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Delineation of terrestrial reserves for amphibians: post-breeding migrations of Italian crested newts (*Triturus c. carnifex*) at high altitude

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Abstract

Little is known about the terrestrial phase of high-altitude populations of European amphibians, in spite of potentially important implications for conservation and management. We followed 51 adult Italian crested newts (*Triturus carnifex*) that emigrated from an ephemeral lake (Lake Ameisensee, 1282 m a.s.l., Northern Calcareous Alps, Austria) with radio-tracking. Transmitters were inserted into each newt's stomach and we collected data until it did not relocate for more than 1 week or until the transmitter was regurgitated. Most newts migrated in a north-westerly direction towards an old growth spruce forest. Subterranean shelters, mostly 5–80 cm deep burrows of small mammals located 13–293 m from the lake, were reached in between 4 h and 7.8 days. Twenty percent of *T. carnifex* shared their refuges with other congeneric species. Females migrated significantly further (median distance 168 m) than males (median 53 m). We propose a terrestrial core reserve extending 100 m from the furthermost terrestrial refuges of newts found with radio-tracking linked with patches of old-growth forest. This terrestrial reserve is substantially larger than has been suggested as sufficient in the recent literature.

Keywords: Amphibian conservation; Terrestrial reserve; Migration; Telemetry; Urodeles

1. Introduction

More fundamental information on life-history requirements, habitat use and dispersal behaviour is necessary for conservation and recovery efforts of pond-breeding amphibians (Semlitsch, 2002). At low altitude regions of central Europe, they are confronted with habitat loss and ecological changes through intense agriculture, urbanisation, and pollution (Beebee, 1996). Most elevated alpine regions are less densely populated by humans, but are still affected by different forms of land use such as the construction of logging roads, clear-cutting, skiing or cattle grazing. Timber harvest has generally become easier at higher altitude through the use of heavy vehicles, helicopters and winches.

Conservation-directed research on amphibians is increasingly focusing on the terrestrial habitat, where our ecological understanding does not yet match the knowledge available for the aquatic phase. Nevertheless, only a few studies have addressed the delineation of protected areas around amphibian breeding sites in which any alteration of the natural habitat is prohibited by law. Semlitsch (1998) calculated terrestrial "buffer zones" for protecting various species of *Ambystoma* based on the upper 95% confidence limit of average migration distances, but Dodd and Cade (1998) pointed out that drawing circles around the breeding site does not account for directional components of migrations. For the protection of California red-legged frogs (*Rana aurora draytonii*), Bulger et al. (2003)

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proposed retaining suitable habitats within at least 100 m of occupied aquatic sites.

High-altitude populations of European newts (genus *Triturus*) differ markedly from conspecific lowland populations in life-history traits such as growth and longevity, pond presence and breeding phenology (Miaud et al., 2000). Owing to the flow of water in inclined areas and the rockier terrain, naturally occurring breeding ponds are often less abundant and/or less evenly dispersed in alpine landscapes than for example in river floodplains. Nevertheless, quantitative data on terrestrial migrations at high altitude sites are so far mostly lacking, a striking fact as pond connectivity is an important determinant for risk of population extinction (Halley et al., 1996; Griffiths and Williams, 2000; Joly et al., 2000; Marsh and Trenham, 2001).

The Italian crested newt (*T. carnifex*) has a disjunct distribution, with the subspecies *T. c. carnifex* ranging from the Alps to the Apennines, and *T. c. macedonicus* covering southern parts of the Balcany. North and east of the Alps, *T. carnifex* forms parapatric contact zones with all three other crested newt species (*T. cristatus, T dobrogicus, T karelini*), but always occupies the comparatively higher elevations up to 1500 m altitude (Arntzen, 2003). Populations are low in numbers and genetically differentiated from Apennine populations (Arntzen, 2001), and therefore deserve particular conservation attention.

The technique of radio-telemetry has so far yielded little insight into migration patterns of amphibians at rather remote, high-elevation sites (but see Matthews and Pope, 1999; Piliod et al., 2002). Moreover, despite its decade-long use for frogs and toads, radio-tracking has only recently been applied to urodele amphibians due to difficulties in attaching the transmitters (Madison, 1997; Madison and Farrand, 1998; Jehle, 2000; Jehle and Arntzen, 2000; Riberon and Miaud, 2000; Stöfer and Schneeweiss, 2001; Trenham, 2001). Given their relatively small size and use of burrows and small crevices, the external placement of transmitters is not possible. If carefully performed, surgical implantation is a suitable procedure for permanently attaching radio transmitters to members of the genus *Triturus* (Jehle and Arntzen, 2000; C. Jakob, unpublished), but potential detrimental long-term effects have not been investigated. Because of the conservation status of the studied species, we avoided surgery and inserted radio transmitters into the stomach (see Oldham and Swan, 1992, for anurans).

The aims of the present study are to (1) test the practicality of inserting transmitters into the stomachs of newts under field conditions, (2) delineate a protected area surrounding amphibian breeding sites based on radio-tracking data, and to provide management recommendations for central European high-altitude amphibians based on radio-tracking, (3) document migration pathways of *T. carnifex* when leaving a reproductive site at the upper elevational range of the species, (4) compare the obtained migratory patterns with previous findings from similar studies on a closely related species in lowland areas of western France (Jehle and Arntzen, 2000; Jehle, 2000).

2. Methods

2.1. Study area

Ameisensee is a periodically flooded lake (North-Eastern Calcarious Alps, Austria; 47° 33.27′ N, 13° 27.83′ E; 1282 m a.s.l.) lying adjacent to a 500 m^2 large wetland surrounded by an old growth spruce forest (*Picea abies*), offering a high structural diversity of microhabitats (small bogs, boulder fields, fallen timber, clearings, rich undergrowth, small mammal burrows). A gravel road passes 40 m SW of the lake, bordering extensive alpine pasture used for cattle grazing during summer and leading into a ski resort 0.5 km east. Each April–May, the basin fills with melting snow entering from creeks in the S and SW and through numerous small inflows from the meadow. In 2000 and 2001, the lake reached a maximum area of 100×35 m and a maximum depth of 4.1 m, and dried out in November and August, respectively. During the peak breeding season of newts, Ameisensee was inhabited by 300–800 adult *T. carnifex*, 1000–7000 alpine newts (*T. alpestris*), and 1500–2500 common newts (*T. vulgaris*) (A. Maletzky, unpublished data), as well as populations of the common frog (*Rana temporaria*), common toad (*Bufo bufo*, Schabetsberger et al., 2000) and the yellow-bellied toad (*Bombina variegata*). The population of *T. carnifex* in Ameisensee is among the largest and highest populations known from the Alps (Cabela et al., 2001), with the next known breeding site 23 km away (M. Kyek, pers. comm.).

2.2. Newt capture and insertion of transmitters

The study was conducted in two consecutive years (2000 and 2001). Shortly before the onset of emigration from the lake after the breeding period, *T. carnifex* that had started to change into their terrestrial phase (rough skin) were caught by dip netting or snorkeling in shallow shoreline regions. They were transported to a climate chamber at the University of Salzburg (12 °C) and kept in a terrarium (60×40×20 cm) at a light–dark rhythm of 16:8 h (darkness 21:00–05:00 local time). Mosses, stones and rotten wood were provided for shelter, and mealworms were provided for food. Animals were held captive between 1 and 2 weeks, to ensure that they had completely changed over to their terrestrial phase.

For transmitter insertion, newts were returned to the study site and anaesthetised in a solution of MS 222 for 10–20 min. Snout-vent length (2000, 2001) and body weight (2001) were determined. Body weights of animals caught in 2000 were calculated from a length–weight regression. Three types of transmitters were used, all with an internal helix antenna: Holohil Systems Limited model LB-2 (weight: 0.48–0.57 g, battery life: 8–21 days), BD2A (weight: 0.69–0.78 g, battery life: 25–35 days) and BD-2G (weight: 1.19 g, battery life: 9 weeks or more). In 2001 only type BD-2A transmitters were employed. Transmitters were cleaned, inserted into the mouth and gently pushed down into the oesophagus with a rounded plastic stick (4 mm diameter), and positioned in the stomach by gentle pressure from outside.

2.3. Radio-tracking and data collection

After recovery from anesthesia, approximately equal numbers of female and male newts were released at dusk on the same day (18:00–21:00), at two points west (point A) and north (point B) of the lake where most emigrating newts were observed (Fig. 1). A TRX 1000S receiver (Wildlife Materials; frequency range 151.000–151.999 MHz) with a hand-held Yagi antenna was used. Individuals could be located with an accuracy of ca. 50 cm and shorter movements were ignored. The detection range of the signal varied between 20 and 80 m, depending on the position of the animal above or below ground.

Newts were radio-tracked between 5 September and 4 October 2000, and between 9 August and 24 September 2001. During the first night after release the newts' positions were recorded every 2–4 h in both years. Thereafter they were tracked at intervals of 1–3 days (2000), or three times during the first day after release followed by daily intervals (2001) until tracked individuals remained in a terrestrial refuge without apparent movement for at least 1 week. Each fix was marked with a numbered flag. Thereafter the study individuals or regurgitated transmitters were carefully recovered by digging, using small garden tools.

Distances and bearings between location points were measured with a measuring tape (precision: 0.1 m) and a compass (precision: 1°). Positions of animals found >50 m away from the last fix were additionally recorded with a GPS System (Garmin GPS 12). Trigonometric functions were used to plot the localisation points into a grid system that was later superimposed on geographical coordinates. Finally, the migratory trajectories were plotted on an aerial photograph with overlaid contour lines using GIS technology (ArcView). The final graphs were done in Corel Draw.

Due to a smaller sample size in 2000, unless stated otherwise the data of both years were either pooled or data only from 2001 were analysed. Data collected from both release points were pooled as no significant differences in migration distances were detected (Mann–Whitney *U*-test; aerial distance to refuge: $P=0.242$; migrated distance to refuge: $P=0.231$). Four out of the eight animals tracked to their refuge in 2000 were rediscovered after being lost, and were not included in the analysis of migration duration and speed. To analyse migratory directions, standard vectors were calculated for both years separately and tested for deviations from a random distribution using the Raleigh test (Batschelet, 1981).

2.4. Delineation of terrestrial reserves

We compared five different potential terrestrial reserves: (1) a circular zone encompassing the upper 95% confidence limit of the mean linear distance of terrestrial refuges from the lake (Semlitsch, 1998) for both sexes; (2) the same for females alone, assuming that the distances were normally distributed; (3) as for (2) but assuming that the distances were log-normally distributed; (4) a zone encompassing all the peripheral refuges plus an additional 100 m circle around each; (5) as (4) but extended to include adjacent patches of woodland habitat generally preferred by overwintering newts.

3. Results

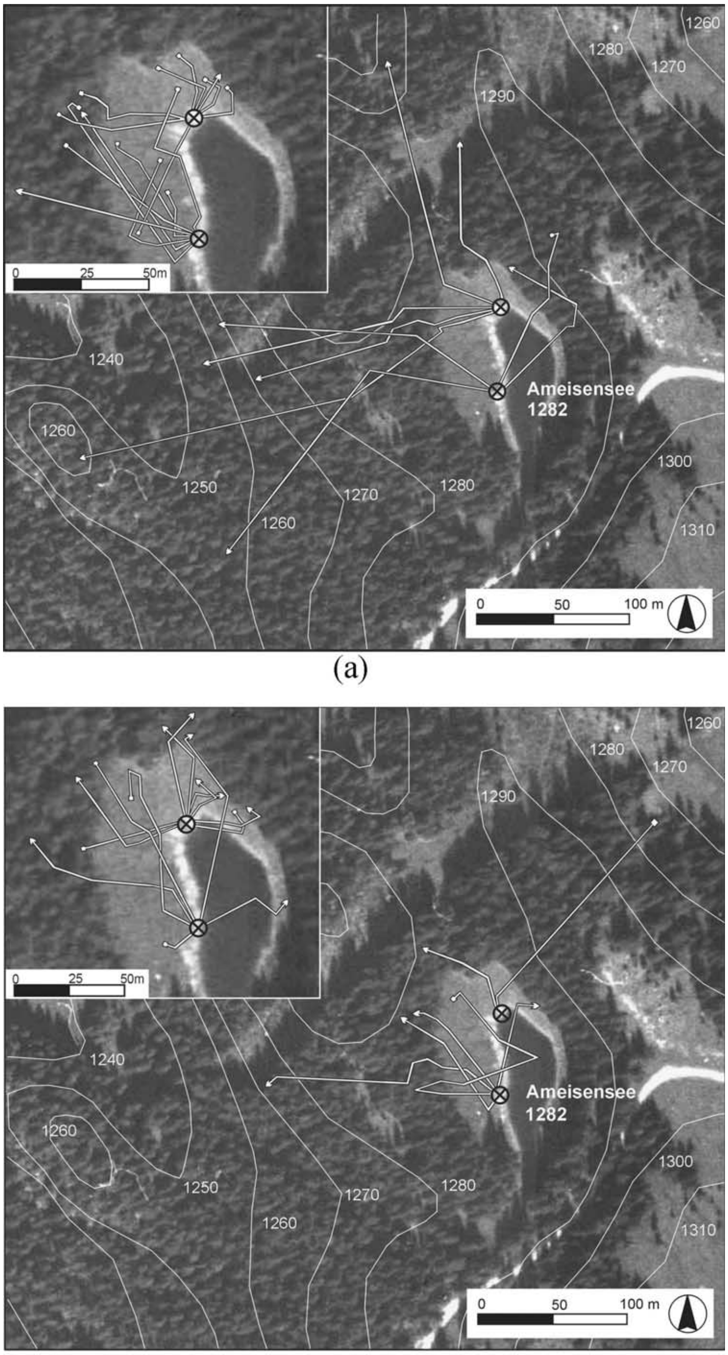
3.1. Radio tracking

Average snout–vent lengths of *T. carnifex* were 88.1 (70–89) and 79.2 (71–98) mm in females and males, respectively (Table 1). With an average mass of 15.1 (7.8–20.0) for females and 11.4 (6.7–14.3) g for males, the relative weight of transmitters in no case exceeded 10% of the body weight. Relative weight of transmitter was significantly less in females than in males (females: average = 6.45%, range = 5.2–8.5%; males: average = 7.75%, range = 6.3–9.8%; *t*-test: $P=0.004$). Four (7.1%) of the tracked animals still had the transmitter in their stomachs after being recovered, seven (12.5%) transmitters were found in shelters next to the animals, seven (12.5%) transmitters were retrieved from underground shelters without the animal present, and in seven (12.5%) cases the signal was detected underground where the transmitter could not be recovered. Ten (17.9%) transmitters were found regurgitated on the soil surface after the animals had moved with the transmitter for at least 20 m. In 16 cases (28.6%) the signal was lost, and five (8.9%) individuals regurgitated the transmitters immediately after insertion (these were not included in Table 1).

3.2. Migrations

Newts were located at 2–8 different positions (average = 3.4), moving for between 4 h and 7.8 days after release. Both sexes moved during night and day with significant deviation from random expectation (2001: χ^2-test; $P<0.001$). During the first night after release, 89% of females and 62% of males changed their position between localizations, whereas the next day these proportions dropped to 20 and 9%, respectively.

Individuals migrated 13–299 m before reaching their terrestrial refuge (Table 1; Figs. 1 and 2). In both sexes, the aerial distance from the lake-shore to the refuge was not significantly correlated with body size (Spearman rank correlation; females: $r_s=0.400$, $P>0.1$; males $r_s=0.236$, $P>0.1$; Fig. 3) or relative transmitter weight



(a)

(b)

Fig. 1. Aerial photographs of the area around Ameisensee (1282 m) with overlaid contour lines (white lines) and altitude above sea level. Migration trajectories of females (a) and males (b) from the two points of release are shown for both years. Arrows at the end of the trajectory point to the newts' terrestrial refuge, whereas squares indicate that the animal was lost on its way. Each change in direction corresponds to a localisation during radio-tracking. Shorter migrations are shown in the enlarged photograph. The black arrow indicates north.

(females: $r_s = -0.337$, $P > 0.1$, males: $r_s = -0.279$, $P > 0.1$). The aerial distance of the terrestrial refuge from the lake, the total migrated distance estimated from tracks and the proportion of the total distance covered during the first night after release were all significantly different between females and males (Mann–Whitney U-tests; aerial distance to refuge 2001: $P = 0.021$, both years: $P = 0.004$; migrated distance to refuge 2001: $P = 0.027$, both years: $P = 0.006$; proportion covered during first night 2001: $P = 0.013$, both years $P = 0.001$). Maximum altitude gained was ca. 40 m.

The median duration of the migration in 2001 was 3.7 days for females and 1.2 days for males with no significant sex-specific difference (Mann–Whitney U-tests; 2001: $P = 0.207$, both years: $P = 0.191$). The maximum recorded speed was 32.5 in females and 27.5 m h^{-1} in males, corresponding to 357 and 353 body lengths,

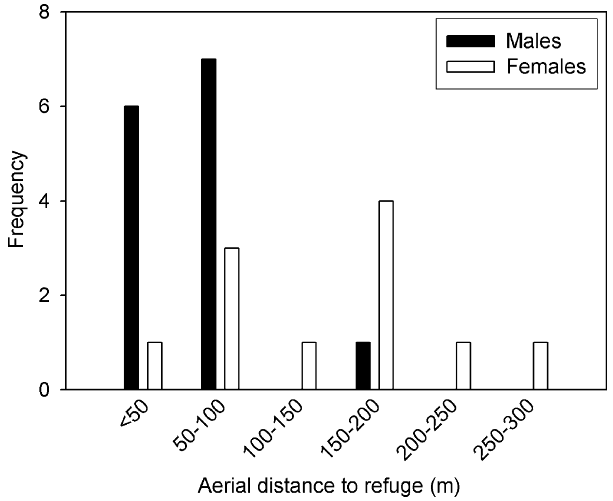


Fig. 2. Frequency distributions of aerial distances of terrestrial hiding places in female and male Italian crested newts.

Table 1
Post breeding migrations of female and male Italian crested newts *(Triturus carnifex)* during the 2-year study period at Ameisensee (1282 m)[a]

	2000		2001	
	Females	Males	Females	Males
Number of newts released (from A or B)	10 (5/5)	10 (5/5)	17 (9/8)	14 (7/7)
Mean snout–vent lengths (range))	88.6 (83.0–94.0)	78.1 (74.0–88.0)	87.9 (71.0–98.0)	79.9 (70.0–89.0)
Animals tracked to refuge (continuously from A or B)	5 (0/1)	3 (1/2)	6 (3/3)	11 (6/5)
Total number of movements	27	27	59	62
Migrated distance to refuge (m) (aerial distance from point of release to refuge)				
Minimum	13 (13)	23 (13)	63 (62)	29 (9)
Maximum	235 (204)	101 (81)	299 (293)	175 (156)
Median	197 (187)	61 (51)	127 (100)	57 (54)
Time to reach refuge (h)				
Minimum	6	13	40	4
Maximum	–	37	135	186
Median	–	15	88	29
Distance moved during first night (%)				
Minimum	20	61	15	45
Maximum	100	99	100	100
Median	37	80	49	96
Migration speed during first night (m/h)				
Minimum	0.8	0.6	1.3	0.8
Maximum	21.6	19.4	32.5	27.5
Median	6.5	3.5	6.0	7.3
Migration speed to refuge (m/h)				
Minimum	2.2	1.8	1.2	0.3
Maximum	–	4.1	2.2	14.3
Median	–	2.7	1.7	3.3
Refuge (% of total)				
In burrows of mammals	3 (60.0)	2 (66.6)	5 (71.4)	8 (80)
In and under rocks	2 (40.0)	–	1 (14.3)	2 (20)
In rotting tree-trunks	–	1 (33.3)	1 (14.3)	–

[a] Newts were released from two points west (A) and north (B) of the lake.

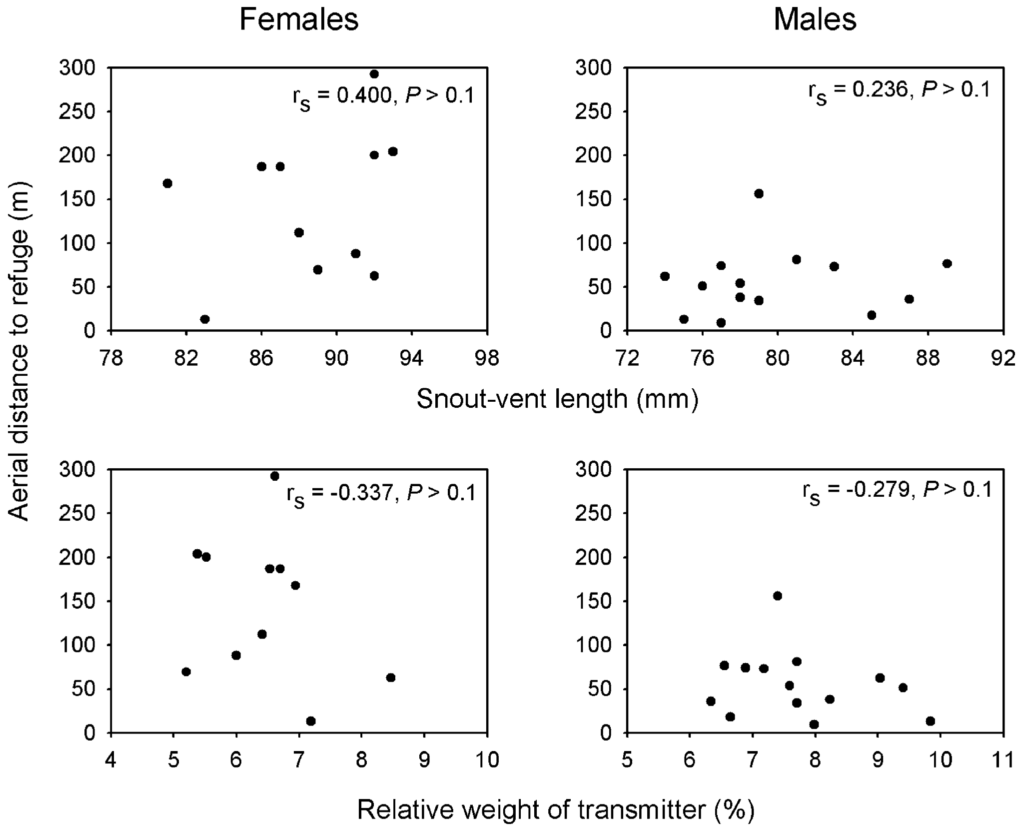


Fig. 3. Linear distance to refuge in relation to snout–vent length (top) and relative weight of transmitter (bottom) in female (left) and male (right) Italian crested newts. The Spearman rank correlation coefficient (r_s) and the probability that there is no correlation is given on top of each panel.

respectively. Average migration speed to the refuge did not differ between sexes, either during the first night after release (2001: $P=0.251$; both years: $P=0.474$) or until arrival at the refuge (2001: $P=0.841$, both years $P=0.551$; Table 1). In both years, the newts preferred a north-westerly direction (Raleigh test; 2000: standard vector length $r=0.575$, azimuth = 310°, $P<0.001$; 2001: $r=0.426$, azimuth = 319°, $P<0.001$). No animal crossed the gravel road southeast of the lake.

3.3. Terrestrial refuges

Twenty-five individuals (49%) could be followed to their terrestrial refuges (Table 1) at the edge of or in the forest. Eighteen (72%) of these were recovered from burrows of rodents under tree roots, five (20%) were hiding in cavities under flat, overgrown rocks probably accessed through burrows or hiding in cracks of large boulders, and two (8%) were located inside rotting tree stumps. The depths below ground ranged from 5 to 80 cm (median: 25 cm). Five individuals were found in their refuges (if unspecified, small mammal burrows) together with other newts: one individual was discovered with one other adult *T. carnifex,* two adult *T. vulgaris*, one adult *T. alpestris* and two juvenile *T. alpestris*, one was located with three adult *T. carnifex* and one adult *T. vulgaris* (rotting tree stump), two individuals shared the shelter with one and two juvenile *T. alpestris*, respectively, and one individual was found together with one adult *T. alpestris.*

3.4. Terrestrial reserves

The inner circular reserve (option 1) had a radius of 125 m, giving an area of 4.9 ha, and included only 68% of the terrestrial refuges (Fig. 4). When specifically protecting the female part of the population (option 2 assuming normal distribution), the reserve enlarged to 199 m radius and 12.4 ha and encircled 84% of refuges. However, some females moved exceptionally long distances (Fig. 1a) and the distances were not distributed normally (χ^2 test; $P<0.001$). Thus, assuming a negative binomial distribution of distances between the refuges and the points of release (option 3), the upper confidence limit increased to 234 m (17.2 ha), and protected 96% of all refuges (Fig. 4).

Option 4, formed by drawing circles with 100 m radius around each observed terrestrial refuge and using the outer edge of all overlapping circles as the boundary of the reserve was actually 1.6 ha smaller than option 3, i.e. 15.6 ha. Finally, in option 5, adjacent patches of old growth forest were linked up with this core reserve including some remaining woodland across the gravel road. A patch of grassland east of the reserve cutting

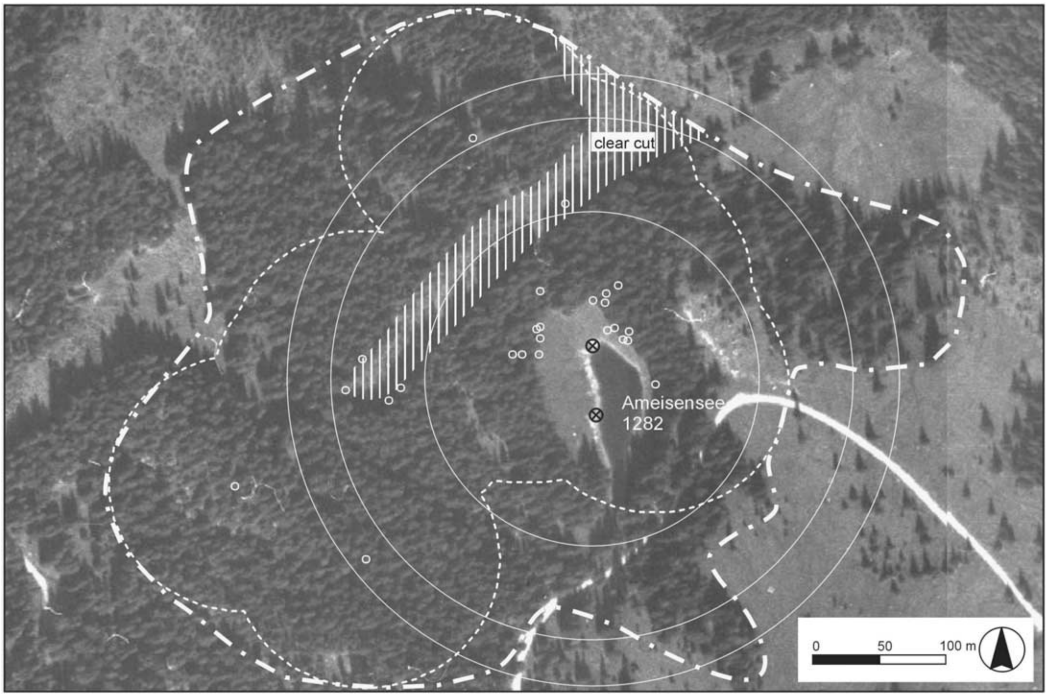


Fig. 4. Boundaries of potential nature reserves around Ameisensee. Concentric terrestrial reserves are based on different ways of calculating the upper 95% confidence limit of migration distances (solid lines; see methods for detailed description). Alternative reserves were derived from drawing circles with 100 m radius around the observed shelters of newts (short dashed line) and adding patches of old-growth forest to this core reserve of overlapping circles (dotted and dashed line). Small circles indicate terrestrial refuges of newts.

into the forest <100 m from the lake was also included for potential reforestation giving a total zone of 22.2 ha.

4. Discussion

4.1. Methodology

The insertion of transmitters into the stomachs of newts is a practical alternative to surgical implantation. Major drawbacks are the limited tracking time and uncertainties such as whether underground signals come from inserted or bare, regurgitated transmitters. However, transmitter size constraints do not allow a battery life capable of tracking individuals for more than a few weeks, and previous studies showed that the vast majority of movements take place during the first phase of tracking (Jehle and Arntzen, 2000). Transmitters which can safely be forced down the oesophagus should be used, thus allowing the potential for regurgitation. The obstruction of intestines by transmitters passing the pylorus would probably cause the death of the tracked animal. Although we observed no such cases, particular care needs to be taken to ensure that transmitters are large enough to remain in the stomach.

The adjustment of study individuals to terrestrial conditions in the laboratory might have disrupted the natural migration behaviour, but cages exposed near the breeding site would have been at risk of disturbance by hikers, and a drift fence was impossible to set up as cattle were present. Releasing animals immediately after capture in the middle of the lake would have also increased the risk of losing regurgitated transmitters in the lake sediment. However, the directionality of movements suggests that the newts were not disoriented once they were released in the field.

4.2. Migrations and terrestrial refuges

We did not record any movements exceeding 1 m after the newts reached their underground shelters. Because of the onset of night frosts shortly thereafter, we concluded that these locations were hibernation sites. Burrows of small rodents in the vicinity of trees, rotting tree stumps or rocks were used most frequently, confirming earlier results for American salamanders (Genus *Ambystoma*; Loredo et al., 1996; Madison, 1997; Madison and Farrand; 1998) and European newts (Jehle and Arntzen, 2000). Individuals of different species and reproductive conditions were found together even at the most distant refuge sites, in line with the observation that newts can follow chemical trails left on the substrate (Hayward et al., 2000), and indicating that even trails of other congeneric species could be used. This behaviour would, for example, ensure that juveniles used shelters that have proven to be frost safe by older individuals.

Terrestrial refuges of *T. carnifex* were 4–8 times further away than those of *T. cristatus* and *T. marmoratus* in a lowland area in western France (Jehle and Arntzen, 2000). Migration speed was roughly the same, but in contrast to this comparative study their migration generally lasted more than 1 day. No snake presence was recorded at Ameisensee, whereas three tracked *T. cristatus* and *T. marmoratus* in France were eaten by snakes (10%), indicating that a higher predation risk could have reduced their migratory activity (see also Sullivan et al., 2002). Alternatively, extended migrations could result from the large numbers ($>10\,000$) of adults of three species competing for suitable shelters. Theory predicts that the metabolic energy costs for locomotion are comparatively lower in larger animals (McNeill Alexander, 1999). The larger Italian crested newts may have gained from occupying more distant hibernation sites (i.e. Ponséro and Joly, 1998), especially if they continued to feed on potentially limited prey resources underground (e.g. earthworms). This implies that suitable shelters around the lake are indeed a limited resource, which may also explain why we found aggregations of newts in 20% of all hibernation sites. This would also imply that narrower terrestrial reserves would probably increase competition for shelter. However, the demands of newts on their hibernation sites and the mechanisms that would explain the observed utilisation patterns remain unknown.

To the best of our knowledge this is the first study revealing sex-biased migration distances in European urodeles. It is unlikely that the considerably longer migration distances of females resulted from the relative transmitter weight being 1.3% less than in males, as migration distances within each sex were unaffected by this parameter. The fact that there was no significant correlation between body size and migration distance indicates that other factors than metabolic advantages in larger individuals may be involved.

Sexual asymmetries in the level of intrasexual resource competition have been identified as a cause for sex-biased dispersal in vertebrates (reviewed in Lambin et al., 2001). Both sexes may compete for frost-safe hibernation sites and/or limited food underground and may therefore have developed spatial niche segregation. Males may tolerate less optimal and more crowded hibernation sites close to the lake for the reward of short migration distances and hence earlier arrival at the breeding site (i.e. Harrison et al., 1983; Griffiths, 1984; Schabetsberger and Jersabek, 1995; Verrell and Halliday, 1985; Arntzen, 2002), which is believed to enhance their reproductive success through a larger number of successful encounters with receptive females (Semlitsch et al., 1993; for a review see Morbey and Ydenberg, 2001). Females in turn could take advantage of optimal conditions in more distant hibernation sites and still have a broad choice of mates when arriving after them. On the other hand, timely arrival at the breeding site is important for both sexes, since the short breeding seasons at high altitude increases the risk of complete failure of a cohort of larvae (Schabetsberger and Jersabek, 1995, personal observation at Ameisensee in 2001). Therefore the majority of migrations in the breeding population probably do not exceed the observed range of 300 m. Tracked individuals needed several days to reach the more distant hibernation sites. Spring migration could be more time consuming than emigration after breeding, since fat reserves of newts are at their minimum and cold temperatures reduce metabolic rates, hence potentially leading to reduced reproductive success. However, more data from different populations are needed before any final conclusions can be drawn.

4.3. Implications for conservation

Whereas Ameisensee itself is protected by legislation from any alteration, the clear-cut in the northwest of the lake (Fig. 4) intercepts migration routes of *T. carnifex,* and exemplifies potential threats in the vicinity of the lake. Salamander abundance has shown to be negatively affected by logging, although the extent of damage caused by different intensities of timber harvest and the time needed for recovery are disputed (Raymond and Hardy, 1991; Petranka et al., 1993; Ash 1997; Harpole and Haas, 1999; Grialou et al., 2000; Hicks and Pearson, 2003). Proposed factors reducing abundance are an increase in ground temperature, decreases in soil moisture, litter input and availability of frost-free hibernation sites (DeMaynadier and Hunter, 1998; Hicks and Pearson, 2003). Apart from direct effects on the terrestrial habitat, logging activities and the concurrent construction of logging roads could permanently change the hydrology of this ephemeral water body (Trombulak and Frissell, 1999; Saunders et al., 2002), potentially diminishing the time available for development to the point where no larvae can reach metamorphosis. The habitats provided by the forest seem of utmost importance for the persistence of high-elevation populations coping with harsh climatic conditions and short reproductive seasons and should be protected from any alteration.

None of the tracked newts migrated in a southerly or south-easterly direction and crossed the gravel road to hibernate in ranchland. Since no animals were released on the steeper southern and eastern shore, we cannot fully rule out the possibility that a fraction of the population chose this direction for emigration. Nevertheless, the strong directionality of movements towards the old-growth forest (see also Malmgren, 2002; Gibbs, 1998; Guerry and Hunter, 2002) supports the concept of delineating terrestrial reserves according to preferred habitats rather than constructing a circular reserve around the lake (Dodd and Cade, 1998).

Considering that only minimum values of migratory ranges could be assessed, the recorded distances covered were surprisingly high. With increasing diameter, the concentric reserves contained increasing proportions of less suitable pasture despite still excluding distant hibernation sites in the forest. Sex-specific differences in migration distances had to be taken into account and the data had to be log-transformed to generate a reserve that encompassed $>95\%$ of observed refuges. However, our alternative approach of adding a 100 m zone to the endpoints of the migrations and including additional patches of viable habitat to this core reserve should protect the majority of existing hibernation sites and is recommended for delineating terrestrial reserves based on radio-telemetry. More data are required to assess whether this is a general feature of high-altitude populations or specific to our study site and species.

Potential migration corridors for long distance dispersal could not be investigated. *Triturus cristatus* adults are reported to move 1290 m within about 1 year (Kupfer, 1998; Kupfer and Kneitz, 2000), However, such long distance migrations may be more frequent between less isolated, lowland breeding sites or alternatively may occur in non-reproducing individuals. We recommend a survey of small water bodies in the area to detect other newt populations, potentially allowing conservation management at the metapopulation level (Richter et al., 2001; Marsh and Trenham, 2001; Ray et al., 2002; Storfer, 2003). We also argue that a monitoring programme should be launched at the lake to ensure that conservation agencies can react to any population decline or further intensive land use. Finally, five other species of amphibians inhabit the lake and are likely to have different habitat requirements that need to be studied.

In conclusion, Italian crested newts at high altitude moved larger distances than previously found in the closely related crested and marbled newts in lowland habitats. More data from other high altitude populations are needed to see if terrestrial reserves in alpine regions have to generally be larger than at lower altitude. Until then, any alterations within the proposed reserves should be prohibited. Remote alpine lakes or ponds outside national parks are under less surveillance than lowland habitats and thus large scale logging activities and their impacts on amphibian populations may go undetected. There is an urgent need for control of logging activities, further information for additional alpine amphibian species and for large-scale surveys to assess connectivity of breeding sites in order to create effective terrestrial reserves.

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