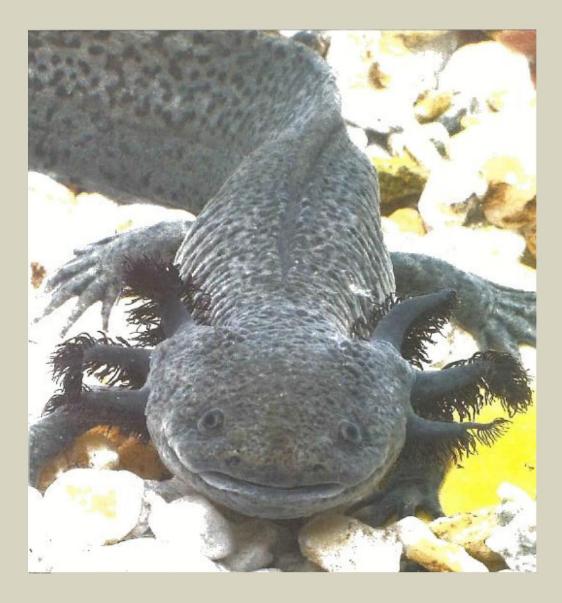
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THE HERPETOLOGICAL BULLETIN

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).

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Front cover illustration. Mexican axolotl, Ambystoma mexicanum. See article on page 4. Photograph © Ian Bride.

Meet the Council....

Dr. Chris Gleed-Owen, Research Committee Chair

I have been the BHS Research Committee Chair since 2003, and am happy to be taking a productive part in the Society's activities. I have always been enthusiastic about amphibians and reptiles, and wildlife and the countryside in general, but growing up in Mansfield, Nottinghamshire, I had little chance to exercise my interest in herpetofauna. We had a resident garden toad and I saw a lizard in the garden on the day we moved in, but other than that it was just my dad's tongue-in-cheek insistence that there were grass snakes at the bottom of the garden that kept my imagination going.

It was only when I began a PhD at Coventry University in 1993, on the history of the British herpetofauna from the Ice Ages to the present day, that I really began to study amphibians and reptiles seriously. It took me four and a half years to teach myself everything I needed to know and complete my doctorate, and there were very few people in Europe, let alone in Britain, who could help me learn to identify the fossil bone assemblages I was working on. I began by developing my own comparative collection of amphibian and reptile skeletons. This was no mean feat (nor a pleasant one!) and there are many of you out there who helped me by providing corpses of unfortunate animals.

I spent long hours learning the skeletal anatomy of British and European species, identifying the diagnostic characters of different bones and picking out the differences between species. Then I put my knowledge to the test, and applied it to subfossil assemblages recovered from caves, archaeological digs and other sites - whatever I could get my hands on. This had hitherto been a much neglected area of palaeontology (the study of past life), and relatively little was known about the history of the British herpetofauna across a timescale of 500,000 years of changing climate. I studied assemblages from over forty sites, and built up a picture of which species lived where and when. This gave me indications of how climate had changed, indeed fluctuate many times during and after the Ice Ages. For example, Aesculapian snakes, tree frogs, Pond terrapins and other exotic species - at least a dozen in total - which inhabited Britain in the warmer parts of the last half million years.

I joined the BHS in 1993, as well as the local herp conservation group, Warwickshire Amphibian



and Reptile Team, and I began to attend annual *Herpetofauna Workers' Meetings*. These were all instrumental in getting to know the many herpetologists I know now, and for learning 'by osmosis' from their extensive knowledge. Thanks to all of you.

After a short career in archaeology (punctuated by a highlight of finding 1000-year old Pool frog bones in East Anglia!), and short stints at English Nature and the Ordnance Survey, I entered herpetology professionally. I work for The Herpetological Conservation Trust (The HCT) as the Research & Monitoring Officer, a post that began in order to set up a national database and geographical information system (GIS) of rare herpetofauna records held. The job now encompasses collation of records, survey, monitoring. liaison. volunteer coordination. licensing, and currently the development of a National Amphibian and Reptile Recording Scheme (NARRS). Aside from HCT duties, I am Chair of the newly formed Dorset Amphibian and Reptile Network (DARN).

As BHS Research Committee Chair, I initiated the Student Grant Scheme in 2004, thanks to £1,000 from the Society. There are currently five grant recipients, and their research will be published in the *Bulletin* or *The Herpetological Journal* in due course. We hope that a similar scheme will continue to run in future years. Following on from Richard Griffith's sterling efforts in organising last year's meeting on the *Ecology of British Snakes*, this year we are holding a meeting at the Open University, organised jointly with The HCT, and entitled *Herpetofauna ecology & conservation – targeting research where it's needed.* A programme flyer is available via the BHS website. We look forward to seeing many of you there.

VETERINARY VIEW

Possible effects of antibiotic therapy on digestion in a Solomon Island skink, Corucia zebrata

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THE Solomon Island skink (Corucia zebrata) is currently under threat from collecting for the pet trade, habitat degradation and a limited geographical distribution (McCov, 1980; Hoover, 1998). Captive breeding programmes may have a part to play in its recovery but if these are to contribute usefully it is important that attention is paid to all aspects of the species biology (e.g. Parker, 1983; Honneger, 1985; Cooper, 2000; Harmon, 2002; Mann & Meek, 2004). As with other true herbivorous reptiles, C. zebrata has an enlarged partitioned colon that slows the passage of digesta through the gut and provides microhabitats for the nematodes and microbes that have a key role in the digestive process (Iverson, 1979). There is even the possibility that the natural food plants of herbivorous reptiles influence the ecology of the intestinal fauna. For example, Testudo hermanni consumes several species of plants that contain toxic compounds (Meek, 1985; 1988) and it has been suggested these may regulate population growth nematode (Longepierre & Grenot, 1999). This complex method of digestion has significance for both the husbandry and medical aspects of herbivorous reptiles, since the delicate microbe and nematode populations may be adversely affected by certain antibiotics (e.g. Cooper; 1980; Innes, 2001) and hence information on potential problems in this area of interest should be highlighted. Here we briefly record a possible single incident of adverse affects concerning the use of antibiotics in C. zebrata.

A subadult *C. zebrata*, one of a small colony of these lizards housed in a naturalistic enclosure (7.5

x 10 meters horizontally and 3.2 metres vertically) at Huddersfield Technical College, showed signs of a skin infection. The animal was taken to the local veterinary surgery for treatment and given an initial treatment of Baytril (dosage=1ml per 5kg body weight) repeated at 5 and 10 day intervals. The lizard was then given liquid recovery diet orally using a syringe and subsequently appeared to have recovered, since it began feeding well on its normal diet of a mixture of fruits and vegetables and occasional giant mealworms: we presume it was also feeding on the vegetation growing in the enclosure which was normal practise for the colony. However, some weeks later it was noticed that there was a gradual decline in condition, despite a continuing good appetite. We considered the possibility that the antibiotic treatments may have had an adverse effect on the lizard's microbe and nematode population and hence we decided to induce 'artificial coprophagy' in an attempt to 'reintroduce' an intestinal fauna (Iverson, 1979; Troyer, 1982). This was achieved by offering several giant mealworms smeared with the faeces of its cage mates, a procedure that was repeated twice within the following week. In a relatively short time period, 2 weeks or so, the lizard began to regain condition and within approximately a 2 month period was back at normal weight.

The potential for the elimination of the intestinal faunas of herbivorous reptiles through the application of certain antibiotics has already been recognised, and indeed Innes (2001) has cautioned against their use pointing out that animals should be monitored for maldigestion

after antibiotic applications. Additionally, the Tewksbury Institute of Herpetology, which has an ongoing research programme on C. zebrata, avoids the regular use of anti-parasitic drugs such as Metronidazol unless potentially harmful protozoa have been identified as present (Richard Ogust, pers. communication). We suspect that this instance with C. zebrata was a case of maldigestion through the application of the antibiotic, although our evidence for this is circumstantial. Indeed there were several curious aspects concerning the incident. For instance, why we should have had to induce 'artificial coprophagy' rather than the animal performing this naturally is not immediately obvious. It was perhaps also unexpected that there was even a decline in our animal's condition, since in Iguana iguana microbe fermentation contributes to only around one third of daily energy requirements; juvenile iguanas without microbes still grow, but less quickly than those with microbes (Troyer, 1982). There are of course other possible explanations, for example social interactions could have constrained this individual to areas in the enclosure with sub-optimal temperatures; in I. iguana it is known for example that as a result of dietary differences between juveniles and adults the former require and regulate to higher body temperatures (Troyer, 1984). However, recent research on the C. zebrata population in question was unable to indicate any major differences in body temperatures between individuals (Mann & Meek, 2004) and in any case the subsequent recovery of the lizard would mitigate against this.

ACKNOWLEDGEMENTS

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Conservation of the axolotl (Ambystoma mexicanum) at Lake Xochimilco, Mexico

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ABSTRACT — Although the Mexican axolotl (*Ambystoma mexicanum*) is well known as a popular laboratory and aquarium animal, in the wild it is almost extinct and confined to the remnant canals of Lake Xochimilco on the edge of Mexico City. Loss of habitat, introduced fish, pollution and illegal collection for food and medicines have all played a role in its decline. Capitalizing on its high profile within local culture, a multidisciplinary conservation programme is being developed using the axolotl as a flagship species for the wider Xochimilco system. The programme is focusing on raising the profile of the axolotl and other species by promoting nature tourism and conservation education within the local community. Complementing these socio-economic initiatives is biological research on population ecology, survey methods and threat mitigation. The axolotl has been bred in captivity very successfully both in Mexico and elsewhere. However, reintroduction to Lake Xochimilco will not be a realistic option until the threats facing the species have been addressed. Equally, the disease and genetic risks posed by the release of captive bred stock need to be evaluated prior to any reintroduction.

N 1989 the relationship between the axolotl (Ambystoma mexicanum) and those who studied it was aptly described as 'schizophrenic' by Shaffer (1989). At that time, researchers fell into two distinct camps - a large group of biologists, geneticists developmental and endocrinologists on the one hand, and a smaller group of evolutionary biologists on the other. In recent years, however, a third research front has opened up, albeit driven by a mere handful of dedicated field workers in Mexico. Work in this new area has been stimulated by heightened concern for the status of the axolotl in its last remaining natural habitat on earth - the remnant canals of Lake Xochimilco on the edge of Mexico City. Even 15 years ago the future of the axolotl

was known to be precarious (e.g. Griffiths & Thomas, 1988; Shaffer, 1989; Brandon 1989; Smith, 1989a,b), but it has taken a renewed global interest in the plight of amphibian populations to precipitate action. The ground that needs to be made up is best illustrated by Smith's (1989a) comment that out of some 4656 works on the axolotl published up to that time, not a single one dealt with field studies. The axolotl (Fig. 1), then, is something of a paradox - immortalized in murals in the National Palace by the celebrated Mexican master, Diego Riviera, and in the writings of Julio Cortazar; widely known and widely used throughout the world as a popular laboratory and aquarium animal; yet almost extinct in the wild.



Figure 1. The Mexican axolotl, *Ambystoma mexicanum*. Photograph © Stuart Harrop.

THREATS TO AXOLOTLS

Lake Xochimilco is the last remnant of a once extensive wetland system that covered much of the volcanic basin in which Mexico City now sits. This closed aquatic system was maintained by a network of natural springs, rainwater and surrounding meltwater from volcanoes. Development of the wetland for agriculture stems from pre-Aztec times, possibly as early as 1000 BC (Rabiela, 1991), but intensified following the foundation of the Aztec capital city of Tenochtitlán on an island in the lake. Farmers reclaimed land by piling up mud and vegetation inside corrals of the water-loving willow (Salix bonplandiana) thereby forming raised fields known as 'chinampas' and developing an extensive lacustrine economy. The significance of this economy is neatly summed up by Deevey (1955): 'Four centuries of scholarship have not sufficed to bring limnological knowledge of the Valley of Mexico up to the stage attained by the Aztecs, many of whom spent most of their lives in canoes and depended on knowledge of the lacustrine flora and fauna for their livelihood'. The axolotl was a significant component of this economy, as alluded to by the Franciscan Friar

Bernardino de Sahagún in his *Historia General de las Cosas de Nueva España*, when he commented 'it is good to eat, it is the food of lords'.

The chinampas are still very evident today, but are now used mainly for the production of vegetables, flowers and plants. Surrounded by remnant canals that were once part of the extensive lake, the chinampas have become known as the 'floating gardens', even though they are not floating at all. Present-day water bodies cover a mere 2.3 square kilometres, and this reduction is largely the result of the diversion of natural springs over 100 years ago to meet the water demands of a burgeoning human population. In order to try and restore water levels, discharge of tertiary-treated sewage back into

the system was initiated in 1957, and in 1990 the government signed the 'Accord of Democratic Co-operation for the Ecological Rescue of Xochimilco' which included plans to restrict development, construct lagoons to control water levels, and improve the treatment of the water put back into the system (Wirth, 1997). Although these actions have probably stopped Lake Xochimilco disappearing completely, water quality and eutrophication are still major issues, alongside continued illegal settlement. Exacerbating the water quality problem is additional pollution from the wide variety of pesticides that have been used on the chinampas. For example, heavy metals have been detected in both axolotls and fishes sampled from the lake (Gonzalez et al., 1997). Moreover, recent surveys have found a strong female bias in the sex ratio of the axolotls captured (Vergara, 1990; Graue, 1998). Hormonal disruption resulting in 'feminization' has been linked to pollution in other amphibians (e.g. Hayes et al., 2002), and presents a worrying spectre for the axolotl.

In addition to water quality and pollution problems, the axolotl is also threatened by introduced fish and possibly by collection for food and medicines (Fig. 2). It is likely that the axolotl was once the top predator in the Xochimilco system. Indeed, most of the other native fish species - including endemic cyprinids and goodeids - are relatively small-bodied, and coevolved with the axolotl. In the second half of the 20th century large carp (Cyprinus carpio) were introduced to the lake as a food source, as were African Tilapia in the 1980's. Through direct predation - and possibly competition - these fish have accelerated the decline of the amphibian population. The axolotl has been widely regarded as a delicacy endowed with medicinal properties since prehispanic times. In fact, 'axolotl syrup' is still produced from a closely related neotenic species, Ambystoma dumerilii, and has been used to treat chest problems for centuries. Although the axolotl is listed on CITES Appendix II - which theoretically means that trade is controlled in a way that does not threaten the survival of the species - axolotls are still illegally collected. Enforcement of the legislation is difficult, but the government authorities have recognised the danger to human health posed by the consumption of fish and axolotls contaminated by heavy metals. Paradoxically, this has created something of an incentive to remove the introduced fish and discourage the consumption of fish and axolotls that have been fished from the lake.

POPULATION STATUS OF THE AXOLOTL AT LAKE XOCHIMILCO

The starting point of any conservation programme for a threatened species should be the establishment of the exact status of the wild population. Once this is known, those factors that have led to its decline should be identified - and hopefully neutralised - before a recovery programme begins. Unfortunately, carrying out population censuses of axolotls is difficult. The only established methodology for finding the animals is that developed and used by local fishermen. This involves casting a 6 m wide throw-net (or 'atarraya') from a stationary canoe, and drawing in the net along the bottom of the canal (Fig. 3). This is a very skilled procedure, and not one that is suitable for all parts of the system or that can be learnt quickly by researchers or students. A census carried out at 12 sampling sites using the services of a reliable local fisherman between 1995-1996 captured 76 animals. This translates into a population density of about 60 individuals per hectare. Although direct comparisons with other amphibians are difficult due to differences in sampling protocols, this is an order of magnitude lower than the densities of ambystomatid salamanders reported elsewhere, which can run to several thousand per hectare (e.g. Husting, 1965; Pechmann et al., 1991). A more recent survey of axolotls carried out in January-February 2002 – again using the traditional fishing method - yielded more worrying findings, as no axolotls were captured at all (Jones, 2002). It may well turn out that surveys need to be conducted later in the year when axolotls are more active, as the earlier surveys indicated that May seems to be a peak month. Despite these disappointing survey results, some unscrupulous fishermen certainly know where axolotls occur and how to catch them. as a recent investigation found axolotls continue to be illegally sold in local markets (McKay, 2003). Future work will refine the design and timing of the field surveys and attempt to gain the confidence of local fishermen who remain suspicious of researchers asking questions about their activities. Tests are also currently being carried out using a variety of funnel trap designs with a view to establishing a standardized method for determining the status of the population.

DEVELOPMENT OF A CONSERVATION STRATEGY

With multiple threats stacked against it, and census methods in an embryonic stage of development, the axolotl could be perceived as having not much going for it. However, as a result of its long history within Aztec mythology and its prominent position within the ancient lacustrine economy of the region, it has become something of a cultural icon. Moreover, Lake Xochimilco is an extremely popular recreational area for the people of Mexico City, and as well as being on the tourist trail for overseas visitors, was inscribed on the UNESCO list of World Heritage Sites in December 1987 and designated under the Ramsar Convention on 2nd February 2004. Highly decorated barges (or 'trajineras') cruise the lake at weekends, while their passengers are serenaded by Mariachi bands and plied with food and drink

from sellers on accompanying canoes (Fig. 4). For many visitors, Xochimilco provides a brief respite from the pressures and bustle of the third largest city in the world. Although the demands of a growing Mexico City might be the ultimate source of the axolotl's problems, local people could also be an integral part of the solution.

With generous pump-priming funding from the British Council and the Declining Amphibian Population Task Force (DAPTF), a series of meetings were held between DICE (University of Kent) and the UAM (Unidad Xochimilco) in 2000 and 2001 to devise a strategic framework for the conservation of the axolotl. During these meetings we talked to local fisherman, boatmen (remeros), farmers and artisans: tour operators, schoolteachers, researchers, and representatives from zoos and conservation organisations. It became obvious that these people valued Lake Xochimilco in different ways; and although the vast majority knew of the axolotl and appreciated its cultural importance, few of the local stakeholders were aware of its precarious status. To our minds, then, there seemed great potential for raising the whole profile of the cultural and ecological importance of the Xochimilco system by using the axolotl as a 'flagship' species for a conservation education and nature tourism programme. This view was reinforced by the fact that the Mexico City authorities had recently granted UAM extra land for the expansion of CIBAC (Centro de Investigaciones Biologicas y Acuicolas de Cuemanco), its research and education field station on the shore of Lake Xochimilco (Fig. 5). With an axolotl breeding and research facility already in place at CIBAC, this opportunity was particularly timely, as we could seek to develop our plans for a conservation education and tourism programme around this existing facility, using the axolotl as a flagship. However. this would all cost money. Strengthening our proposal by enlisting the support of a range of national and international organisations, notably the Mexican conservation authorities (CONABIO and SEMARNAT); Chapultepec, Toronto and Chester Zoos (who all have breeding colonies of axolotls); DAPTF and

the British Herpetological Society; a bid was submitted to the British Government's Darwin Initiative programme to fund a three-year project entitled 'Aztecs and Axolotls: Integrating Conservation and Tourism at Xochimilco, Mexico'. Singling out the project in a statement to the British media, the British Government's Environment Minister announced that the bid had been successful in April 2002.

THE DARWIN INITIATIVE PROJECT

The Darwin Initiative project is taking a multidisciplinary approach to the conservation of the Xochimilco system, and is using the axolotl as the centrepiece of this strategy. The project aims to develop CIBAC as an information and education centre with a view to enhancing understanding of the ecology and conservation of Xochimilco among local people and visitors. This is being undertaken in parallel with an educational outreach programme; ongoing research into the threats facing the axolotl and other endemic fauna; population assessment; and breeding and reintroduction protocols. To achieve these goals, a series of training workshops for staff and students of UAM - as well as local stakeholders - have been held at CIBAC (Fig. 6). These have covered conservation education, nature guiding for local boatmen, souvenir production for unemployed artisans, amphibian biology and conservation, and captive breeding and reintroduction methodologies. These workshops have been informed by social survey work carried out by a team of Mexican undergraduate 'investigators', and have drawn upon the expertise of our project partners both in Mexico and elsewhere. In addition, Alejandro Melendez - a UAM staff member - completed the MSc in Tourism and Conservation at DICE in 2003. Alejandro is continuing to oversee the development of the project in Mexico. Despite the pressures on Lake Xochimilco, there is still much for the naturalist to see, particularly in terms of its birdlife (over 160 species have been recorded at the site). However, as it is unlikely that visitors will have the opportunity to see live axolotls in the lake itself. future nature tours will conclude with a visit to

CIBAC, where visitors will be able view axolotls being used for the captive breeding and conservation research programme, and learn more about the natural history and conservation of the Xochimilco system. Posters, information leaflets, T-shirts, school work-packs, a website and souvenirs produced by local craftsmen are providing material support for the project, and will hopefully continue to do so when the project is over. It is anticipated that these products will help the axolotl become marketed as a flagship for wildlife conservation throughout Mexico City, as well as nationally and internationally. We anticipate that educational displays focusing on the axolotl will be running in parallel at the partner institutions of Chapultepec Zoo (Mexico), Toronto Zoo (Canada), the Indiana Axolotl Colony (USA) and Chester Zoo (UK). To conclude the Darwin Initiative project, in December 2004 we are organising an international workshop at CIBAC, entitled 'Conservation of the Axolotl and Xochimilco' which will allow all the contributing parties to report their successes (and failures!), and launch an action plan for the future.

A ROLE FOR CAPTIVE BREEDING AND REINTRODUCTION?

Amphibians are potentially excellent subjects for captive breeding and reintroduction programmes. Unlike many mammals and birds, the high fecundity of many amphibians can be utilized to produce large numbers of offspring quickly. Equally, the feeding and general maintenance of amphibians in captivity is often straightforward and relatively inexpensive, and animals for reintroduction do not need long periods of prerelease training so that they know what food to eat and what predators to avoid when released into the wild (e.g. Bloxam & Tonge, 1995). Axolotls have the added advantage of having a long history of captive propagation. Many of the animals currently in laboratories and aquaria around the world are descended from 34 animals sent to the Museum of Natural History in Paris in 1863, and aquaculture techniques for breeding and rearing this species are probably the most sophisticated for

any amphibian. However, there are a number of important issues that need to be addressed before a reintroduction programme can be seriously instigated.

Trade-offs exist between different methods of rearing axolotls in captivity. A recent study by one of us (McKay, 2003) compared the performance of axolotls raised in enclosures in a semi-natural canal (i.e. 'low maintenance' regime) with those in aquaria (i.e. 'high maintenance' regime). Axolotls raised in the enclosures grew much faster than those raised in aquaria, but survival was much lower. A 'high maintenance' regime may therefore result in more animals produced at a smaller size, but at a significantly higher cost.

The genetic management of any animals earmarked for reintroduction needs careful evaluation. Inbreeding depression in captive bloodlines initiated by a small number of founders can be a problem, and could lead to animals that are maladapted for life in the wild. Preliminary work using starch-gel electrophoresis indicated that a captive colony contained a lower degree of genetic variation than the wild population (Graue, 1998). This was, perhaps, to be expected given the relatively small number of founders of the captive colony. However, both the captive and the wild stock analysed displayed less genetic variation than that observed in other ambystomatids and in other amphibians in general (Nevo, 1978). If the wild population has itself now been reduced to a small remnant population, breeding from a sample of these animals may also accelerate inbreeding depression. One possibility might be to augment inbred 'wild type' with alleles from carefully selected captive bloodlines, but this remains work for the future.

A second important issue concerning the reintroduction of animals to the wild is that related to disease. Animals bred under captive conditions may be exposed to a variety of novel pathogens that they may not necessarily experience in the wild. Even if such pathogens appear to have benign effects on captive stock, it is crucially important that they do not find their way into natural systems. If wild animals are already

Conservation of the axolotl



Figure 2. Axolotls are still used to produce general purpose health tonics, bottles of which can be purchased locally. Photograph © Richard Griffiths.



Figure 4. Highly decorated 'trajineras' take visitors on leisurely cruises along the canals of Lake Xochimilco. Photograph © Richard Griffiths.



Figure 5. Richard Griffiths presents Virginia Graue with a set of BHS journals at CIBAC – the field station on the banks of Lake Xochimilco. Photograph © Ian Bride.



Figure 3. A local fisherman using the traditional netting method ('atarraya') for catching axolotls. Photograph © Richard Griffiths.



Figure 6. Participants and facilitators of a training workshop on board the project's own appropriately named trajinera. Photograph © Ian Bride.

suffering from, for example, immunosupression as a result of pollution, attack by a novel pathogen inadvertently introduced by releasing captive-bred stock could prove detrimental to the existing wild populations. Emerging infectious diseases, such as chytridiomycosis and ranaviral disease, have already been shown to have catastrophic effects on amphibian populations in different parts of the world (Daszak et al., 2003). Indeed, ranaviruses have been associated with mortalities observed in wild populations of the closely related tiger salamander (Ambystoma tigrinum) in North America (Jancovich et al., 1997; Bollinger et al., 1999). To minimise the risks that captive-bred stock may pose for wild stock, a sound reintroduction policy should focus on targeting and restoring habitats where there are no extant wild populations, coupled with a rigorous health screening of animals earmarked for release. However, this process might be compromised by the uncontrolled release of captive bred specimens by well-meaning local people - a practice that project members have been told has already occurred. This in turn raises the biggest issue of all in reintroduction programmes. Can it be certain that the factors that led to the decline - and perhaps extinction - of the original populations have been removed? If not, there is no point in releasing more animals that may go the same way as their predecessors. Some of these problems are already being addressed at CIBAC. The effectiveness of using plants as natural water treatment systems (bioremediation) is being tested as a method for cleaning up axolotl habitats. Other work is investigating the impact of various landuse regimes on the water quality and fauna and flora, as well as the overall landscape, whilst plans are afoot for the creation of an experimental in-situ restoration study site from which exotic species will be removed. Radio-tracking studies of axolotls may shed some light on how much movement and gene flow there is between subpopulations within the lake system, and the survival of eggs, larvae and adults are being compared under semi-natural conditions with a view to determining the most efficient stage for any future reintroduction programme.

CONCLUSIONS

Flagship species for conservation projects are invariably highly charismatic species that can engage the interest and imagination of people. This creates a sense of purpose in trying to save them, while the measures taken to protect the species - be it removing alien predators or saving the habitat - will also help protect other, less charismatic species in their wake. Amphibians, including the axolotl, seem to be unlikely candidates for flagship species. Although the threats that it faces seem almost overwhelming, the axolotl has three things going for it that other amphibians unfortunately lack: (1) a long history of importance as an icon of Aztec heritage and culture; (2) widespread familiarity throughout the world as a result of its longstanding use as a laboratory model and aquarium exhibit; and (3) an association with an area that local people and tourists alike value as a place to enjoy both themselves and the wildlife that surrounds them. Only time will tell whether these three factors will provide the foundations for bringing the last remaining wild population back from the brink of extinction, but ultimately, all will depend upon the understanding and support of the people of Xochimilco.

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POSTSCRIPT

Dr Virginia Graue, who instigated this project and co-authored this paper, sadly passed away in January 2004 after a long battle against serious illness. Her enthusiasm, knowledge and sense of humour will long be remembered, and the Darwin Initiative project will be dedicated to her memory.

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A review of environmental conditions along the coastal range of the Diamondback terrapin, *Malaclemys terrapin*

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ABSTRACT — The Diamondback terrapin, *Malaclemys terrapin*, is distributed along the east coast of North America from Cape Cod, Massachusetts to Corpus Christi Bay, Texas. Six characteristic sections occur along this narrow coastal range, and the individual ranges of the seven subspecies of *M. terrapin* correspond closely to them. From north to south and west these are the Embayed Section (*M. t. terrapin*), Sea Island Section (*M. t. centrata*), Floridian Section (*M. t. tequesta* in the north, *M. t. rhizophorarum* in the mangrove thickets of the Florida Keys), East Gulf Coast Section (*M. t. macrospilota*), Mississippi Alluvial Plain Section (*M. t. pileata*), and West Gulf Plain Section (*M. t. littoralis*). Each section is described using the following environmental factors: the underlying geology and geological history, beach conditions, major inflowing rivers, inshore and beach vegetation, ocean currents, tides and wave action, and air and water temperatures. A discussion is presented of the most important of these, in regards to possible influence on subspeciation (geological features and history, environmental temperatures, tidal ranges, and the mangrove vegetation of southern Florida and the Florida Keys).

THE Diamondback terrapin, Malaclemys terrapin (Testudines: Emydidae) occupies a narrow North American coastal range that extends from Cape Cod, Massachusetts, to Corpus Christi Bay, Texas, and includes the Florida Keys (Conant and Collins, 1998; Ernst and Bury, 1982; Ernst et al., 1994). It occupies various habitats along the edge of the coastal plain, such as salt marshes, brackish estuaries and lagoons, tidal creeks and flats, and sounds behind barrier islands (Ernst et al., 1994; Palmer and Cordes, 1988).

Within this range, seven subspecies are currently recognized (Ernst and Bury, 1982): the Northern diamondback terrapin, *Malaclemys terrapin terrapin*, ranges along the Atlantic Coast from Cape Cod, Massachusetts to Cape Hatteras, North Carolina; the Carolina diamondback terrapin, *M. t. centrata*, is found on the Atlantic Coast from Cape Hatteras to northern Florida; the Florida East Coast diamondback terrapin, *M. t. tequesta*, occupies the Atlantic Coast of Florida to the Keys; the Mangrove diamondback terrapin, *M. t. t. rhizophorarum*, lives on the Florida Keys; the Ornate diamondback terrapin, *M. t. macrospilota*, ranges north from Florida Bay in the south along the Gulf Coast to Mobile Bay; the Mississippi diamondback terrapin, *M. t. pileata*, is found from Mobile Bay west along the Gulf Coast to western Louisiana; and the Texas diamondback terrapin, *M. t. littoralis*, ranges from western Louisiana to Corpus Christi Bay, Texas. Zones of intergradation occur where the various subspecific ranges meet (Ernst and Bury, 1982; Ernst et al., 1994).

It is interesting that the subspecific ranges correspond closely to the six characteristic sections of the North American Coastal Plain described by Thornbury (1965). From north to south and west these are the Embayed Section, Sea Island Section, Floridian Section, East Gulf Coast Section, Mississippi Alluvial Plain Section, and West Gulf Plain Section. The six sections exhibit somewhat different biological, geological and oceanographic characters, which possibly played roles in the evolution of the observed subspecific ranges within *M. terrapin*.

METHODS

In this paper we examine and describe the characteristics of each of Thornbury's six sections as presented in Duncan & Duncan (1987), Kumpf

et al. (1999), Myers & Ewel (1990), and Thornbury (1965), and several primary sources. The major environmental factors examined for each section are those that probably play major roles in shaping the biology of the species. These are as follows:

Underlying Geology and Geological History. Geology provides the topographic features of the coastal range of *M. terrapin*. As such, it affects the path of ocean currents, tidal range, beach depth, and the plants present.

Beach Conditions. Beaches provide nesting habitat for the turtle. Sand beaches are preferred, although some beaches contain gravel, and others are almost nonexistent due to rocky outcrops. The beaches near Cape Cod are generally narrower than those farther south.

Major Rivers. The major watersheds entering the section provide varying amounts of freshwater, depending on the upland area drained, season and local storms. M. terrapin and some of its prey species depend on freshwater inflow to lower the salinity of the coastal waters. The salinity of ocean water, approximately 35 parts per thousand, varies according to the temperature, degree of evaporation, and the amount of freshwater influx (Zottoli, 1978). The turtle will acclimate to high salinity concentrations, but can not withstand, especially hatchlings, permanent exposure to seawater (Bels et al., 1995; Bentley et al., 1967; Cowan, 1981; Davenport & Macedo, 1990; Dunson, 1970, 1985; Gilles-Baillien, 1973a, 1973b, 1973c; Robinson & Dunson, 1976). Rivers also provide the nutrients and trace elements necessary for many of the prey species of M. terrapin, and molluscan and crustacean breeding areas are more intense in estuaries or near the mouths of major rivers (Kumpf et al., 1999).

Inshore and Beach Vegetation. Inshore vegetation provides foraging areas for all life stages and hiding places for hatchlings and juveniles. Beach vegetation provides nesting habitat and protection from the sun and predators during nesting.

Ocean Currents. These currents, depending on the source and direction of flow, are largely responsible for the temperature of the water along

the shore. The rapidity of inshore currents may make it dangerous for *M. terrapin* to move along the shoreline.

Tides and Wave Action. Malaclemys terrapin must nest above the high tide line, and extreme high tides and severe wave action can erode nesting beaches, destroy established nests, or alter foraging habitat. Waves also cause turbidity, the amount of which may affect prey species. Presented tidal data are from the United States Department of Commerce (1987).

Air and Water Temperatures. Both temperatures vary with season and with latitude. Generally, temperatures average cooler in the north and warmer in the south, and may cause northern populations to hibernate in the winter (Lawler & Musick, 1972; Yearicks et al., 1981). These affect both daily and annual cycles of activity and have a profound effect on successful nesting. Incubation temperatures may also affect the sex ratio of hatchlings. Malaclemys terrapin practices temperature-dependent sex determination; incubation temperatures of 24-29°C produce almost all males, eggs incubated at 30°C produce only females (Ewert & Nelson, 1991; Sachsse, 1984). Seasonal temperature data were obtained from two websites:

www.nws.noaa.gov/climatex.html, and www.usatoday.com/weather/climate/usa.

RESULTS

Section Descriptions

The Embayed Section. Thornbury's (1965) Embayed Section, ranging from Cape Cod, Massachusetts, to a little south of the Neuse River in North Carolina, contains many estuarine embayments that divide the Atlantic Coastal Plain into several peninsular tracts, and an inner lowland on lower Cretaceous Raritan clays. Offshore sandbars are particularly common in the north. This section corresponds to the range of *M. t. terrapin*. Its most outstanding geomorphic characteristics are related directly or indirectly to the most recent submergence of the Atlantic Coastal Plain (greater in the north than in the south) caused by the weighing down of northeastern North America by Pleistocene glaciation, and to the subsequent postglacial rise in sea level upon return of large volumes of melted ice runoff to the oceans. Beaches in New England and around Cape Hatteras are rather narrow, but all others are fairly broad.

The major freshwater drainages entering the section from north to south are the Narragansett Bay complex; Connecticut River; Hudson River; Delaware River and Bay; Chesapeake Bay complex, including the Susquehanna, Potomac and James rivers; Chowan River emptying into Albemarle Sound; Pamlico River and Sound; and Neuse and Cape Fear rivers. These waterways, depending on upland rainfall, may add much freshwater to the coastal Atlantic Ocean, and their mouths and estuaries are very productive zones for the important mollusk and crustacean prey of *M. t. terrapin*.

Algae cling to the more rocky shores of New England; these are productive areas for snails (Littorina sp.), an important food source. Farther south offshore seagrass (Cymodocea filiforme, Halodule wrightii, Thalassia testudinum) beds are more numerous, providing habitat for crabs (Callinectes sp., Gelasimus sp., Sesarma sp., Uca sp.), small bivalves (Anomalocardia cuneimens, Gemma gemma, Macoma sp., Mya arenaria, Mytilus edulis, Tagelus sp.), snails (Littorina sp., Melampus sp., Nassarius obsoletus), and marine annelids (Nereis sp.) (Allen & Littleford, 1955; Coker, 1906; Ernst et al., 1994; Mitchell, 1994; Palmer & Cordes, 1988; Roosenburg, 1994; Roosenburg et al., 1999; Whitelaw & Zajac, 2002). Most populations of M. terrapin are associated with saltmarshes, in which the predominate vegetation is Cordgrass (Spartina alterniflora). Beach vegetation often includes Ammophila breviligulata, Myrica pensylvanica and Phragmites sp. (Duncan & Duncan, 1987; Palmer & Cordes, 1988).

The New England coast from Cape Cod, Massachusetts, to about the eastern tip of Long Island, New York is influenced by the cold Labrador Current which originates in the Arctic (Thurman, 1994). From Long Island south to Florida, the Atlantic coast is bathed by the warm Gulf Stream that originates in the Caribbean Sea as the Caribbean Current. Mean water temperatures in January vary from 4.4°C at Boston Harbor, Massachusetts, to 9.4°C at Cape Hatteras, North Carolina, and from 18.9°C and 25.0°C in July for the two sites, respectively. Northern coastal waters become cold enough in winter to stun marine turtles, often with fatal results (Morreale et al., 1982). Mean air temperature corresponds accordingly from north to south, and may be so cold as to force *M. terrapin* to hibernate as far south as Virginia (Lawler & Musick, 1972; Yearicks et al., 1981).

Tides, and subsequent wave action, vary within the section. Average tide ranges on 15th June (the turtle's nesting season) for the section vary from a high of 2.9 m at Boston, Massachusetts, to a low of 0.7 m at Hampton Roads, Virginia. The entire section is subject to occasional hurricane events during the summer and fall which may cause much beach erosion and damage to tidal marshes.

The Sea Island Section. This region covers the youthful to mature terraced coastal plain from about the Neuse River, North Carolina, south to northern Florida. It contains fewer estuaries than the Embayed Section but has a low border of barrier islands. It covers most of the range of M. t. centrata. The amount of submergence is less than that north, and the drowned mouths of its rivers are shallower. Beaches are narrow around Cape Hatteras but broad south of there. Offshore sandbars are less common and are replaced by a series of coastal sea (barrier) islands. The underlying geology is similar to the Embayed Section, but the Miocene rocks of the sea islands do not extend to the inner margin of the Coastal Plain, where they are replaced by Eocene and Cretaceous rocks. Near the beaches is a tract of young terraces, largely unmodified by stream erosion, with extensive swamps on them. The chain of sea islands is separated from the parallel mainland by salt marshes, passes, tidal creeks ('guts'), sounds or lagoons which are good feeding areas for the turtles. Three types of islands are present along the coast (Zeigler, 1959): erosion remnant islands, marsh islands, and beach ridge islands; and the islands serve as important nesting sites for the turtles.

Environmental conditions along coastal range of Malaclemys terrapin

The prevailing rivers can be dated to either the pre-Wisconsinian (Santee, Edisto, Savannah, Saltilla) which drain from the Piedmont across the coastal plain, or the post-Wisconsinian (Midway, Newport, Turtle) which head near the escarpment and form the inner boundary of the Pamlico terrace (Zeigler, 1959).

Some seagrass beds (*Thalassia testudinum*) occur offshore. Beach vegetation is similar to that of the Embayed Section, but palmetto (*Sabal* sp.) is present on some barrier islands and inshore borders of continental beaches. Animals reportly consumed by this section's *M. terrapin* include most of those invertebrates previously listed for the Embayed Section, and the bivalves (*Geukensia demissa*), crabs (*Uca pugnax*), and small adult fishes (Atlantic Silversides, *Menidia menidia*) (Middaugh, 1981; Tucker et al., 1997).

Fed by the Gulf Stream, the offshore waters are relatively warm. Mean January water temperatures vary from 9.4°C at Cape Hatteras to 10.6°C at Savannah, Georgia; mean July water temperatures at these two sites are 25.0°C and 28.3°C, respectively. Mean air temperatures in January and July at these two sites are 7.1°C and 9.4°C and 25.8°C and 27.8°C, respectively. Summer and fall hurricanes are not infrequent in this section. Normally, however, the tidal range is from about 1.3–2.3 m.

The Floridian Section. This coastal region extends along the Atlantic coast of Florida. Its northern boundary blends into the southern Sea Island Section; however, it has certain distinctive features of its own. It is comprised of a recently emerged (Eocene to Pleistocene) terrace with carbonate rocks and extensively developed karst features. Its sandy beaches are usually broad. Offshore sandbars or limestone keys (small islands) border much of the coast, and its southernmost area is a series of Atlantic Coastal Ridge limestone keys. Lagoons lie behind the sandbars. Prominent tidal marshes and swamps are present, and extensive marine terraces occur on the east and south around the higher central peninsula of Florida (Thornbury, 1965). The edge of the continental shelf is only a few miles east off the coast. Major freshwater drainages of the region are the St. Johns and Indian rivers and the Everglades. This section corresponds closely with the ranges of M. t. tequesta and M. t. rhizophorarum.

Vast tidal saltmarshes of Cordgrass (Spartina alterniflora, S. patens), Eelgrass (Zostera sp.), Saltwort (Salicornia sp.), brown algae (Ascophyllum nodosum, Fucus vesiculosus), and mats of green algae (Cladophora sp., Enteromorpha sp.) and blue-green Algae (Calothrix sp., Lyngbya sp.) may be present (Duncan & Duncan, 1987; Zottoli, 1978). These create important crab (Callinectes, sp., Sesarma sp., Uca sp.), snail (Littorina sp., Melampus, sp., Nassarius sp.), bivalve (Macoma sp., Mytilus sp.) and annelid worm (Nereis sp.) habitat (Montague & Wiegert, 1990; Zottoli, 1978).

The predominant vegetation changes in the southernmost parts, especially the Florida Keys, where extensive stands of mangrove occur; Rhizophora mangle is the most common species, but Avicennia germinans and Laguncularia racemosa may also be present along the shoreline. The mangroves create a new habitat, and their rich invertebrate and vertebrate faunas are much different than those of the more northern portion of the Floridian Section (Odum & McIvor, 1990; Zottoli, 1978). This is the habitat of M. t. rhizophorarum. Unfortunately, prey reports for this subspecies are generalized, small bivalves (possibly, Anomalocardia cunimeris, Mya sp. and Mytilus sp.) and snails (possibly Littorina sp., Melampus sp. and Nassarius sp.), but one was observed feeding on a small dead fish (Red snapper, Lutjanus compectanus; Wood, 1992). Immediately north and west of the Florida Keys, M. t. rhizophorarum intergrades with M. t. tequesta and M. t. macrospilota, respectively (Ernst, pers. obs.).

Climate of the entire Floridian Section is influenced by the warm Gulf stream which flows offshore. January mean water temperatures vary from 10–11°C in the north to 21.7°C at Miami, Florida and 20.6°C at Key West, Florida. Correspondingly, mean January air temperatures at these sites are 9–10°C, 19.6°C and 15.6°C, respectively. July mean water and air temperatures at these three sites are 27–28°C and 27–28°C; 30.6°C and 28.2°C; and 30.0°C and 29.4°C, respectively.

Frequent hurricanes and tropical storms affect the section during the summer and fall. Tidal ranges in the north are 2–3 m, and at Key West, 0.4 m.

The East Gulf Coastal Plain Section. The range of M. t. macrospilota, is found in this region, from southwestern Florida to Mobile Bay, Alabama. Intergradation with at least M. t. rhizophorarum occurs in southwestern Florida (Ernst, pers. observ.). It is a youthful to maturely dissected, belted coastal plain with a series of alternating cuestas (formations with a cliff on one side and a gentle slope on the other) and lowlands. Coastwise terraces are present along the outer margin (Thornbury, 1965). There is an increase westward in number and thickness of the Cretaceous and Eccene formations, resulting in a widening of the coastal plain, causing a sharp contrast with the inland Piedmont. The 'Fall Line' is distinct on its rivers. The greater part of this section consists of belted Pleistocene coastal plain, including a series of lowlands on weak rock, usually limestone or clay shales, bordered seaward by cuesta scarps and dip slopes on stronger, commonly sandstone, rocks. Inland, adjacent to this is a narrow stripe of coastwise terraces. The major rivers of this region, from south to north, include the Caloosahatche, Peace, Withlacoochee, Waccasassa, Suwannee, Auchilla, Ochlackonee, Apalachicola, Choctawhatchee, Escambia, Tensaw, and Mobile.

The vegetation is rich and grades from mangroves in the south to more herbaceous plants as the coastal dunes are transversed northward. Forbs and grasses present include Alternanthera ramosissima, Ambrosia hispida, Aristida patula, Chloris petraea, Croton glandulosus (var. floridanus), Flaveria floridana, Muhlenbergia capillaris, and Schizachyrium semiherbe (Johnson & Barbour, 1990). Sea oat (Uniola paniculata) and Phragmites sp. also occur on the dunes, and Spartina sp. is ever present in the tidal marshes (Duncan & Duncan, 1987). Stable dunes are dominated by either small palms (Sabel sp.) or Gramma grass (Bouteloua hirsuta). The only report on the diet of M. t. macrospilota was that of Carr (1952) who noted that one had fed on a

Pointed venus clam, Anomalocardia cuneimeris, but the snail genera Littorina and Nassarius, and the bivalve genera Macoma and Mytilus are also present.

The predominate offshore current is the warm Gulf Stream. Air temperatures in January average $9-10^{\circ}$ C and in July 27–28°C; January and July water temperatures average $10-11^{\circ}$ C and 28.5–30.0°C, respectively. The turtles seldom, if ever, are forced to hibernate in the winter. Normal tidal ranges are 0.7–1.0 m, but this section frequently experiences tropical storms and hurricanes with high wave action.

The Mississippi Alluvial Plain Section. This coastal region consists of alluvial and deltaic plains, with alluvial terraces inland and coastwise deltaic terraces along the seaside. It covers most of the range of M. t. pileata. Most of the deltaic area is composed of meandering branches of the Mississippi/Atchafalaya River complex, mostly formed in the last 2,000 years, but the Pascagoula and Sabine rivers contribute freshwater in the east and west, respectively. Saltmarsh and dune plants are similar to those of the preceding section; barrier islands may contain Juncus sp. (Duncan & Duncan, 1987; Johnson & Barbour, 1990). Cagle (1952) reported the intestinal contents of M. t. pileata from this section contained only 'fragments of small clams and snails'. Present are the bivalve genera Macoma and Mytilus, and the snail genera Anomalocardia, Littorina and Nassarius, popular prey of M. terrapin elsewhere.

The Gulf Stream keeps the section warm, allowing the turtles to remain active all year long. January and July mean air and water temperatures are, respectively: 9.5–15.0°C, 27.5–28.0°C; 10.6–16.0°C, 28.7–30.0°C. The normal tide range is 0.7–1.0 m, but the coast is subject to severe tropical storms and hurricanes each year.

The West Gulf Coastal Plain. This is Thornbury's (1965) most western section, and it is here that M. t. littoralis is found. The section's inner portion comprises a wide belted coastal plain with inconspicuous cuestas; the seaward margin is a deltaic coastal plain. This Quaternary coastal plain consists of a series of coalescing deltaic and Environmental conditions along coastal range of Malaclemys terrapin

alluvial Pleistocene terraces built by rivers; from east to west, the Sabine, Neches, Trinity, Brazos, Colorado, Lavaca Guadalupe, Nueces, and Rio Grande. These terraces decrease in age and elevation toward the sea, and each is thought to have developed during a high sea level. The western end of the section contains a series of fault systems, with the westernmost quite pronounced. Many igneous intrusions are found within the fault zone, and salt domes are more plentiful than in Thornbury's more eastern sections. Coastal vegetation resembles those of the last two sections. No specific data relating to the diet of M. t. littoralis has been published, but the common prey genera of bivalves and snails are present in this region.

Once again, the warm Gulf Stream bathes the region; air temperatures in January average $11-13^{\circ}$ C and in July 28–30°C. The coastal water averages $12-14^{\circ}$ C in January and 29–30°C in July. The region experiences several tropical storms or hurricanes each year, but normally the tidal range is 3.1-1.2 m.

DISCUSSION

The section descriptions above clearly indicate that core environmental conditions vary along the coastal range of *Malaclemys terrapin*. The most variable are geological morphology (including beach conditions), air and water temperatures, and tidal range. All sections have large rivers contributing freshwater, and the beach and tidal marsh vegetation are relatively constant regarding the major plants, with the exception of the mangrove area of southern Florida.

Diversification based on geology is supported by studies of other western Atlantic and Gulf of Mexico marine and coastal animals continuously distributed throughout the range of *M. terrapin*: Horseshoe crab (*Limulus polyphemus*; Saunders et al., 1986), Stone crab (*Menippe* sp.; Bert, 1986), Virginia oyster (*Crassostrea virginica*; Reeb & Avise, 1990), Black sea bass (*Centropristis striata*; Bowen & Avise, 1990), Menhaden (*Brevoortia tyranus, B. patronus*; Bowen & Avise, 1990), Atlantic sturgeon (*Acipenser oxyrhynchus*; Bowen & Avise, 1990), the Dusky seaside sparrow (Ammodramus maritimus; Lamb & Avise, 1992), and *M. terrapin* (Avise, 1992). Most of these studies used mtDNA as the primary marker of diversity within species.

Two clear clades appeared in M. terrapin, north and south of approximately Cape Canaveral, Florida (28° 27'N; Avise, 1992). Avise (1992) did not speculate about which geological features may have led to such distinctions, but Lamb and Avise (1992) suggested that Atlantic and Gulf Coast Diamondback terrapins may have been isolated during the late Pleistocene glaciation. However, five other species with the same split (Toadfish, Opsanus sp.; American oyster; Horseshoe crab; Dusky seaside sparrow; and Black sea bass) showed much higher genetic diversity, leading to the theory that the various populations of Malaclemys may have had more recent evolutionary contact than the other five animals (Avise et al., 1992). Because of the correlation between geological features and subspecies ranges (Thornbury, 1965), strengthened by genetic evidence, underlying geologic history may have played a role in the subspeciation within M. terrapin.

The air and water temperature regimes experienced by M. terrapin within the various geological sections may also have played some role in subspeciation. The greatest differences occur between the New England populations, adapted to the cold waters of the Labrador Current, and the southern Florida and the Gulf of Mexico populations that are adapted to the warm waters of the Gulf Stream. However, although these differences may affect the sex ratios of clutches or possibly the number of clutches a female produces each year, no pressure for subspeciation is readily apparent. Populations of M. t. terrapin bridge the gap between the cold New England waters and those of the warm Gulf Stream without apparent significant changes in phenotypic characters. Nevertheless, along the Gulf Coast from the Florida Panhandle to southern Texas two subspecies, M. t. pileata and M. t. littoralis, are different in both pattern and morphology (Ernst et al., 1994), although they experience almost identical temperature variation during the year.

Practically no research has been done on the effects of tides on M. terrapin. Females prefer to nest above the high tide line (Auger and Giovannone, 1979; Burger and Montevecchi, 1975), but how this would affect subspeciation is unknown. However, the tidal regimes, like the underlying geology, have a correlation with the subspecies ranges. Three, M. t. macrospilota, M. t. pileata and M. t. littoralis, experience noncontiguous tidal periods. Because of limited data on the tidal activity of Malaclemys, no firm conclusions can be made about the tide's potential effect on subspeciation. The correspondence of the three Gulf of Mexico subspecies with tidal periods mark tidal activity as a promising prospect for further study.

As noted, the only major difference in vegetation type within the ranges of the subspecies of *M. terrapin* is that of the mangrove habitat of *M. t. rhizophorarum*. The mangrove habitat may have encouraged the development of both the solid black adult carapace and bulbous keel knobs of *M. t. rhizophorarum* as camouflage; the dark monocoloration to hide it among the mangrove roots, and the knobs as mimics of the breathing pneumatophores (air roots) of the mangroves.

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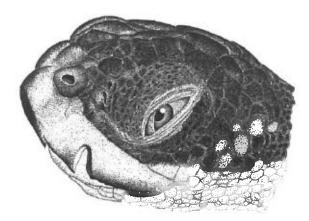
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Head detail of hatchling Leatherback sea turtle, *Dermochelys coriacea*. Reproduced with kind permission of the artist/author, Julian C. Lee, from *The Amphibians and Reptiles of the Yucatán Peninsula* (Cornell University Press, 1996).

Anomalepis mexicanus Jan (Serpentes, Anomalepididae) in Honduras

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Anomalepididae Taylor. Jan, in Jan & Sordelli (1860) gave 'Mexique' as the locality for his specimen of A. mexicanus (Jan, 1857, gave 'Messico' as the locality for his Anomolepis mexicanus, a nomen nudum). No subsequent specimens of this species or family have been collected in Mexico, and that locality is considered erroneous (Kofron, 1988; McDiarmid et al., 1999). Kofron (1988), in the most recent review of the species, recorded A. mexicanus from Peru, Panama, and Costa Rica.

By sheer coincidence, in 2003 (143 years after the species was first made known to science), two specimens of Anomalepis mexicanus were collected by separate workers in two countries to the north of its previous known range. Köhler et al. (2004) reported the first specimen of this species from Nicaragua (collected 19th July 2003). On 10th December 2003, Tomás Manzanares collected the first specimen of this species from Honduras. In addition, I collected a second Honduran specimen of A. mexicanus on 18th May 2004. Both were collected near a campsite known as Urus Tingni Kiamp (14°54.639'N, 84°40.829'W) in primary rainforest at 160 m elevation in the Mosquitia of northeastern Honduras. This locality lies about 170 km NNE of the Nicaraguan locality reported by Köhler et al. (2004). The two Honduran specimens are discussed below.

The two Honduran specimens (UF 141964–65) have total lengths of 155 and 100 mm, respectively (sexes of both unknown). Pertinent scale counts (those identified by Kofron, 1988, as diagnostic of the species in the genus) are: number of dorsal scales 261-262; scale row formulas 22-22-22 and 24-24-22. These data agree with those of Kofron (1988) in that Central American snakes have fewer dorsal scales than those from Peru, although there is overlap in the respective ranges. The Honduran specimen with 24 scale rows at midbody (UF 141964) is the only specimen of *A. mexicanus*

known from Central America to have 24 scale rows at midbody, although that count has been recorded in at least one specimen from Peru (Kofron, 1988). Colour in life of UF 141965 was recorded as follows: all dorsal and ventral surfaces Chestnut (colour 32 in Smithe, 1975–1981), but internal organs visible through translucent ventral skin; iris black.

The Honduran specimen collected in 2003 was under a log on a bank above a stream and the second specimen was inside a rotten log on a hillside. Both situations were moist from recent heavy rainfall. These specimens also represent the first records of the family Anomalepididae from Honduras.

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Behaviour and time allotment in the West Indian snake Alsophis rufiventris (Colubridae)

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T one time, eleven species of West Indian Aracers (Colubridae: Alsophis) occurred on more than 100 islands in the Bahama Islands. Greater Antilles, and Lesser Antilles (Henderson & Sajdak, 1996). The five that occur in the Lesser Antilles had a historical range encompassing 16 islands. This range has been reduced to nine islands, likely due to introductions of the Mongoose (Herpestes javanicus; Sajdak & Henderson, 1991). Alsophis rufiventris, one of the five Lesser Antillean species, is listed as endangered on the IUCN 'Red List of Threatened Animals' (Day, 1996). The species is endemic to the Saba and St. Christopher (St. Kitts) banks, but it has been extirpated from St. Kitts and Nevis (Barbour, 1930). Although Saba and St. Eustatius evidently support healthy populations in the absence of mongoose, these islands represent only 11% of the species' original range (Sajdak & Henderson, 1991).

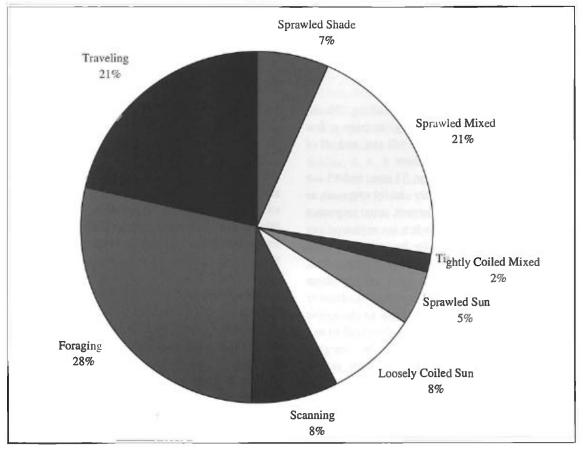
The biology of *A. rufiventris* has not been studied extensively. Henderson and Sajdak (1996) included the species in their analysis of West Indian *Alsophis* diets, and, in her bioinventories of Saba and St. Eustatius, Rojer (1997a, 1997b) commented on basic ecology and distribution. Our study sought to identify components in the behavioural repertoire of *A. rufiventris* and to place these components into the context of time. Henderson and Winstel (1997) noted the paucity of information regarding daily activity and time budgets in snakes, and the difficulties inherent with accumulating those data (e.g., ability to maintain visual contact with subjects). Although several studies have provided information on patterns of activity (e.g., Slip & Shine, 1988), fewer have provided percentages of time devoted to various activities (Henderson, 2002; Secor, 1995). Our observations, although of short duration, add to this small body of knowledge and provide groundwork for future observations of *Alsophis* ecology.

From 13th-22nd June 2004, we conducted focal animal studies along the main access trail to The Ouill, a dormant volcano on the southeastern end of St. Eustatius, Netherlands Antilles. The trail ascends the western slope from approximately 165-400 m elevation. Vegetation consists of semievergreen seasonal forest, but deciduous seasonal forest is present at lower elevations and dry evergreen forest occurs near the crater rim. All but the latter are dominated by Pisonia spp., whereas the crater rim is characterized by Coccoloba / Chionanthus stands (unpubl. data, St. Eustatius National Parks Association). Anolis lizards (especially A. schwartzi, but also some A. bimaculatus), presumably the primary prey of Alsophis rufiventris (Henderson & Sajdak, 1996), are abundant throughout the study area, especially in association with rock outcrops or slides, but also in leaf litter.

The area of The Quill in which the work was conducted was relatively devoid of undergrowth that had the potential of interfering with observing snakes for prolonged periods. This was in large part due to numerous goats that foraged over much of the island, cropping vegetation from elevations ranging from sea level to the crest of The Ouill. We scanned both sides of the trail for snakes for the full line of sight, but rarely spotted snakes more than 3.0 m off the trail (although sometimes we were able to see them as far as 10 m from the trial). Upon encountering an animal that did not appear startled by our presence, we noted substrate, extent of insolation (shade, filtered light, full sun), and microhabitat. An observer would watch the snake for 15 min, until the animal was lost from view, or if we felt the animal was responding to observer presence. We noted and timed behaviours in six categories based on position, movement, and

presence or absence of tongue-flicking, with some sub-categories for clarification: (1) Stationary, (a) sprawled, stretched along the substrate, with no part of the body touching another, (b) loosely coiled, one or a few large coils causing the animal to touch itself in at least one place (c) tightly coiled, multiple or S-coils involving broad contact between body sections, (d) scanning, head elevated at roughly a 45 degree angle to substrate with no tongue-flicking (a similar but more pronounced behaviour has been recorded in another racer-type snake, *Masticophis flagellum*; Secor, 1995); or (2) Moving, (a) foraging, movement over substrate with tongue-flicking and short pauses to nose through leaf litter, roots, and deadfall, (b) traveling,

Figure 1. Behavioural time allotments in Alsophis rufiventris on The Quill, St. Eustatius, Netherlands Antilles.





An adult male Alsophis rufiventris basking in full sun on the rim of the Quill at an elevation of \sim 400 m Photograph © John S. Parmerlee, Jr.

steady movement with no tongue-flicking. We did not include a 'basking' category, as only a few snakes were clearly basking in full sun, and all of these were on the rim of the crater.

We recorded a total of 5 hr, 33 min, and 45 sec of data on 27 snakes. We were careful to remain as unobtrusive as possibly. However, some responses to observers were evident when we reviewed our data. Snakes might pause for less than a minute during their foraging activities, remaining still, with no tongue-flicking. At least some of these instances could have been responses to observer presence. Because we were unable to determine whether or not such pauses were the result of our presence and despite statements by Gregory (2004) indicating that snakes are not overly responsive to the presence of observers, we chose to err on the side of caution and disregarded all ambiguous observations from the data set, thereby reducing the total observation time to 167 min and 45 sec. Although the remaining data cover a relatively short period of time, based on our subjective evaluations of *A. rufiventris* behaviour and that of congeners observed on other islands, we believe that our results accurately represent behaviour and time allocations of these snakes.

We observed individual Alsophis rufiventris on The Quill moving nearly 50% of the time (Fig. 1). Slightly more time was spent foraging than traveling. While stationary, most snakes were in sun-dappled shade, some time was spent loosely coiled or sprawled in full sun or shade, with most of the latter involving short pauses during foraging. We observed tight coiling only in sun/shade mosaic and loose coiling only in full sun. The vast majority of time (43%) involved resting in or moving through mixed and full shade. Of the two snakes observed loosely coiled in

full sun, one was on rocks of the rim of the volcano and the second was in a patch of mostly bare ground on the slope. The majority of encounters and observations took place on the slopes, where breaks in the canopy that allowed full sun to reach the forest floor were relatively uncommon. We did not attempt to discern when a snake was stationary for thermoregulatory purposes, simply scanning the environment, or resting.

We saw snakes loosely coiled in full sun only in the morning (07:40 hrs, 09:50 hrs). We observed traveling in both afternoon and early evening and foraging at all times of day. In the middle of the day, we observed snakes sprawled in conditions of mixed lighting.

Percentages reflected by the data agree with our experiences with and observations of this and other species of *Alsophis*. *Alsophis rufiventris* is an active forager (Schwartz & Henderson, 1991), moving over and through leaf litter and along deadfall and rocks in search of prey. We observed snakes assessing their immediate environments both chemically (tongue-flicking) and visually (scanning). For this study, the two were considered to be mutually exclusive, as tongue-flicking rarely occurred while a snake was stationary, even in the extended data set.

Of interest also were behaviours not previously documented. During one focal animal observation and again during a concurrent study, we observed tail movement involving approximately the last 8.0 cm of the tail, while the rest of the body and tail was sprawled and motionless. The motion was apparently deliberate, with the tail curled slightly and the movement mostly horizontal to the ground. Thus, the tail would flip or writhe from one position to another, with occasional pauses and vertical curls. Similar behaviours have been implicated in caudal luring (e.g., Heatwole & Davidson, 1976), but we were unable to attribute any obvious motive to these movements.

Although no record exists of this species eating sympatric ground lizards (*Ameiva erythrocephala*), we observed a snake investigating five different holes, presumably *Ameiva* burrows. The snake inserted 10–15% of its body into cavities for up to 3 min 55 sec, alternating between probing the burrow and pausing. Henderson & Sajdak (1996) noted that other species of *Alsophis* are known to consume ground lizards.

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A recent population assessment of the American crocodile (*Crocodylus acutus*) in Turneffe Atoll, Belize

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ABSTRACT — We investigated the status of the American crocodile (*Crocodylus acutus*) in Turneffe Atoll, Belize during 2002 and 2004. A combination of spotlight surveys and counts of recently hatched nests were used to census the crocodile population. A total of 49 crocodiles were observed along 40.1 km of survey route (1.2 crocodiles/km) during spotlight surveys in 2002. This encounter rate was not significantly different from that reported in surveys conducted during the mid-1990's. Eight and 20 recently hatched nests were found in 2002 and 2004, respectively. The number of nests found in 2004 exceeds the previously reported maximum count of 15, suggesting that recruitment of breeding females into the population may be occurring. Crocodile nests were found at four sites in Turneffe Atoll. The most significant nesting beach in Belize is located on Northern Cay and currently threatened by a proposed tourist development. Failure to protect this beach could have potentially devastating consequences for *C. acutus* in Belize.

HE American crocodile (Crocodylus acutus) **L** has one of the most extensive distributions of any crocodilian in the New World, occurring along the Atlantic and Pacific Coasts of Mexico, and Central and South America as well as the Caribbean islands of Cuba, Jamaica, Hispaniola, and the southern tip of Florida (Thorbjarnarson, 1989). American crocodile populations throughout this range have declined due to past overexploitation, continued illegal hunting, and habitat destruction (Thorbjarnarson, 1989). Crocodylus acutus is currently recognized as 'vulnerable' by the International Union for the Conservation of Nature and Natural Resources (IUCN), listed on Appendix I of the Convention on International Trade in Endangered Species of Fauna and Flora (Thorbjarnarson, 1992; Ross, 1998), and considered threatened by the Belize Department of Fisheries (McField et al., 1996; Platt & Thorbjarnarson, 2000a).

Owing to the paucity of reliable population estimates, surveys of C. acutus in Belize were accorded high priority by the IUCN Crocodile Specialist Group (Thorbjarnarson, 1992; Ross, 1998). Preliminary surveys of offshore cays (islands) were initiated during 1994 and 1995 (Platt & Thorbjarnarson, 1996), and a countrywide survey of offshore and mainland habitats was completed in November 1997 (Platt & Thorbjarnarson, 1997, 2000a; Platt et al., 1999b). Platt & Thorbjarnarson (2000a) estimated that fewer than 1000 non-hatchling C. acutus inhabit Belize; the largest populations occurred on offshore cays and the Turneffe Atoll, while only scattered individuals were found in mainland coastal habitats.

Turneffe Atoll harbours the largest *C. acutus* population and highest concentration of nesting activity in Belize (Platt et al., 1999a; Platt & Thorbjarnarson, 2000a). An estimated 200 to 300

non-hatchling crocodiles inhabit the atoll, including 15-25 breeding females. Moreover, Turneffe Atoll is thought to serve as a source population for C. acutus elsewhere in the coastal zone, and as such plays a vital role in regional metapopulation dynamics (Platt & Thorbjarnarson, 2000a). Reproduction of C. acutus in Turneffe Atoll is highly dependent on elevated beach ridges composed Suitable nesting of coarse sand. beaches are rare in the atoll owing to combination of natural and a anthropogenic factors (Platt & Thorbjarnarson, 2000a). Because nesting beaches are increasingly threatened by development, Platt & Thorbjarnarson (2000a) concluded that the conservation status of C_{-} acutus in the Turneffe Atoll should at best be considered tenuous, and recommended a long-term monitoring program based on nest counts and spotlight surveys to determine population trends. We here provide a recent assessment of the American crocodile in Turneffe Atoll using survey data collected in 2002 and 2004.

Significantly, this is the first assessment undertaken since completion of the country-wide survey in 1997 (Platt & Thorbjarnarson, 1997).

Study area

Turneffe Atoll (Figure 1) is the largest of three atolls in Belize, and one of only four atolls in the Western Hemisphere (Stoddart, 1962). It is located approximately 35 km from the mainland, and is 50 km north-south and 16 km east-west with an estimated surface area of 533 km² (Perkins, 1983). The atoll consists of a chain of islands partially enclosing three shallow lagoons: Southern, Central, and Northern (shown as Vincent's Lagoon on some maps). Most of Turneffe Atoll is dominated by mangrove swamps (*Rhizophora*

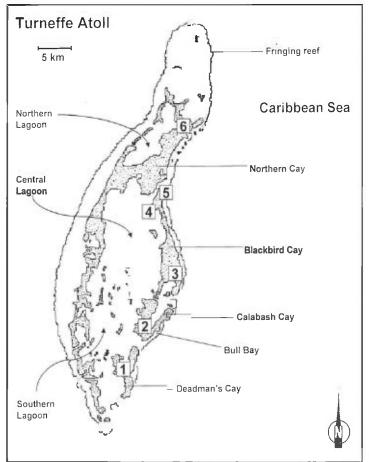


Figure 1. Map of Turneffe Atoll showing localities mentioned in text. Numbers correspond to nesting beaches listed in Table 1. Coordinates of nesting beaches are provided in Platt & Thorbjarnarson (1997, 2000b).

mangle, Avicennia germinans, and Laguncularia racemosa), while beach ridges are characterized by cay littoral forest (Stoddart, 1962; McField et al., 1996). The topography, climate, vegetation, biodiversity, and history of the atoll are fully described elsewhere (Stoddart, 1962; Stoddart, 1963, Perkins, 1983; McField et al., 1996; Platt et al., 1999a; Platt et al., 2000). Turneffe Atoll remains sparsely populated; four resorts, a research centre, and scattered fishing camps are the only permanent dwellings found in the atoll (Platt et al., 1999a).

1				2004
I	0	0	0	0
NA	0	0	l	2
NA	5	3	1	3
1	1	2	0	0
0	0	0	0	4
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METHODS

Fieldwork in the Turneffe Atoll was conducted from 27th June to 15th July 2002, and 20th to 25th July 2004. We censused the crocodile population in 2002 using a combination of spotlight surveys (Bayliss, 1987) and nest counts, but only the latter were conducted during 2004. Spotlight surveys were conducted from a 5 m motorized skiff beginning 15 to 30 minutes after sunset. Crocodile eyeshines were detected using a 400,000 candlepower Q-beam spotlight and 12-volt headlights. All crocodiles sighted were classified by total length (TL) as hatchlings (TL < 30 cm), juveniles (TL = 30-90 cm), subadults (TL = 90-180 cm), or adults (TL > 180 cm). Crocodiles that submerged before TL could be determined were classified as 'eyeshine only' (EO). The beginning and endpoints of each survey route, and the distance traversed was determined with a Garmin® GPS 12. Encounter rates were calculated as the number of crocodiles observed per kilometer of survey route (Platt & Thorbjarnarson, 2000a).

We revisited nesting areas identified during previous surveys (Platt & Thorbjarnarson, 1996, 1997) and searched for recently hatched nests during July of 2002 and 2004. American crocodile Table 1. Counts of American crocodile (*Crocodylus acutus*) nests found at various beaches in the Turneffe Atoll (1994 to 2004). Data from Platt & Thorbjarnarson (1997) and present study. Note that 1995 counts are based on incomplete survey data. NA = Not available. Location numbers correspond to Figure 1.

eggs hatch from late June to mid-July following the onset of the annual wet season (Platt & Thorbjarnarson, 2000b). Female crocodiles typically excavate nests to remove neonates, leaving a readily obvious hole containing eggshell fragments and membranes (Figure 2). In addition to known nesting areas, during both years of this survey we searched potentially suitable beaches where nesting has yet to be documented.

RESULTS

Spotlight surveys

We conducted spotlight surveys along the eastern and western shores of Blackbird and Calabash Cays in 2002. Beginning and endpoints, and a description of each survey route are contained in field notes archived in the Campbell Museum (Clemson University, Clemson, South Carolina, USA). We observed a total of 49 *C. acutus* along 40.1 km of survey route (encounter rate = 1.2

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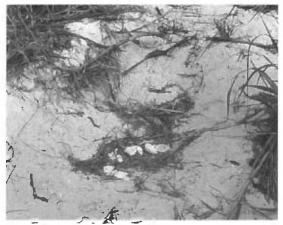


Figure 2. An American crocodile nest recently excavated by female to release hatchlings. Note eggshell membranes remaining in hole. Blackbird Cay, Turneffe Atoll (12th July 2002). All photographs © Steven G. Platt.



Figure 3. American crocodile nesting beach on Northern Cay, Turneffe Atoll (21st July 2004). This beach is the most significant American crocodile nesting site in Belize.



Figure 4. Shallow mangrove lagoon adjacent to the crocodile nesting beach on Northern Cay, Turneffe Atoll (28th June 2002). This lagoon provides critical nursery habitat for hatchling American crocodiles.



Figure 5. American crocodile nesting beach on Calabash Cay, Turneffe Atoll (22nd July 2004). Note the elevated beach ridge and cay littoral forest vegetation. Such sites are rare in Turneffe Atoll and constitute critical nesting habitat for American crocodiles.

crocodiles/km). Of these, 16 (32.6%) were classified as EO, and 33 (67.3%) were approached closely enough to estimate size; these included 1 (3.0%) juvenile, 17 (51.5%) subadults, and 15 (45.4%) adults. Additionally, we observed a pod of 12 to 15 hatchlings during a spotlight survey of Bull Bay (Calabash Cay) on 11th July 2002. A large (TL ca. 120 cm) Boa constrictor (*Boa constrictor*) appeared to be attempting to prey on the small crocodiles; it was found about 2 m away and moving towards the hatchlings in shallow water. The following day some of the hatchlings were relocated in an eroded, water-filled hole at the base of a Coconut palm (*Cocos nucifera*).

Nest counts

We found eight and 20 recently excavated nests in 2002 and 2004, respectively, at four sites in Turneffe Atoll (Table 1). The GPS coordinates of each nest are contained in field notes archived in the Campbell Museum. Although mound nesting has been reported among *C. acutus* in the Turneffe Atoll (Platt & Thorbjarnarson, 2000b), we found only hole nests during the current study. Of the 28 nests found during 2002 and 2004, 17 (60.7%) occurred at a single beach on Northern Cay (Fig. 3). We also observed two large adult crocodiles and approximately 20 to 30 hatchlings in a nursery lagoon (Fig. 4) adjacent to this beach on 21st July

2004. Neither adults nor hatchlings were observed at this site in 2002, although tracks and drag marks indicated crocodiles were indeed present at that time.

Additional nesting areas occur on Calabash Cay (Fig. 5) and at several sites on Blackbird Cay. Previous surveys (Platt & Thorbjarnarson, 1997) found no evidence of crocodile nesting on Calabash Cay, but we documented a single nest here in 2002 and found two nests at the same location during 2004. An old excavation containing dried eggshells was also present at the site, most likely dating from the 2003 nesting season.

We found nests at two sites on Blackbird Cay during the current investigation. Nests occurred on a high beach ridge along the eastern shore, approximately 3 km north of Blackbird Resort in 2002 and 2004, and in 2004 we located an additional nesting area at the northern tip of Blackbird Cay, adjacent to Turneffe Flats Resort. The latter site is located on a densely vegetated ridge adjacent to an open marsh. Several crocodile wallows were found in the marsh, and one of us (SN) encountered a female crocodile with neonates in a wallow during 2000 and 2001. Crocodiles apparently no longer use a nesting area on the western shore of Blackbird Cay. This low, poorly drained beach ridge is composed largely of peat rather than coarse sand, and is the only site where mound nesting by C. acutus has been observed in Belize (Platt & Thorbjarnarson, 1997, 2000b). Likewise, no evidence of nesting activity has been found on Deadman's Cay since 1995, although the site appears to remain suitable habitat.

DISCUSSION

The encounter rate in Turneffe Atoll during 2002 was somewhat greater than previously reported (0.96 crocodiles/km; Platt & Thorbjarnarson, 1997), although this difference was not significant ($\chi^2 = 2.03$; df = 1; p>0.05). Because of the variability inherent in spotlight counts, long-term monitoring is generally required to detect population changes (Bayliss, 1987). The high proportion of subadults and adults noted during our investigation is likely due in part to sampling bias; juveniles remain concealed in mangrove vegetation and escape detection during spotlight surveys (Platt & Thorbjarnarson, 2000a).

The 20 crocodile nests we found in 2004 exceed the previous maximum count of 15 nests in 1997 (Table 1). These data suggest that recruitment of breeding females is occurring in Turneffe Atoll, and possibly reflect an overall population increase since the previous surveys were conducted. However, given the small number of breeding females in the atoll and the annual variability in nesting effort, these data should be interpreted with caution.

previous Our current and (Platt & Thorbjarnarson, 1996, 1997, 2000a) investigations underscore the importance of the Northern Cay nesting beach to the Turneffe Atoll crocodile population. Indeed, Platt & Thorbjamarson (1997) regarded it as the most significant C. acutus nesting site in the entire coastal zone of Belize. This beach consists of a high ridge composed of coarse sand, with an adjacent shallow brackish lagoon that provides excellent nursery habitat for hatchlings, and undoubtedly enhances neonate survival (Platt & Thorbjarnarson, 2000a, 2000b). This beach was greatly improved by Hurricane Keith in 2000 when tidal over-wash deposited large amounts of sand at the eastern end of the nursery lagoon and created additional nesting habitat.

Our recent surveys indicate that with the exception of Northern Cay, crocodile nesting beaches in Turneffe Atoll remain relatively undisturbed with little sign of human disturbance other than occasional visits by fishermen and coconut collectors. However, the Northern Cay nesting area is now in imminent danger of destruction due to the proposed development of a tourist resort. If this project is allowed to proceed an irrevocable loss of critical nesting habitat will occur. Given that Northern Cay hosts the largest concentration of C. acutus nesting activity yet identified in Belize, this development constitutes a grave threat to the continued viability of the crocodile population in Turneffe Atoll. Even more importantly, because Turneffe Atoll appears to serve as a source population for *C. acutus* in other areas of the coastal zone (Platt & Thorbjarnarson, 2000a), destruction of the Northern Cay nesting beach has potentially devastating consequences for this endangered species elsewhere in Belize. Therefore it is imperative that development be immediately halted. Additionally, some form of permanent legal protection is urgently needed for Northern Cay, as well as other nesting beaches in the atoll, to avoid future conflicts with development interests.

Our observations provide further evidence that mound nesting occurs infrequently among C. acutus in Turneffe Atoll. During a previous study (1994-1997) only 6 of 41 (14.6%) nests found in the Turneffe Atoll were mound nests (Platt & Thorbjarnarson, 1997). In general, mound nesting appears to be rare among C. acutus, and largely confined to populations in southern Florida, USA (Beard et al., 1942; Ogden, 1978; Kushlan and Mazzotti, 1989; but see Russell [1929] for an account of mound nesting in the Yucatan region of Mexico). Mound nesting is thought to be an adaptive response to waterlogged soils (Thorbjarnarson, 1989). Significantly, the only site in Belize where we found mound nests is a low-lying beach composed of shallow and often wet peat soil.

Finally, to our knowledge predation by *Boa* constrictor on hatchling *C. acutus* has not been previously reported (Thorbjarnarson, 1989). *Boa* constrictor are common throughout Turneffe Atoll and frequently feed on *Ctenosaura similis* (Platt et al., 1999a); thus consumption of hatchling crocodiles is not unexpected.

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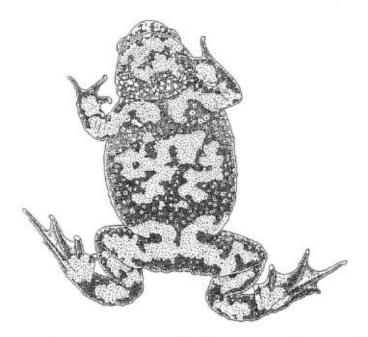
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