0314	2002-09-29; 16:35 h	48	94	3.0	23°25'46"N, 120°28'58"E
GN0394	2002-12-05; 10:56 h	55	109	5.2	23°25'44"N, 120°28'55"E
GN0426	2002-01-23; 14:11 h	49	100	3.3	23°25'48"N, 120°29'07"E

Table 1. The collection data and measurements of the five *A. sagrei* males, that had vertebrate prey in their stomachs.

broken; the animal was weighed to the nearest 0.1g with an YC-model e68 digital scale and dissected by making a mid-ventral incision. The stomach was removed for stomach content analysis and placed in a vial filled with 75% alcohol. At the end of the collection period the stomach content of every lizard was spread in a petri dish and all the prey items were identified down to order level and, if possible, to family level. All the specimens, except for the stomach contents and the stomachs (preserved only in 75% alcohol), were first fixed in 10% formalin and then preserved in 75% alcohol. In addition to the morphology, the head, sub-caudal, and sub-digit scalation were used for the identification of the saurian prey isolated from the other prey items, and the SVL and TL of the complete saurian prey (n=2) were measured to the nearest mm with a transparent plastic ruler. Abbreviations are as follows: *Abbreviations:* SD – standard deviation; SVL – snout-vent length; TL – tail length; BM – body mass

RESULTS

The average temperature for the study period was 22.71°C; June 2002 being the hottest month and February 2003 being the coldest; and during the same period 1453 mm rain fell, of which the most fell in July 2002.

Five *A. sagrei* males, about 1% of all the lizards, had vertebrate prey in their stomach contents, and had a SVL, TL, and body mass that ranged from 47 to 55 mm, 86 to 109 mm, and 2.3 to 5.2g respectively; with an average SVL, TL, and body mass of 49.8 mm (SD=3.114), 96.4mm (SD=8.62), and 3.58g (SD=1.112) respectively (Table 1).

GN0010 was collected from a betel-nut palm (*Areca catechu*) plantation on a hill. But unlike in other betel-nut palm plantations, the farmer kept the area very tidy and the ground was virtually bare. GN0180 was collected in a field used for the cultivation of bamboo (*Bambusa atrovirens*). The areas surrounding the bamboo stands were bare because the farmer regularly raked the leaves and other litter into piles around the bases of the bamboo stalks. This practice is often observed in fields where bamboo is cultivated in Taiwan. GN0314 and GN0394 were collected from the border of a field that was left to lie fallow since August 2002. Prior to that, the field was a lemon (*Citrus limonia*) orchard. The trees were grown in rows, and along the western part of the orchard many were overgrown by *Mikania micrantha.* In general, through out the lemon orchard, species like *Amaranthus spinosus*, *Bidens pilosa*, *Celosia argentea*, and *Chloris barbata* grew in the lanes among the trees. Although the farmer did spray herbicides from time to time, which reduced the vegetation in the lanes, some form of vegetation litter always covered the ground. Many of the *C. limonia* were infected by *Anoplophora malasiaca* and were dying. All the trees were thus uprooted and piled in the center of the orchard in July 2002 (Fig. 1), and were burned at the end of the year. To the end of the study no attempts were made by the farmer to cultivate any crops in the field. GN0426 was collected from an orange (*Citrus aurantium*) orchard, where the farmer regularly raked the ground among the trees, and the ground was thus bare at all times.

The only vertebrate prey items recorded in this study were three *A. sagrei* hatchlings, a tropical house gecko (*Hemidactylus frenatus*) hatchling, and a skink – most likely a hatchling of an Indian forest skink (*Sphenomorphus indicus*); and belonged to three families – the most common of which was Polychrotidae. Vertebrate prey comprised about 0.16% of the total number of items in the lizards' stomachs, and only 0.17% of

Figure 1. The lemon (*Citrus limonia*) orchard after the trees have been uprooted and piled in the middle of the field. This field is bordered on three sides by betel-nut palms (white arrows), which are used by *A. sagrei* males as perches.

the prey items (all stomach items except the consumed sloughs).

Since the digestive process was very advanced, it is not possible to give an exact predator/prey SVL ratio of the scincid, and two of the *A. sagrei* hatchlings. As for the remaining *A. sagrei* hatchling (GN0394) and the *H. frenatus* hatchling (GN0010); the predator/prey SVL ratios were 3.24:1 and 3.13:1 respectively.

DISCUSSION

The Brown anole (*A. sagrei*) is a sit-and-wait predator (ambush predator) that feeds during the entire day (Schwartz & Henderson, 1991), and as ambush predators, they would be expected to prey on more active prey (Huey & Pianka, 1981), that is mobile, on the surface, and visually conspicuous (Pianka & Vitt, 2003).

Anolis sagrei saurophagy has been recorded before and involved cannibalism on other anoles (Lee, 2000; Nicholson *et al.*, 2000; Campbell & Gerber, 1996; Campbell, 1999; Gerber, 1999). Intraguild predation by *A. sagrei* on *A. carolinensis* hatchlings has been shown to be severe enough to result in the rapid decline of sympatric populations of *A. carolinensis* in Florida, USA (Meshaka *et al.*, 2004). Although *A. sagrei* cannibalism is not out of the ordinary, Gerber (1991) has demonstrated that adult male *A. sagrei* selectively prey on hatchling *A. carolinensis*.

Although *H. frenatus* is primarily a nocturnal gecko (Cox *et al.*, 1998; McCoid and Hensley 1993; Meshaka *et al.*, 2004), McCoid and Hensley (1993) has reported a shift in activity patterns by the hatchlings and juveniles of this species in Guam, and suggested that it may be a heretofore unrecognized activity shift in young of *H. frenatus* to reduce cannibalism. Such activity patterns have not been confirmed in the present study area, but it is worth noting that *H. frenatus* has been observed on the trunks of *A. catechu* during the day (Norval, pers. observation). Still, the hatchling that fell prey to GN0010 could have been disturbed in its shelter by anthropogenic activities. Many of the fields are bordered by betel-nut palms, which are used by *A. sagrei* as perches. Another factor that could thus contribute to the risk of predation by *A. sagrei* on small lizards is the response of these lizards to agricultural activities such as tilling. As stated above, *A. sagrei* often utilizes the vegetation bordering fields as perches, and emigration of small lizards, such as the hatchlings of *A. sagrei*, to these areas would naturally lead to an increase of predation by adult *A. sagrei* males. This was more than likely the case for GN0314 and GN0394, because although throughout the year individuals were collected from this area, these two saurophagy cases were recorded after the orchard was cleared and the uprooted trees were burned. *Anolis sagrei* hatchlings were observed in this area, and had to emigrate to the areas bordering the cleared orchard when all the available cover was removed.

Since none of the predation events were observed, one can only speculate about how they occurred. But interestingly, all the saurophagy cases I recorded were in areas with no or little ground covering, and very high anthropogenic disturbances. As part of another study, 230 *A. sagrei* were collected between January 2004 and February 2005 from a small betel-nut palm plot (15 x 40m) in the same study area for stomach content analysis. And although the understory vegetation was sparse from time to time, the ground was never bare. Not a single case of saurophagy was recorded (Huang & Norval, unpublished data)! It thus seems that *A. sagrei* saurophagy is more likely in cleared open habitats, with no ground cover, than in

habitats with ground covering. And from a conservation perspective, farmers in Taiwan should be encouraged not to remove all the ground covering in areas where *A. sagrei* occurs to lessen the risk of hatchlings of indigenous species falling prey to large *A. sagrei* males.

The question still remains, why would some *A. sagrei* males be cannibalistic? According to Rodriguez Schettino (1999), one *A. sagrei* of each sex occupies a territory, in which may be established a family composed of one male, several females (of which one dominates), and juveniles and hatchlings that may stay in the territory for several weeks before they disperse to other areas. Paterson & McMann (2004) have demonstrated that *A. sagrei* males can distinguish between neighbours and non-neighbours, and Tokarz (1992) found that *A. sagrei* males behaved differently with familiar females than with unfamiliar females. So, if *A. sagrei* males have the ability to distinguish among familiar and nonfamiliar classes of males and females, would they also be able to distinguish between their own offspring and that of others? An empirical study to determine if *A. sagrei* males are able to recognize their own offspring would not only determine if *A. sagrei* males are capable of kin-recognition, but it would also help clarify the question of whether cannibalism is truly just opportunistic predation, or whether it is a form of intraspecific competition.

As far as can be determined, this appears to be the first published description of a gekkotan and scincid falling prey to Brown anoles.

ACKNOWLEDGEMENTS

Special thanks are extended to Prof. Jonathan Losos, and Dr. Jean-Jay Mao for their comments and for reviewing this paper.

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The presence of *Chamaeleo chamaeleon* (Reptilia) on the Maltese islands, with a note on the occurrence of this species on Cominotto Island and its possible effects on the endemic local lizard

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ABSTRACT – The Mediterranean chameleon *Chamaeleo chamaeleon* is one of nine terrestrial reptile species that occur in the Maltese islands. Because it is an introduced species very few studies have been conducted in Malta and much of the available knowledge is derived from research made abroad in a different environment. This study tackles some of data in circulation and the discovery of this reptile on the islet of Cominotto, and endeavours to investigate its potential impact on the local population of *Podarcis filfolensis*.

CHAMAELEO chamaeleon is not indigenous to Malta, having probably been introduced between the dates of 1846–1865, but has subsequently become established, spreading to practically every corner of the Maltese Islands. This species has few predators locally and is generally difficult to spot. Also it is generally found in shrub and tree habitats where it encounters few other reptiles. With juveniles it is almost impossible to distinguish between the sexes but adults can be more readily distinguished from the structure of the skull and especially from the coloration during the mating season. Moreover, males tend to grow much larger than females. The cloaca tends to differ as females have a wider opening when compared to the size of the specimen than males while the later especially in mating season have an almost inflamed section in the rear of the cloaca where the hemipenis is contained. The animal is oviparous, the female laying about 12-22 eggs in April to June which hatch in the following August to November. Coloration is very variable depending on a number of factors, example: a tensed specimen is usually black while a relaxed specimen tends to be green. Sick or dying specimens tend to be pale. Remarkably, even females in heat or pregnant, can be distinguished by colour. Females on heat are black covered systematically with orange spots. When they become pregnant, purple spots usually follow, tending to repel off males accompanied also by the aggressive behaviour from the females. Whatever colour the specimen changes to, it always has a white stripe on its belly (based on examples observed by the author at Melliha region, especially in Ghadira nature reserve from 1997–present).

Literature, distribution and possible effects

Chamaeleo chamaeleon was first recorded in the Maltese literature by Giovanni Gulia in 1890. It was reportedly introduced by Jesuit priests at St. Julians (Gulia, 1890) possibly from North Africa. While Gulia considered it to have become naturalised, Despott (1915) could not obtain any specimens and did not include it in his list of Maltese herpetofauna. There is now no doubt that the animal has established itself and spread. It is likely, however, that this spread has occurred from more than one locality. Recent records include numerous specimens from all over Malta especially in the north. This species was also found at various localities in Gozo. In Comino it has more established itself in the hotel and valley area but can also be found sparsely scattered all over the island.

Through the past years the author has been visiting various islands and islets to study the behaviour of the different populations of *Podarcis filfolensis*. One island, which enjoys easy access and scant human interference, is Comino, and therefore, due to this factor, it was the island most frequenty visited. The monitoring of all populations found is also continued but usually preference is given to the smaller islands, which need more monitoring for conservation such as Selmunett Island and Cominotto. Besides the target, while on the field, notes of its prey and predators and the flora and fauna are taken. The earliest records from Cominotto date back to the summer of 1996, and since that time the following herpetofauna on this island have been recorded. These are *Tarentola mauritanica, Hemidactylus turcicus*, *Chalcides ocellatus* and the endemic yet

unnamed population of *Podarcis filfolensis*. This lizard differs from the mainland and other population stocks in size, behaviour and also the level of degree in melanism. The latter is quite common on the island but prey is scarce when comparing the area and the population to other islands such as Comino and Selmunett. (These two are the opposite because there is an abundance of prey and much less lizards). This is why a large number of *P. filfolensis* are found at point A. (Figure 1) this is because in the summer time, it is an ideal location because they feed on any left overs left by humans.

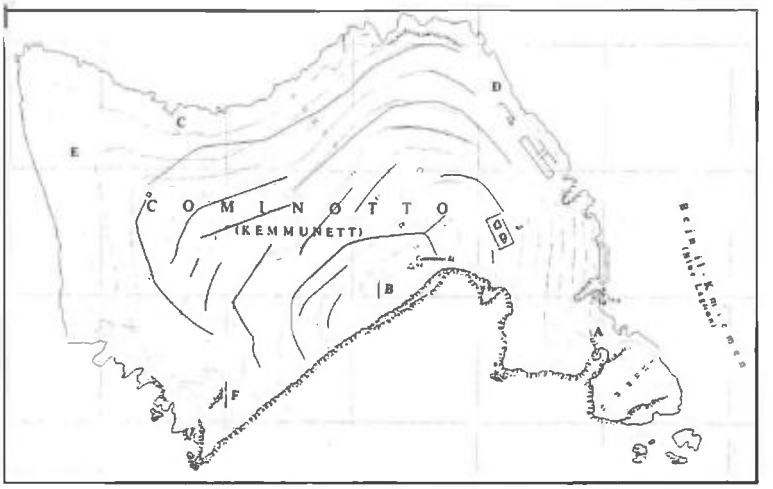

Figure 1. Cominotto. Points as indicated in text.

On 20th August 2000 three faecal pellets where taken from Cominotto at point B and one of them resulted to belong to a small specimen of *C. chamaeleon*. This was the first indication that this species might thrive on this island. On 6th July 2001 a complete skull and the first 7neck bones were found under a *Lamiaceae sp.*shrub in a 2-5cm deep soil at point C. On 17th June 2002 a female specimen was observed at point D with a total length of 16 cm, and on the same day at point E a male with a total length of 14 cm was also noted. On 16th April 2004 a shed skin of 5.2 cm long x 3.2 cm wide was taken from point F. After careful examination, it was found that this also belonged to a *C. chamaeleon*.

The presence of this species on the island is not a worrying situation at present but if the population of this reptile increases exponentially, it maybe however be a treat to the local population of *P. filfolensis*. The latter are already challenged by natural predators and other problems. Of all the other populations observed, these lizards are the ones that suffer most from a type of red mite (unknown species) often found under the neck, behind the ear pore or close to the hind legs. From observation this population is also the one most often found with disabilities such as missing toes due to severe combat in mating seasons and for territory. Also, *C. ocellatus* was recorded on 28 separate occasions feeding on *P. filfolensis* juveniles from this island. Since prey is scarce and *C. chameleon* has to share the same habitat with *P. filfolensis* – unlike the situation on the main islands where *C. chamaeleon* is more likely to be found in trees – there is a higher possibility of encounters between the two species which will result in further predation on *P. filfolensis*.

Chamaeleo chamaeleon feeds on a variety of arthropods including Arachnida, Diptera, Blatodea, Orthoptera and Lepidoptera. It catches its prey by shooting its extendable tongue towards prey. In adults, this can be twice their body length. In captivity one specimen also took lizards. (Savona-Ventura, 1983). The author recorded this behaviour from the main island on juveniles on 32 separate occasions.

The yet unnamed population of *P. filfolensis* present on Cominnotto Island is of extreme ecological and scientific importance due to its endemism, and the introduction of an alien species such as *C. chamaeleon* will certainly not improve its chances of survival and conservation.

ACKNOWLEDGEMENTS

The author would like to thank Esther Schembri and Jeffery Sciberras for their continuous support and assistance in the field and during my studies on the hepterofauna. The author would like also to thank Sammy Vella for the reading of the script and his useful comments.

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NATURAL HISTORY NOTES

LERISTA BOUGAINVILLII (Bougainville's skink): **PREDATION, DIURNAL ACTIVITY**. There are few published records of predators of Australian lizards identified to species level, or of predation by invertebrates, and little on times of activity in the genus of small semi-fossorial lygosomine scincids *Lerista*, the most speciose terrestrial vertebrate genus in Australia. This note documents an instance of diurnal activity and invertebrate predation on *Lerista bougainvillii*. At 15:50 h (Australian Eastern Standard Time), 2nd October 1990, the first author was searching through leaf litter and loose grey sandy soil at the base of a low dome granite rock outcrop in remnant dry sclerophyll forest dominated by *Eucalyptus caliginosa* with a mixed heath/grassland understorey on top of a small hill at Lot 10 Kirby Road, Armidale, New South Wales, at 30°28'.397S 151°38'.561E, 1073m elevation (GARMIN GPSII, WGS84 grid), and disturbed an adult *Lerista bougainvillii* with a complete original tail; the *L. bougainvillii* was apparently active in the litter when detected, rather than inactive in a refugium, hence demonstrating diurnal activity. The lizard ran under the loose litter along the base of the rock for *ca.* 0.5 m and was then seized by a large (*ca.* 100 mm) adult scolopendrid centipede *Erythmostigma rubripes* situated under the litter adjacent to the rock; this predatory action was noticed due to the violence of the disturbance in the litter and partial emergence of the protagonists to view. Removal of some of the leaf-litter and closer examination revealed that the lizard had been seized by the centipede with its jaws and anterior three pairs of legs in such a manner as to grip the lizard ventrolaterally over the anterior body and neck region, with more posterior pairs of legs apparently being used to hold and subdue the body and tail of the writhing lizard and maintain a grip on the substrate, although there was no continuous grip maintained with these posterior legs such as that of the anterior three pairs; the lizard had been deeply bitten at least twice in the ventral neck and left ventrolateral axillary region, with a considerable amount of blood-loss evident; tail autotomy did not occur. The lizard was beyond aid and was left with its predator.

This predatory interaction was induced by disturbance of the lizard by the observer, but there can be no doubt as to the predatory response of the centipede, which on this account would appear to be a 'lie-in-wait' rather than an 'active-search' type of predator, at least of small scincids active in litter by day. It is probable that large scolopendrid centipedes are a significant predator of *Lerista* spp. wherever they coincide; they themselves occasionally fall prey to large *Urodacus manicatus* scorpions at the above site (*eg.*, pers obs., earlier the same day at 14:00 h, 2nd October 1990, a large adult *U. manicatus* was observed consuming a *ca.* 80 mm *E. rubripes* in a short chamber excavated beneath a 20 cm diameter stone at *ca.* 70 m south of the above locality).

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