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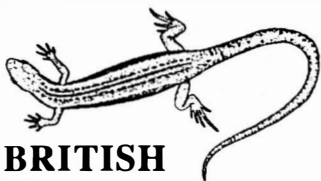
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FRONT COVER: Development of the belly pattern in *Triturus cristatus* (S. F. M. Teunis).

## A STRUVITE FAECOLITH IN THE LEATHERBACK TURTLE *DERMOCHELYS CORIACEA* VANDELLI: A MEANS OF PACKAGING GARBAGE?

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### ABSTRACT

A large stone-like object was collected from the rectum of a leatherback turtle beached at Midway Atoll, Hawaiian Islands. It consisted of biomineralized faecal material, the mineral being struvite ( $\text{NH}_4\text{MgPO}_4 \cdot 6\text{H}_2\text{O}$ ). Much material of anthropogenic origin (plastics in sheet and linear form, plus other packaging materials and monofilament nylon) was incorporated into the faecolith structure. It is hypothesized that the formation of struvite stems from the interaction of the leatherback's osmotic physiology with the metabolism of faecal bacteria. While the formation of the faecolith may be pathological, it could alternatively be an adaptive response to package garbage (whether natural or man-made).

### INTRODUCTION

Beached adult specimens of the leatherback turtle *Dermochelys coriacea* Vandelli have almost invariably been drowned in nets, injured/killed by shark attack or in collision with boats. They may therefore be presumed to have been healthy beforehand. Necropsy sometimes reveals hard, round objects in the gut, particularly the hind gut. For example, the large male leatherback beached at Harlech in North Wales, UK (Eckert & Luginbuhl, 1988) had a hard, clay-like ball at the junction between the small and large intestines, while the rectum of a turtle beached at Midway Atoll in the northwestern Hawaiian Islands contained a hard, smooth, ovoid ball (the subject of this article). The aim of this investigation was to analyze the nature of this object, and perhaps elucidate the reasons for the occurrence of such faecoliths.

### MATERIALS AND METHODS

A large (13 cm in diameter), smooth, stone-like object was collected (on 1.4.91) from the rectum (at the junction with the cloaca, but displaced to one side of the gut in an outpouching of the rectum) of a freshly-stranded specimen of *Dermochelys coriacea* at Midway Atoll at the northwestern end of the Hawaiian archipelago (28° 13' N, 177° 21' W) (see Fig. 1). Leatherbacks are known to forage in the pelagic habitat to the north of Midway Atoll where they are not uncommonly entangled in Japanese, Taiwanese and Korean driftnets (Balazs, 1982). However, this was the first leatherback ever known to strand at Midway. The turtle had clearly been the victim of a shark attack as it had been decapitated very recently and lost all four flippers. Fresh blood was still flowing from its wounds and several sharks were swimming in shallow water immediately off the beach where the turtle stranded. On dissection (which revealed perfectly fresh tissues) the object was found immediately, so cannot have been an artifact of post-mortem deterioration.

The object was divided into two portions, one being sent to the UK for detailed analysis, while the other was used only for gross investigation. The faecolith portion sent to Britain was held for a few days in a water-saturated atmosphere. This caused the structure to soften. It was broken up and studied beneath a binocular microscope. During these observations, numerous small, hard, transparent crystals were seen embedded in the brown material of the softened faecolith structure. The crystals were dense and insoluble in water; they were separated from the rest of the material by washing and stirring. Crystals were prepared for X-ray probe microanalysis by freeze drying and attachment to an aluminium stub with double-sided adhesive tape. Crystals were studied in a scanning electron microscope (SEM) fitted with an energy dispersive X-ray microanalyser. A total of 10 faecolith crystals were investigated.

Once the elemental composition had been established, further crystals were investigated by X-ray diffraction. 20-30 of the larger and cleaner crystals were hand-picked under a binocular microscope and ground in an agate pestle and mortar under deionized water. The resultant slurry was spotted onto a glass slide and allowed to dry at room temperature. During drying the slurry was mixed using a scalpel blade in an attempt to minimize any preferred orientation. A diffractometer trace was obtained from this slide using  $\text{CuK}\alpha_2$  radiation in a Philips diffractometer.

### RESULTS

#### GENERAL DESCRIPTION OF FAECOLITH

At the macroscopic level it was found that the smooth, rounded faecolith contained much material of anthropogenic origin (see Table 1). The rest of the faecolith appeared to be of an amorphous brown nature, with a strong faecal odour.



Fig. 1. Photograph of stranded leatherback, showing faecolith in situ.

At the microscopic level it could be seen that the brown material was made up of lamellae of soft material, which presumably consisted mainly of faecal bacteria (large numbers of bacteria were visible in early 'dirty' SEM preparations of the faecolith crystals). Between each of the lamellae were huge numbers of crystals (ca. 0.2-0.3 mm length, flattened and coffin-shaped). The crystals were transparent, colourless, hard, brittle and apparently insoluble in water.

#### FAECOLITH CRYSTAL COMPOSITION

First, it was noticed that the crystals prepared for X-ray microanalysis by freeze-drying appeared white and chalky rather than transparent; this indicated that the original crystals contained water of crystallization. All ten faecolith crystals subjected to X-ray microanalysis showed very similar patterns to that shown in Fig. 2. There are three obvious peaks. The Al comes from the stub on which the crystal is mounted; the Mg and P are the major elements of the crystal itself. Particularly surprising is the low amount of Ca; the faecolith was clearly not calcified.

X-ray microanalysis is largely qualitative, and calculation of peak areas yields only semi-quantitative information (see Morgan, 1985 for discussion). However, calculation yielded the following mean compositions (SD in parentheses): Na 1.6 (0.5)%, Mg 32.2 (1.9)%, Si 0.9 (0.3)%, P 67.1 (2.3)%, Cl 0.7 (0.8)%, K 0.3 (0.5)%, Ca 2.2 (1.5)%. From these values it may be seen that virtually all of the identified elemental material present in the crystals consists of Mg and

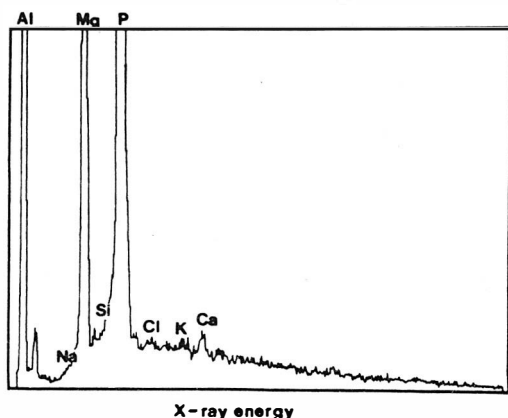


Fig. 2. Trace derived from X-ray dispersive microanalysis of faecolith crystals. Al is from the stub on which the crystal was mounted.

1. 300 mm length of tangled, blue polypropylene twine (5 mm thick).
2. 4 strands (120 mm, 105 mm, 120 mm, 130 mm) of old, unravelled polypropylene tarpaulin fabric, all 1 mm wide.
3. 160 mm length of monofilament nylon fishing line (approx. 8 lb breaking strain).
4. 4 pieces of green, hard, flat plastic (9x13 mm, 10x7 mm, 6x5 mm, 6x5 mm).
5. Piece of flat, white hard plastic (9x5 mm; 2 mm thick).
6. Piece of flat, yellow-orange hard plastic (5x5 mm).
7. 3 small strands of plastic (20 mm, 20 mm and 30 mm in length).
8. 6 small pieces (approx. 4 mm diameter) of expanded polystyrene foam.
9. Piece of unknown hard substance (6x5 mm).
10. Numerous polystyrene beads (< 1 mm diameter).
11. 3 pieces (each approx. 20 mm diameter) abraded material from polythene bags

TABLE 1. Material of anthropogenic origin incorporated in faecolith

P, with some crystal surfaces (particularly clean ones with no contaminating material visible on the surface) approaching levels of 100%. The technique is not capable of detecting the presence of elements with an atomic number below 11 (e.g. C, H, I or O), so although the X-ray microanalysis results, combined with the observation of crystalline rather than amorphous structure, strongly suggest that the crystals are almost pure magnesium phosphate, the technique cannot discriminate between different types of phosphates (e.g. between various orthophosphates, some of which contain H, and pyrophosphate), and cannot eliminate the possibility of the presence of ammonium in the crystals (as in struvite,  $\text{NH}_4\text{MgPO}_4 \cdot 6\text{H}_2\text{O}$ ).

The magnesium phosphates are all insoluble or only very slightly soluble in water, so degree of solubility cannot separate the forms, but the X-ray diffraction pattern gave a near-perfect match for struvite (JCPDS pattern number 15-762). The morphology of crystals is very similar to that recorded by LeGeros & LeGeros (1984) from struvites synthesized in gel systems. A good general description of struvite (also known as guanite) may be found in Palache *et al.* (1951).

#### DISCUSSION

Faecoliths are present in some stranded leatherbacks, but certainly not all; Den Hartog & Van Nierop (1984) did not report any in the six *Dermochelys* they studied. At present it is difficult to decide whether their presence indicates a pathological condition, or is a normal feature of turtle biology. Except for the injuries caused by the shark attack, the Midway turtle showed no obvious signs of disease and there was no compaction of plastic in the gut. The adaptive formation of hard nodules in the gut of marine animals is not unknown; the heart urchin *Echinocardium* ingests fragments of wood or stone which act as a substratum for the formation of bacterial nodules which fix and detoxify sulphur as insoluble metal sulphides. There is also a general tendency in marine invertebrates

for detoxification by binding metals in insoluble, granular form. It is feasible that the formation of a smooth, rounded object around non-biodegradable garbage may facilitate later defaecation. Leatherbacks not only swallow plastic bags and man-made garbage such as the twine and polystyrene reported here; they are also known to swallow wood, feathers, sand and seaweed (e.g. Brongersma, 1969; Den Hartog & Van Nierop, 1984)). It would appear that they will swallow almost any material swimming or floating at the sea surface; some of this material was presumably difficult to pass through the gut even before man started to throw non-biodegradable garbage into the sea. However, there is an extensive veterinary literature concerned with the consequences for captive animals of swallowing of foreign bodies (see Frye, 1991 for reptilian examples), but except in the case of crocodilian gastroliths (swallowed deliberately for control of buoyancy and/or digestive efficiency) the responses of animals seem to be pathological rather than adaptive. The occurrence of hard masses in the intestine of chelonians is not uncommon either (see Frank, 1981), but these are usually formed from masses of chitinous parts of insects or accumulated indigestible cellulose fibres. Such masses can cause constipation, though intestinal parasitic nematodes may help to break the masses down.

From the form of the leatherback faecolith studied here it is clear that its hardness stems from biomineralization, presumably by the gut bacteria rather than the leatherback itself, since the mineral crystals are deposited between the bacterial lamellae. It is most interesting that the mineral is non-calcareous and composed of struvite which may be formed in the laboratory by mixing magnesium sulphate solution with an acid solution of ammonium phosphate (Palache *et al.*, 1951). Struvite is not a common biomineral in a global sense, although it is well recognized in medical and veterinary circles. The principal occurrence in live organisms seems to be as a component of urinary stones in mammals (including cats and humans) resulting from alkalization due to bacterial infection (e.g. Prien & Frundel, 1947; LeGeros & LeGeros, 1984; Lowenstam & Weiner 1989). Geological struvite occurrences have unusual bulk compositions and are non-marine (e.g. within fossil cave guano deposits); struvite has also been found in dung-peat mixtures and in canned food (Palache *et al.*, 1951). In these occurrences too, bacterial activity is probably significant.

In view of the association with bacterial lamellae in the faecolith, a similar origin seems likely in this case. A further factor may be enrichment of the hindgut fluids of the leatherback turtle by divalent ions. *Dermochelys* has to drink seawater like any other marine reptile (or teleost fish). It can only absorb water by pumping Na across the gut wall until sufficient osmotic gradient exists for water to flow osmotically from gut lumen to blood. In consequence, the hind gut

fluid is likely to contain relatively high concentrations of magnesium, calcium and sulphate ions, but little sodium or chloride. However, the ammonium and phosphate ions of struvite are presumably derived from the faecal bacteria. LeGeros & LeGeros (1984) report that struvite can be formed in a calcium-rich medium at pH values between 7 and 9, and that formation of small crystals is actually promoted by high calcium concentrations, so it is not necessary to postulate a calcium-poor or acid environment in the hindgut.

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## RELEASE AND RECAPTURE OF CAPTIVE-REARED GREEN SEA TURTLES, *CHELONIA MYDAS*, IN THE WATERS SURROUNDING THE CAYMAN ISLANDS

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(Accepted 17.9.92)

### ABSTRACT

Cayman Turtle Farm released 26,995 yearling and hatchling green sea turtles, *Chelonia mydas*, into the waters surrounding the Cayman Islands, between 1980 and 1991. Released turtles were the offspring of the farm's captive breeding colony. Tagged turtles were regularly recaptured and re-released locally and demonstrated growth rates of 3.0 kg/year. With turtles recaptured from other regions of the Caribbean, recapture rate for turtles released as yearlings was 4.1%. 66% of the locally recaptured turtles were infected with cutaneous fibropapillomas, a condition increasingly observed among turtle populations worldwide.

### INTRODUCTION

Historically, the Cayman Islands supported a huge turtle rookery and subsequently the "turtling industry" provided a means of support for the islands through the export of hawksbill shell and green turtle meat (King, 1982). The Cayman Islands fishing fleet obtained turtles from foreign turtle populations. Cayman Turtle Farm, CTF, began operation in 1968 to commercially raise the green sea turtle. Currently CTF is a major tourist attraction on Grand Cayman and produces turtle products for local consumption. The farm's breeding herd produces an average of 10,500 hatchlings per year. Hatchling and yearling green sea turtles are tagged and released into the waters surrounding the Cayman Islands as part of a continuing study to assess turtle survival and the establishment of a resident turtle population.

Most tagging programmes focus on mature adults to monitor breeding populations simply because the turtles are accessible for tagging while on the nesting beaches. Limited studies have been done on juvenile populations to assess growth rates of the populations (Bjorndal & Bolten, 1988; Frazer & Ehrhart, 1985). The development of an autograft tag has the potential to monitor turtles as part of a population group (Hendrickson & Hendrickson, 1981). Effective tagging and recovery methods are critical in determining the success of population management programs and to allow for the determination of basic questions of sea turtle biology such as how long turtles live and do sea turtles return to their natal beaches to nest.

### METHODS

Facilities and husbandry procedures at CTF have been previously described (Wood, 1991). Turtles designated for release were released as either hatchlings or as yearlings. Several tagging methods have been used. All hatchlings released since 1983 received a "living tag" which involves transfer of a 4 mm disk from the plastron to the carapace. The location of the graft was designated by the carapace scute and identified a release age group. A surgical biopsy punch was used to puncture the dermal layer of the plastron and carapace. The disks were then removed with a scalpel and interchanged. The graft was secured with a surgical glue (@Histoacryl, B. Braun Melsungen AG, Melsungen, Germany).

Mutilation tags were used in 1980-1983. The trailing marginals of the turtle were notched to identify the release age

group. Yearlings released prior to 1984, received individually, numbered plastic tags in the rear flipper (Dalton Supplies, England). Titanium tags (Stockbrands Pty Ltd, Western Australia), individually numbered and identified with the inscription "Premio remitir, Turtle Farm, Grand Cayman, BWI" have been used for yearling turtles since 1984. Tag location was the trailing edge of the left front flipper. Tag size for yearling turtles was 50 x 6 mm. A larger titanium tag, 69 x 8 mm, was used for larger (>15 kg) turtles captured during local tag-recapture efforts. Fig. 1 illustrates the various tags used. Local recaptures were done by setting traditional hanging turtle nets. The freely-floating bottoms of the net (varying in surface length from 12 - 25 m with a net depth of approximately 3 m) allowed a captured turtle to surface easily until removed. Nets were set and checked on a daily basis for one to two week periods throughout the year. Since 1985, nets have been set a total of 863 net days resulting in 218 turtle captures. Nets have been set during each month except March, April and November with turtles captured during all months nets were set. Occasionally, turtles were seen or caught by locals and reported to the farm. Overseas recoveries of tagged turtles were most often from fishermen.

On release of farm stock, some yearlings were individually weighed and measured. Curved carapace length, CCL, was measured with a fiberglass sewing tape from the leading edge of the nuchal scute to the notch between the two supracaudals. Curved carapace width, CCW, was measured at the widest part of the carapace from the edge of the marginals. If the turtles were not individually weighed, the average stock weight for the group was used as the release weight. Upon recapture, the turtles were weighed and measured. Reported sizes for overseas recaptures were considered approximate and not included in statistical analysis.

The general health of local recaptures was noted. Particularly, with the common occurrence of cutaneous fibropapillomas, turtles were graded as to the extent of the infection according to the following designations:

*Grade 0:* no cutaneous fibropapillomas.

*Grade 1:* cutaneous fibropapillomas less than 6 mm.

*Grade 2:* cutaneous fibropapillomas 7 mm - 50 mm.

*Grade 3:* cutaneous fibropapillomas 5 mm - 100 mm.

*Grade 4:* cutaneous fibropapillomas greater than 50 mm which must physically hamper movement or have resulted in blindness.

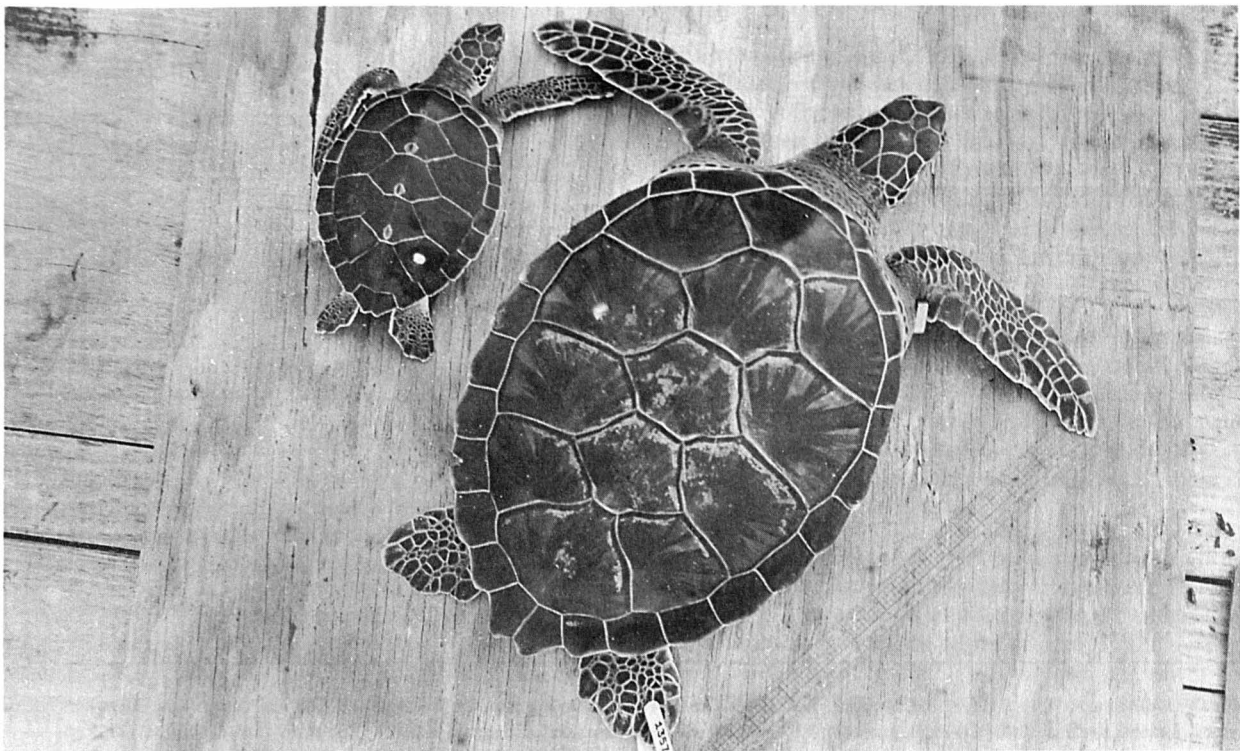


Fig. 1 Captive reared green turtles, six months old and 18 months old specimens, with representative tags. The younger turtle on the left has a living tag in the right coastal no. 4 scute. The older turtle on the right has a living tag in the left coastal no. 2 scute; a plastic roto-tag in the right rear flipper; a titanium tag in the trailing edge of the right front flipper; and a mutilation notch in a left marginal.

A one way analysis of variance and/or the Student-Newman-Keuls multiple range test were used to compare sample means.

RESULTS

Table 1 summarizes the release of turtles from CTF since 1980. Fig. 2 designates release sites on Grand Cayman and the number of turtles released from each site. Of the 26,995 turtles released, 14,100 turtles released as hatchlings were tagged by "living tag" only. This would identify the year of release only. 2,322 hatchlings and 1,944 yearlings were released with no tag. 1,283 yearlings were released with a

	weight (kg)	CCL (cm)	CCW (cm)
mean	11.9	45.7	40.8
SD	5.4	6.8	6.4
maximum	24.5	58.0	53.0
minimum	5.5	36.0	31.5

TABLE 2. Size data for 18 hawksbill sea turtles captured in North Sound, Grand Cayman. CCL is curved carapace length; CCW is curved carapace width.

year of release	no. of hatchlings released	no. of yearlings released	tagging comments
1980	/	1208	mutilation tag only
1981	79	1685	60 yearlings; mutilation tag; 1331 yearlings with rototags
1983	4405	71	all hatchlings with "living tag"
1984	/	2000	titanium tags
1985	3107	/	2641 hatchlings with "living tag"
1986	/	1936	all with titanium tags; 938 with "living tag" also
1987	5559	500	5082 hatchlings with "living tag"; all yearlings with "living tag" and titanium tag
1988	/	1202	"living tag" and titanium tag
1989	2800	1769	1500 hatchlings with "living tag"; 119 yearlings with titanium tag
1990	/	104	"living tag" and titanium tag
1991	472	98	hatchlings with "living tag"; yearlings with titanium tag
total	16422	10573	

TABLE 1. Number of hatchling and yearling green sea turtles released by CTF, 1980-1991. If tag designation is not entered, turtles were released without a tag.

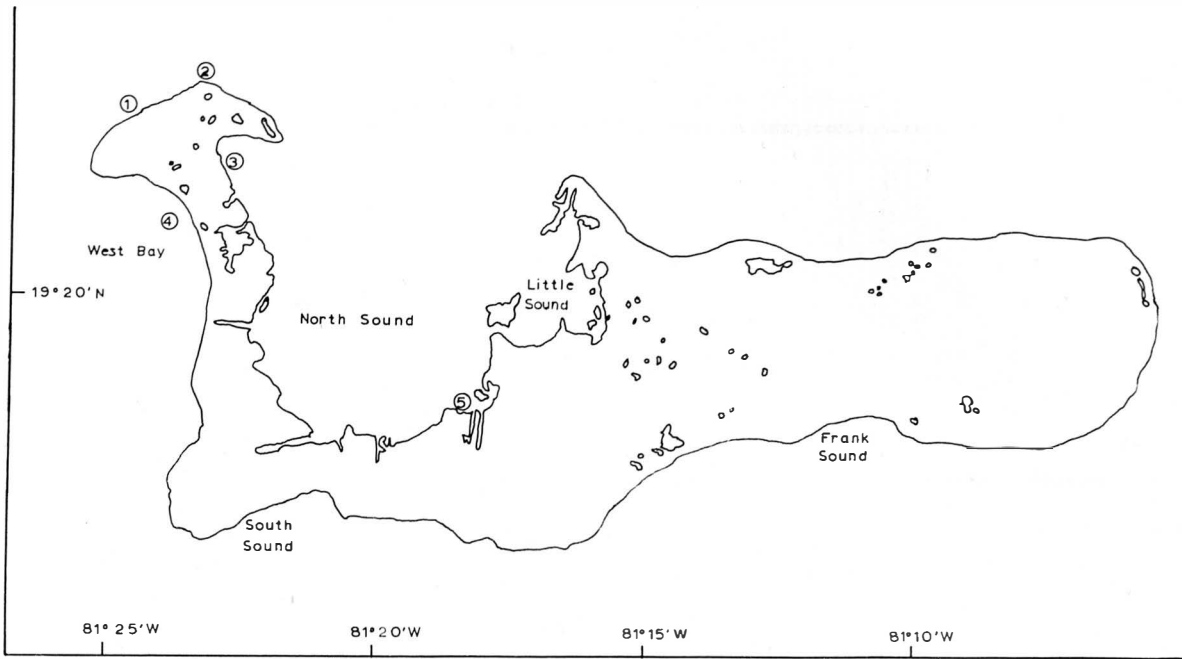


Fig. 2 Outline map of Grand Cayman, Cayman Islands, BWI. Numbers in circles represent the following: 1, Cayman Turtle Farm; 2, Barkers release site; 3, Batabano release site; 4, West Bay release site; 5, North Sound release site.

release site	no. released	recapture site				Total
		North Sound	Other, local	Cuba	Other, foreign	
North Sound	2336	104 (4.5)	/	35 (1.5)	3 (0.1)	142 (6.1)
Batabano	530	5 (0.9)	2 (0.4)	4 (0.8)	/	11 (2.1)
Barkers	909	24 (2.7)	1 (0.1)	13 (1.4)	/	38 (4.2)
West Bay	2184	8 (0.4)	2 (0.1)	62 (2.8)	8 (0.4)	80 (3.7)
Total	5959	141 (2.4)	5 (0.1)	114 (1.9)	11 (0.2)	271 (4.5)

TABLE 3. Number of turtles recaptured and site of recapture for released yearling turtles. Numbers in parentheses represent % of the released turtles subsequently recaptured.

no. years between release and recapture	no. local recaptures	no. foreign recaptures	total recaptures recaptures	% of total recaptures in year designated
1	45	22	67	23.2
2	55	22	77	21.6
3	51	39	90	31.1
4	8	11	19	6.6
5	5	20	25	8.7
6	2	4	6	2.1
7	1	4	5	1.7
total	167	122	289	

TABLE 4. Time between release and recapture for locally and foreign recaptured turtles.



fibropapilloma infection grade	time between release and recapture (yrs)			
	<1	1-2	2-3	>3
0	32	15	9	8
1	7	8	5	2
2	3	13	23	5
3	1	18	8	0
4	1	1	6	1
total	44	55	51	16

TABLE 5. Degree of fibropapilloma infection among 166 locally recaptured turtles.

mutilation tag only identifying year of release, 1,387 yearlings were released with a roto-tag and 5,959 yearlings were released with a titanium tag.

Since 1984, 294 green turtles tagged by CTF have been recaptured either in local waters or overseas. In addition 69 other turtles, including 18 hawksbill sea turtles have been captured, tagged and released during tag recapture efforts of CTF in North Sound, Grand Cayman. All the hawksbills captured were subadults. Table 2 gives size data for the hawksbills captured. All the hawksbills were in good condition; two had small barnacles on the carapace. One hawksbill was missing rear marginals as if it had been bitten by a shark. Two of the hawksbills were recaptured in the same location, one within 13 days. The other hawksbill was recaptured 321 days later and had gained 6.7 kg (recapture weight = 13.7 kg) and increased in CCL 10.6 cm (recapture length = 50.0 cm).

Fifty-one green sea turtles were captured in North Sound without a "living tag", flipper tag, or obvious tag scar. Mean weight ( $\pm$ SD) was  $11.0 \pm 5.3$ , range 3.3-24.5 kg; mean CCL was  $45.8 \pm 6.9$  cm, range 31.8 - 59.5 cm. The sizes of these turtles were similar ( $P > 0.1$ ) to sizes of known release turtles. One hundred and twenty-eight turtles captured in North Sound with titanium tags had a mean weight ( $\pm$ SD) of  $10.0 \pm 4.9$ , range 2.7-29.9 kg; mean CCL was  $43.9 \pm 7.2$ , range 29.0-66.0 cm. Eight of these turtles were subsequently recaptured in the same location within one year. One turtle was subsequently reported taken in Nicaragua 1,178 days later.

Of the 294 recaptures of turtle identified as released by CTF, 271 had a titanium tag which enabled the turtle to be identified as to exact release site and release date. The other recaptures were identified by "living tag" as a CTF release, but individual data was incomplete for analysis or because of incomplete information from overseas recaptures, the turtle's history remained incomplete. Table 3 identifies the number and site of recaptures for yearlings released and tagged with a titanium flipper tag. Of the 271 recaptures listed, 28 are repeat captures of the same turtle. The net rate of turtles recaptured is 243 individual turtles of the 5,959 individually tagged yearlings, or 4.1%. Of the 243 turtles recaptured with a titanium tag, 40 were noted as having a visible "living tag" at release. Of these 40, 26 were noted as having a "living tag" on recapture.

One hundred and twenty-nine recaptures have been reported from outside the Cayman Islands. One hundred and

seventeen of these were from Cuba, five from Honduras, two from Belize, and one each from Mexico, Nicaragua, USA, and Venezuela. The recapture reported from Venezuela was the farthest distance traveled, 1,931 km. The turtle was recaptured 274 days after release, traveling 7.1 km/day. The sea speed record goes to a turtle released as a two-year old from the west shore of Grand Cayman which was recaptured within 24 days, 644 km away in Honduras, traveling 26.9 km/day.

Table 4 summarizes recaptures for 289 turtles on the basis of recapture site and time between release and recapture. Time between release and recapture ranges from 13-2,511 days, mean  $795 \pm 511$ . There is a statistically significant difference for the number of days from release to recapture between turtles recaptured locally ( $n = 167$ , mean ( $\pm$ SD) =  $697 \pm 421$ ) and those recaptured overseas ( $n = 122$ , mean ( $\pm$ SD) =  $931 \pm 589$ ;  $P < 0.0001$ ).

Sixty-eight percent of all green sea turtles recaptured in local waters had cutaneous fibropapillomas present. None of the hawksbill sea turtles were infected. Table 5 summarizes the relationship between the degree of infection and time between release and recapture. Seventy-two percent of the turtles recaptured within less than one year from release showed no fibropapillomas, while only 26% of the turtles recaptured after more than one year after release showed no fibropapillomas. Eight turtles were recaptured more than once in North Sound, Grand Cayman. In two instances, the turtles had fibropapillomas on initial capture and no fibropapillomas upon recapture after periods of 11 and 21 months. In the other six instances of recaptures, five turtles were first captured with no fibropapillomas present and subsequently developed fibropapillomas after periods of 10, 11, 13, 14, or 14 months. One turtle recaptured within 11 months increased in the degree of fibropapilloma infection.

Sixty of the turtles recaptured in North Sound were individually weighed at the time of release. Table 6 summarizes the parameters of weight and age at release and recapture and observed weight gain. For the sixty turtles recaptured, the mean ( $\pm$ SD) weight gain was  $3.04 \pm 1.11$  kg/year. These turtles ranged in age from 11 to 15 months at release and mean time between release and recapture was 583  $\pm$  384 days. All turtles were recaptured in good condition with the presence of cutaneous fibropapillomas ranging from grade 0 to 3. There was no significant difference in observed weight gain among groups of turtles of various degrees of infection with fibropapillomas. (Respective weight gain, means  $\pm$  SD, for grade 0, 1, 2, and 3 fibropapilloma infection were  $3.13 \pm 0.88$ ,  $3.23 \pm 1.10$ ,  $3.32 \pm 1.36$ ,  $2.35 \pm 1.05$ ,  $F = 2.11$ ,  $P = 0.109$ .) Mean gain in CCL for 22 of the recaptures for which CCL was measured at release was  $8.4 \pm 3.1$  cm/year. At release, these 22 turtles were 13 to 14 months old and mean CCL was  $30.4 \pm 3.1$  cm, range 24.0 - 34.0 cm. Mean CCL on recapture was  $41.5 \pm 7.3$  cm, range 29.0 - 56.0 cm. Mean number of days between release and recapture was  $506 \pm 375$  days, range 41-1199 days. Thirty-two overseas recaptures were reported which included a weight measurement for turtles individually weighed at release. One of these turtles was 13 months old at release, the others were 14 months old. Mean weight gain for these turtles was  $7.83 \pm 3.46$  kg/year. There was a significant difference in weight gain between local and overseas recaptures ( $P < 0.0001$ ). Mean time from release to recapture for this group of overseas recaptures was  $773 \pm 295$  days, and as

with the larger subgroups quantified in Table 4, there was a significant difference in the time from release to recapture between the local and overseas recaptures ( $P < 0.05$ ).

### DISCUSSION

The turtle recapture rate of 4.1% for yearlings tagged with a titanium tag is not unusual. Excluding the local recaptures, which represent an active recovery effort, the overseas recapture rate is 2.0%. Witham (1976, 1980) reported tag recovery rates of 0.7-0.9% for over 10,000 captive reared yearling green sea turtles released in Florida, USA. Tag recoveries for yearling Kemp's ridley sea turtles released in Texas, USA, averaged 4.8% (Fontaine *et al.*, 1989). None of the captured turtles in North Sound without a titanium tag showed tag scars. Locally captured turtles up to 30 kg successfully retained the smaller titanium tag. The longest known retained tag is 82 months from release to recapture.

Turtles released on the north side of the island are more likely to be captured locally than those released on the west shore. Possibly contributing to this observed tendency are the strong offshore currents on the open west shore as opposed to the barrier reef enclosed release sites on the north shore. Also, recapture efforts focus on the abundant north shore turtle grass beds. Approximately 60% of the 80 km<sup>2</sup> of North Sound is covered with *Thalassium testudinum* (turtle grass) interspersed with green algae of the genera *Halimeda*, *Penicillus*, and *Rhipocephalus* and an abundant population of bivalves (Roberts, 1977). Often associated with these turtle grass beds are populations of jellyfish, particularly of the genera *Aurelia* and *Cassiopeia*. South Sound and Frank Sound, on the south coast of Grand Cayman, also have extensive turtle grass beds.

The incidence of cutaneous fibropapillomas among locally recaptured turtles is similar to that reported for other populations recently (Balazs & Pooley, 1991). Significantly, some of the recaptured turtles have shown complete remission of the infection. None of the overseas recaptures were reported as having any fibropapillomas present, but because of the limitations in overseas reporting, the presence of fibropapillomas cannot be precluded. Nonetheless, the local recaptures occurred within protected sound areas of the island and the probable decrease of water circulation as opposed to open ocean habitats may influence the incidence of fibropapillomas. Although, both tagged and untagged turtles had fibropapillomas, there was a tendency for fibropapillomas to be associated with the titanium tags. Turtles that had fibropapillomas and a titanium tag, consistently had fibropapillomas enveloping the tag.

As expected with an altered diet, recaptured turtles showed a decrease in weight gain from the average projected weight gain from 6.6 kg/year for captive reared turtles in the size range sampled to 3.0 kg/year for the recaptured turtles. Although the rate of growth is significantly reduced, the appearance of the recaptured turtles is good with individuals showing no signs of emaciation. The turtles appear to adapt readily to feeding on the turtle grass beds around the island. As overseas size measurements were unconfirmed, the reasons for the difference noted between local and overseas weight gains remains speculative.

As summarized by Boulon & Frazer (1990), mean growth rates among juvenile green turtles are dependent upon geographical location and size class. Boulon & Frazer (1990) used straight line carapace length with recalculations of some of the data presented to establish uniformity because of differences in how the carapace length was measured. For the captive population of turtles at CTF, the relationship between straight line carapace length (SCL, measured from the leading edge of the nuchal scute to the notch between the supracaudals) and CCL is 0.96 and is linear for the size range reported here. Using this relationship to convert the mean growth rate (cm/yr) based on CCL to SCL, the mean growth rate for turtles released and recaptured in the Cayman Islands for a size class of 30 - 40 cm, SCL, is  $8.26 \pm 2.95$  cm/year. This is in the range of growth rates reported for other populations,  $8.8 \pm 1.0$  cm/year for the Bahamas (Bjorndal & Bolten, 1988) and  $4.96 \pm 1.72$  cm/year for the U.S. Virgin Islands (Boulon & Frazer, 1990).

Head-starting as a conservation technique is controversial (Woody, 1990; Allen, 1992). Part of this controversy stems from the criteria by which such a program is judged a success or failure. If head-started turtles must be shown to be reproductively successful, then this program has not been proven to be beneficial, if for no other reason than insufficient time for reproductive maturity has not passed. If however, success is defined by adding turtles to their natural environment and documenting their ability to survive in this environment for a number of years, then this study can reasonably be considered as positively benefiting the wild population. Such turtles augment the wild stock and perhaps even relieve some natural and human predation. There is no reason to believe that once the animals reach sexual maturity they will not become reproductively successful as well.

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## SUMMER AND WINTER REFUGIA OF NATTERJACKS (*BUFO CALAMITA*) AND COMMON TOADS (*BUFO BUFO*) IN BRITAIN

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### ABSTRACT

We have investigated the refugia used by *Bufo calamita* and *Bufo bufo* throughout the year on heathland, sand dune and saltmarsh habitats in Britain. On the first two habitats, natterjacks mainly lived at depths of >20 cm in burrows of their own making and these burrows insulated animals very effectively against temperature fluctuations during the summer. In saltmarsh habitats natterjacks used a variety of refugia and at all sites common toads were found in mammalian burrows and under stones, logs and piles of leaf litter. Natterjacks at the saltmarsh site vacated areas following tidal inundation with no evidence of mortality attributable to this event. At the heathland site, male natterjacks adopted two distinct strategies for refugia use during the breeding season: commuters travelled to and from the ponds every night, returning before dawn to their summer burrows, while residents took up temporary abode near the ponds for the duration of the breeding season. On heaths and dunes natterjacks usually used the same burrows for hibernation that were used in the summer months, but buried themselves more deeply. Common toads also used similar sites to those occupied in summer, but often these were selected following an autumn move towards the breeding ponds. At the saltmarsh and other coastal sites in Cumbria, most natterjacks and all common toads hibernated under piles of stones or logs, or in the burrows of small mammals.

### INTRODUCTION

The natterjack is the rarest amphibian in the British Isles and is declining over much of its European range. Information on the habitat components that are important for breeding and foraging by this species is now extensive (e.g. Beebee, 1983; Banks & Beebee, 1987a; 1988; Sinsch, 1989a; Denton, 1991), but much less is known about refugia use, especially during the winter months. Indeed, there have been very few studies on the hibernacula of European amphibians with most information on this subject being anecdotal and often the result of accidental, unsystematic discoveries. However, attempts have been made to identify winter refugia of tree frogs *Hyla arborea* in the Netherlands (Stumpel, 1990), common toads have been studied in winter by the use of thermosensitive radiotransmitters (Van Gelder *et al.*, 1986), and there have been more general reports on hibernation sites of several species (e.g. Hagström, 1982; Sinsch, 1989b). We have recently quantified summer refugia selection by natterjacks and common toads at four study sites in Britain (Denton & Beebee, 1992). Natterjacks mostly used burrows of their own making on sandy sites while common toads usually sought shelter beneath debris. Burrowing behaviour is highly adaptive with benefits including protection against temperature extremes, desiccation and predation (Hoffman & Katz, 1989). In this study we set out to characterise the refugia used by the two toad species on the three habitats in which both can be found in Britain, notably lowland heath, coastal dunes and upper saltmarsh.

### STUDY SITES

Observations were carried out over four years (1988-1991 inclusive) at the following sites:

- (1) Woolmer Forest, a lowland heath in southern England supporting a relict population of about 100 natterjacks and with an even smaller number of common toads.
- (2) Ainsdale and Birkdale sand dunes, on the Merseyside coast of north-west England. This extensive (several hundred

ha) dune system supports several thousand natterjacks and tens of thousands of common toads.

- (3) Dunnerholme, an upper saltmarsh in Cumbria (north-west England) supporting several thousand natterjacks and a much smaller number of common toads.

In addition, some observations were made at Millom iron-works, another coastal site in Cumbria consisting mainly of rocks and debris with a shallow pond and several thousand natterjack toads. All these sites are described in detail elsewhere (Beebee, 1989; Denton, 1991).

### METHODS

All the study sites were visited many times by day and any likely refugia investigated. Natterjack burrows on banks were often identified by the characteristic semicircular opening; those on flat ground were found by searching for newly-exposed sand piles on the surface. Other refugia were detected by systematic lifting of stones, logs and other debris (Denton & Beebee, 1992). Refugia use was also studied by radiotelemetric monitoring of tagged animals. For the hibernation studies, totals of 14 natterjacks and two common toads were tagged on Merseyside; six natterjacks and five common toads at Woolmer; and 12 natterjacks and one common toad at Dunnerholme. Tags were implanted and tracking carried out as described elsewhere (Denton, 1991; Denton & Beebee, 1993). Hibernation sites were investigated by implanting toads with 100-day transmitters in late autumn and following the animals into hibernation, and transmitters were removed the following spring. At Woolmer, individual natterjacks were marked by toe-clipping or identified by individual throat-spot patterns.

At all sites, some of the refugia were subjected to detailed study. Depth, temperatures and relative humidities at the point occupied by the toad were measured in 18 burrows at Merseyside and in 25 at Woolmer. Air, ground-surface and burrow temperatures and humidities were recorded using a Hanna H8564 thermohygrometer. Burrow depths and substrate types were also recorded.

## RESULTS

## GENERAL FEATURES OF SUMMER REFUGIA

The numbers of refugia investigated for both species at all study sites are listed in Table 1. At dune and heath sites, natterjacks almost always used refugia on sandy substrates. This was true whether refugia consisted of true burrows or of cells dug under debris, but in the Cumbrian sites where sand was rare or (as at Millom) completely absent, typical refugia for this species included mammalian burrows, hollows under large stones on clay soils, and gaps in piles of slag or drystone walls. Most natterjacks in summer burrows lived at depths of >20 cm from the burrow entrance, though on dunes this was usually a horizontal rather than a vertical distance. Thus the average depth at which toads were found in 18 burrows on Merseyside was 30 cm (range 10–45 cm). At Woolmer, however, burrows were dug vertically into virtually flat ground. Toads in 25 burrows at the heathland site averaged 23 cm below ground, with a range of 5–45 cm. Only in spring and autumn was there any substantial use of surface refugia, mostly as cells dug immediately beneath flat tiles, at Woolmer (Denton & Beebe, 1992). Common toads were only found in surface refugia or in burrows dug by other animals at all sites; as shown in Table 2, dense vegetation, especially moss at the base of *Salix repens* stems in wet slack basins was a favourite place and rabbit burrows were utilised on both dunes and heathland. Common toads of all sizes were

study site	refugia numbers	
	total investigated	studied by radiotelemetry
<i>Merseyside</i>		
natterjack	45(42)	28
common toad	23(0)	12
<i>Dunnerholme</i>		
natterjack	143(21)	17
common toad	14(0)	2
<i>Woolmer</i>		
natterjack	57(55)	15
Common toad	11(0)	4
<i>Millom</i>		
Natterjack	83(0)	0
common toad	4(0)	0

TABLE 1. Numbers of refugia studied, 1988–1990. Refugia constituted by self-dug burrows are given in parentheses.

refugia	site	
	Merseyside	Woolmer
logs or litter	5	6
dense vegetation	14	3
rabbit holes	4	2
total	23	11

TABLE 2. Characteristics of common toad refugia.

frequently found under logs and other debris, including metal sheets.

Burrows dug by natterjacks in sandy substrates were effective homeostatic refugia protecting the animals within from extremes of heat and drought. The daily fluctuations of ground air, ground surface and natterjack body temperatures around and inside one particular burrow at Merseyside over a twelve hour period in August are shown in Fig. 1, a single example from the 18 investigated. Whereas sand surface temperatures fluctuated over a range of 48°C during this time, with a maximum of about 60°C at midday, the thermally-tagged natterjack 30 cm below ground level maintained a temperature of around 24°C ( $\pm 1^\circ\text{C}$ ) throughout. Sand surface temperatures of >50°C were recorded regularly on these dunes in summer while night-time temperatures often dropped to <12°C. During such hot dry periods, natterjacks remained inactive in their burrows for up to several weeks at a time. At Woolmer, minimum temperatures in summer were much lower than on the dunes and often dropped to around 0°C. Night-time (22.00–24.00 hours) temperatures in 25 burrows with aestivating natterjacks at this site were always warmer than ground surface temperatures, by an average of 1.6°C on one particular and typical summer night ( $t=2.14$ ,  $df=24$ ,  $P<0.03$ ). Mean humidity was also significantly higher in burrows, averaging 90% compared with 60% in surface air ( $t=9.09$ ,  $df=24$ ,  $P<0.0001$ ) on this same occasion.

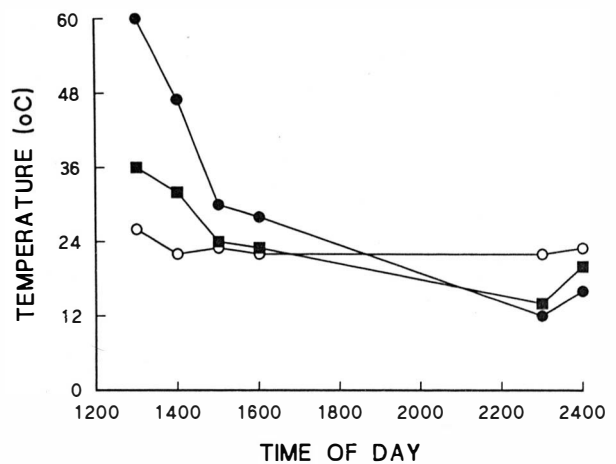


Fig. 1. Temperatures in and around a natterjack burrow. Measurements were made at Merseyside during a single day in August 1990. filled circles, sand surface; filled squares, ground air; open circles, toad in burrow with thermal transmitter.

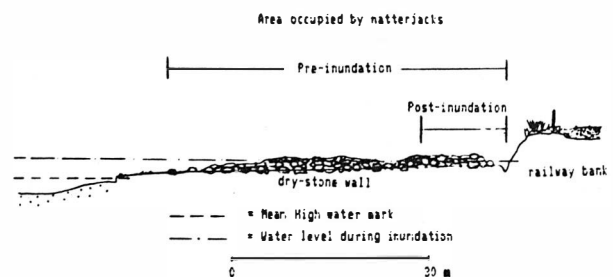


Fig. 2. Refugia changes associated with tidal inundation. The figure shows the distribution of natterjacks in refugia before and after a tidal inundation at Dunnerholme during September 1989.

Refugia use	n	number of animals seen		
		1 season	2 seasons	>3 seasons
Nightly migration to pond from winter/summer burrows	18	2	5	11
Temporary occupation of new refugia near ponds	21	8	5	8

TABLE 3. Refugia selection by breeding male natterjacks at Woolmer. Observations were cumulative over four breeding seasons (1988-1991 inclusive). *n*=total number of individuals monitored. Each individual was observed a minimum of three times in each breeding season.

Refugia selection by natterjacks at saltmarsh sites was influenced by episodes of tidal inundation. At Dunnerholme the distribution of natterjacks varied from month to month through the summer on this account. Thus in June 1988 a drystone wall which extended from a railway embankment across grazed saltmarsh to the beach (Fig. 2) was occupied by over 80 animals. These were found under collapsed stones along the entire length of the wall. In September 1988, following a tidal inundation, only 15 toads were found in the wall and none were found more than 15 m from the railway embankment end. Many of the more seaward stones concealed marine crustaceans at this time. Natterjacks had also abandoned strand-line flotsam which, before the inundation, was heavily used as a refugium. How toads survived these episodes was not discovered, but no dead animals were found in the flooded areas.

REFUGIA SELECTION BY NATTERJACKS DURING THE BREEDING SEASON

Bufonids of all species are compelled to visit ponds during the breeding season, and this inevitably entails movement away from previously-occupied refugia. Male natterjacks were studied individually at Woolmer, and two equally favoured strategies were apparent at this time (Table 3). Throughout the breeding season, some males commuted to the ponds on every night that they were encountered, returning before dawn to their summer (and winter) home range areas in round trips of up to 300 m. Other males adopted refugia in the vicinity of the ponds for at least one night and often for much longer during the 8-10 week calling period. These males either made new burrows near the pond or hid under debris or in dense vegetation such as *Molinia* tussocks, and invariably started calling before the commuters arrived. The resident strategy seemed slightly more hazardous than the commuter strategy since a substantial proportion of males adopting the former (40%) were seen only for a single breeding season, whereas the comparable figure for commuters was just over 10% (Table 3). Nevertheless, comparing survival rates for up to two seasons with those for more than two seasons there was not quite a significant difference between the two strategies ( $\chi^2=3.53$ , *df*=1, *P*>0.05). Since all males were recorded during their calling bouts, these data were not biased by differential capture probabilities. Females almost invariably commuted to the pond for a single night, spawned, and returned to the summer/winter home range immediately afterwards. Only on eight recorded occasions out of more than 50 observations, when temperatures dropped low enough to pre-

study site	n	no. animals using:	
		same refuge as in summer	new site
<i>Merseyside</i>			
natterjack	14	8	6
common toad	2	0	2
<i>Dunnerholme</i>			
natterjack	12	4	8
common toad	1	0	1
<i>Woolmer</i>			
natterjack	6	6	0
common toad	5	1	4

TABLE 4. Hibernacula selection by natterjacks and common toads. All data were from radiotracked animals. *n*=number of individuals tracked into hibernation.

vent spawning (Banks & Beebee, 1987*b*) did females remain in the vicinity of the ponds for an extra day.

HIBERNACULA SELECTION BY NATTERJACKS AND COMMON TOADS

Animals were followed into hibernation by radio-tagging in late autumn, and results are summarised in Table 4. Individual natterjacks at Woolmer always hibernated in the same burrows they occupied during the summer months, but dug down to depths of >50 cm in winter. These hibernacula were invariably on flat, level ground and not in the various banks available at the site. In addition to radiotracking data, 43 natterjacks with known home ranges at Woolmer were first observed in spring in the same areas they occupied the previous summer, also indicating hibernation sites in or near the refugia used in summer months. Some burrows were occupied by more than one individual, and juveniles (<40 mm long) were found with adults. On mobile dunes at Merseyside, natterjacks hibernated in burrows at the base of marram (*Ammophila*) clumps, 8 out of 14 using the same ones occupied during the summer. All four of the radio-tracked natterjacks using burrows on the most seaward dune ridge, however, moved to burrows on the east-facing leeward side of the ridge for hibernation, perhaps minimising risk of exposure by wind erosion on the seaward facing slopes during winter gales.

The Dunnerholme site was dominated by saltmarsh habitat with only small outcrops of mobile dunes. Eight of the 12 natterjacks followed into hibernation by radiotracking moved from their summer refugia into new sites for the winter: two moved less than 5 m, and secreted themselves at depths of around 25 cm in burrows of small mammals; one moved from a pile of railway sleepers into a bank of loose clinker; one moved from a drystone wall, and two more from under stones, to bury themselves in a sand bank; and two dug new burrows within 10 m of their summer refugia in the same sand bank. By contrast, two remained in the sleeper pile, one remained in the drystone wall and another in its summer sand burrow. One male hibernated at the base of a bank >20 cm below the level reached by high winter tides. At Millom, where no sand at all was available, natterjacks hibernated in spaces between

coarse slag particles in large banks of this material. In April 1991 63 natterjacks emerged at this site from three holes less than 10 cm apart, all of which led to underground cavities formed among piles of building debris.

The hibernation sites selected by common toads were similar at all three study sites. Radio-tracked animals resorted to hiding places in dense vegetation, under piles of logs or in leaf litter. Both tagged animals at Merseyside, the one at Dunnerholme and four out of five at Woolmer moved to new sites for the winter. Some individuals made substantial (>500 m) moves towards the breeding ponds in autumn before settling in a hibernation site, a behaviour never seen with natterjacks. Mammalian burrows, especially rabbit and vole holes, were also used at Woolmer and Birkdale.

## DISCUSSION

Both toad species of this study probably spend more than 90% of their lives in refugia, yet there have been few reports on the nature and location of these places, especially with regard to hibernation sites. Our observations extend those of others on natterjacks which, for the most part, were the results of chance encounters in both summer and winter (reviewed in Beebee, 1979; 1983). Water availability may be a major factor governing refugia selection by amphibians in the sandy, relatively arid habitats favoured by natterjacks in Britain. Burrowing enables natterjacks to utilise substrate moisture, whereas common toads are dependent on surface water sources. Sand is also a poor conductor of heat and temperature fluctuations dampen rapidly as a function of depth from the surface; yellow dunes favoured by natterjacks are subject to daily temperature variations which are much greater than those on the more mature grey dunes (Chapman, 1964) and the ability to burrow is therefore an important adaptation of *Bufo calamita* for existence in otherwise exposed, open habitats. *Bufo bufo*, by contrast, generally selected equable conditions by utilising surface refugia in dense vegetation. At Woolmer, three out of eight common toads radio-tracked in their summer home ranges were eaten by grass snakes *Natrix natrix* while none of six tagged natterjacks were lost to this predator. The snakes caught toads by day, and it seems likely that surface refugia were more accessible to them than the burrows (often completely covered by collapsed sand) inhabited by natterjacks.

The survival of toads in areas subject to occasional tidal inundation needs more study. The duration of these episodes rarely exceeded two hours and it is possible that animals survived in air spaces during the flooding period. Subsequent vacuation of flooded sites may be a behavioural response to residual salinity in groundwater; juvenile natterjacks avoid substrates saturated with >46% seawater when given a choice (Pearce, 1978). Although *B. calamita* is considered to be a euryhaline amphibian, its upper limit of salt tolerance is lower than that of *B. viridis* and is lower in winter than in summer, probably because reduced metabolic rates in cold weather limit the accumulation of plasma urea (Sinsch, Seine & Sherif, 1992).

We do not know whether the two strategies adopted by male natterjacks at Woolmer during the breeding season are used at other sites. Both have apparent dangers; moving long distances every suitable calling night for several weeks risks

being caught by nocturnal predators (though we have seen no evidence of such at Woolmer) and being immobilised by falling temperatures. We have found males moving away from ponds late at night almost immobilised by cold, with body temperatures <4°C, but again we have no evidence of consequent mortality. Residents, on the other hand, often hide in vegetation rather than burrows and may be at increased risk from snake attack during daytime. This might be a particular feature of the Woolmer site, where burrowing opportunities around some of the best breeding ponds are severely limited by dense vegetation and impacted substrates; residence may well be a safer and more common strategy at other natterjack localities where burrowing is easier near the breeding pools.

Natterjacks in Britain only inhabit non-sandy sites at coastal localities in Cumbria and Scottish Solway. The climate of these places is strongly influenced by the Gulf Stream and is characterised by mild winters with few severe frosts. Toads living at such sites may be under less pressure to live and hibernate in deep sandy burrows, and thus be free to occupy slightly wider ecological niches, than elsewhere in Britain. Inland natterjack populations in southern and eastern England occur on sites that experience not only severe winter frosts but sub-zero temperatures at night at any time of year between September and June (unillustrated data). This may well deter natterjacks from moving off sandy substrates in these areas.

Our observations have some implications for conservation management of natterjacks. Clearly it is important that in places without sandy substrates alternative hibernation sites (drystone walls etc) are always available. Areas surrounding breeding ponds may benefit from management designed to provide abundant burrowing facilities, such as banks of soft sand without dense or rank vegetation, thus making life safer for resident males. Finally, removal of log and litter piles may help to disadvantage competitively-superior common toads which can, in some situations, cause local extinction of natterjacks when numbers rise to the point where their tadpoles dominate the breeding ponds (e.g. Banks & Beebee, 1987c; Griffiths, 1991; Griffiths, Edgar & Wong, 1991). There is some evidence that in open habitats refugia availability is an important factor governing common toad population density (R. Oldham, personal communication).

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## THE EFFECTS OF SALINITY AND TEMPERATURE ON APPETITE IN THE DIAMONDBACK TERRAPIN *MALACLEMYS TERRAPIN* (LATREILLE)

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### ABSTRACT

The appetite of saltmarsh diamondback terrapins (*Malaclemys terrapin*) is extremely large (mean satiation ration on a diet of mussel flesh at 25°C = 7.2% body weight), some 8-10 times that of closely related freshwater emydid turtles. When held in sea water without access to fresh water the appetite of diamondbacks is gradually depressed, reaching (after 18 days in sea water) 22-54% of the average satiation ration recorded when fresh water is available. Between 20 and 35°C appetite in *Malaclemys* is stable ( $Q_{10} = 1.1$ ). Between 15 and 20°C  $Q_{10} = 20.7$ , indicating a shift to a hypometabolic state below 20°C.

### INTRODUCTION

The diamondback terrapin *Malaclemys terrapin* (Latreille) is a small emydid turtle which inhabits saltmarshes and lagoons on the eastern coast of the United States, from New York State to Texas. Emydid turtles are normally characteristic of freshwater ecosystems in the Americas, Europe, north Africa and Asia. Although a handful of species have colonized productive estuarine areas (e.g. Dunson & Seidel, 1986), most cannot survive in full sea water for more than a few days because they become osmotically dehydrated and salt loaded. Such species can survive periodic exposure to high salinities by avoiding drinking or eating when salinities are high (e.g. *Batagur baska*; see Davenport & Wong, 1986; Davenport *et al.*, 1992), but only *Malaclemys* is physiologically capable of spending several weeks in sea water without periodic access to fresh water. The species has attracted a great deal of study by W. B. Dunson and co-workers who have demonstrated that the species can choose to drink only low salinities, has a low integumentary permeability to salts and water, plus a reasonably powerful lachrymal salt gland, and has the remarkable ability to increase extracellular fluid volume dramatically when fresh water is available (Dunson 1970, 1976, 1985; Robinson & Dunson, 1975). However, diamondbacks cannot survive indefinitely in sea water; their blood gradually becomes more concentrated and loaded with urea (Gilles-Baillen, 1970). Davenport & Macedo (1990) recently demonstrated that diamondbacks have well-developed direct behavioural responses to the vibration of rainfall which allow them to spend the summer months in fully-marine conditions. The turtles exploit the transient availability of freshwater during occasional rainstorms. However, in their coastal habitats they may well face periods of 2-4 weeks when no rain falls, yet they continue to feed. Coker (1906) long ago showed that diamondbacks are carnivores which eat a range of saltmarsh invertebrates (crabs, littorinid snails, nereid worms). All of these prey items will be isosmotic with sea water, so will have body fluids more than twice as concentrated as terrapin blood. Terrapins will take in some sea water with their food (Dunson, 1985; Dunson & Mazzotti, 1989), though they avoid deliberate drinking of high salinity media.

It therefore seemed likely that terrapins ought to respond to lack of availability of fresh water by reducing food intake; this hypothesis is tested in the present study. Experience of keeping *Malaclemys* and a variety of freshwater emydids in captivity also suggested that diamondback terrapins had an unusually large appetite: accordingly the study was broadened to investigate appetite, appetite return and the influence of temperature on food intake.

### MATERIALS AND METHODS

#### COLLECTION AND MAINTENANCE

Six terrapins, all mature males, were used in these experiments. Initially purchased from a dealer, they had been held in captivity for several years, were extremely tame and fed readily in the presence of observers. They were held under constant illumination in large tanks of circulating sea water (34‰; 25±1°C) which had floating rafts on which vessels full of fresh water for drinking could be mounted. The terrapins were fed routinely upon flesh of mussels (*Mytilus edulis* L.) collected from the shore of the Menai Strait (North Wales).

#### FEEDING AND MEAL SIZE ASSESSMENT

During feeding experiments terrapins were each fed individually in a separate feeding tank. Each terrapin was weighed to the nearest 0.1 g on a Mettler P1200 toploading balance before a meal, so that the meal size could subsequently be expressed in terms of % body weight. To determine the size of a meal, a quantity of mussel meat was weighed out, and that amount offered piecemeal to the terrapin under investigation. When the animal had refused more food for a period of 10 min it was assumed to be satiated. Uneaten food in the feeding tank was retrieved, water drained from it, and added to the unoffered food. All of this food was weighed and the meal size obtained by deducting this weight of mussel flesh from the original weighed amount. In the light of pilot experiments it was found that maximal appetite occurred after a 48 hr food-deprivation period, and throughout this paper, a meal taken after such a deprivation period will be referred to as a 'standard satiation meal'.

### RETURN OF APPETITE

To find out when food was first taken after a standard satiation meal, the terrapins were offered food at one hour intervals following a standard satiation meal. Food acceptance was first observed after 6 hr. This allowed the following experiment to be designed. Three of the terrapins were each given a standard satiation meal (i.e. after 48 hr of food deprivation). Each was then deprived of food for an experimental period before being fed to satiation. The sequence of 48 hr food deprivation, standard satiation meal, deprivation period and experimental satiation meal was repeated until all three animals had yielded data for the following deprivation times: 6, 12, 18, 21, 48, 60 and 72 hr.

### APPETITE UNDER FULLY-MARINE CONDITIONS

Three terrapins were maintained under the standard feeding regime for four feeds (days 0-6) from which a mean standard meal size was calculated for each terrapin. Immediately after the fourth standard meal, the terrapins were deprived of fresh water. They continued to be fed to satiation at 48 hr intervals, the meal size being recorded in each instance. Fresh water was restored to the diamondbacks after 18 days of deprivation (i.e. after the feed on day 24 of the experiment); food consumption continued to be monitored at 48 hr intervals up to day 32.

### EFFECT OF TEMPERATURE ON APPETITE

Three terrapins were maintained under the standard feeding regime for four feeds at a temperature of 25°C to allow a mean standard meal size to be calculated for each terrapin. After this the water temperature was changed to, and maintained at, an experimental temperature for 96 hr. Two satiation meal assessments were carried out, at 48 hr ('first feed') and at 96 hr ('second feed'). These two assessments were performed to test for adjustment of physiology to a new temperature. After the second feed the animal was transferred to the next experimental temperature and the whole process repeated. The terrapins were exposed to the following temperatures in an order designed to avoid either a systematic rise or fall in temperature throughout the period of study- 15°C, 25°C, 35°C, 30°C, 20°C.

## RESULTS

In considering the results it has to be accepted that the sample size is rather small. Although the animals have been long-captive (carrying the risk of development of unusual behaviour patterns), this has the advantage that the turtles were not shy and would readily feed in the presence of observers.

### RETURN OF APPETITE

The mean satiation ration recorded for the three turtles at 25°C was equivalent to 7.2% body weight. The results of the return of appetite study are shown in Fig. 1. Although no return of appetite occurs until six hours after a standard satiation meal, the diamondback is then capable of consuming 33-41% of a standard satiation meal. Appetite returns completely within 48 hr. Food intake probably reflects the amount of 'space' available in the stomach, but attempts to construct a 'square-root' gastric emptying model of the type described for lower vertebrates by Jobling (1981) failed be-

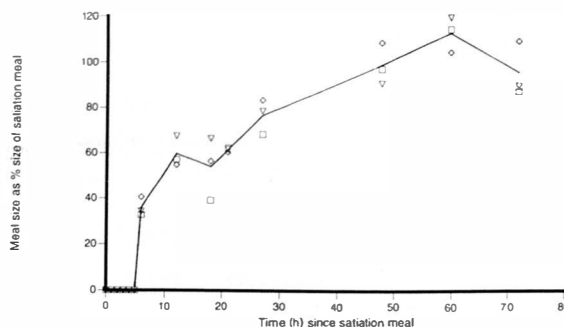


Fig. 1. Return of appetite in *Malaclemys terrapin* at 25°C. Solid line represents mean; symbols represent individual turtles.

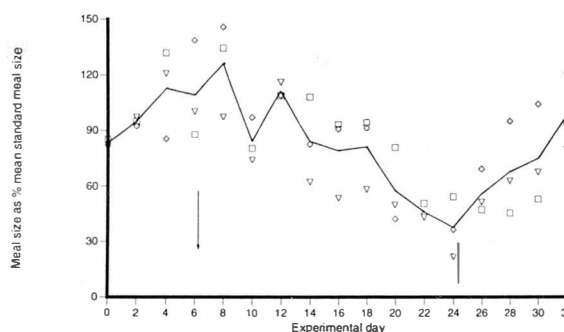


Fig. 2. Effect of lack of access to fresh water on appetite in *Malaclemys terrapin* at 25°C. Downwardly directed arrow indicates onset of water deprivation. Upwardly directed arrow indicates renewed access to fresh water. Solid line represents mean; symbols represent individual turtles.

cause of the steep rise in appetite between 5 and 6 hr after a standard satiation meal. After 60 hours of food deprivation there are signs of an overshoot to higher levels of appetite, but not to a statistically significant extent.

### APPETITE UNDER FULLY-MARINE CONDITIONS

The data displayed in Fig. 2 demonstrate that exposure to full sea water without access to fresh water gradually depresses appetite so that, after 18 days of water deprivation, the diamondbacks' appetite has fallen to 22-54% of the average satiation ration recorded when fresh water was available. During this period there was a steady fall in body weight of the diamondbacks (Fig. 3), most of which is due to osmotic water loss as described by Robinson & Dunson (1976), since it may be seen that body weight rapidly climbs to its initial value as soon as fresh water is made available again, whereas appetite takes 6-8 days to recover completely (Fig. 2).

### EFFECT OF TEMPERATURE ON APPETITE

The effects of temperature on appetite in *Malaclemys* are shown in Fig. 4. As would be expected, lowering the temperature depresses appetite, whereas a rise in temperature stimulates it. However, the temperature effects are far from linear (Fig. 4). At 15°C appetite is considerably depressed at the first feed (to around 16% of the average standard meal size at 25°C) and does not show significant signs of recovery by the time of a second feed. At 20°C the picture is different. Initially appetite is depressed, but there is a highly significant ( $P < 0.001$ ) recovery of appetite by the time of the second feed. At 25°C there was no significant difference in appetite re-

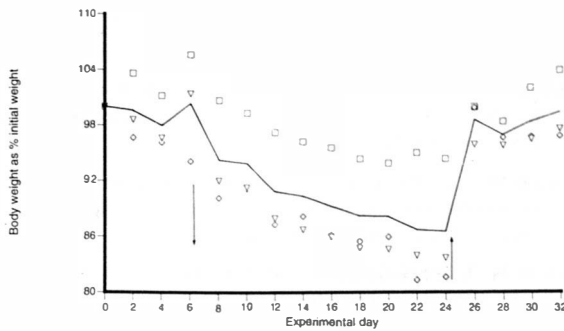


Fig. 3. Effect of lack of access to fresh water on body weight in *Malaclemys terrapin* at 25°C. Downwardly directed arrow indicates onset of water deprivation, Upwardly directed arrow indicates renewed access to fresh water. Solid line represents mean; symbols represent individual turtles.

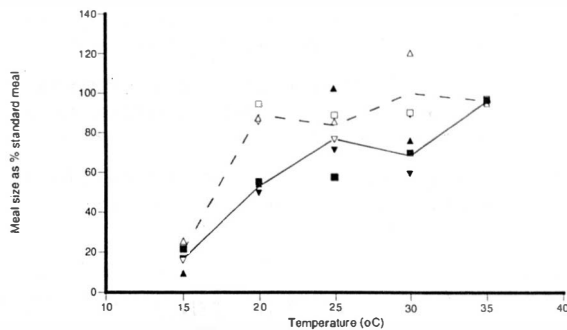


Fig. 4. Effect of temperature on appetite in *Malaclemys terrapin*. Data represent three individuals. Closed and open downward triangles represent one individual at first and second feeds after transfer to new temperature respectively (see text for details). Corresponding symbols for individuals 2 and 3 were closed and open boxes, and closed and open upward triangles respectively. Solid line represents mean appetite at first feed; dashed line represents mean appetite at second feed.

Temperature range (°C)	$Q_{10}$ for appetite			
	Turtle 1	Turtle 2	Turtle 3	Mean
15-20	30.2	19.8	12.2	20.7
20-25	0.8	0.9	1.0	0.9
25-30	1.4	1.0	2.0	1.5
30-35	1.2	1.1	0.6	1.0
20-35*	1.1	1.0	1.1	1.1

TABLE 1. Effect of temperature on appetite in *Malaclemys terrapin*;  $Q_{10}$  values for second feed data.\*  $Q_{10}$  is presented for this range to show contrast with that for 15-20°C range.

corded between the two feeds, while at 30°C there was a significant difference ( $P < 0.05$ ), with the appetite at second feed being higher. At 35°C there was no significant difference between appetite levels recorded.

Table 1 shows  $Q_{10}$  values for appetite calculated from the second feed data. Clearly appetite in *Malaclemys* is remarkably stable between 20 and 35°C, but is severely depressed below 20°C. The high  $Q_{10}$  value for the 15-20°C interval indicates a fundamental change in metabolism below 20°C, rather than a simple thermal response.

## DISCUSSION

Diamondback terrapins with access to fresh water for drinking proved to have unusually large appetites (mean satiation ration 7.2% body weight at 25°C, corresponds to 3.6 % body weight  $d^{-1}$  assuming complete return of appetite in 48 hr), particularly for carnivorous adult turtles past the phase of rapid growth. For comparison, Birse & Davenport (1987) recorded satiation rations of 3.7% body weight for juvenile (fast-growing) loggerhead sea turtles (*Caretta caretta* L.) at the same temperature, but values for freshwater emydids relatives of *Malaclemys* are much lower; Kepenis & McManus (1974) recorded  $<0.5\%$  body weight  $d^{-1}$  for young painted turtles (*Chrysemys picta* (Schneider)), while Davenport & Kjörsvik (1988) recorded an intake rate of 0.045% body weight  $d^{-1}$  for adult *Mauremys caspica* (Gmelin) males (101-173 g body weight; also at 25°C) feeding on a dry pelleted diet, which corresponds to about 0.2% body weight  $d^{-1}$  on a wet weight basis. If mussel flesh is assumed to have a water content of 75-80%, then adult male diamondbacks consume about 7-9 g dry matter  $(kg\ body\ wt)^{-1}\ d^{-1}$ . This is 2-3 times the dry matter intake reported for a range of herbivorous turtles (Björndal, 1985) eating much poorer quality diets, so the available evidence indicates that *Malaclemys* has a relatively enormous appetite. Davenport *et al.* (1992) recently described a similarly large appetite in another estuarine emydid, the river terrapin *Batagur baska* (Gray) (a largely herbivorous species).

Davenport *et al.* (1992) suggested that river terrapins were responding to a food-rich estuarine ecosystem by maximizing food intake and processing food quickly and relatively inefficiently (a strategy compatible with the resource-utilization hypothesis of Sibly, 1981). This may also be true of *Malaclemys*, since their salt marsh habitats contain an abundance of littorinid snails and crabs (the main items of their diet), so they may be able to afford to waste energy in a manner not tolerable in food-poor freshwater systems. However, an additional factor needs to be considered. Diamondback terrapins spend much of the productive summer period in fully marine conditions, only able to fully-hydrate themselves when fresh water becomes available due to rainfall (there is strong element of water storage involved, since diamondbacks exhibit swollen subcutaneous tissues after a drinking bout; Robinson & Dunson, 1976). The results of the study reported here demonstrate that prolonged exposure to full sea water substantially depresses appetite, presumably because the animals have to strike a physiological balance between the intake of salts and energy. It therefore seems possible that diamondbacks are adapted to respond to the availability of fresh water by enhanced appetite (hyperphagia) and energy storage, so that average intake of energy is maximized.

Three features of the response of appetite of diamondbacks to temperature are interesting. First, the ability of the terrapins to adjust to temperatures between 20 and 35°C, but not to be able to acclimate (at least in the relatively short-term experiments reported here) to 15°C appears to be a novel observation in turtles. Second, the relative independence of appetite shown by acclimated terrapins between 20 and 35°C perhaps reflects the wide geographical range of the species (roughly from 26-41°N on the eastern coast of the United States), encompassing warm and cool temperate regions. It

contrasts with the limited data available for other chelonians, which tend to show temperature dependence (e.g. *Caretta caretta*; Birse & Davenport, 1987). Finally, a sharp decline in appetite below 20°C indicates that the species enters a depressed metabolic state at such temperatures.

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## A SIX YEAR STUDY ON THE POPULATION DYNAMICS OF THE CRESTED NEWT (*TRITURUS CRISTATUS*) FOLLOWING THE COLONIZATION OF A NEWLY CREATED POND

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### ABSTRACT

The population dynamics of the crested newt, *Triturus cristatus*, in a newly created aquatic habitat in a dune area in northwestern France was studied over a six year period. After a rapid colonization of the pond in year 1, and a fast initial increase to reach 335 newts in year 5, the adult population size dropped dramatically to 16 in year 7. Variation in the adult population among years was largely due to variation in juvenile recruitment. In the longer term, the population stabilized at about 40 newts. Since the population has survived for five times the minimum generation time of the species, the colonization was judged to be a success. An estimated 50% of the juveniles joined the breeding population at age 2; those that did not breed by then spent the third year on land. The average annual survival rate for the juveniles was 0.22. For the adults survival was 0.49 and showed almost no fluctuations over time or with age. Given a short distance to disperse, the crested newt can be an opportunistic species.

### INTRODUCTION

In the historic past amphibians have been favoured by agricultural practices. More breeding sites became available through the creation of ponds for cattle drinking. Also the terrestrial component of the amphibian habitat was favourable because of diversification in land use. This trend is now in reverse, mainly as a result of the intensification of agricultural practice. Field size enlargements, urban extensions and an increase in monoculture have reduced the diversity and availability of terrestrial habitat. In areas under continuous agricultural use there has been an increase in the arable to pasture ratio, with a concomitant decline in numbers of amphibian breeding sites (Oldham & Nicholson, 1986). Additionally, widespread improvement of pasture has increased soil nutrient levels, accelerating the rate of eutrophication, hydrosere succession and consequent loss of water bodies from grassland (Beresford & Wade, 1982). The loss of ponds and the decrease in terrestrial habitat suitable for amphibians are synergistic effects, and movements between local populations becomes increasingly difficult. Extinction probabilities may increase significantly with increased interpopulation distance (Sjögren, 1991; Sinsch, 1992).

In the United Kingdom a national survey of one species, the crested newt, *Triturus cristatus*, has shown a decline in breeding sites of 37% during ten years, attributable mainly to agricultural development and pond neglect (Oldham & Nicholson, 1986). Extensive studies in northwestern Germany have shown *T. cristatus* to be the rarest of the four indigenous newt species (Blab & Blab, 1981; Feldmann, 1981). It was found almost exclusively in ponds where other newt species also occurred. Similar observations were made in Denmark, Switzerland and northwestern France (Arntzen & Gerats, 1976; Grossenbacher, 1977; Bisgaard *et al.*, 1980). Clearly, *T. cristatus* has habitat requirements that are more demanding than that of most other palaearctic newt species. One consequence of a specialized habitat choice might be that

for dispersal fewer 'stepping-stones' are available for such a species than for those with less stringent ecological requirements. This raises the question of how successful the crested newt can be in colonizing new habitats for breeding. This is particularly important in view of programmes at the more practical side of nature conservation that aim to improve aquatic and terrestrial habitats and create new ponds. In the present paper we describe the colonization of a new pond by *T. cristatus* and we followed the success of the newly established population.

### MATERIAL AND METHODS

#### SITE DESCRIPTION

The study was carried out in an abandoned sand-quarry in a coastal dune system in northwestern France (Fig. 1). The quarry is located in the département (province) Pas-de-Calais, approximately 1 km southeast of the village of Ambleteuse and 800 m from the sea. The quarry pond was discovered as an amphibian breeding site in 1975, at which time it was shallow relative to its area and almost devoid of macrophytes (maximum surface approximately 160 m<sup>2</sup>, maximum depth 30 cm). For two years the only amphibian species observed to be

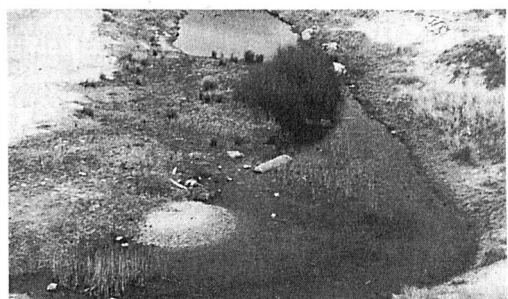


Fig. 1. Study pond in abandoned quarry in northwestern France. The part of the pond in the foreground is an original dune slack; that in the background is newly created (Photo: H. Kersten).

year	number of visits	first visit	last visit	total catch	different individuals caught	$\hat{N} \pm SE^a$	sampling efficiency <sup>b</sup>	observer <sup>c</sup>
1979	3	24 April	18 June	40 adults	40	c. 60	c. 2 out of 3	WW & AZ
1980	8	8 April	3 Sept.	70 adults	70	c. 105	c. 2 out of 3	FH & AZ
				23 juveniles (age class 0+) <sup>d</sup>	23	-	-	
				178 juveniles (age class 1+)	150	309 $\pm$ 49	49%	
1981	7	14 March	14 May	283 adults	153	169 $\pm$ 15	91%	ST & JA
1982 <sup>e</sup>	6	5 April	5 July	335 adults	235	346 $\pm$ 35	68%	HK & JA
				35 juveniles	26	44 $\pm$ 17	59%	
1983 <sup>e</sup>	11	20 March	18 May	706 adults	201	182 $\pm$ 9	100%	HK & JA
				19 juveniles	15	23 $\pm$ 16	65%	
1984	3	27 April	29 April	22 adults	14	16 $\pm$ 6	88%	JA & HK
				0 juveniles	0	0	-	
1992	8	8 April	1 June	94 adults	53	55 $\pm$ 10	96%	CA & JA
				0 juveniles	0	0	-	

TABLE 1. Recording programme and estimates of sampling efficiency and population size of *Triturus cristatus* in a pond in northwestern France. Notes: a, determined by capture-recapture approach (weighted mean method of Begon (1979)). For 1979 and 1980 estimates see text. b, No. individuals caught/estimated population size  $\times 100$ . For 1983 maximum estimate of population size ( $\hat{N} \pm 2 SE$ ) is used instead of  $\hat{N}$ . For 1979 and 1980 estimates see text. c, initials; to identify observers see acknowledgments and authors names. d, specimens just metamorphosed, captured on September 3 (see text and Fig. 2). e, see Kersten (1984) for a more detailed account.

breeding in it was the natterjack toad (*Bufo calamita*). At this time, the absence of crested newt eggs from the pond suggested that a breeding population had yet to be established. Eggs deposited by crested newts are easy to spot and can be distinguished from eggs of the other newts species occurring in this part of France (Arntzen, 1990). In the summer of 1977 the pond was enlarged. An excavation (7 x 20 m, maximum depth > 1.2 m) was made at the eastern side of the original pond, approximately doubling its surface (Fig. 1). Three ponds inhabited by crested newts, as observed in 1975 and in later years, are situated at distances of between 120 to 360 m to the south and southeast of the quarry.

#### METHODOLOGY

The presence of *T. cristatus* in the study pond was noted for the first time in 1978. The population of crested newts was studied over six consecutive years (1979-1984) and in 1992. In the spring of 1979 and 1980 adult newts were counted, while from summer 1980 to 1984 the population was studied in more detail through a capture-recapture approach. In 1981, 1982, 1983 and 1992 the crested newt population was followed over a major part of the aquatic season, including the period when most adult newts were expected to be in the water (at this latitude the second half of April and the first half of May (Kowalewski, 1974; Blab & Blab, 1981; Verrell & Halliday, 1985)). In 1984 the capture-recapture experiment was confined to the end of April. Metamorphosing specimens, hereafter called 'efts' (characterized by the presence of remnants of gills) appeared in late summer and are about six months old (age class 0+). Efts

were recorded in 1980 only, when the study was continued into September. The size of the aquatic portion of the juvenile cohort, efts excluded, was estimated each year, from 1980-1984. Details of the recording programme are given in Table 1.

Crested newts were detected by torching the shallow part of the pond in the period from dusk to midnight and caught by hand or by using a dip-net. All newts were classified as adults (with distinct male or female secondary sexual characteristics), juveniles (with no or indistinct such features) or efts. Snout-vent length (SVL) was measured on plastic coated millimetre graph paper, from the tip of the snout up to and including the insertion of the hind legs. For practical purposes this measurement of body size is the same as the more widely used measurement up to and including the anterior edge of the cloacal opening. To allow individual recognition upon recapture, the belly pattern of the newts (an irregular array of black spots on a yellow or orange background) was recorded photographically (Hagström, 1973). Efts and juveniles had generally not yet fully developed the highly individual distinctive patterns as found in the adults, and consequently individual recognition was more difficult. In almost all the juveniles, however, sufficient clues were available either from spots on the belly, mostly on the anterior side of the body between the fore-legs, or, if these were absent, from the pattern marking the ventrolateral margin of the belly. Photographs were taken in the field and the newts were released immediately.

A null hypothesis of random catch was tested for males versus females by comparing the number of each sex among specimens captured for the first time with the number of recap-

year	captures		recaptures		sex-biased catchability <sup>a</sup>	sex-ratio <sup>b</sup>
	males	females	males	females		
1979	18	22	-	-	-	0.82
1980	32	38	-	-	-	0.84
1981	79	74	71	59	NS	1.13
1982	115	120	49	51	NS	0.96
1983	100	101	249	256	NS	0.98
1984	7	7	8	0	**	2.14
1992	25	28	18	23	NS	0.84
total	376	390	395	389	NS	0.99

TABLE 2. Number of captures and recaptures for male and female *T. cristatus*. No significant differences ( $P>0.05$ ) were observed in the catchability of males and females in the years that population size estimates were made (except for 1984). Sex ratio is not significantly different from unity in all cases. Notes: a, one-tailed *G*-test of independence; NS,  $P>0.05$ ; \*\*,  $P<0.01$ . Williams' correction for continuity is applied in case sample size is small. b, sex ratio is expressed as total no. males / total no. females and tested against unity by *G*-test goodness-of-fit.

tured specimens (Arntzen & Hedlund, 1990). Total population size ( $\hat{N}$ ) was estimated for each year in which capturing - recapturing experiments were done, using the weighted mean algorithm of Begon (1979) for adults and juveniles separately. Sampling efficiency was calculated for both groups in each of these years by dividing the estimated population size by the total number of different individuals caught that year. These figures were used to obtain an estimate of the number of recaptures from previous years had sampling efficiency been 100 %. This value in turn was used to estimate yearly survival rate (*S*).

To determine the age of the newts two methods were used: (i) directly, by capture and later recapture of one year old juveniles (age class 1+, see below for initial age determination), and (ii) indirectly, on the basis of observed population structure. Because the population was a newly established one, we infer that no newts hatched in this pond prior to 1977 and conclude that adults observed in 1979 (with the exception of occasional immigrants) had age  $\leq 2$ , adults caught in 1980 had age  $\leq 3$  etc. Since adult crested newts were at least two years old (two years being the minimum age of maturation observed in the wild (Dolmen, 1983a; Francillon-Vieillot *et al.*, 1990; and present study)), it can be concluded that adults in 1979 were two years old, while adults in 1980 were  $2.5 \pm 0.5$  years old, adults in 1981 were  $3 \pm 1$  years old, etc., with the accuracy of the estimate declining with more year classes contributing to the population. So, by combining a high sampling efficiency, a high recapture rate and some knowledge of the onset of the population expansion, we circumvented the tedious techniques that are generally used for aging newts (Francillon-Vieillot *et al.*, 1990).

## RESULTS

### JUSTIFICATION OF METHODS

The number of crested newts observed is given in Table 2, partitioned for specimens captured for the first time (with or without being recaptured later on in the same year) and recaptures. In three cases out of four no significant departure from the expected pattern of random catch was observed. In all years the observed sex-ratio was close to unity, bolstering our

confidence that the method used to detect and catch adult newts is essentially unbiased. A deviating pattern with no females recaptured was observed in 1984. In accordance with the effort put into it, the sampling efficiency for juveniles was inferior to that for the adults (Table 1).

A histogram of the body-size for all newts captured in 1980 is presented as an example (Fig. 2). The histogram shows a distinctly bimodal distribution, in which the large animals are adults and the smaller animals are efts and juveniles. Within the latter group a bimodal size distribution is observed when samples for the third week of July are compared with the sample from the first week of September (Fig. 2 insert). The latter group consists almost exclusively of efts. The larger sized juveniles, clearly forming a single cohort, hatched in the preceding year and hence were about 18 months old (age class 1+, see below).

The belly pattern of *T. cristatus* can be shown not to be fixed. Both the number of black dots and their size tend to increase over time. However, change is gradual and we are confident in having correctly identified all adult specimens and all those juveniles that were recaptured within the season, or in the next year; recognition of a young animal in a subsequent year, however, may be problematical. For instance, to establish the identity of the 1980 juvenile depicted in Fig. 3 in 1982 and 1983 (Fig. 3 c,d) would have been difficult if the 1981 record had not been available. The high sampling efficiency in a population of moderate size helped to narrow down the number of unrecorded animals which in turn increased the reliability with which the juveniles could be identified. Summarizing the above points, we claim correct recognition of adults as well as juveniles (excluding efts) within a season and beyond, provided that no gaps exist in the annual recording.

### JUVENILE GROWTH, MATURATION AND BREEDING

As shown in Fig. 2 growth of juveniles over the summer was fast with an average increase of SVL of 8.3 mm in 10 weeks. Assuming growth continued at this rate until early September and slowed down towards hibernation, a body size increase with another 6 mm to almost adult SVL of 52 mm by

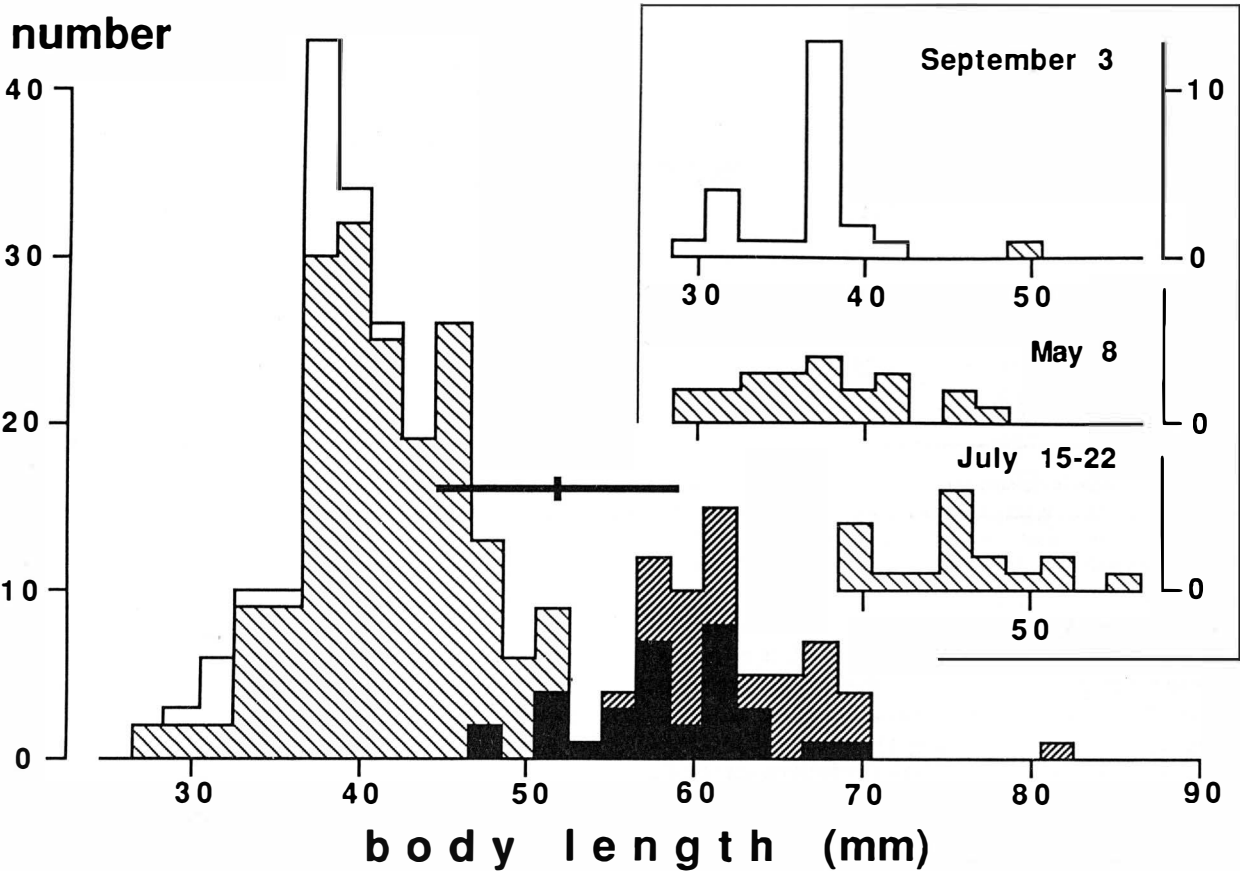


FIG. 2. Histogram of body-size for *Triturus cristatus* collected in 1980. Histograms are additive. Adult specimens are indicated by black bars (males) and densely shaded bars (females); newly metamorphosed juveniles (efts) are indicated by white bars and juveniles of age class 1+ by lightly shaded bars. The insert shows the size distribution of (almost exclusively) efts in September and juveniles of age class 1+ in May and July. The horizontal bar shows mean and range of the hypothesized size distribution of juveniles towards hibernation at the end of their second year, demonstrating that approximately half of the cohort may by then have reached adult size (details see text).

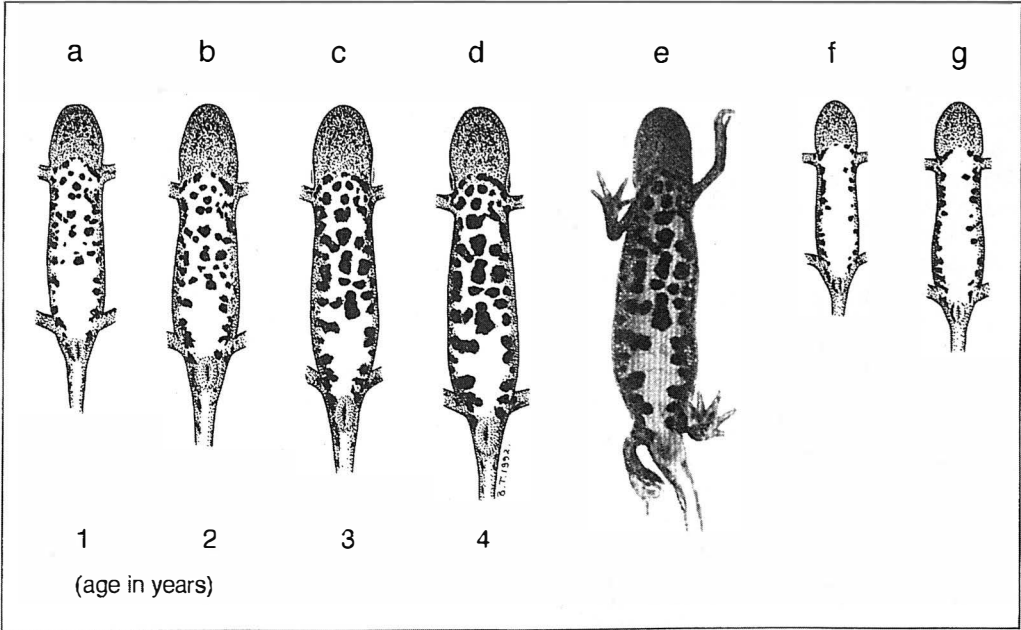


FIG. 3. Development of the belly pattern of a female *Triturus cristatus* over four consecutive years. Note that it would have been difficult to recognize the adult specimen in years 4 and 5 (C and D) from the juvenile belly pattern in year 2 (A) had not the specimen been recorded in the intervening year (B). The drawings are taken from photographs (compare D and E). Particularly indistinct juveniles (G and H) can be identified by their ventro-lateral patterning, even in the absence of mid-ventral spots.



the start of the third year would be expected (Fig. 2). Of the 30 juveniles that were observed over three 2-year periods (1981-1982, 1982-1983, 1983-1984) all had matured by the year of recapture (17 were males and 13 were females). Average SVL ( $\pm$  SD) of these young adults was  $58.5 \pm 5.6$  mm and  $61.4 \pm 4.4$  mm for the males and females, respectively. These data indicate that all specimens that come to the pond in their third year have become sexually mature. Interestingly, these recruits to the breeding population were on average significantly larger as juveniles than their cohort counterparts that were not observed to join the breeding population (SVL  $44.4 \pm 4.0$  mm ( $n=30$ ) compared to  $42.0 \pm 5.3$  mm ( $n=202$ );  $P<0.05$  in  $t$ -test), suggesting that rapid growth and early maturation are in some way related.

Of the ten animals in 1982 that had been previously caught in 1980, eight were also observed in the intervening year 1981. Considering the efficiency of sampling in 1981 (91%), this is about the number expected under the null hypothesis that all adult crested newts come to the pond to breed each year. A similar observation can be made regarding the data of 1981 to 1983, when ten specimens out of 51 were not observed in the intervening year 1982 when sampling efficiency was 68%. These data taken over two 3 yr periods support the notion that the entire adult population of crested newts is present in the pond every year (Table 3). No significant difference was observed for male and female newts ( $G$ -test of independence,  $P>0.05$ ).

### estimated population size

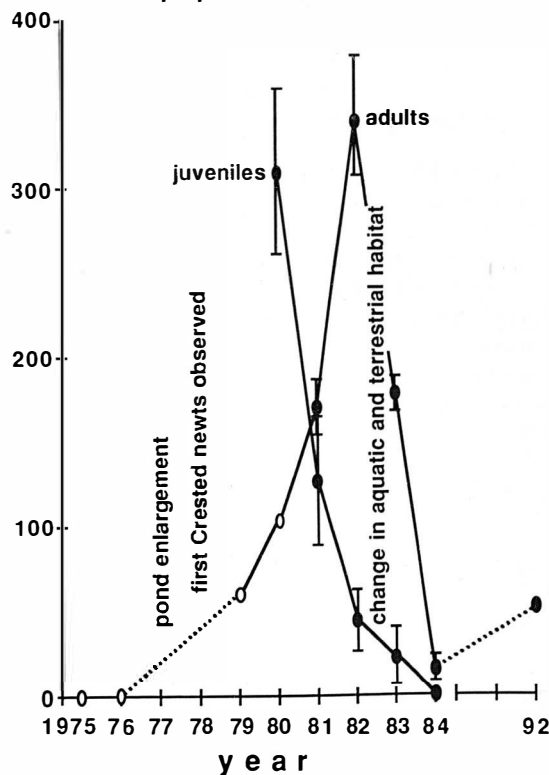


FIG. 4. Development of population size of *Triturus cristatus* over the period 1975 to 1982. Solid dots refer to population size estimates made by capture - recapture experiments. Bars indicate the standard error of the estimate. Open dots refer to less rigorous estimates (details see text).

year	capture	recapture two years later	intervening year	
			specimens observed <sup>a</sup>	specimens not observed
1980	juv./male	male	3	0
	juv./female	female	5	2
	total		8	2
1981	juv./male	male	16	5
	juv./female	female	25	5
	total		41	10

TABLE 3. Capture-recapture data for *Triturus cristatus* over two 3-yr periods. In both cases the number of specimens not observed in the second year is not significantly different from expected ( $P>0.05^b$ ). Expectations are drawn from sampling efficiency (see Table 1), testing the null hypothesis that adults breed every year. Notes: a, note that all juveniles observed in the second, intervening year were classified as adults in the third year; b, one-tailed  $G$ -test of goodness of fit is applied with Williams' correction for continuity if the sample size is small.

### POPULATION DEVELOPMENT

The first population size estimate for adults on the basis of capture-recapture data was made in 1981 ( $\hat{N} = 169$ , Table 1). In 1982 the population size had gone up to approximately 350 individuals ( $\hat{N} = 346$ , SE = 35). In 1983 the population was down to about 180 individuals. A dramatic drop in population size was observed in 1984, when  $\hat{N}$  was down to 16 adults. In 1992 the population was estimated at 55 adults. In each of the years sampling efficiency was high, ranging from an estimated 68% in 1982 to approaching the 100% level in 1983 (Table 1).

In the absence of recapture data, only a rough adult population size estimate could be made for 1979 and 1980. To this end we assumed a catching rate lower than that obtained for adults in the years 1981-1984 (when sampling efficiency averaged 85%, weighted value) since less effort was made these years. On the other hand sampling efficiency must have been substantially higher than that for the juveniles (1980 - 1983 : 49%, weighted value). At the intermediate catching rate of two out of three, the population size for 1979 can be estimated at roughly 60 individuals. Applying the same catching rate to the figure of 1980, a population size estimate of  $\hat{N} = 105$  is obtained. The juvenile cohort in 1980 was estimated from capture-recapture data to equal approximately 300 individuals. In the years following, the number of juveniles in the pond went down gradually to reach a zero level of observation in the year 1984. Data on the development of the newt population over a 18-year period are summarized in Fig. 4.

### SURVIVAL

Altogether 540 individuals (273 males and 267 females) were captured that were not recorded in any of the subsequent years; 71 males and 88 females were recaptured between years.

With the exception of 1984, when only a single newt was recaptured out of the 216 different specimens recorded in

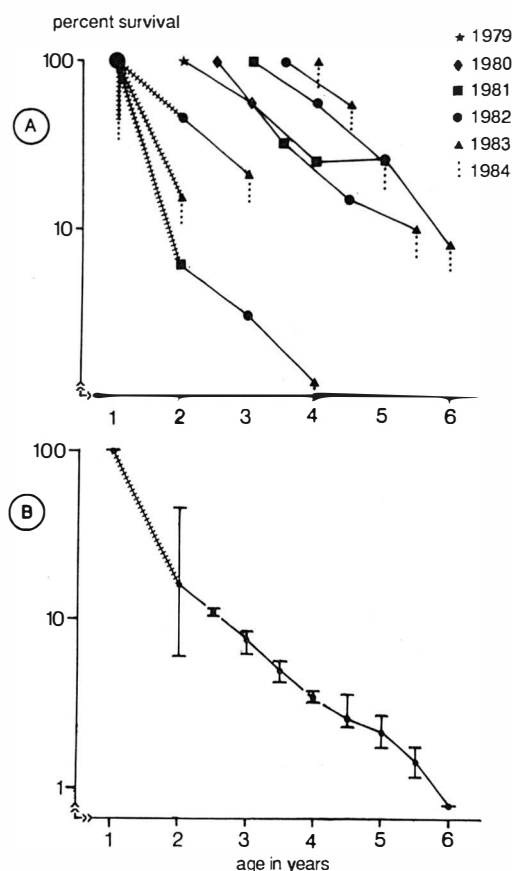


FIG. 5. Survivorship curves of *Triturus cristatus*. Juvenile survival is indicated by barred lines, adult survival by solid lines. The survival rate of juveniles is likely to be an underestimate (details see text). (A) Year to year comparisons for eight cohorts; (B) totals over the years, per half year, excluding the data for 1983 to 1984 when survival rate was close to zero. The observed range is indicated by vertical bars. Note that the y-axis has a logarithmic scale.

1983, the survival rate of adult newts ( $S_a$ ) from the year of initial recording to the following year ranged from 33% for 1980-1981 to 57% for 1979-1980 (Table 4), averaging at 48% (weighted mean = 47%). Taking the recaptures over the subsequent years also into account, but again excluding the aberrant results for 1983 - 1984,  $S_a$  was 51% (weighted mean = 47%). No significant difference was observed in the yearly survival of males and females (Table 5). Survivorship curves are presented in Fig. 5. From the approximately parallel running lines in Fig. 5a, and from the straight line that can be drawn through the data points in Fig. 5b it can be concluded that  $S_a$  shows little variation with adult age. For the whole of the study  $S_a$  was estimated at 49%. For juveniles  $S$  ranged from 7% for 1980 - 1981 to 45% for 1981-1982 (Table 4) averaging at 22% (weighted mean = 17%).

## DISCUSSION

Neither eggs nor adults of the crested newt were observed in the pond in 1975 and 1976. Breeding was observed in the spring of 1978, but may have occurred in 1977, the year that the pond was enlarged. By comparing the size of the adults as measured in 1977 against the growth curve for this population (J. W. Arntzen, in prep.) four animals (three males and one female) stand out. Their large size makes it unlikely that they hatched in the quarry pond (considering its age) and we as-

sume that these newts are colonizers from nearby ponds. Considering the small population sizes in neighbouring ponds it is unlikely that they would have supplied more than a few adult newts. We therefore argue that a breeding population became established in 1977. This makes the crested newt a rapid colonizer in this sandy habitat. Evidently some of the colonizers were adults. No data are available for juveniles that seem to be mainly responsible for dispersal in other amphibian species (Gill, 1978a,b; Berven & Grudzien, 1990). A similar rapid colonization of newly created ponds in an agricultural environment was reported by Lenders (1992). Within a year of construction all four newt species locally present (*T. alpestris*, *T. cristatus*, *T. helveticus* and *T. vulgaris*) had colonized a set of six ponds at distances of up to 300 m from an existing pond. All these species were present in all the dune ponds neighbouring the quarry, although *T. helveticus* was locally rare (Arntzen, 1986). *T. alpestris* was observed for the first time in the quarry in 1981. Joly & Miaud (1989) reported a remarkable breeding site fidelity for *T. alpestris*, that might explain its late arrival, but unfortunately no comparisons were made with other newt species. Crested newts may be found at distances of up to 800 m away from their breeding ponds (Simms, 1969; Viertel, 1976). Studying the colonization rate of a large number of newly created ponds it was found that all ponds colonized by the crested newt were situated within 1000 m from a locality known for the species (Laan & Verboom, 1990). Dispersal rate was estimated at an average of 1 km per year (Arntzen & Wallis, 1991). The fact that a large population increase can occur as in the quarry pond suggests that *T. cristatus* can be an opportunistic breeder and may forage and reproduce in new ponds given the opportunity and it suggests that the difficulties *T. cristatus* may have establishing itself in new habitats (see for example Hagström, 1980a) originate from its localized distribution rather than from poor colonizing abilities *per se*.

As illustrated by the data from 1980 (Fig. 2), four groups of aquatic crested newts could be recognized: adult males, adult females and two cohorts of immatures ('juveniles' and 'efts'). These were the same groups as Dolmen (1983a) identified in an extensive study on the population structure of this species in Norway. Hagström (1977, 1979), also working in Scandinavia, concentrated on the adult stages, as the belly patterns of most juveniles could not be used for unequivocal individual recognition. Compared to Swedish crested newts, juveniles from the study site appeared to have a more obvious ventral spotting, all showing a unique ventral pattern, although with varying degrees of distinctiveness (Fig. 3; cf. Hagström 1977 : Fig. 6).

With the possible exception of 1980, less attention was given to the sampling of juveniles compared to adults, explaining the relatively low calculated sampling efficiency for the former (Table 1). Three additional factors affecting sampling efficiency that apply more strongly to juveniles than to adults could be: (i) size - the small size of juveniles could make them more difficult to detect; (ii) behaviour - the juveniles may behave differently from the adults, for example they may avoid the shallow part of the pond where adults forage; (iii) aquatic mode - where it is known that adults are aquatic over most of the breeding season and beyond and hence do approximate a 'closed population', juveniles - mostly leading a terrestrial life (Hedlund, 1990) - may stay in the pond for a short while only, where recorded animals may

year of initial capture	no. of different specimens caught	year of recapture	age at year of recapture	estimated age in year of recapture <sup>a</sup>	no. of recaptures <sup>b</sup>	survival relative to previous year		estimated yearly survival rate
						observed	expected	
1979	40	1980	≤3	3	15 (22)	38%	57%	57%
		1981	≤4	4	9 (10)	23%	25%	45%
		1982	≤5	5	7 (10)	18%	26%	100%
		1983	≤6	6	3	8%	8%	30%
		1984	≤7	7	0	0%	0%	0%
1980	no recapture data due to our inability to individually recognize efts from their belly patterns							
	23 <sup>c</sup>	1981	2	2	9 (10)	6%	7%	7%
		1982	3	3	4 (6)	2%	3%	60%
		1983	4	4	2	1%	1%	33%
		1984	5	5	0	0%	0%	0%
	150 <sup>d</sup>	1981	2	2	9 (10)	6%	7%	7%
		1982	3	3	4 (6)	2%	3%	60%
		1983	4	4	2	1%	1%	33%
		1984	5	5	0	0%	0%	0%
	70	1981	≤4	3.5±0.5	21 (23)	30%	33%	33%
		1982	≤5	4.5±0.5	7 (10)	10%	15%	43%
		1983	≤6	5.5±0.5	7	10%	10%	70%
		1984	≤7	6.5±0.5	0	0%	0%	0%
1981	56 <sup>d</sup>	1982	2	2	17 (25)	30%	45%	45%
		1983	3	3	12	21%	21%	48%
		1984	4	4	0	0%	0%	0%
	153	1982	≤5	4±1	58 (85)	38%	56%	56%
		1983	≤6	5±1	38	25%	25%	45%
		1984	≤7	6±1	0	0%	0%	0%
1982	26 <sup>d</sup>	1983	2	2	4	15%	15%	15%
		1984	3	3	0	0%	0%	0%
	235	1983	≤6	4.5±1.5	104	44%	44%	44%
		1984	≤7	5.5±1.5	1	0%	0%	0%
1983	15 <sup>d</sup>	1984	2	2	0	0%	0%	0%
	201	1984	≤7	5±2	1	0%	0%	0%

TABLE 4. Survivorship of *Triturus cristatus* over a six year period. Notes: a, on the (substantiated) assumption that juveniles have age 1 and adults have age ≥2 in the year of initial capture (for details see text); b, number of recaptures expected when no animals escape detection are in parentheses; c, newly-metamorphosed newts (efts); d juveniles (efts excluded).

year of first capture	recaptured in subsequent year(s)		not recaptured in subsequent year(s)	
	males	females	males	females
1979	5	10	13	12
1980	8	14	24	24
1981	28	23	51	51
1982	30	40	85	80
1983	0	1	100	100
total	71	88	273	267

TABLE 5. Capture-recapture data for *Triturus cristatus*. No significant differences ( $P>0.05$ ) were found in capture-recapture rate applying a one-tailed *G*-test of independence (1983 sample too small for testing).

Country, area	<i>S</i>	method	reference
Sweden, Gothenburg	0.78	A	Hagström (1979)
United Kingdom (?)	0.42	?	Frazer (1983)
Germany, Westphalia	0.50	A	Glandt (1981)
France, Mayenne	0.65	B	Francillon-Vieillot <i>et al.</i> (1990)
Sweden, Öland	0.65	A	Hedlund (1990)

TABLE 6. Published rates of yearly survival (*S*) for adult *Triturus cristatus* as estimated from A, capture-recapture studies; B, age distribution (see survival curve in Amtzen & Hedlund, 1990: Fig. 3).

Country, area	$\hat{N}^a$	method	reference
Switzerland, Zurich	330±90	A <sup>b</sup>	Blankenhorn et al. (1969)
	415±14	A <sup>b</sup>	
Switzerland, canton of Zurich	500-1000	E	Escher (1972)
United Kingdom, Oxfordshire	93±36	A <sup>b</sup>	Bell (1979)
	30	B	
Sweden, Gothenburg	342±84 <sup>c</sup>	A	Hagström (1979)
France, Bourbon	482±78	A	Zuiderwijk (1980)
Germany, Westphalia	20-40	A <sup>b</sup>	Feldman (1981)
Germany, Münsterland	>60	C <sup>b</sup>	
France, Mayenne	462±129	A	Schoorl & Zuiderwijk (1981)
Germany, Münsterland	101±15 <sup>c</sup>	A	Glandt (1982)
	1	B	
	3	B	
United Kingdom, Bucks.	c. 140±13	A	Verrell & Halliday (1985)
United Kingdom, nr. Huntingdon	264±123	A	Cooke (1985)
	56±31	A	
France, Mayenne	40±5	A	Bouton (1986, pers. comm.)
	85±20	A	
	440±100	A	
France, Mayenne	126±21	A	Zuiderwijk & Sparreboom (1986)
Germany, Northrhine-Westphalia	111±8	A	Sinsch (1988)
England, Sussex	102	C,D	Beebee (1990)
Sweden, Öland	172±26 <sup>c</sup>	A	Hedlund (1990)
	<30	B?	
	75	B?	
	400	B?	

TABLE 7. Published population size estimates ( $\hat{N}$ ) for *Triturus cristatus*. Methods: A, capture-recapture; B, true census, exhaustive search; C, pond draining; D, funnel traps; E, unspecified. Notes: a, SE as published (in some papers SD is given instead of SE) or estimated from population data; b, juveniles not explicitly excluded; c, average over 4-6 consecutive yrs.

be replaced by unrecorded ones. Moreover, it could be argued that a sub-cohort of juveniles exists that escaped detection entirely, because of a fully terrestrial mode of life. If so, the real size of the juvenile population may well have been underestimated. The proportion made up by the terrestrial group is unknown, but it could be substantial. The observation that all juveniles recaptured at age 2 are recruits to the breeding population does not necessarily mean that *all* specimens of that age have sexually matured. What the data do tell us, though, is that if age 2 immatures existed, they were not aquatic but terrestrial.

Fig. 2 suggests that in 1980 about 50% of the newts had not reached adult size at the end of the second and start of the third year, and that only juveniles relatively successful in their phase of somatic growth matured at age 2. This is in line with Smith (1954) who stated that in optimum conditions, crested newts mature at age 2, more commonly at age 3, or at age 4 if the conditions are adverse. In Scandinavia maturation is also recorded at age 2 or 3 but in poor upland habitats they may not breed until they are at least four years of age (Dolmen, 1983a). Francillon-Vieillot *et al.* (1990) studying skeletal growth rings in a population of crested newts in central-western France, observed that a certain pattern of growth rings, which they associated with the onset of maturation, was present in newts of age 2 in 11 out of the 23 newts (48%) in which the pattern was observed; the remainder showed this feature at age 3 (48%) or at age 4 (4%). Accordingly, about half of the juvenile population of 1980 will have been breeding in 1981 for the first time, and almost all of the survivors

will have been breeding by 1982. Similarly, the eft of 1980, forming the juvenile cohort of 1981 ( $\hat{N} = 126$ ) will have contributed to the adult population size of 1982 and 1983 (Fig. 4). Assuming, for the sake of argument, a high yearly survival rate as for the adults ( $S = 49\%$ ), the cohort of 1979 estimated at 309 juveniles in 1980, would be reduced to approximately 150 in 1981 and to 75 by then fully mature specimens in 1982. The new cohort of 1980, estimated at 126 juveniles in 1981, would have contributed a further 60 specimens of which about half would have matured, giving a total explained population increase of about 100 specimens. Clearly, this does not fully explain the observed adult population size increase from 1981 and 1982 ( $\Delta\hat{N} = 177$ ). To account for the difference, we once more are forced to conclude that by restricting observations to the aquatic specimens the size of the juvenile population is underestimated.

The largest and the second largest juvenile cohorts observed were those of 1980 ( $\hat{N} = 309$ ) and 1981 ( $\hat{N} = 126$ ). These cohorts gave rise to the biggest observed adult population of  $\hat{N} = 335$  in 1982, for which in terms of reproduction, the basis was laid in 1979. This was the year after the first adult crested newts were observed and only two years after the pond had been enlarged.

The estimated annual survival rate for adults was around 49%. This is at the lower end of the range of published data (Table 6), when we exclude Frazer's (1983) estimate for which methodology and data are not specified. Juvenile survival is more variable (Table 4) and larval survival, as

indicated by juvenile recruitment, is simply erratic. We conclude that variation in the adult population among years was largely due to variation at those earlier life stages.

Absence of newts from the breeding population that could not be attributed to mortality was noted by Hagström (1979). With a sampling efficiency of averaging at 47%, this observation is of limited value since the large majority of gaps in the records can be explained by census oversights. With a sampling efficiency close to 100%, Hedlund's (1990) data are more informative. Over three different years she estimated the frequency of newts skipping breeding opportunities to average 14% (range 6% to 22%). We have found no such indications but admittedly, as in Hagström's study, sampling efficiency was inadequate to signify absence of newts at that level (see Gill, 1985, 1987; Nichols *et al.*, 1987).

With the data at hand a preliminary life table can be drawn up for *T. cristatus*. The fecundity part of the life table has been determined from dissection of females. Approximately 200 eggs are laid by an average adult female each year (published estimates range from 189 to 220: Hagström, 1980b; Arntzen & Hedlund, 1990; Hedlund 1990). Due to a highly unusual chromosome syndrome, 50% of the developing embryos die off at tail-bud stage (Macgregor & Horner, 1980). Mortality of the embryos in the field has not yet been studied as the eggs are deposited singly on aquatic vegetation all over the pond, but loss is bound to be substantial due to predation and oophagy (see below) and drying out of ponds. No data are available on the survival rate of larvae. In a Swedish population, Hedlund (1990) was able to estimate that out of all offspring 0.5% were recruited to the breeding population. With  $S_j$  at 22% it can be estimated by interpolation that, out of a single batch of eggs, on the average four to five larvae survive up to and including metamorphosis. This must be considered a minimum estimate because the survival rate for efts is likely to be lower than that for juveniles and two years (occasionally three years) may be required for an eft to become sexually mature (Francillon-Vieillot *et al.*, 1989; Arntzen & Hedlund, 1990). With  $S_j$  at 50% and one pair of newts per year giving rise to effectively a single adult, a net reproductive rate of unity is just maintained.

Of the twenty-six populations estimated for size that we could find in the literature (Table 7) eight are of equal size or larger than the quarry population in 1982. This overall picture, however, almost certainly is strongly biased towards the larger populations, that were singled out for the purpose of study. Indeed, to quantify a small population by capture-recapture, the most popular and most reliable method, is relatively labour intensive. Glandt (1982) and Sinsch (1988) remarked that some of the populations they studied were among the largest ones in the district. In typical crested newt ponds in Westphalia, Germany, population size was in the order of 20-40 individuals (Feldmann, 1981) and in only 3 out of 230 (1.3%) crested newt breeding sites was the observed number over a hundred. According to Bell (1979) the average population size of the crested newt is 10-20 individuals of reproductive age. Irregular inspection of the study pond and two newly created dune slacks in the remodelled quarry since 1984, including a capture-recapture study in 1992, indicated that the population of crested newts is more or less stable at 20-60 adult individuals.

In the five years following the colonization of the quarry

the crested newt developed a sizable population that subsequently collapsed to approximately modal size. No definition seems to be generally agreed upon when to call a colonization 'successful'. As in the case of man-mediated translocations, for such a claim the burden of proof is on the investigator (Dodd & Seigel, 1991) and we echo the call for long term monitoring to ascertain 'success'. With the survival of the newly established population at approximately modal size for a time span exceeding five times the minimum generation time of the species, the colonization of the quarry by the crested newt undoubtedly can be considered a success.

Few studies are long term. A population of crested newts studied by Glandt (1982) over four consecutive years was remarkably stable ( $\hat{N}$  ranging from 89-108). On the other hand, in two populations that were studied over a six year period a substantial year to year fluctuation in size was observed where  $\hat{N}$  ranged from 150-223 (Hedlund, 1990) and from 230 to 500 (Hagström, 1979), but the observed decline of the quarry population from 1983 to 1984 seems unprecedented. Two aspects of the decline require particular discussion: (i) the low recruitment in the population from the early eighties onwards, and (ii) the very low adult survival from 1983 to 1984. Considering the decline of the population from 1983 to 1984 it cannot be excluded that newts have been collected from the pond for purposes of research or trade. As we have shown, the sampling efficiency can be high in the shallow part of the pond. Another, perhaps more likely possibility is that adult newts died in their terrestrial habitat in the summer and autumn of 1983, being buried when the quarry was remodelled in an attempt to restore the quarry to the original dune habitat.

Considering the lack of recruitment, intensive predation on the pre-metamorphosis stages seems the most plausible explanation. The most sizable animal species in the pond apart from adult crested newts were three-spined sticklebacks (*Gasterosteus aculeatus*), introduced into the quarry pond in 1981. They feed on a wide variety of items (Wootton, 1976), including fish eggs and fish larvae and - presumably - crested newt eggs and hatchlings as well. Only indirect evidence is available suggesting a detrimental effects of the presence of fish on the occurrence of crested newts (Escher, 1972; Clausnitzer, 1983). A strong negative correlation between the presence of fish and the crested newt was found by Beebee (1985). 'Sticklebacks' as predators are named by Bell (1979) and Dolmen (1982), and ten-spined sticklebacks (*Pungitius pungitius*) by Cooke *et al.* (1980). Other potential predators on amphibian larvae in the quarry are the larvae of the dragonflies *Aeshna* sp., *Ischnura elegans* and *Libellula depressa* (Pritchard, 1965; Thompson, 1978; Askew, 1988).

The observed pattern of population development (Fig. 4) with no or little recruitment when adult number peaks suggests intraspecific density-dependent regulation of population size. A substantial spatial and temporal niche segregation is observed between the larval and adult stages of the crested newt (Griffiths & Mylotte, 1987; Dolmen, 1983b) suggesting that cannibalism is reduced, but, as in other studies (Crump, 1992), no estimates are available that quantify the effects of cannibalism on the level of the population. Occasional observations were made on crested newts (*T. cristatus*) adult and larvae, respectively, consuming the adults and larvae of smaller newt species (Hagström, 1971; Dolmen & Koksvik, 1983; Frazer, 1983). Inter- and intra-specific oophagy were

reported by Avery (1986) and Arntzen (1988), respectively. The occurrence of cannibalism is also reported in some closely related species, without information on the life stages involved (Terent'ev & Chernov, 1949) for *T. karelini*, or by adults on larvae in *T. dobrogicus* (Lac, 1957). In each of the other extensive studies on newt foraging, however, indications of cannibalism (excluding oophagy) are absent (Kühlhorn, 1959; Avery, 1968; Bruno, 1973; Pellantova, 1973; Diaz-Paniagua, 1980; Dolmen & Koksvik, 1983; Stoch & Dolce, 1985; Griffiths, 1986; Griffiths & Mylotte, 1987; Kuzmin, 1991). The fluctuations in the study population may not be controlled by predation and anthropogenic disturbances alone and our interpretation of the data has to be taken with reservation. Drought and other factors may also influence the dynamics of amphibian populations (Berven, 1990). In a long-term study in the southeastern United States juvenile recruitment in particular could be associated to drought, with pond drying being largely responsible for recruitment failures (Semlitsch, 1987; Pechmann *et al.*, 1989; 1991).

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## SHORT NOTES

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## MICROHABITAT PARTITIONING IN A MOUNTAIN LIZARD COMMUNITY IN JEBEL AKHDAR, OMAN

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Jebel Akhdar is the highest sector of the Hajar, a continuous mountain range extending from the Musandam peninsula to the easternmost tip of Arabia at Ras al Hadd. Jebel Akhdar, composed largely of eroded Permian to late Cretaceous limestones (Glennie *et al.*, 1974), extends for about 80 km in an east-west direction, and reaches a maximum elevation of 3009 m. The mountains are sufficiently high to induce orogenic rainfall, which allows the development of relatively dense vegetation cover at the higher elevations and in the valleys or wadis (Ghazanfar, 1991). Many wadis have some surface water for much of the year.

The lizard fauna of the mountains reflects these conditions, showing a typical pattern of mountain endemism and range restriction (Arnold & Gallagher, 1977; Arnold, 1987). The montane lizard fauna totals 14 species from four families: Lacertidae (2 species), Scincidae (2 species); Agamidae (1 species) and Gekkonidae (9 species). The lizard fauna of Jebel Akhdar has received little study other than descriptions of collections, though notes on lizard habits and habitats have been published for the more northerly sectors of the Hajar range (Arnold, 1972; Arnold & Gallagher, 1977; Arnold, 1977; Bischoff, 1989; Böhme & Leptien, 1990).

The study site, at the head of Wadi Halfayn is an eastward draining valley that cuts deeply into the limestone strata of the 2000 m high Saiq plateau. There is some permanent surface water in the upper reaches, and sub-surface flow supports a well developed wadi vegetation including moderate sized trees at lower elevations. The trees include *Ziziphus spina-*

*christi*, *Moringa peregrina*, *Acacia tortilis*, *Ficus salicifolia*, *Maerua crassifolia*, and *Acridocarpus orientalis*. The vegetation falls within the mountain wadi associations described by Mandaville (1977), and the hillsides immediately above the wadi bed belong to the *Acacia tortilis-Rhazya-Moringa* plant association (Ghazanfar, 1991). Eight species of lizards were encountered along a 3 km stretch of the wadi at altitudes of 700 m to 800 m. These were a large lacertid, *Lacerta jayakari*, a skink (*Mabuya tessellata*), three nocturnal geckos (*Asaccus elisae* sens. lat., *Ptyodactylus hasselquistii*, *Hemidactylus persicus*), and three species of diurnal geckos (*Pristurus rupestris*, *Pristurus gallagheri*, and *Pristurus celerrimus*). This paper reports a preliminary study of the habitat partition within this lizard community, particularly of the diurnal species.

Field observations were made on six days, at irregular intervals between November 1988 and August 1992 (21.11.1988; 12.12.1988, 7.7.1989; 28.8.1991, 28.2.1992, 24.8.1992), encompassing both summer and winter observations. Forty-two man hours of observations were made between 0600 and 1600 hrs. The location of each lizard on first sighting was recorded using the following pre-assigned microhabitat categories: substratum (ground; rock face; tree; cave), height above ground ( $\leq 0.5$  m;  $>0.5$  m and  $\leq 1.0$  m;  $>1.0$  m and  $\leq 2.0$  m;  $>2.0$  m), tree species (for arboreal sightings), sun or shade. Sightings were made by walking slowly up the valley with one observer on the wadi bed and the other on a disused drystone falaj (water conduit) about 5 m above the wadi bed on the northern side. No attempt was made to estimate relative abundance of the species. Rather, a range of different microhabitats were preferentially searched, so trees, caves and rock faces were searched with far greater intensity than the large areas of gravel and scree. The nocturnal species were found in their daytime retreats.

Table 1 summarises 285 lizard sightings. The data illustrate the clear microhabitat resource partitioning between the three *Pristurus* species. Based on these microhabitat categories, Levins' standardised niche breadth (Hurlbert, 1978) is 0.175 for *Pristurus rupestris*, 0.335 for *P. gallagheri* and 0.319 for *P. celerrimus*. Niche overlaps, calculated using Piankas' (1973) symmetrical formula, are very low between *P. rupestris* and *P. gallagheri* (0.110) and between *P. celerrimus* and *P. gallagheri* (0.020), and rather higher between *P. rupestris* and *P. celerrimus* (0.390). At this site, *P.*

lizard species	microhabitat category									
	ground	cave	rock base	low rock	mid rock	high rock	tree base	low tree	mid tree	high tree
<i>Pristurus rupestris</i> (106)	50.9	-	34.9	1.9	-	0.9	6.6	4.7	-	-
<i>Pristurus gallagheri</i> (101)	3.0	-	-	1.0	-	1.0	13.9	19.8	28.7	32.7
<i>Pristurus celerrimus</i> (16)	6.3	-	25.0	12.5	37.5	18.8	-	-	-	-
<i>Ptyodactylus hasselquistii</i> (30)	-	56.7	3.3	13.3	6.7	20.0	-	-	-	-
<i>Asaccus elisae</i> (19)	-	-	100.0	-	-	-	-	-	-	-
<i>Hemidactylus persicus</i> (2)	-	100.0	-	-	-	-	-	-	-	-
<i>Lacerta jayakari</i> (10)	70.0	-	10.0	-	-	10.0	-	-	10.0	-
<i>Mabuya tessellata</i> (1)	-	100.0	-	-	-	-	-	-	-	-

TABLE 1. Daytime microhabitat resource utilization by eight lizard species in Wadi Halfayn. The data represent the microhabitat category in which the lizard was first sighted, as percentages within each species. The total number of observations was 285. For the rock and tree categories, the following definitions apply: base  $\leq 0.5$  m; low  $>0.5$  m and  $\leq 1.0$  m; mid  $>1.0$  m and  $\leq 2.0$  m; high  $>2.0$  m above ground level. Sample size are given in parentheses.

*rupestris* is a rupicolous species found on the ground, gravel and scree and rarely venturing onto larger boulders, rock faces or trees. *P. gallagheri* is an arboreal species, very rarely seen outwith trees, while *P. celerrimus* is a gecko of cliff faces and large boulders.

Although low overlap in microhabitat use must greatly reduce competition in a community, one cannot reliably conclude that competition has been the causal factor in bringing about the observed resource utilization (e.g. Schoener, 1982, Pianka, 1986). However, the microhabitats used by two of these *Pristurus* species have been observed to vary over the species' ranges. Hence, over most of its range *P. rupestris* is usually encountered on rocks, stones and other hard objects (Arnold, 1977, 1980), but in the *Prosopis cineraria* woodlands bordering the Wahiba Sands, eastern Oman, this species is arboreal (Gallagher & Arnold, 1988). At this locality, *P. celerrimus* and *P. gallagheri* are not found, but the sandy substrate under the trees is home to *Pristurus minimus*. *P. celerrimus*, in the northern part of its range, as at Ruus al Jibal, appears to be less restricted to steep rock faces and may be found on rocky ground and scree. This lability in habitat use does suggest that the more restricted resource usage in the Wadi Halfayn community is likely to have arisen in order to reduce past or present competition. Ninety six individuals of *Pristurus gallagheri* were sighted in trees of the following species: *Moringa peregrina* (51.0%), *Ziziphus spina-christi* (21.9%), *Acacia tortilis* (17.7%), *Ficus salicifolia* (6.3%), *Maerua crassifolia* (2.1%), dead trees (1.0%). This apparently indicates a strong preference for *Moringa* which is far from being the commonest tree species, both *Ziziphus* and *Acacia* being much more abundant.

The majority of these sightings were of lizards on the trunk or a major branch facing head down on the shady side of the tree. The body was often held well off the bark and the geckos appeared to be highly alert. Ants were seen to be taken on occasion, with the gecko using a 'sit and wait' strategy until the ant approached within a few centimetres.

The observations of *Pristurus gallagheri* confirm the arboreal habit of this species, alluded to from the collection data for the type series (Arnold, 1977, 1986), and the similarity of its habits with those of its sister species, *Pristurus flavipunctatus* (Arnold, 1990).

*Lacerta jayakari* and *Mabuya tessellata* are basically ground dwellers, though both are able to climb agilely on rocks and drystone walling. *Asaccus elisae* sens. lat. and *Hemidactylus persicus* were only found in two small caves, and were presumably using these as daytime refuges. Both caves contained traditional egg laying sites, which appeared to have been used for many years. The only fresh gecko eggs were three pairs found in August 1991 and August 1992. Two heavily gravid *A. elisae* sens. lat. were observed in August 1992 in one cave. *Ptyodactylus hasselquistii* was usually found in caves and shady crevices, but some individuals were seen in the open, in deep shade on vertical cliffs at the edge of the wadi. These individuals did not appear to be active. This analysis of daytime microhabitats does not indicate differences in microhabitat utilization between the three nocturnal gecko species. These species are of approximately the same size and all have scansorial pads for climbing on rock faces. In order to determine their niche relationships, one would need to investigate other parameters such as microhabitat utilization

during the geckos' active periods, timings of activity, or dietary differences.

**Acknowledgements.** We would like to thank Shahina Ghazanfar for plant identifications, and Nick Arnold, Martin Fisher and Henk Strijbosch for helpful comments on the manuscript.

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# ON THE TAXONOMIC STATUS OF *HYLA CARINATA* ANDERSSON, 1938 (ANURA: HYLIDAE)

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Among the 32 species of the genus *Hyla* currently reported from Bolivia (De la Riva, 1990; Reynolds & Foster, 1992), several species are poorly known or have uncertain taxonomic status. This may be attributed to: (1) loss of the type specimen (*H. roeschmanni* De Grys, 1938); (2) erroneous type locality: species may come from other countries (*Hyla molitor* Schmidt, 1857); and (3) absence of information on the species since their descriptions (*H. albonigra* Nieden, 1923 [= *H. zebra* Duméril & Bibron, 1841]; *H. carinata* Andersson, 1938; *H. charazani* Vellard, 1970; *H. ocapia*, Andersson, 1938). The status of each of these species is under review. In this note, I deal with the case of *H. carinata*.

Since its description, *H. carinata* has only been mentioned in general catalogues (Duellman, 1977; Harding, 1983; Frost, 1985), but no further information is available on this species. Andersson (1938) described *Hyla carinata* based on three adult males which (according to Andersson) were collected by C. Hammarlund on 2 February, 1934, at San José, Tarraco, ca. 50 km W La Paz (Provincia Ingavi, Departamento La Paz, Bolivia [16°23'68"25']). This locality lies on the Altiplano (a high plateau ranging from S Peru to N Argentina) near Lake Titicaca, on the Andean mountains, at an elevation of 3800 m. Andersson provided a suitable description of the species and, among the characters he emphasized, were the increased ossification of the skull (with strong, broad frontoparietals, their margins forming a prominent ridge over tympanum), and the presence of two external vocal sacs. Based on these characters and Andersson's description alone (without reference to the type specimens), I discounted the possibility that *Hyla carinata* is a synonym of any other Bolivian hylid, although it seemed that it might be a member of the genus *Osteocephalus*. Andersson (1938) noted the similarity of his *H. carinata* to *H. taurina* and *H. planiceps* (= *Osteocephalus taurinus*). The lack of more recent data on *H. carinata* is puzzling because the area surrounding Lake Titicaca has been well collected. The only amphibians reported in the area are *Bufo spinulosus*, *Pleurodema cinereum*, *P. marmoratum*, *Telmatobius albiventris*, *T. culeus*, *T. marmoratus* and *Gastrotheca marsupiata*. *Hyla pulchella* occurs in the nearby valley of La Paz, but does not reach the Altiplano. I suspected that the type locality was erroneous, and *H. carinata* may be a lowland species.

Examination of the three syntypes (NHRM 1874) confirmed that they did not belong to any hylid known from Bolivia or its neighbouring countries. They showed some peculiar features such the presence of a dermal fold in the chest, a single very expandible bilobated vocal sac (not two vocal sacs, as Andersson reported) and a supratympanic bony ridge (not formed by the frontoparietal but by the squamosal). Such a combination of characters is characteristic of some species

of Hylidae of the genus *Smilisca* Cope (Duellman, 1970; Duellman & Trueb, 1966; Starrett, 1960), which occurs mainly in Middle America. Comparison of the syntypes of *H. carinata* with a large sample of *Smilisca phaeota* (Cope, 1862) in the collection at the University of Kansas (see Appendix 1) left little doubt about their identity. *Smilisca phaeota* occurs from Nicaragua to northeastern Colombia and Ecuador. Measurements, colour and pattern of the syntypes of *H. carinata* fall well within the range of variation reported by Duellman (1970) and Duellman & Trueb (1966) for *Smilisca phaeota*, a species showing little geographical variation in pattern. However, Duellman (1970), described differences in size in specimens from different areas. The mean snout-vent length in the three syntypes of *H. carinata* (56.6 mm after Andersson, 55.4 mm after personal observations) is similar to that of specimens of *S. phaeota* from the Chocoan region of Colombia (56.0 mm), which are presumably similar to those from Ecuador.

It seems odd that Andersson (1938) did not provide any data on activity or habitat of *H. carinata*, unlike other species collected by Hammarlund in Bolivia and quoted or described in the same paper. Data on several amphibians from western Colombia and Ecuador obtained by the same collector, are provided in Andersson's paper. I suggest, therefore that the specimens of *S. phaeota* described as *H. carinata* by Andersson (1938) were captured in one of these countries and that a mistake occurred in the cataloguing of the specimens. Thus, *Hyla carinata* Andersson, 1938, is a junior synonym of *Smilisca phaeota* (Cope, 1862) and it does not occur in Bolivia.

**Acknowledgments.** I am grateful to E. Ahlander and S. O. Kullander of the Naturhistoriska Rijkmuseet (NHRM) for loaning the syntypes of *H. carinata*. W. E. Duellman and L. Trueb provided space and facilities during my stay at The University of Kansas (KU). R. F. Inger provided useful comments in an early stage of this study. My trip to Kansas was financed by an aid from the Plan de Formación del Profesorado during my stay at the Universidad de Las Palmas de Gran Canaria.

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#### APPENDIX I

*Material examined:* *Hyla carinata*: SMNH 1874 (3 specimens); *Smilisca phaetota*: Columbia: KU 169614-19; 169621-26; 169628-33. Costa Rica: KU 25723-24; 32212-47; 32262-65; 36808-10; 37133-35; 37168; 64267-69. Ecuador: KU 142646; 146567-75; 146563-66; 164475-76.

### BOOK REVIEWS

*The Snakes of Iran.* Mahmoud Latifi (Translated by Sepideh Sajadian). (1991). 159pp. Society for the Study of Amphibians and Reptiles, Oxford, Ohio, USA. cloth: \$22.00

Dr. Latifi was prevented from final supervision of the original Pharsi edition (1985) due to the Iran/Iraq conflict. The finished product was almost certainly not as the author himself would have wished it and the English translation is not a new edition. The editorial supervisors, Alan E. Leviton and George R. Zug, state that they "have been faithful to the author's original manuscript". The corrections made on p.64 in collaboration with the author do not invalidate this claim and whereas the reader must judge if more could have perhaps been done I feel a fair balance has been struck.

The first of the two chapters deals with generalities about snakes. The zoogeographical discussion though interesting could with advantage have been amplified with statistics on climate and more detail on vegetation and forest types. The large number of snake species found in Iran is due precisely to the wide variety of ecosystems. The figures depicting morphology are explicit and well-drawn. Twenty-five pages are devoted to snake bite and related topics: venom characteristics, symptoms, first aid, after care. Here the author is clearly in his element. Dr. Latifi is a member of the International Society of Toxicology and sits on the consultative panel for Characterisation of Snake and Scorpion Venoms and Antivenoms of the WHO. Far-reaching research has been carried out at the Razi Institute in Tehran where Dr. Latifi is Director. I found this section the most absorbing of the whole book. *The Illustrated Guide to the Snakes of Iran* makes an attractive centrepiece. There are 22 colour plates depicting 65 taxa/morphs and accompanying maps. Distributions are colour coded: venomous land snakes red, rear-fanged orange, non venomous blue and sea snakes purple. The drawings vary in quality but those depicting sand boas, vipers and elapids are acceptably realistic. Colour photographs would have enhanced the presentation.

Chapter Two is prefaced with a b/w plate of the Iranian provinces and the species listed according to province. This gives such a clear picture that it seems wasteful to repeat all this in the text under "Species Distribution". Data on "habitat" is meagre. The author's personal records and observations on some 128,000 snakes over a 24 year period could have contributed much of value. Each species receives

a detailed diagnostic description which is as comprehensive as one could wish, though the figures on "size" are rather ambiguous. Mention is made of diet, reproduction and where relevant, locomotion.

The few complaints that I have are as follows. In the index the text *Eirenis* follows *Elaphe* but otherwise is placed at the end of the Aglypha. Within the Elapidae, Hydrophidae and Viperidae genera and species are listed alphabetically but this practice is not followed elsewhere and there is no logical order at all in the colour illustrations. An alphabetical system eliminates inconsistency and avoids hierarchal assumptions. The use of English names for certain species needs watching. *Coronella austriaca* (smooth snake) is called both wolf snake and leopard snake. *Coluber ravergeri* is also called leopard snake, the name commonly applied to *Elaphe situla*, not found in Iran. *Elaphe quatuorlineata* is called whip snake and all three *Telescopus* spp. vipers. English vernacular in the translation should have been checked against that in general usage. The statement on p.20 that the Zanjhani viper (*Vipera xanthina*) and the Iranian horned snake (*Pseudocerastes persicus*) belong exclusively to Iran is not corroborated on p.85. The condensing of information into lists is a sound notion but there is rather a lot of this. The snakes are "listed" in one form or another no fewer than eight times, four of which are virtual duplications.

Recent research necessitated the need to revise the author's taxonomy in a table of taxonomic equivalents. Sixty species have been increased to 70, partly accounted for by including *Hydrophis gracilis*, *H. lapemoides* and *Lapemis curtis* as possible strays in Iranian waters and allowing the revised nomenclature of certain *Coluber* spp. and snakes within the *V. xanthina* complex. Discussion is wisely avoided due to prevailing controversy and disagreement. Incorrect subspecific designations have been rectified but the inclusion of *Natrix n. natrix* is wrong: the form inhabiting Iran is *N. n. persa*.

The book is thoroughly researched with over 140 sources in the main bibliography and 39 in the editorial supplement and is good value at \$22, whatever the state of the pound. The print is bold, layout spacious with no feeling of visual claustrophobia. It reads so effortlessly that one soon forgets it is indeed a translation. Snakes of Iran, unique in being the only book dealing with Iranian herpetofauna, is indispensable to layman and specialist both as a sound reference source and field guide.

Richard Clark  
Arendal, Norway

*Encyclopedia of Australian Animals: Frogs.* Michael J. Tyler. (1992). 109 pp. Angus & Robertson, Pymble, NSW.

*Encyclopedia of Australian Animals: Reptiles.* Harald Ehmann. (1992). 495 pp. Angus & Robertson, Pymble, NSW.

Recent years have seen the publication of a number of authoritative and well-illustrated books dealing with the herpetofauna of Australia. These two volumes continue the tradition of combining high quality photographs with a scholarly text. Both books have arisen from the Australian

Museum's National Photographic Index of Australian Wildlife. In compiling this photographic collection, it was realised that the pictures could form the basis of natural history books of general interest. *Frogs* and *Reptiles* therefore form companion volumes to those dealing with *Birds* and *Mammals*, which together must form the most comprehensive photographic record of the Australian fauna ever assembled.

Both books comprise a brief introduction to zoological classification, and outline the system used to describe the distribution, abundance and status of each species listed. Although any scoring system for such parameters is open to errors of judgement and personal opinions, all too many books provide little or no information on the conservation status of the species concerned, and the inclusion of such a system is therefore to be welcomed. A further novelty is the inclusion of phonetic spellings to assist in the correct pronunciation of all scientific names, as well as a translation of the Latin or Greek species name.

The rest of the text presents each species in a systematic fashion, including a colour photograph, a couple of paragraphs of basic natural history, summary information on habitat, size, abundance and status, and a distribution map. Some of the common names are as colourful as the accompanying photographs (Booroolong Frog, Popplebonk and Tinkling Froglet were new ones on me!). Not every species described is illustrated, and the photographs vary in size with a few of the pictures in the *Reptiles* volume being rather small. However, the standard of photography is consistently high throughout both books. The volumes conclude with a breakdown of the orders, suborders, families and genera within the respective classes, a glossary, index, and a short list of further reading.

Once again Australia has produced two books which will be of interest to both the naturalist and research biologist. Both books serve to emphasize the astounding diversity of the Australian herpetofauna, and how little is known about many of its most enigmatic species. It is particularly fitting that they should be published shortly before the Second World Congress of Herpetology in Adelaide at the end of this year. If you are going to this meeting I can recommend no better reading to get you in the right mood. If you are not going, then these books may persuade you to change your mind.

Richard Griffiths  
University of Kent

## INDEX FOR THE HERPETOLOGICAL JOURNAL VOLUME 1

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2. Three copies of all submissions, and illustrations, should be sent to the Editor. All papers will be subject to peer review by at least two referees
3. Authors should consult a recent issue of the Journal regarding style. Papers should be concise with the minimum number of tables and illustrations. They should be written in English and spelling should be that of the *Oxford English Dictionary*. Papers should be typed or produced on a good-quality printer (at least near-letter quality, avoid worn ribbons), and double-spaced with wide margins all round. Typesetting is greatly assisted if accepted manuscripts can be supplied on microcomputer diskettes. Authors are therefore strongly encouraged to produce manuscripts using a wordprocessor (preferably on a PC-compatible microcomputer).
4. For all papers the title page should contain only the following: title of paper; name(s) of the author(s); address of the Institution where the work was done; a running title of 5 words or less. The text of the paper should begin on page 2 and be produced in the following order: Abstract, Text, Acknowledgements, References, Appendices. Full papers and reviews should have the main text divided into sections. Short notes (generally less than six manuscript pages and accompanied by a single data set) should be produced as continuous text. The first subhead will be centred in capitals, the second shouldered in lower case, and the third run on in italics. Footnotes are not permitted.
5. The usual rules of zoological nomenclature apply.
6. Tables are numbered in arabic numerals, e.g. Table 1; they should be typed double spaced on separate sheets with a title/short explanatory paragraph underneath.
7. Line drawings and photographs are numbered in sequence in arabic numerals, e.g. Fig. 1. Colour photographs can only

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

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

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

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

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

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

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

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