POPULATION ECOLOGY OF THE GREAT CRESTED NEWT (*TRITURUS CRISTATUS*) IN AN AGRICULTURAL LANDSCAPE: DYNAMICS, POND FIDELITY AND DISPERSAL

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Aspects of the population ecology of the great crested newt (*Triturus cristatus*) were studied over a period of seven years (1989-1995) in an agricultural landscape of the Drachenfelser Ländchen, south-west of Bonn, Germany. Seven ponds – three natural and four man-made – were monitored by drift fences and pitfall traps. The numbers of adults increased from 1992. The number of juvenile emigrants showed marked fluctuations between years at all ponds and in some years juvenile production failed completely at the temporary ponds. A total of 63% of the adult newts identified in 1994 at four sites were recaptured in the subsequent year. Ninety-nine percent of the newts recaptured returned to the place of the first capture. In contrast to the adults, a number of juvenile great crested newts moved to neighbouring ponds, migrating a maximum distance of 860 m within the year of metamorphosis. Two out of four artificially constructed ponds were colonized naturally.

Keywords: population ecology, pond fidelity, dispersal, colonization, *Triturus cristatus*

INTRODUCTION

The great crested newt can be found in most parts of central Europe (Arntzen & Borkin, 1997). Throughout its wide distribution it is regarded as an endangered species and it is legally protected in Germany and across Europe (Corbett, 1994; Beutler *et al*., 1998). The decline of the great crested newt is mainly a result of the loss of suitable ponds for breeding, the destruction of the terrestrial habitat, the fragmentation of landscape and the introduction of modern farming methods in agricultural areas (Beebee, 1975; Feldmann, 1981, Grosse & Günther, 1996).

Other studies available on the population ecology of great crested newts or other members of the *cristatus* super-species have covered periods ranging from one season up to ten years (e.g. Hagström, 1979; Blab & Blab, 1981; Glandt, 1982; Verrell & Halliday, 1985; Arntzen & Teunis, 1993; Cooke, 1995; Ellinger & Jehle, 1997, Baker, 1999). However, most studies have been carried out only at a single breeding site, and in most cases the emigration of juvenile newts after metamorphosis has not been reported. The aim of the present paper is to give an overview of the dynamics of neighbouring local populations of the great crested newt over a period of seven years. Capture-mark-recapture methods have been used to investigate possible movements of adult individuals between the ponds. Further aspects of the study were the dispersal behaviour of juveniles and the colonization of newly-created ponds.

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MATERIAL AND METHODS

SITE DESCRIPTION

Research was carried out continuously from 1988 to 1995 within a 4 km^2 area south-west of Bonn (North Rhine-Westfalia, Germany, Central Europe), located within a mosaic of farmland, urban areas and patches of forest (Schäfer & Kneitz, 1993, Kneitz, 1998). The climatic conditions of the study area are sub-Atlantic, with an average air temperature of 7.8 ° to 8.5 ° C and an annual precipitation between 600 mm and 650 mm. Usually, the winters are mild and humid. Most of the summers are hot and dry.

During the research, seven ponds were studied (Fig. 1); three ponds were natural (ponds 1 to 3) and four were created artificially in 1988 (ponds A to D). The older sites had maximum areas between 200 m^2 and 1200 m^2 and their water levels fluctuated greatly. The areas of newly created sites ranged from 64 m^2 to 80 m^2 and their water levels were more stable, owing to the plastic liners that were used in their construction. The distances between neighbouring ponds ranged from 430 m to 1940 m (Table 1).

Great crested newts shared their breeding sites with smooth newts (*Triturus vulgaris*), alpine newts (*T. alpestris*), agile frogs (*Rana dalmatina*), common frogs (*R. temporaria*), common toads (*Bufo bufo*) and pool frogs (*Rana lessonae* / *R.* kl. *esculenta*).

Great crested newts were present in all of the older sites at the beginning of the study, in 1989; however, the population at pond 2 consisted of only a few individuals (Schäfer, 1993). To augment this population at site 2, ten adult specimens were released in spring 1992. At site C, six adults were introduced in spring

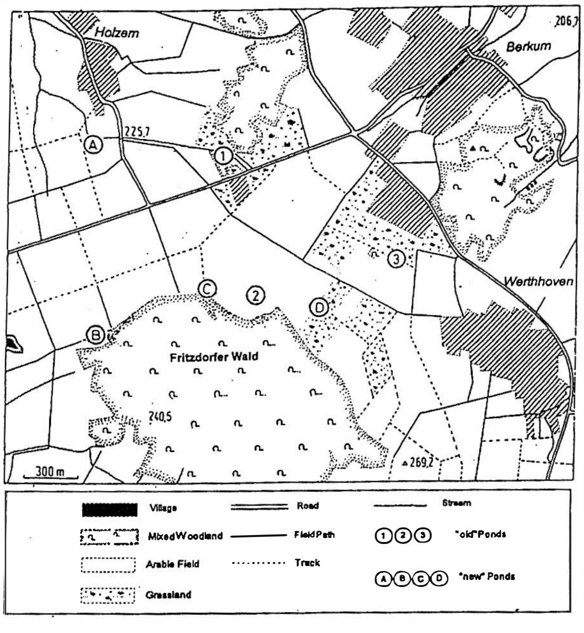

FIG. 1. Map illustrating the structure of the study area and the locations of the ponds.

1991 to establish a population. The donor-site for both these introductions was a clay pit 3.5 km distant (for further details see Schäfer, 1993).

POPULATION MONITORING

All migrating amphibians at the seven study ponds were monitored by a drift fence and pitfall system. The ponds were encircled by drift fences, 70 cm in height, consisting of plastic-covered metal gauze (Fig. 2). About 30 cm of the fence was buried in the ground and a plastic gutter was placed on its top to prevent newts from climbing over the fence undetected. On both sides of the fence, 35 cm deep plastic buckets (80 l capacity) were sunk into the ground at five-metre intervals. The edge of every bucket was taped with a plastic strip to prevent the newts from escaping (for further details see Kneitz 1998). The fence efficiency (FE) for great crested newts was estimated in 1995, both for immigration (FEi) and emigration (FEo), using the Lincoln Index (Table 2). Fence efficiency was defined as the percentage of the population approaching the fence which was caught in the pitfalls (for methodology see Arntzen, Oldham & Latham, 1995). For adults the FEi varied between 67 % (pond 2) and 100 % (pond C), while FEo varied between 32 % (pond 1) and 83 % (pond C).

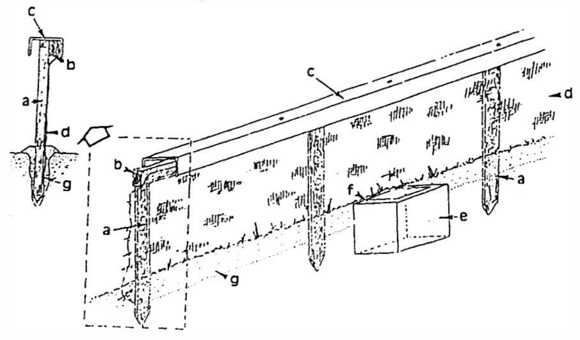

FIG. 2. Schematic representation of the drift fence/pitfall system at the ponds: a, post; b, gutter; c, plastic gutter; d, drift fence; e, pitfall trap; f, plastic tape; g, buried drift fence.

To investigate the emigration of juvenile amphibians at pond 2, a different type of terrestrial trap was used in the summers of 1994 and 1995. The trap consisted of two flower boxes (98 x 14 x 16 cm each) with a fence, 50 cm high, fixed at the back of the boxes in the direction of emigration. The edge of every box was taped with a plastic strip to prevent animals from escaping. The terrestrial traps were sunk into the ground of the surrounding fields at distances of 10 m to 110 m from the edge of pond 2 (Fig. 3). Terrestrial traps were also placed at the edge of the forest. These traps consisted of two buckets, as described above, at the centre of a radial array of four 5 m-long drift fences (Hartung & Glandt, 1988, see Kneitz, 1998 for further details).

All pitfall traps were checked for animals daily in the morning hours (Kneitz, 1998). The trapping systems at the ponds and in the forest were erected in summer

TABLE 1. Description of pond parameters. Terrestrial habitat types found within 100m of the pond were identified: 1, arable farm land; 2, pasture farm land; 3, mixed wood; 4, deciduous wood; 5, scrub; 6, garden.

Pond	Maximum area (m²)	Maximum depth (m)	Scrub cover	Open water	Terrestrial habitat	Inter-pond distance, mean and range (m)
1	1200	1.5	high	80%	2, 3, 6	995 (700-1220)
2	450	1.2	low	30%	1, 5	773 (300-1200)
3	200	0.9	moderate	30%	1, 2, 5	1242 (530-1850)
A	80	0.9	low	25%	1, 5	1315 (730-1940)
B	64	1	moderate	40%	4, 5	1215 (710-1340)
C	64	1	moderate	40%	1, 3	795 (300-1140)
D	64	1.2	low	40%	1, 2	1007 (430-1940)

TABLE 2. Estimated fence efficiencies for drift fences used at four study ponds in 1995, with 95% confidence intervals.

Pond	Estimated fence efficiency (%) immigration	emigration
1	81 (71-91)	32 (19-44)
2	67 (53-80)	46 (26-67)
3	94 (88-100)	76 (71-82)
C	100 (100)	83 (100)

1988 and were removed in December 1995 (Schäfer, 1993; Kneitz, 1998). The terrestrial traps used near pond 2 were set up on 1 June 1994 and dismantled on 24 October 1994. In 1995 the traps were used from 15 June to 3 August and from 1 October to 30 November.

To monitor movements of newts between the ponds, adult newts at sites 1, 2, 3 and C were identified by their individual belly patterns in 1994 and 1995 (e.g. Hagström, 1973). The pattern was recorded photographically (Minolta X 700, Metz CT-4 flashlight). The juveniles at sites 1 and 2 were marked by toe clipping during the emergence of newly-metamorphosed newts in 1994 and 1995 (August and September). Two toes were clipped in each animal and the code used identified the pond and the direction of emergence. We were able to identify marked animals up to the spring immigration of the following year. In some cases the regenerated toes were still recognizable in the summer. The captured animals were released subsequently to the marking procedures on the opposite side of the fence to that on which they were captured.

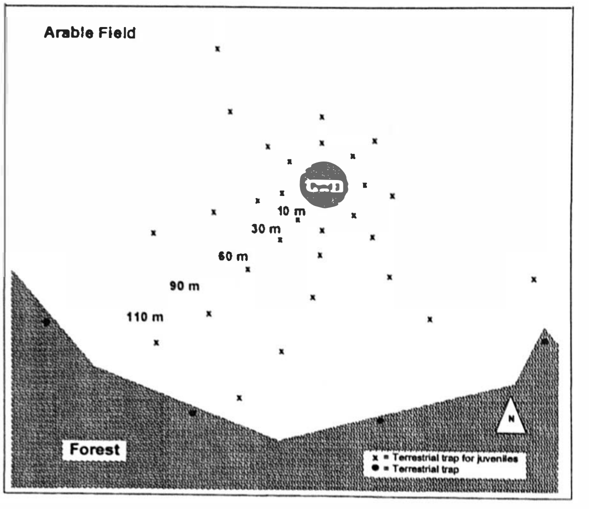

FIG. 3. Map of the pitfall system applied to monitor emigrating juveniles at pond 2 in 1994 and 1995.

To check for the presence and breeding activity of great crested newts in the years following the removal of the drift fences, the seven ponds were searched for eggs from April to June in 1996 and 1997.

TABLE 3. Population sizes of *Triturus cristatus* at four neighbouring breeding sites from 1989 to 1995 (data from January 1989 to June 1992 obtained from Schäfer, 1993). The sizes are presented as the numbers of immigrating adults and sub-adults and the numbers of emerging juveniles. The mean juvenile production per female is defined as the number of emigrating juveniles divided by the number of reproductive females.

	Pond 1						Pond 2					
Year	Males	Females	Total	Subadults	Juvs	Juv/Fem	Males	Females	Total	Subadults	Juvs	Juv/Fem
1989	11	15	26	1	133	8.9	-	-	-	-	-	-
1990	13	20	33	4	55	2.75	-	-	-	-	-	-
1991	14	20	34	6	164	8.2	-	-	-	-	-	-
1992	23	43	66	21	26	0.6	6	4	10	-	112	28
1993	43	32	75	5	3	0.1	1	2	3	1	32	16
1994	44	53	97	-	106	2	13	15	28	-	176	11.7
1995	36	55	91	12	13	0.4	15	11	26	3	43	4.7

	Pond 3						Pond C					
Year	Males	Females	Total	Subadults	Juvs	Juv/Fem	Males	Females	Total	Subadults	Juvs	Juv/Fem
1989	1	2	3	-	17	8.5	-	-	-	-	-	-
1990	2	3	5	-	-	-	-	-	-	-	-	-
1991	3	4	7	-	-	-	3	3	6	-	23	7.6
1992	1	1	2	-	53	53	2	3	5	-	40	13.3
1993	1	1	2	3	-	-	3	1	4	-	-	-
1994	6	2	8	1	1	0.5	1	1	2	2	-	-
1995	6	10	16	-	-	-	2	4	6	-	-	-

TABLE 4. Capture and recapture data for adult *Triturus cristatus* in 1994 and 1995. The belly patterns of 132 out of 135 newts immigrating in spring were recorded photographically. Only one adult female was recorded at a different site in the second year (at pond C instead of pond 3).

	Pond 1			Pond 2		
	captures (1994)	recaptures (1995)	%	captures (1994)	recaptures (1995)	%
males	35	23	66	11	9	82
females	49	32	65	12	5	42
total	84	55	66	23	14	61
	Pond 3			**Pond C**		
	captures (1994)	recaptures (1995)	%	captures (1994)	recaptures (1995)	%
males	10	5	50	-	-	-
females	13	7	54	2	2	100
total	23	12	52	2	2	100

RESULTS

POPULATION STRUCTURES AND DYNAMICS

The largest number of adult great crested newts was found at site 1 (Table 3). Adult numbers increased from 26 at the beginning of the study to 97 individuals in 1994 (mean=60±11). Numbers of newly-metamorphosed juveniles fluctuated from year to year (Table 3): the greatest number was observed in 1991, followed by a sharp decrease in 1993. An increase in the number of new juveniles emerging was always followed by an increased number of adult newts two years later. Sub-adult newts were encountered almost every year when a large number of juveniles had left the pond the previous year.

Since the introduction of great crested newts in 1992 a moderate number of adult crested newts was found at site 2 (mean=17±6). From 1992 to 1995 the adult part of the population increased from 10 to 28 individuals. As in pond 1, juvenile newts showed marked fluctuations in numbers, with peaks in 1992 and 1994 and lower numbers in 1993 and 1995.

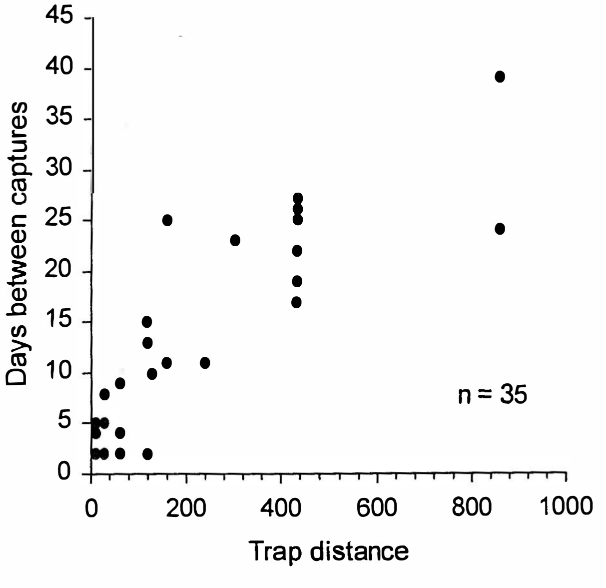

FIG. 4. The relationship between the distance between traps (m) and the number of days between captures.

Small numbers of adults were observed at pond 3 and in the seven years of study juveniles emerged only in 1989 (*n*=17), 1992 (*n*=53) and 1994 (*n*=1); in other years juvenile recruitment failed completely. At pond C we found no adults before six were introduced, in 1991. Twenty-three juveniles were produced in 1991 and 40 the following year, but no juveniles were produced in the years 1993-1995.

The yearly mean number of juveniles per female ranged from zero to about nine juveniles per female at pond 1 (Table 2). The highest values observed at ponds 2, 3 and C all occurred in 1992 (> 10 juveniles per female); this was the most successful year in terms of juvenile recruitment at ponds 3 and C, in the run of seven years. We found no significant correlation between the numbers of immigrating females and emigrating juveniles.

CAPTURE AND RECAPTURE OF ADULT NEWTS

Of 132 adults individually identified by their belly patterns in 1994, 83 (i.e. 63 %) were identified in the subsequent year (Table 4). Eighty-two newts returned

TABLE 5. Presence of *Triturus cristatus* at two newly-created ponds, B and D, from 1989 to 1997; ad, adult; sub, sub-adult; juv, juvenile; –, great crested newts not present.

year	Pond B	Pond D
1989	-	-
1990	-	-
1991	-	-
1992	-	1 juv
1993	-	-
1994	-	8 juv
1995	1 ad., 1 sub.	1 ad., 8 sub.
1996	eggs	eggs
1997	eggs	eggs

to the pond of their first capture, while only one adult female was recorded at a different site (pond C instead of pond 3). A total of 70 newts were recaptured entering the pond during the spring immigration. Thirteen newts were recaptured elsewhere and at different times of year. Of the latter, four animals were captured near the ponds, but did not enter them; three animals were not recorded at the breeding site in spring, but entered the ponds in autumn; six animals were found only in the inner traps of the drift fence in summer 1994 and may have hibernated in the ponds or passed the drift fence undetected.

DISPERSAL OF JUVENILES AND COLONIZATION

Of 176 juveniles marked at pond 2 in 1994, a total of 35 were recaptured in traps at distances ranging from 10 m to 860 m. Seventeen newts were caught in terrestrial traps in the surrounding field between 10 m and 60 m from the pond after an average of four days. Seven juveniles were captured in traps at the edge of the forest at distances from 120 m to 240 m after an average of 11 days. Thirteen juveniles were captured in the outer traps of the neighbouring ponds (ponds C, D and 3) at distances of 300 m to 860 m after an average of 23 days. The maximum distance travelled away from the natal pond was 860 m (to pond 3). There was a significant positive correlation between the trap distance (second capture of a juvenile newt in a terrestrial trap after moving away from the pond) and the days between captures (r=0.872, P<0.0001; Fig. 4).

At pond D, one juvenile great crested newt was caught in 1992 and eight juveniles were caught in 1994; subsequently, between 8 August and 9 September 1995, nine animals were captured by drift fences (Table 5). Of the latter, one newt was an adult male (SVL=73 mm), five animals were identified as subadult males (SVL=65.4 ± 5 mm) and three as sub-adult females (SVL=66.7±2 mm). In 1996 and 1997 breeding activity was confirmed by the presence of eggs at the pond (Table 5).

In 1995, one female great crested newt was captured at Site B during the spring immigration (4 April) and again during the emigration (14 September). A subadult male (SVL=60 mm) was captured on 27 October. In 1996 and 1997 eggs were found at pond B, indicating breeding activity at this site.

Site A was monitored together with the other ponds from 1989 to 1997. Throughout this period there was no record of great crested newts at all. This site was not colonized by this species.

DISCUSSION

In accordance with previous work by several authors (e.g. Gill, 1978; Blab & Blab, 1981; von Lindeiner, 1992; Schäfer, 1993; Griffiths, 1996), the population sizes are presented in terms of estimated numbers of immigrating adults and subadults and emigrating juveniles. The drift fence system used at the ponds during the course of the study captured immigrating *Triturus cristatus* quite effectively. It was estimated that 67-100 % of the breeding population was trapped during the immigration. This relatively high value may be compared with the data on the Danube crested newt at Donauinsel near Vienna (see the comparison of fence efficiencies in Arntzen, Oldham & Latham, 1995). However, the fence efficiency during the emigration was much lower (32-83%). The possibility cannot be excluded that newts either circumvented the fences or hibernated within the fenced area. Another explanation for a lower apparent fence efficiency might be a higher mortality of adult animals in the course of the breeding season. The actual mortality was not analysed in the present study.

The neighbouring populations revealed fluctuations in the numbers of adults and juveniles. In general the trend was towards an increase in numbers of adults. The largest population of great crested newts, at pond 1, increased from 26 individuals in 1989 to 97 in 1994. The increase might indicate the successful recruitment of newly-matured newts, following a series of years of sustained production of juveniles. Similar dynamic processes within the adult component of a population had been observed at other long term studies on *Triturus cristatus* around Europe (Hagström, 1979; Blab & Blab, 1981; Glandt, 1982; Arntzen & Teunis, 1993; Baker, 1999). In Westfalia, for example, the adult population size remained fairly stable during the course of four years, at between 89 and 108 individuals (Glandt, 1982). In other cases the adult population size underwent heavy fluctuations: in north-west France the population size ranged from 16 to 346 individuals (Arntzen & Teunis, 1993) and in England the population size varied between 67 and 242 individuals (Baker, 1999).

Massive fluctuations in juvenile recruitment were observed at all four ponds where breeding occurred. The two larger ponds produced juveniles almost every year, the smaller ponds 3 and C frequently had no juvenile recruitment. Although they might have suffered from the failure to produce metamorphosed juveniles, neither of the smaller populations became extinct during the study period. A possible cause for the lack of juveniles at pond 3 was the lowering of the water level in the summer months, and the consequent failure of newt larvae to complete metamorphosis The pond drying process is not uncommon, leading to a loss of a juvenile production in many amphibian species that breed in ponds (Berven, 1990; Pechmann *et al*., 1989). The failure in juvenile recruitment at pond C following the introduction in 1992 may have been associated with high predation by numerous dragonfly larvae (*Aeshna cyanea*) and diving beetles (*Dytiscus marginalis*). Declines in juveniles of other syntopic amphibian species at the pond were observed prior to the introduction (Kneitz, 1998).

Eighty-three adults (63%) of 132 adults captured in 1994 were recaptured in 1995 and identified by their belly patterns. All adults except one female were recaptured at the same ponds in which they had first been captured. This suggests strongly that the movement of adult individuals between the ponds was rare between 1994 and 1995. The failure to move to other ponds may have been a function of the distance between ponds and the structure of the area. The ponds were located within an agricultural landscape at distances of not less than 300 m apart and pond 1, which held the largest local population of *Triturus cristatus*, was potentially isolated by a frequently-used road. Nevertheless, homing experiments by Blab (1978) and Müllner (1991) on adults of *Triturus cristatus* indicated an ability to move up to 800 m to a breeding site after being displaced during the breeding season. Other studies on breeding populations of great crested newts in France (Miaud, Joly & Castanet, 1993) and Germany (Wenzel, Jagla & Henle, 1995) indicated an exchange of adult individuals within the breeding season. However, these sites were located within 100 m of each other and the habitat between the ponds was suitable for newts. In contrast to the latter studies, the adult newts in our study expressed a high fidelity for their breeding pond.

In contrast to the adults, recently-metamorphosed great crested newts moved to neighbouring ponds up to 860 m away within a year of metamorphosis. The dispersal distance fits well with the presumed genetic dispersal rate of 1 km per year in a moving hybrid zone of *Triturus cristatus* and *T. marmoratus* in western France published by Arntzen & Wallis (1991). Pond D was probably first colonized effectively by juvenile newts in 1994. Given the pattern of production of juveniles in 1994 (Table 3), it is likely that the colonizers came from pond 2, 430 m away (Fig. 1). Sub-adult newts were recorded at pond D in 1995, and in 1996 and 1997 breeding activity was evidenced through egg counts. However, it was not possible to prove that the newts captured as juveniles in 1992 and 1994 were the breeders of 1996.

Although there are studies available on the colonization of newly-created ponds by great crested newts, it is not clear whether juveniles are the first animals to enter new ponds. For example, in a long-term study on the Danube crested newt, individuals entered two ponds at distances of 200 m and 700 m from the pond of emergence (Greßler, 1997). In Vienna, newly created ponds were colonized after at least two years. In another case study, in Britain, farm ponds were colonized at distances of up to 400 m from existing ponds (Baker & Halliday, 1999). Lenders (1996) recorded adult great crested newts colonizing ponds in the Netherlands in the first year after construction, within distances of 100 m.

In the present study the creation of new breeding habitats seemed a success for great crested newts. Two of the four newly-created habitats were used as breeding sites. However, the first immigrating great crested newts were found after three years (pond D) and six years (pond B). The relative success of colonization was confirmed by means of egg counts after seven years at both sites. A more precise method of measuring successful recruitment should be obtained by quantifying metamorphosing juveniles.

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