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Reproductive ecology of Bombina variegata: Habitat use

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Reproductive ecology of *Bombina variegata*: Habitat use

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Introduction. -- Reproduction in variable habitats is characterized by uncertainty and requires selection of suitable conditions. Environmental variability may be temporal, spatial, or both. The same site may differ in its suitability for reproduc-tion at different times within a reproductive period, and several associated sites may differ at any one time (Stearns, 1992).

The appropriate response to temporal variability depends on the predictability of the environment. In periodically changing habitats, reproduction at predictably successful times is the normal case, whereas in an unpredictable and changing habitat, assessing and reacting to rapidly changing conditions may be essential. Anurans spawning in rain-filled ponds of unpredictable duration may be expected to synchronize their spawning with rainfall, reproduce more than once per season in favorable years and skip reproduction in unfavorable years (see Barandun and Reyer, 1997a,b, Barandun et al., 1997 and literature therein).

The response to spatial variability is more complex. In patchily distributed breeding sites there are three possibilities: 1) individuals can return to their natal site throughout their life, provided the site persists over sufficient time, 2) they can disperse to new sites as juveniles and thereafter remain sedentary as adults, and 3) they can remain nomadic and search for new sites throughout their lives. Dispersal is a common phenomenon among all groups of organisms (Hanski and Gilpin, 1991) and can lead to genetic exchange among populations, colonization of new habitats, and recolonisation after local extinction (Greenwood, 1982; Hansson, 1991). When a local population is saturated, dispersal can be favored even when there is only a small chance for individuals to become established in another population (Hansson, 1991). Dispersal does not exclude the possibility that some individuals may return to their natal sites. Whether or not sexually mature individuals exhibit site fidelity depends on the scale of environmental variability and life expectancy. When reproduction is likely to be successful at the same site throughout an individual's life, site fidelity may be the best choice. Several species of anurans breeding in stable and permanent ponds seem to choose this strategy (Heusser, 1960; Berven and Grudzien, 1990; Reading et al., 1991). Dispersal to new sites will be favored when the suitability of the habitat changes quickly or is unpredictable. Ovipositing in different ponds also spreads the risk of reproductive loss (Kaplan and Cooper, 1984). Empirical data, however, are scarce for anurans, mostly because of methodological constraints. Juvenile dispersal seems to be widespread, but adult dispersal and spawn distribution is poorly documented (Merrell, 1970; Daugherty and Sheldon, 1982; Reading et al., 1991).

Bombina variegata uses various ponds for reproduction, most of them temporary (Bauer, 1987). We studied a population in a habitat with a variety of different temporary ponds, where pond conditions change unpredictably within and among years, mainly due to climatic conditions and human activities(Barandun and Reyer, 1997a). The question was whether individuals spawn in a single pond or spread the risk of reproductive failure, mainly due to desiccation (Barandun and Reyer, 1997b), by ovipositing in different ponds within a breeding season.

Materials and Methods. -- The study area is situated northeast of Zürich in a military training area, 440 m above sea level. One third of the area is covered by a closed mixed forest with little ground vegetation. The remaining open area is a sparsely vegetated sheep pasture on clay soil.

We studied *Bombina variegata* between 1990 and 1993 on a ca. 10 ha area with a high density of both ponds and toads. All ponds were artificial, created when amoured vehicles compressed the soil. In June 1991, 10 ponds were destroyed when 1 ha was graded by bulldozers. Disturbance by military activities changed the size, depth, shape and vegetation of most ponds, mainly in winter and early spring each year. Some ponds even disappeared totally and new ones appeared in other places. Only two ponds remained undisturbed during the study period. During the annual sampling period from April to September, single ponds were occasionally disturbed. Eighteen ponds have existed since at least 1989, although their shapes have repeatedly changed. Some ponds may have existed for up to ten years. In the open area, 44 - 46 ponds were studied each year. Temporary ponds situated in the forest (up to 15/year) were also investigated. All forest ponds were completely shaded, smaller than six m^2 and contained no aquatic vegetation. Further details about the species, the study area and some general methods are provided by Barandun and Reyer (1997a,b)and Barandun et al.(1997).

Toads were caught by hand after sunset on 26 nights in 1990 (ca. every 5 days), 7 nights in 1991 (twice per month), 14 nights in 1992 (twice per month plus on nights after transfer) and one night in 1993. Only ponds, including nearly dry ones, were sampled because animals were rarely found on dry land. Toads were identified, measured and returned to their pond of origin within two hours of capture. Males and females resumed courtship within one hour following release. Disturbance through capturing is therefore considered minimal. To identify individuals, the belly pattern was photographed and the pictures were used to identify recaptured animals. Snout-vent-length was measured to the nearest mm. Sexually mature males were identified by their swollen and pigmented nuptial pads. Females and juveniles were indistinguishable unless the former carried eggs. The smallest female carrying eggs was 34.8 mm. All individuals larger than this size which did not have swollen pigmented nuptial pads were classified as females (Barandun et al., 1997). In 1990, 210 juveniles were marked collectively by clipping two toes in four different combinations according to four separate groups of ponds.

To test site fidelity experimentally, 66 females and 151 males were transferred among ponds in 1992. Transfer distances varied from 8 m to 420 m. The location where the toads were found last in the same season was compared with the pond into which they had been transferred. Statistics were performed with the software JMP (SAS Institute Inc., Cary, NC, 1995). Hypotheses tested and tests used are given in the results.

Results. -- The reproductive period of *Bombina variegata* lasted from the first heavy rain in May to early August. Within this period, adults were caught almost exclusively in the spawning area during times of actual breeding activity, whereas during dry periods and in autumn a substantial proportion of toads was found in moist places in the forest (Fig. 1). The difference between proportions caught in the two areas with a similar distribution of sampling effort during the three periods is significant for both males and females (both $\chi^2 > 174$, $p<0.001$, df=2). Males always outnumbered females in spawning ponds where they were up to five times as abundant as females during periods of breeding activity. In the forest, the sex ratio among captured toads was more balanced (Fig. 1). Most adult males seemed to be synchronously active in spawning ponds, whereas only a small proportion of females stayed there at any one time. However, females were also found repeatedly in spawning ponds during periods of reproductive inactivity, suggesting that they used ponds for purposes other than spawning or waited for suitable breeding conditions.

No calling, mating, or spawn was ever recorded in the forest, nor was there calling activity during dry periods in the spawning area. However, calling and spawning started and reached highests levels within hours after heavy rain, when the ground was wet and temporary ponds were flooded. The activity dropped during heavy rain and cold weather. Within 3-5 days following rain, the number of animals found in ponds declined and calling activity ceased.

The changing proportion of toads in the forest and the fast behavioral response to rainfall indicates that individuals staying in the forest must have moved directly to a spawning pond. Depending on weather conditions, they probably move repeatedly between the forest and the spawning ponds during a summer, but times between successive catching periods were too long to demonstrate such short-term movements directly. Although the distances moved between the two areas ranged between 50 - 240 m, 48 % of the movements were less than 50 m. Only four out of 802 recaptured individuals, i.e. 0.5%, visited ponds across the whole spawning area, suggesting that the proportion of adults potentially leaving the study area must have been neglegible.

Individuals were found in the same pond in 1121 out of 2038 (55 %) recaptures outside the forest. Within a season, 78% of the recaptured toads were found in the pond where originally marked or in ponds less than 50 m away (Fig. 2a). After one or two winters, 62% were recaptured within 50 m of the original pond, of which about half were found in the same pond which they had used in the previous year (Fig. 2b). Females tended to show higher site fidelity than males within years (χ^2=4.4; df=2; p=0.1) and were significantly more philopatric between years (χ^2=9.2; df=2; p=0.01). Of the 210 juveniles marked in 1990, 35 were recaptured in 1992, seven (=20%) in the same group of ponds, 12 (=34%) in other ponds, and 16 (=46%) in the forest. Assuming an annual mortality rate of about 40% (cf. Brandun et al., 1997), the 35 recaptured toads represent about 40% of the surviving cohort members. These data indicate that adults are highly philopatric and few juveniles disperse far from their natal area. The actual mobility of juveniles and adults was probably higher than recorded because short excursions to other ponds were likely to have been overlooked, and migrations between the spawning area and the forest or other hiding places were rarely recorded.

Results of the transfer experiment also indicated strong site fidelity (Fig. 3). Among those displaced more than 50 m, 28 % were not recaptured in the same year, 10 % remained in their transfer pond or less than 50 m away from it, 32 % were found in or within 50 m of their home pond, and another 30 % were found in a different area or in the forest. Compared with the number of individuals staying in the transfer area or moving to new areas, a higher than expected number of toads returned home (χ^2=22.6; df=2; p<0.001), with no significant difference between the sexes (χ^2=2.6; df=2; p>0.05). Some individuals returned to their home area across the whole study area.

Discussion. -- Our results indicate that individuals seem to have precise knowledge of their habitat. Although making excursions from time to time, they immediately return to a particular breeding pond after rainfall, remain in the same pond or its surroundings within and between years, and return to their home pond more often than expected when experimentally displaced.

Potentially suitable breeding ponds existed at similar locations within the study area every year. However, essential factors for tadpole development like duration, temperature, and pond vegetation changed unpredictably both within and among years. Each year most metamorphs emerged from only two or three ponds but their location partly differed among years. Because successful reproduction differed not only in space, but also in time (Barandun and Reyer, 1997a,b), the toads were expected to distribute their eggs among different ponds (Kaplan and Cooper, 1984), but females were not observed to do so. Rather, individuals returned to a restricted area and reproduced at the same place even when conditions changed dramatically. Similar site fidelity has been reported by Kapfberger (1984) and Seidel (1987) for *Bombina variegata*, by Reading et al. (1991) for *Bufo bufo*, and by Sinsch (1992) for *Bufo calamita*. In the latter species, however, males were also observed searching for new ponds immediately after rain. It seems likely that differences among species and populations reflect differences in the relative importance of various environmental conditions for reproductive success. Where quick reaction to climatic conditions is more important for reproductive success than spreading the risk of reproductive failure through spatial spawn distribution, we expect site fidelity to a small known area which reliably contains suitable spawning sites. Because rainfall and pond desiccation were the best predictors of reproductive success in our study area (Barandun and Reyer, 1997b), this dependence on climatic conditions may explain why most individuals, both males and females, remained in the same pond or area all summer and regularly returned to it after moving to the forest during dry periods or when experimentally displaced. On the other hand, using new ponds within the near neighborhood allows the toads to cope with disturbance and drastic habitat changes which occur frequently and may spatially shift suitability or even totally eradicate ponds.

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LITERATURE CITED

BARANDUN, J., AND REYER, H.-U. 1997a. Reproductive ecology of *Bombina variegata*: characterisation of spawning ponds. Amphibia-Reptilia 18:143-154.

————. 1997b. Reproductive ecology of *Bombina variegata*: Development of eggs and larvae. J. Herpetol. 31:107-110.

————, AND ANHOLT, B. 1997. Reproductive ecology of *Bombina variegata*: Aspects of life history. Amphibia-Reptilia 18:1-9.

BAUER, S. 1987. Verbreitung und Situation der Amphibien und Reptilien in Baden-Württemberg. Beih. Veröff. Naturschutz Landschaftspflege Baden-Württemberg 41:71-157.

BERVEN, K. A., AND GRUDZIEN, T. A. 1990. Dispersal in the wood frog (*Rana sylvatica*): implications for genetic population structure. Evolution 44:2047-2056.

DAUGHERTY, C. H., AND SHELDON, A. L. 1982. Age-specific movement patterns of the frog *Ascaphus truei*. Herpetologica 38:468-474.

GREENWOOD, P.J. 1982. The natal and breeding dispersal of birds. Ann. Rev. Ecol. Syst. 13:1-21.

HANSKI, I., AND GILPIN, M. 1991. Metapopulation dynamics: brief history and conceptual domain. Biol. J. Linn. Soc. 42:3-16.

Hansson, L. 1991. Dispersal and connectivity in metapopulations, p.89-103. *In*: Metapopulation dynamics. M. Gilpin and I. Hanski (eds.). Biol. J. Linn. Soc. 42, Acad. Press, London.

HEUSSER, H. 1960. Ueber die Beziehungen der Erdkröte (*Bufo bufo* L.) zu ihrem Laichplatz II. Behaviour 16:93-109.

KAPFBERGER, D. 1984. Untersuchungen zu Populationsaufbau, Wachstum und Ortsbeziehungen der Gelbbauchunke, *Bombina variegata variegata* (Linnaeus, 1758). Zool. Anz. 212:105-16.

KAPLAN, R. H., AND COOPER, W. S. 1984. The evolution of developmental plasticity in reproductive characteristics: an application of the "adaptive coin-flipping" principle. Am. Nat. 123:393-410.

MERRELL D. J. 1970. Migration and gene dispersal in *Rana pipiens*. Am. Zool. 10:43-52.

READING, C.J., LOMAN, J., AND MADSEN, T. 1991. Breeding pond fidelity in the common toad *Bufo bufo*. J. Zool. 225:201-212.

SEIDEL, B. 1987. Breeding of a *Bombina variegata* population in a habitat with temporary pools. Proc. 4th ord. Gen. Meeting Soc. Eur. Herp., Nijmegen 1987:353-356.

SINSCH, U. 1992. Sex-biased site fidelity and orientation behaviour in reproductive natterjack toads (*Bufo calamita*). Ethol. Ecol. Evol. 4:15-32.

STEARNS, S. C. 1992. The evolution of life histories. Oxford Univ. Press, New York.

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FIGURE CAPTIONS

Figure 1: Average numbers of captures per sampling night in the spawning area (white bars) and in the forest (grey bars) during spawning and dry periods in the breeding season and in autumn thereafter. Standard deviations are shown by lines. Total numbers: 974 captures of females and 1971 captures of males, pooled over all three years of the study.

Figure 2: Site fidelity of females (grey bars) and males (white bars). Plotted are percentages of individuals found exclusively in each of the three distance categories (a) within one season (N=151 females; 337 males) and (b) after one or two winters (N=98 females; 182 males).

Figure 3: Movements of adult females (★; N=44) and males (o; N=113) after experimental transfer. 22 additional females and 38 males were not recaptured after the transfer. Ranges of 50 m around home and transfer areas are indicated by shaded areas.

Figure 1

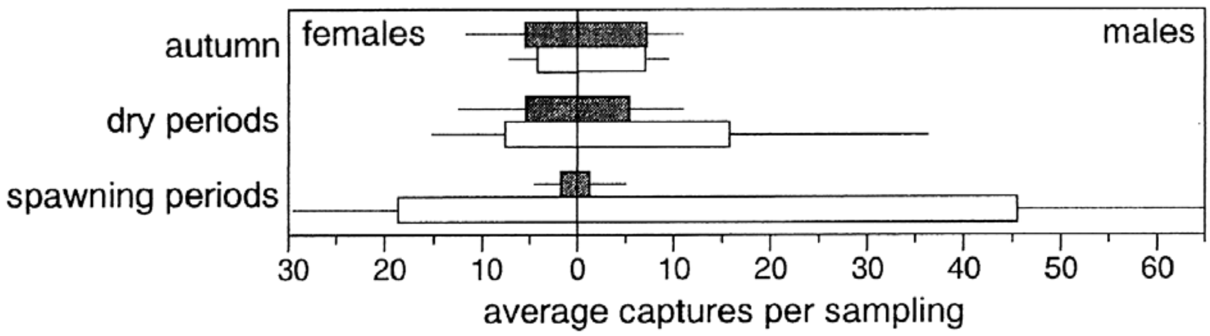

autumn
dry periods
spawning periods
females
males
30 20 10 0 10 20 30 40 50 60
average captures per sampling

Figure 2

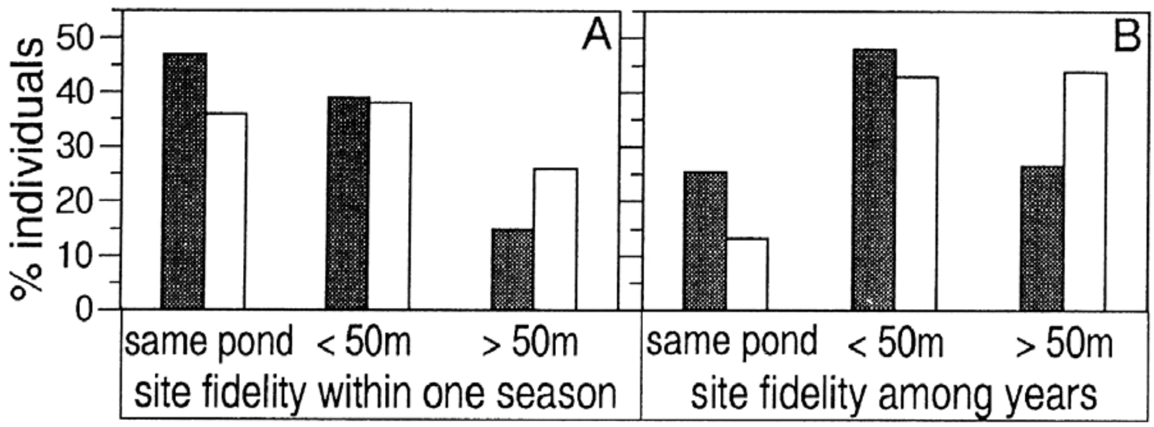
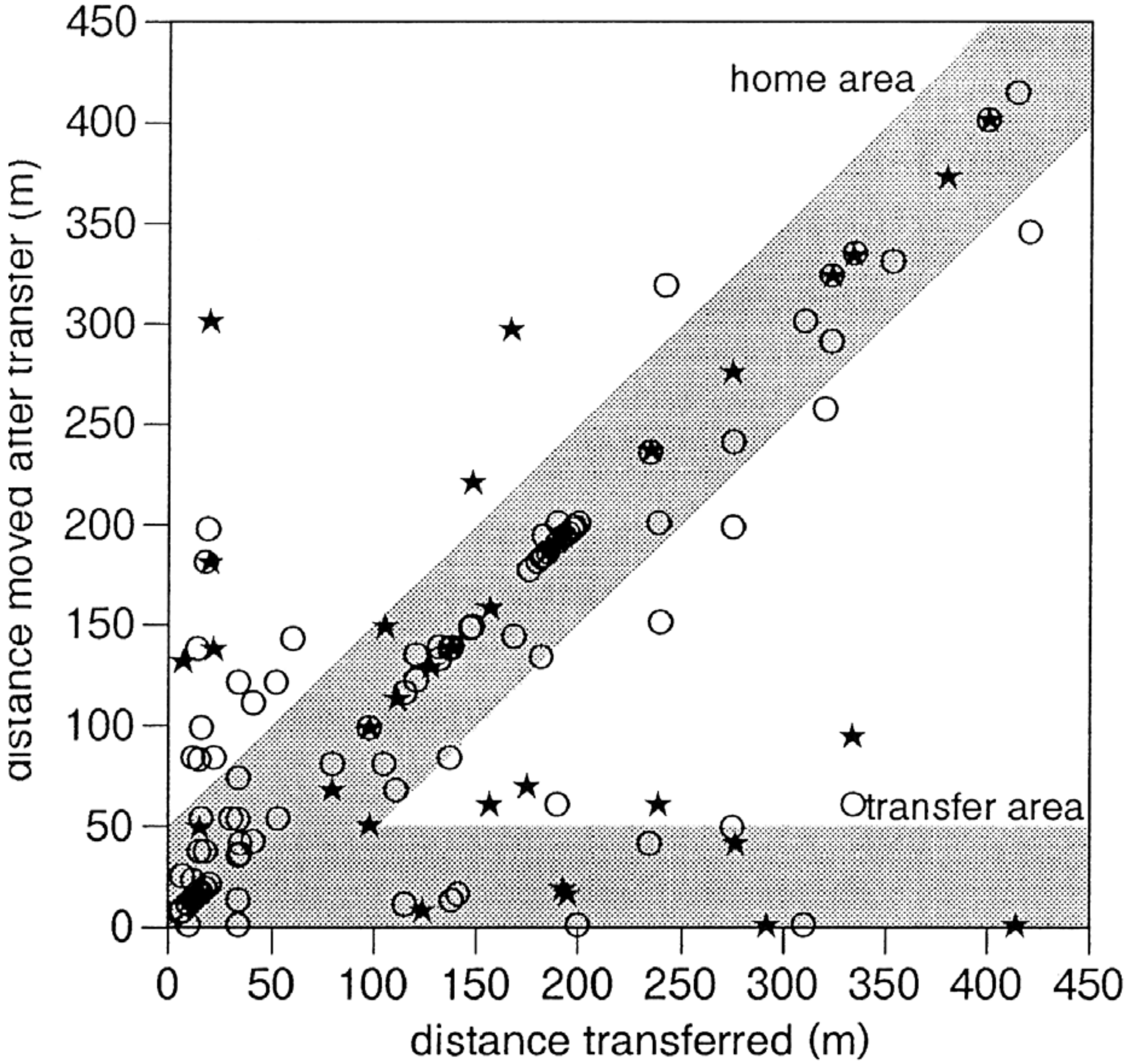

% individuals
50
40
30
20
10
0
A
B
same pond
< 50m
> 50m
site fidelity within one season
same pond
< 50m
> 50m
site fidelity among years

Figure 3


home area
transfer area
distance moved after transfer (m)
distance transferred (m)
0
50
100
150
200
250
300
350
400
450