

AMPHIBIAN COLONIZATION OF NEW PONDS IN AN AGRICULTURAL LANDSCAPE

JOHN M. R. BAKER AND TIM R. HALLIDAY

Department of Biology, The Open University, Walton Hall, Milton Keynes MK7 6AA, UK

Newly constructed ponds on farm land were surveyed for amphibians and compared with long-standing farm ponds. The frequencies of amphibian occupation of the two pond types were similar (65 and 71% respectively), but the species composition differed. *Bufo bufo* was found more frequently in new ponds than in old ponds, whereas *Triturus cristatus* and *T. vulgaris* were found less frequently in new ponds. The differences in the amphibian species assemblage between the two types of pond reflected the ponds' functions and the amphibians' dispersal abilities. New ponds were larger and tended to support fish and waterfowl more frequently than did old ponds. *Triturus cristatus* was not found in any fish ponds. Principal component and discriminant analyses of variables related to ponds and the surrounding terrestrial habitat indicated that, for *T. cristatus* and *T. vulgaris*, the location of new ponds relative to existing ponds was a significant factor in pond colonization. *Triturus cristatus* and *T. vulgaris* did not colonize ponds at distances greater than 400 m from existing ponds. *Rana temporaria* and *Bufo bufo* were not so constrained by dispersal abilities and were able to colonize new ponds at distances up to 950 m from existing ponds. *Rana temporaria* was more likely to be found in new ponds containing submerged vegetation; however, multivariate analyses could not discriminate between ponds that were, and were not, colonized by *Bufo bufo*. The results of this study are discussed with regard to the construction and management of ponds for the conservation of these amphibians.

Key words: amphibian assemblages, farm ponds, colonization, habitat characteristics

INTRODUCTION

Amphibians in Britain have exploited a variety of man-made ponds (Warwick, 1949; Banks & Laverick, 1986; Jeffries, 1991; Beebee, 1997). However, in regions where widespread species (common frogs, *Rana temporaria*, common toads, *Bufo bufo*, great crested newts, *Triturus cristatus*, palmate newts, *T. helveticus*, and smooth newts, *T. vulgaris*) have declined, habitat loss, particularly the loss of breeding ponds, seems to be a major causal factor (Cooke & Scorgie, 1983; Hilton-Brown & Oldham, 1991). In general there has been a decline in the number of ponds in Britain over the course of the twentieth century (Barr *et al.*, 1994; Oldham & Swan, 1997). However, the rate of loss has been lessened by the creation of new ponds. Seven per cent of ponds located by systematic surveys included in the National Amphibian Survey were newly created (Swan & Oldham, 1993), and since the 1960s increases in pond numbers have been recorded in some areas (Oldham & Swan, 1997). Thus, new ponds may represent a significant proportion of all ponds, and amphibian success at such sites is worthy of attention.

While the creation of new ponds in gardens has provided breeding sites for *Rana temporaria*, *Bufo bufo* and *Triturus vulgaris* (Cooke, 1975; Beebee, 1979; Beebee, 1985; Banks & Laverick, 1986; Hilton-Brown & Oldham, 1991), the suburban areas most likely to provide this sort of habitat represent only a small pro-

portion (5.5%) of land in Great Britain (Stott *et al.*, 1993). Furthermore, in the long-term, amphibian populations in such areas may suffer reduced genetic diversity due to inhibition of movement between populations in built-up areas (Hitchings & Beebee, 1998). The fate of amphibians in agricultural landscapes is significant both because of the large area of land involved (48.7%) and also due to the potential for this land-use type to support genetically diverse amphibian populations in the long-term.

The importance of ponds in rural areas, in combination with pond losses tempered by a continuing trend of pond creation, makes amphibian colonization of new ponds on farm land an issue of interest. The purpose of the present study was to compare ponds that have been recently constructed in agricultural areas with older ponds, as amphibian breeding sites. The study compared amphibian presence/absence between samples of old and new ponds, and sought to ascertain the characteristics of new ponds that made them suitable amphibian sites.

Of particular interest was the habitat surrounding ponds. Although water quality can affect the distribution of amphibian species (e.g. Cooke & Frazer, 1976; Denton, 1991), within an area of relatively homogeneous geology the distribution of pond-breeding amphibians is less dependent on the finer-scale variation in water quality. Some pond breeding amphibians appear to be fairly insensitive to water quality, being found widely distributed throughout their ranges (e.g. *Rana temporaria* and *Bufo bufo* [Swan and Oldham,

1993]). Amphibian presence in agricultural areas seems to be largely independent of water quality (Hecnar & McCloskey, 1996), but rather is determined by geology and the nature of adjacent terrestrial habitat (Beebee, 1985; Pavignano, Giacoma & Castellano, 1990; Laan & Verboom, 1990; Swan & Oldham, 1993; Marnell, 1998; Stumpel & van der Voet, 1998), pond vegetation (Ildos & Ancona, 1994; Stumpel & van der Voet, 1998) and age (Laan & Verboom, 1990, Stumpel & van der Voet, 1998). The present study investigated the effects of land use around newly created ponds, the presence of fish, water fowl and vegetation, and the effect of pond age on the presence of amphibians in new ponds.

A particular focus of the present study was the location of new ponds relative to existing ponds. Metapopulation ecology theory (Levins, 1969; Hanksi & Gilpin, 1991) offers a useful framework to understand, manage and conserve discontinuously distributed wildlife populations, including pond-breeding amphibian populations (McCullough, 1996). The status of amphibians within a region is dependent on the outcome of the dynamic processes of the extinction of local populations and the colonization of unoccupied ponds (Savage, 1961; Gill, 1978; Hecnar & McCloskey, 1997; Sjögren-Gulve, 1994, Edenhamn, 1996). As might be expected, amphibians living in such metapopulations are able to colonize suitable, newly created ponds (Gill, 1978; Edenhamn, 1996). A key issue for the conservation management of amphibian populations is the distance between ponds which allows colonization and the long-term persistence of local populations. The present study investigated the distance between ponds and local pond density as potential influences on the colonization of new ponds.

Of the four amphibian species found in the study area (common frogs, common toads, great crested and smooth newts), great crested newts are of particular interest since they are the most scarce and rapidly declining of the widespread British amphibians (Cooke & Scorgie, 1983; Hilton-Brown & Oldham, 1991), and the least successful in the colonization of new pond habitats (Cooke & Scorgie, 1983; Beebee, 1997).

MATERIALS AND METHODS

New ponds constructed through Countryside Commission grants were located with the help of Bedfordshire County Planning Department, Northamptonshire Planning and Transportation Department and Buckinghamshire Farming and Wildlife Advisory Group. Further new ponds were located by interviewing landowners. Ponds that resulted from restoration of existing sites were not included in this study. Pond age was established through local authority records and by interview with landowners. Seventy-eight new ponds, dispersed over 3000 km² of west Bedfordshire, north Buckinghamshire and Northamptonshire were surveyed. Landowners and managers were interviewed to establish the nature of amphibian and fish introductions. The presence of fish was further established

while surveying the ponds for amphibians. The amphibian survey was carried out in three stages, using established techniques (British Herpetological Society, 1990; Griffiths *et al.*, 1996). The first stage consisted of circuiting the accessible shoreline, visually searching for frogs and toads, the spawn of these species and also newt eggs. The second stage repeated the visual search, after dark, using a torch. For the third stage, weed beds were swept with a pond net for newts and amphibian larvae. Funnel trapping was not used due to the logistical problems in visiting sites twice, to set and collect traps.

Pond use by waterfowl (ducks and geese) was noted. Submerged vegetation was also recorded as either present or absent, since some new ponds were devoid of aquatic weed beds.

The nearest neighbouring pond to each new pond was located from maps and by interview with the landowner. In cases where access to these ponds was possible, they were also surveyed for amphibians, providing a control sample of ponds. These ponds will be referred to as 'old' ponds. The terrestrial habitat around new ponds was analysed from 1:25 000 Pathfinder series maps. A 1 cm (=250 m) grid was superimposed over each pond location. The following four variables were recorded within a 1 km radius of the pond: built up areas (the number of grid squares containing buildings the size of an individual farm house or larger), woodland (the number of grid squares containing areas of woodland), riparian habitat (the number of times rivers, streams or canals crossed grid lines), and proximate pond density (the density of water bodies within a 1 km radius of a pond). Pond density within a 2 km radius and the distance between a new pond and the nearest neighbouring pond were also measured.

Six of the eight variables were log-transformed to normalize skewed data and all variables were relativized to ensure that variables with different means did not contribute disproportionately to the overall variance. A principal component analysis was carried out using the terrestrial habitat variables (built-up areas, woodland, riparian habitat, proximate pond density, pond density and distance to nearest neighbouring pond) to see if these habitat variables could be reduced to two vectors. Discriminant analyses were used to determine differences between ponds colonized by amphibians, and those where amphibians were not detected. For each amphibian species, presence/absence was used as the independent variable. The dependent variables used were built-up areas, woodland, riparian habitat, proximate pond density, pond density, distance to nearest neighbouring pond, pond size, pond age, presence of fish, presence of waterfowl and presence of submerged vegetation. The latter three variables were categorical (presence/absence).

All statistical tests used the probability value $\alpha=0.05$ to determine significance. For χ^2 tests of association, Yates' correction was used when expected values were less than five.

TABLE 1. The frequency of occurrence of all fish species, trout, wildfowl (ducks and geese) and amphibians in old and new ponds. χ^2 values are given for comparisons of presence and absence data between old and new ponds. * indicates $P < 0.001$.

	Old ponds (n=49)	New ponds (n=78)	χ^2
Amphibians	71%	65%	3.70
Fish	20%	54%	13.92*
Trout	0%	21%	11.50*
Waterfowl	14%	46%	13.65*

RESULTS

Forty-nine old and 78 new ponds (median age = five years, range = 1 to 20 years) were surveyed. In most cases (at least 77% of new ponds) construction was funded by Countryside Commission grants. Forty-one per cent were constructed primarily for fish or waterfowl, the remainder for other purposes such as wildlife habitat creation or aesthetic value.

The new ponds surveyed were significantly larger than the old ponds (mean sizes = 1704 and 409 m², respectively; $t=3.15$, $df=125$, $P<0.01$; ranges = 13-14 160 and 30-1060 m², respectively) and a greater proportion supported fish, (54%), including trout (*Salmo*) species (21%), and waterfowl (46%) (Table 1). Amphibians were found in similar proportions of old (71%) and new (65%) ponds. The distribution of the number of species found per pond was also similar between the two types of pond ($\chi^2=3.70$, $df=4$, $P>0.05$) (Fig. 1). However, interviews with landowners and managers revealed that amphibians had been introduced to some ponds. The movement of frogspawn was the most common form of amphibian introduction (3 old and 16 new ponds) and potentially created a source of bias in the survey data. To test whether frogspawn introductions were associated with the presence of frogs, the proportion of new ponds where frogs were detected that were also sites of

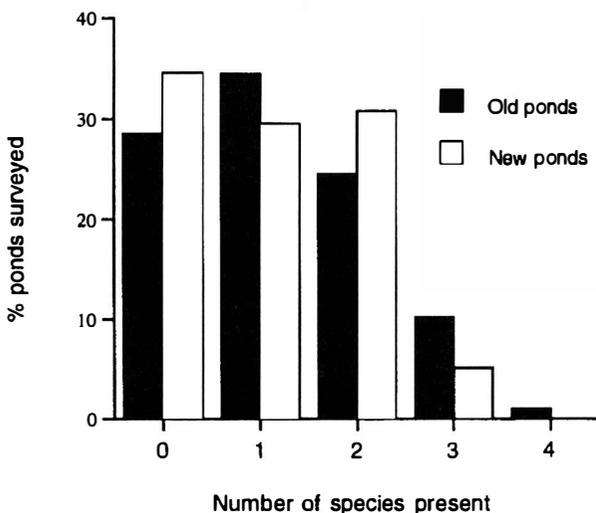


FIG. 1. The number of amphibian species occupying old and newly constructed farm ponds.

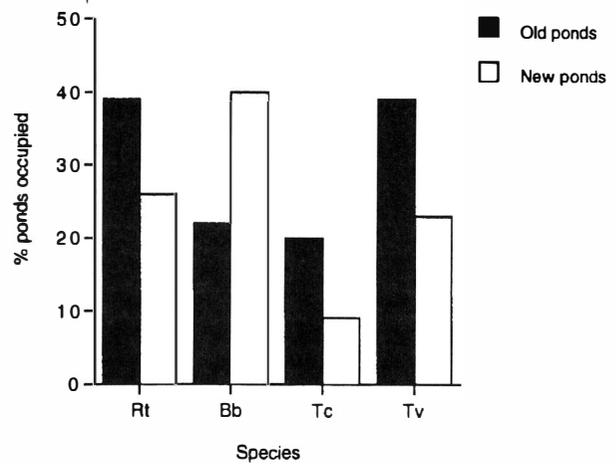


FIG. 2. The percentage of old and newly constructed ponds occupied by *Rana temporaria* (Rt), *Bufo bufo* (Bb), *Triturus cristatus* (Tc) and *Triturus vulgaris* (Tv).

introduction (9/16) was compared with the proportion of ponds where frogs had colonized naturally (16/62). The presence of frogs at new ponds was significantly associated with introductions of frogspawn ($\chi^2=5.412$, $df=1$, $P<0.05$).

To remove any effects of frog introductions on the occupancy of new ponds, the frog occupancy data were analysed after removing all sites where frogs had been introduced. There was no significant difference in the proportions of frog presence/absence between old (39% presence) and new (26% presence) ponds ($\chi^2=2.173$, $df=1$, $P>0.05$). An analysis of the presence/absence of toads, great crested and smooth newts revealed that the distribution of these species differed between old and new ponds ($\chi^2=7.625$, $df=2$, $P<0.05$). Toads were found more frequently in new ponds (40%) than in old ponds (22%) whereas both *Triturus cristatus* and *T. vulgaris* occurred at lower frequencies in new (9 and 23% respectively) than in old ponds (20 and 39% respectively) (Fig. 2).

To examine the relationship between amphibian occupancy and fish and waterfowl presence, sites of frogspawn introduction were included. Similar numbers of both fish ponds and ponds utilized by waterfowl were occupied by at least one amphibian species (Table 2; $\chi^2=0.487$, $df=1$, $P>0.05$ and $\chi^2=0.232$, $df=1$, $P>0.05$, respectively). However, the distributions of amphibian presence/absence, by species, differed between fish, and fish-free, ponds ($\chi^2=11.39$, $df=3$, $P<0.01$). Frogs and toads tended to be found more frequently in fish ponds, while smooth newts were found less frequently and great crested newts were never found to co-exist with fish. A similar pattern was found in ponds used by waterfowl, but this was not statistically significant ($\chi^2=6.64$, $df=3$, $P>0.05$).

Principal component analyses were carried out for six habitat variables (built-up areas, woodland, riparian, proximate pond density, pond density and distance to nearest neighbouring pond), for the 78 new ponds. These variables reduced to two vectors repre-

TABLE 2. Amphibian occupancy of new ponds relative to the presence of fish and waterfowl. n = number of ponds, Any spp. = at least one amphibian species present, Rt = *Rana temporaria*, Bb = *Bufo bufo*, Tc = *Triturus cristatus*, Tv = *Triturus vulgaris*. Figures in brackets represent percentages.

<i>Amphibian and fish presence</i>						
	n	Any spp.	Rt	Bb	Tc	Tv
Fish absent	36	25 (69)	9 (25)	11 (31)	7 (19)	10 (28)
Fish present	42	27 (64)	16 (38)	20 (48)	0 (0)	8 (19)

<i>Amphibian and waterfowl presence</i>						
	n	Any spp.	Rt	Bb	Tc	Tv
Fish absent	42	27 (64)	11 (26)	12 (29)	6 (14)	11 (26)
Fish present	36	25 (69)	14 (39)	19 (53)	1 (3)	7 (19)

sending 68% of the variance in habitat variables. The eigenvector loadings indicate that the first axis primarily represents distance to the nearest neighbouring pond and the second axis primarily represents the amount of adjacent woodland (Table 3). Amphibian species presence/absence was then plotted against the first two axes of the principal component analyses (Fig. 3). Frog presence/absence was plotted only for the 62 ponds where introductions had not occurred. Pond occupancy by frogs and toads is spread evenly across the two principal components. However, in the case of the newts, both species appear to occur on the lower half of the first axis, indicating that newts tended to occupy new ponds in locations where the distance to the nearest neighbouring pond was small (Fig. 4).

TABLE 3. Results of principle component analysis of six variables quantifying terrestrial habitat surrounding new ponds. The variance explained by six new axes and the loadings of each original habitat variable on the first two axes are given. Wood = woodland, Rip = riparian habitat, B = built-up areas, PPD = pond density within a 1-km radius, PD = pond density within a 2-km radius, NN = distance to nearest neighbouring pond.

Axis	Eigenvalue	% of var.	cum. % of var.	Broken-stick
1	0.007	49.62	49.62	0.006
2	0.003	18.55	68.17	0.003
3	0.002	13.15	81.32	0.002
4	0.002	11.07	92.38	0.001
5	0.001	4.70	97.08	0.001
6	0.000	2.92	100.00	0.000

	Factor score coefficients for terrestrial habitat	
	Axis 1	Axis 2
Wood	-0.1637	0.7013
Rip	0.0705	0.3093
B	-0.0413	0.1021
PPD	-0.1608	-0.4869
PD	-0.0970	-0.4057
NN	0.9650	-0.0212

Discriminant analyses detected significant differences between occupied and unoccupied ponds for frogs (at all sites and sites where frogs had not been introduced) and great crested newts, but not for toads. The discriminant function for smooth newts was on the borderline of statistical significance ($P=0.052$). Values of Wilks' λ are given in Table 4. For frogs, univariate tests (Table 4) indicate that the presence of submerged vegetation in new ponds is associated with frog presence, for all sites and for the reduced data set excluding sites of introduction. Correlation between the original variables and those of the canonical discriminant function (Table 5) also indicate the importance of submerged vegetation. Pond age is a significantly different factor using all of the pond data for frogs, but this effect disappears when the sites of introduction are removed (Table 4).

For great crested newts, both measures of pond density and also the presence of fish are significantly different between occupied and unoccupied ponds (Ta-

TABLE 4. Values of Wilks' lambda (λ) for discriminant functions separating occupied from unoccupied ponds for *Rana temporaria*, *Bufo bufo*, *Triturus cristatus* and *T. vulgaris*. F values for univariate tests are given for significantly different variables for *Rana temporaria* (all ponds and ponds excluding sites of introductions) and *Triturus cristatus*. Age = pond age, fish = fish present, PPD = pond density within a 1-km radius, PD = pond density within a 2-km radius, SV = submerged vegetation. NS, $P>0.05$; * $P<0.05$; ** $P<0.01$; *** $P<0.001$.

	Wilks' λ	df	Statistics
<i>R. temporaria</i>	0.669	11	$\chi^2=28.3^{**}$
SV	0.897	1,76	$F=8.74^{**}$
Age	0.926	1,76	$F=6.06^*$
(no introductions)	0.658	11	$\chi^2=22.8^*$
<i>B. bufo</i>	0.781	11	$\chi^2=17.4$ NS
<i>T. cristatus</i>	0.690	11	$F=26.21^{**}$
PD	0.872	1,76	$F=11.19^{***}$
Fish	0.885	1,76	$F=9.88^{**}$
PPD	0.948	1,76	$F=4.15^*$
<i>T. vulgaris</i>	0.758	11	$\chi^2=19.5$ NS

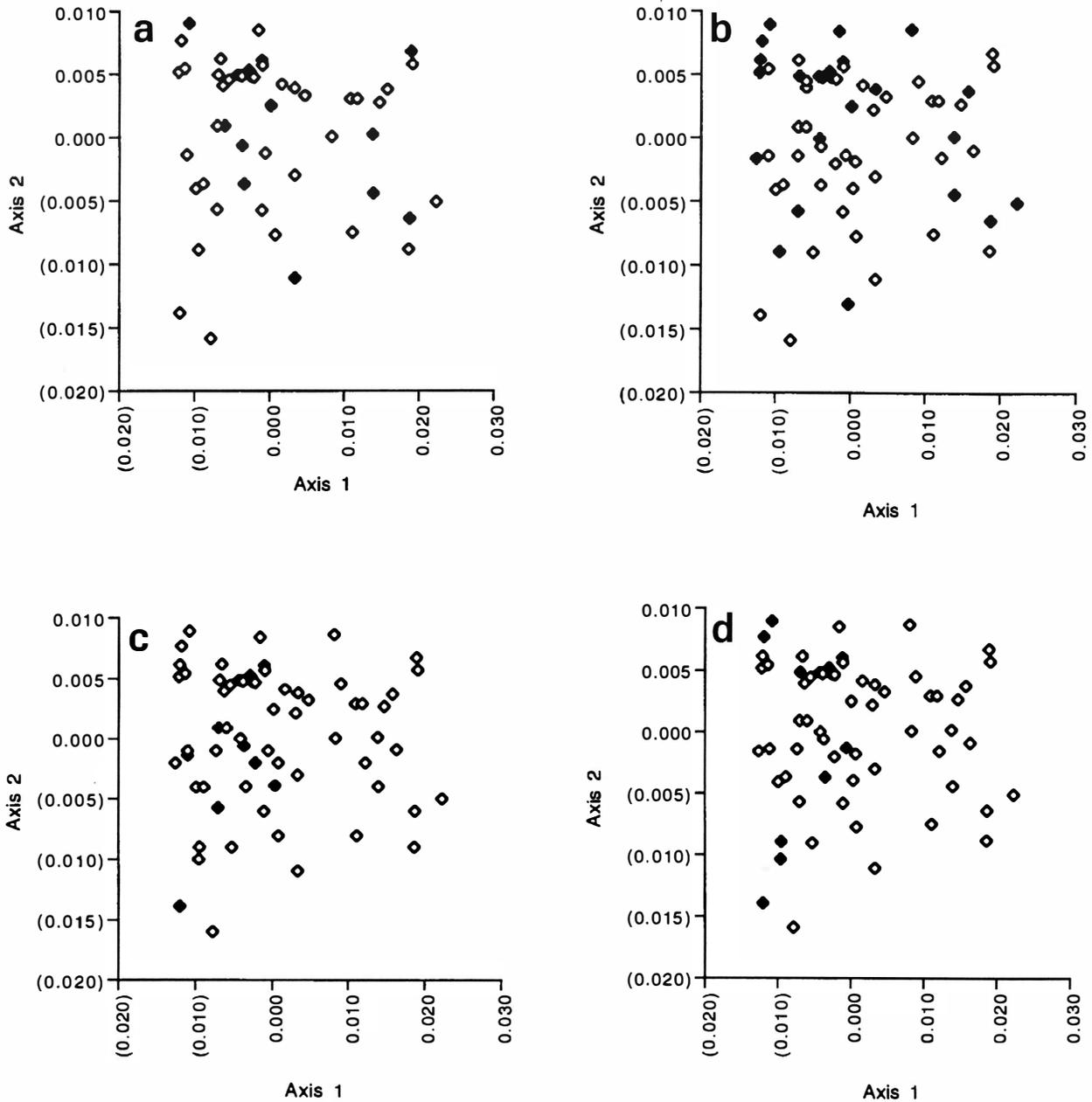


FIG. 3. The distribution of amphibian presence overlaid onto principal component analysis plots of vectors 1 and 2. (a) *Rana temporaria*, (b) *Bufo bufo*, (c) *Triturus cristatus*, and (d) *Triturus vulgaris*. Filled diamonds: present; open diamonds: absent.

TABLE 5. Pooled within-groups correlations between discriminating variables and standardized canonical discriminant function variables for the four largest correlation values, presented in decreasing order of size. *Rt* = *Rana temporaria* (all pond data), *Rt* (no intros.) = *Rana temporaria* (excluding sites of introduction), *Bb* = *Bufo bufo*, *Tc* = *Triturus cristatus*, *Tv* = *Triturus vulgaris*.

<i>Rt</i>		<i>Rt</i> (no intros.)		<i>Bb</i>		<i>Tc</i>		<i>Tv</i>	
SV	0.483	SV	0.466	Wood	0.532	PD	0.572	NN	0.840
Age	0.402	Fowl	0.344	PD	-0.509	Fish	-0.537	Size	0.436
B	0.261	Rip	0.280	Fowl	0.481	PPD	0.348	PPD	-0.233
Rip	0.224	Age	0.252	Fish	0.334	Fowl	-0.305	Rip	-0.216

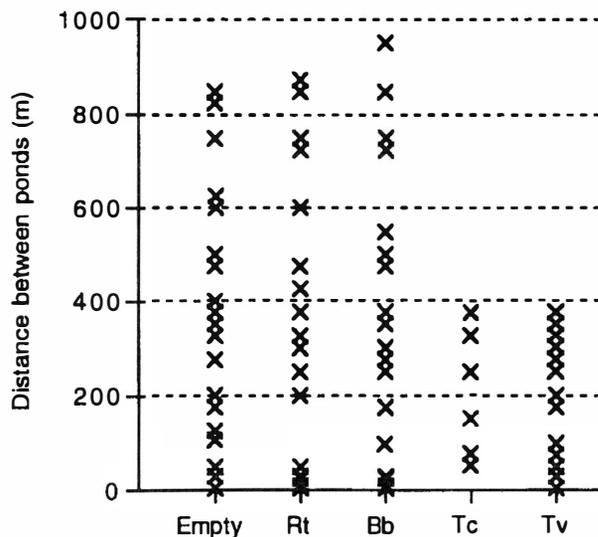


FIG. 4. The distance between old and newly constructed ponds that were either devoid of amphibians (Empty) or occupied by *Rana temporaria* (Rt), *Bufo bufo* (Bb), *Triturus cristatus* (Tc) or *Triturus vulgaris* (Tv).

ble 4). Great crested newts were most likely to colonize fish-free ponds in areas of high pond density. For smooth newts, although the discriminant function is marginally not significant, the distance to the nearest neighbouring pond is the variable most strongly correlated with the discriminant function (Table 5). New ponds colonized by smooth newts tended to be closer to the nearest neighbouring pond than those that were not colonized.

DISCUSSION

The old ponds surveyed seem typical of ponds found on agricultural land in England, in terms of amphibian occupancy and size. Cooke (1975) found frogs and toads in 33-36% and 22-35%, respectively, of ponds in agricultural areas; and the National Amphibian Survey (Swan & Oldham, 1993) found frogs, toads, great crested and smooth newts in 47, 33, 18 and 27%, respectively, of field ponds. The median size of field ponds (length x width) in the National Amphibian Survey (300 m²) was similar to the area of old ponds in the present study (250 m²). However, it cannot be assumed that the present study is representative of all farmed areas: regional variations exist in the pattern of amphibian occupancy of ponds in agricultural areas (e.g. Beebee, 1981).

The new ponds surveyed in this study were clearly different in nature from older ponds on farmland. This difference in part reflects the function of the ponds. It was not possible to determine the original purposes of the long-established ponds, but many ponds in the British countryside were constructed as water sources for livestock (Oldham & Swan, 1997). The new ponds surveyed were constructed for aesthetic reasons, to enhance wildlife habitat and for recreational and business purposes consistent with contemporary rural pursuits (rearing fish, angling and wildfowling). Hence the new ponds more frequently supported populations

of fish (54%) and were heavily used by waterfowl (46%). Many of them were also much larger than old ponds. Although it is impossible to disentangle the confounding effects of age and size between the two groups of old and new ponds, discriminant analyses indicated that within the sample of new ponds neither of these factors was related to amphibian presence.

Although overall amphibian occupancy of old and new ponds was similar, the species composition between the pond types differed. Frogs and smooth newts were the most commonly found amphibians in old ponds (both species found in 39% of ponds), whereas in new ponds toads were the most commonly found species (40%). Occupancy of new ponds tended to be lower for frogs (26%) and significantly so for great crested and smooth newts (9 and 23%, respectively). The differing successes of the four amphibians in new ponds on farm land reflects their dispersal abilities and also the functions of the new ponds. Frogs and toads were able to colonize ponds with nearest neighbouring ponds up to 950 m away. Since the pond densities in this study area were such that the nearest neighbouring ponds were always found within a distance of 950 m, new ponds always fell within anuran colonization range. This relatively effective dispersal ability of common frogs and toads is consistent with data collected by Sinsch (1991) and Beebee (1997), except that Beebee found that frogs were more frequently found in new ponds than were toads. The reverse was true in the present study, demonstrating a greater dispersal ability for toads than found at other sites in north-western Europe (Reading *et al.*, 1991).

Newts colonized new ponds only at sites where the nearest neighbouring pond was within 400 m. This does not imply that 400 m is the maximum migratory distance from the pond of origin, but it does suggest that 400 m is an upper limit to the effective colonization distance between ponds in this particular agricultural landscape over a relatively short time-scale. In other areas newts have been found at greater distances from their ponds of origin (up to 800 m in *Triturus vulgaris* [Simms, 1969]). Amphibian colonization abilities are not absolute. Variation in the migratory limits and colonization success between study areas may be due to differences in the nature of terrestrial habitat between ponds (Reh & Seitz, 1990, Sjögren-Gulve & Ray, 1996) and also the nature of the ponds themselves. The new ponds in the present study were diverse in function and size while other studies have focused on ponds excavated more specifically for wildlife and landscape conservation (Beebee, 1997; Stumpel & van der Voet, 1998).

Many new ponds in the present study were either created specifically for, or supported, fish and/or waterfowl. Fish and waterfowl ponds were favourable for anurans but not so for newts. Fish ponds were never used by great crested newts. The positive association between fish and toads, and the converse for great crested newts has been noted in previous pond surveys (Beebee, 1979; Beebee, 1981; Dolmen, 1982; Beebee,

1985) and the differing abilities of all four amphibians to coexist with predatory fish are well-substantiated. Toad larvae are distasteful to fish (Glandt, 1984) and shoaling may also reduce the frequency of attacks (Watt *et al.*, 1997). The cryptic coloration and avoidance behaviour of frog larvae (Manteifel, 1995) may serve to keep them in microhabitats inaccessible to fish. During the present study frog larvae in trout lakes were found only in dense weed beds. Differences in the behaviour of the newt larvae explain their relative coexistences with fish; smooth newt larvae are benthic, whereas great crested newt larvae are nektonic (Dolmen, 1983), making the latter more vulnerable to fish predation.

The lack of detectable effects of terrestrial habitat, with the exception of neighbouring ponds, on amphibian colonization of new ponds is in contrast to the findings of Beebee (1985), Laan & Verboom (1990), Pavignano *et al.* (1990), and Swan & Oldham (1993). It is possible that terrestrial habitat effects were not detected because the quantification technique used in the present study was not sufficiently sensitive. Alternatively, the mixed farm land surrounding the new ponds may have provided sufficient habitat diversity such that land surrounding all new ponds was equally likely to support amphibian populations. Swan & Oldham (1993) discovered a similar trend, in that although terrestrial habitat did affect amphibian presence in ponds, within a land-use type containing a diverse habitat, habitat features were less predictive of amphibian presence.

The present study showed that amphibians are readily able to colonize new ponds on mixed farmland. However, the issue of whether amphibian presence is a measure of pond quality (Oldham & Swan, 1997) needs consideration. In Britain, areas that are species rich for a particular taxon are not necessarily so for other taxa, and species of high conservation interest do not necessarily occupy areas that are biologically diverse (Prendergast *et al.*, 1993). This may also apply at the finer scale of ponds. For example, in ponds, plant species richness does not correlate with coleopteran diversity (Wilkinson & Slater, 1995). In the present study, although new ponds were frequently colonized by toads, this does not necessarily reflect pond quality. Fourteen (18%) of the new ponds contained no submerged vegetation and presumably were of limited wildlife value. However, toads were breeding in six of these unvegetated new ponds. Future amphibian survey work will be of wider conservation interest if the relationships between amphibian presence and other measures of biological diversity or pond quality are investigated.

The data from the present study are representative of amphibian abundance and colonization abilities in an area of mixed farm land supporting a diverse range of new ponds. They suggest that, within similar land-

scapes, new ponds on farm land can provide suitable habitat for amphibian populations, particularly anurans. However, to benefit newts, some specifications are recommended. Ponds intended to benefit newt populations should not be stocked with fish and it may also be beneficial to avoid heavy waterfowl use of such ponds. In situations where the latter two interests are the objective of pond creation schemes, wildlife agents should advocate the construction of secondary ponds, set aside to benefit native species. New newt ponds should also be sited within 400 m of existing newt ponds. This seems to differ from Swan & Oldham's (1993) recommendation of one suitable pond per km². However, the closer pond proximity represents a distance over which newts have rapidly colonized new ponds; the pattern of pond occupancy reported by Swan & Oldham may have taken longer to develop.

A pond construction programme, based around a strategy of creating areas with relatively small interpond distances is also likely to benefit other species; areas of higher pond density are associated with greater plant diversity (Möller & Rördam, 1985). A proactive conservation strategy for great crested newts, based on maintaining and creating areas of high pond densities, could use this legally protected amphibian as an umbrella species, under which other pond organisms could benefit. Such a strategy is also consistent with current ideas concerning the creation of new ponds for wildlife (Williams *et al.*, 1997).

ACKNOWLEDGEMENTS

This project was funded by a grant to Tim Halliday from the Agriculture and Food Research Council. We wish to thank Ann Morey for statistical help and advice, and Trevor Beebee, Jim Foster and Anton Stumpel for useful comments on the original manuscript. We would also like to thank the following who have helped with the location of new farm ponds: Jeremy Biggs (Pond Action), Michael Gwilliam (Bedfordshire County Planning Department), Sonia Percival (Northamptonshire Planning and Transportation) and Chris Smith (Buckinghamshire FWAG). We also thank the following landowners for allowing access to ponds: Mr. J. Adams, Michael Adams, David Belcher, Mr. A. Bond, Mr. D. Brace, Philip Burt, Mr. W. Butterfield, Bill Capel, Ken and Jane Clarkson, Ian Clifton, Mr. R. Collins, Mr. and Mrs. J. Cook, Mr. and Mrs. LeCount, Bernard Day, Charles Fitzroy, Robin Garrett, Alan and Liz Goffe, Dr. and Mrs. Harrold, Geoffrey Haywood, the Holt family, Mr. J. Jelley, Mr. and Mrs M. Judge, Peter Knight, Roger Kirton, Michael Marlow, Mr. G. Middleton, Mr. and Mrs. J. Moore, Mr. D. Newman, Lady Pritchard, Mr. J. Robinson, John Smith, George Thame, Brian Tustian. We would like to thank Mr. and Mrs. Christie and Martin Ireson for being so generous in sharing their information on local amphibians and ponds.

REFERENCES

- Banks, B. & Laverick, G. L. (1986). Garden ponds as amphibian breeding sites in a conurbation in the north east of England (Sunderland, Tyne and Wear). *The Herpetological Journal* **1**, 44-50.
- Barr, C. J., Howard, D. C. & Benefield, C. B. (1994). *Countryside Survey 1990. Inland water bodies*. London: Department of the Environment.
- Beebee, T. J. C. (1979). Habitats of the British Amphibians (2): Suburban parks and gardens. *Biological Conservation* **15**, 241-257.
- Beebee, T. J. C. (1981). Habitats of the British Amphibians (4): agricultural lowland and a general discussion of requirements. *Biological Conservation* **21**, 127-139.
- Beebee, T. J. C. (1985). Discriminant analysis of amphibian habitat determinants in South-East England. *Amphibia-Reptilia* **6**, 35-43.
- Beebee, T. J. C. (1997). Changes in dewpond numbers and amphibian diversity over 20 years on chalk downland in Sussex, England. *Biological Conservation* **81**, 215-219.
- British Herpetological Society (1990). *Surveying for amphibians: a practical guide*. London: British Herpetological Society.
- Cooke, A. S. (1975). Spawn site selection and colony size of the frog (*Rana temporaria*) and the toad (*Bufo bufo*). *Journal of Zoology, London* **175**, 29-38.
- Cooke, A. S. & Frazer, J. F. D. (1976). Characteristics of newt breeding sites. *Journal of Zoology, London* **178**, 223-236.
- Cooke, A. S. & Scorgie, H. R. A. (1983). *The status of the commoner amphibians and reptiles in Britain*. Huntingdon: Nature Conservancy Council.
- Denton, J. S. (1991). The distribution and breeding site characteristics of newts in Cumbria, England. *Herpetological Journal* **1**, 549-554.
- Dolmen, D. (1982). Zoogeography of *Triturus vulgaris* (L.) and *T. cristatus* (Laurenti) (Amphibia) in Norway, with notes on their vulnerability. *Fauna Norv. Ser. A* **3**, 12-25.
- Dolmen, D. (1983). Diel rhythms and microhabitat preference of the newts *Triturus vulgaris* and *Triturus cristatus* at the northern border of their distribution area. *Journal of Herpetology* **17**, 23-31.
- Edenhamn, P. (1996). Spatial dynamics of the European tree frog (*Hyla arborea* L.) in a heterogeneous landscape. Doctoral dissertation. Swedish University of Agricultural Sciences, Uppsala, Sweden.
- Gill, D. E. (1978). The metapopulation ecology of the red-spotted newt, *Notophthalmus viridescens* (Rafinesque). *Ecological Monographs* **48**, 145-166.
- Glandt, D. (1984). Laboratory experiment on the prey-predator relationship between three-spined sticklebacks, *Gasterosteus aculeatus* L. (Teleostei), and common toad larvae, *Bufo bufo* (L.) (Amphibia). *Zoologisches Anzeiger, Jena* **213**, 12-16.
- Griffiths, R. A., Raper, S. & Brady, L. (1996). *Evaluation of a standard method for surveying common frogs (Rana temporaria) and newts (Triturus cristatus, T. helveticus and T. vulgaris)*. Report number 259. Peterborough: Joint Nature Conservation Committee.
- Hanski, I. & Gilpin, M. (1991). Metapopulation dynamics: brief history and conceptual domain. *Biological Journal of the Linnean Society* **42**, 3-16.
- Hecnar, S. J. & McCloskey, R. T. (1996). Amphibian species richness and distribution in relation to pond water chemistry in south-western Ontario, Canada. *Freshwater Biology* **36**, 7-15.
- Hecnar, S. J. & McCloskey, R. T. (1997). Spatial scale and determination of species status of the green frog. *Conservation Biology* **11**, 670-682.
- Hilton-Brown, D. & Oldham, R. S. (1991). *The status of the widespread amphibians and reptiles in Britain, 1990, and changes during the 1980's*. Focus on Nature Conservation No. 131. Peterborough: Nature Conservancy Council.
- Hitchings, S. P. & Beebee, T. J. C. (1998). Loss of genetic diversity and fitness in common toad (*Bufo bufo*) populations isolated by inimical habitat. *Journal of Evolutionary Biology* **11**, 269-283.
- Ildos, A. S. & Ancona, N. (1994). Analysis of amphibian habitat preferences in a farmland area (Po plain, northern Italy). *Amphibia-Reptilia* **15**, 307-316.
- Jefferies, M. (1991). The ecology and conservation value of forestry ponds in Scotland, United Kingdom. *Biological Conservation* **58**, 191-211.
- Laan, R. & Verboom, B. (1990). Effects of pool size and isolation on amphibian communities. *Biological Conservation* **54**, 251-262.
- Levins, R. (1969). Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bulletin of the Entomological Society of America* **15**, 237-240.
- Manteifel, Y. (1995). Chemically-mediated avoidance of predators by *Rana temporaria* tadpoles. *Journal of Herpetology* **29**, 461-463.
- Marnell, F. (1998). Discriminant analysis of the terrestrial and aquatic habitat determinants of the smooth newt (*Triturus vulgaris*) and the common frog (*Rana temporaria*) in Ireland. *Journal of Zoology, London* **244**, 1-6.
- McCullough, D. R. (1996). *Metapopulations and wildlife conservation*. Washington, DC: Island Press.
- Möller, T. R. & Rördam, C. P. (1985). Species numbers of vascular plants in relation to area, isolation and age of ponds in Denmark. *Oikos* **45**, 8-16.
- Oldham, R. S. & Swan, M. J. S. (1997). Pond loss and amphibians; historical perspective. In British Pond Landscapes. Proceedings of the UK Conference of the Pond Life Project, 3-16. Boothby, J. (Ed.),
- Pavignano, I., Giacoma, C. & Castellano, S. (1990). A multivariate analysis of amphibian habitat determinants in north western Italy. *Amphibia-Reptilia* **11**, 311-324.

- Prendergast, J. R., Quinn, R. M., Lawton, J. H., Eversham, B. C. & Gibbons, D. W. (1993). Rare species, the coincidence of diversity hotspots and conservation strategies. *Nature* **365**, 335-337.
- Reading, C. J., Loman, J. & Madsen, T. (1991). Breeding pond fidelity in the common toad, *Bufo bufo*. *Journal of Zoology, London* **225**, 201-211.
- Reh, W. & Seitz, A. (1990). The influence of land use on the genetic structure of populations of the common frog *Rana temporaria*. *Biological Conservation* **54**, 239-249.
- Savage, R. M. (1961). *The ecology and life history of the common frog*. London: Pitman.
- Simms, C. (1969). Indications of the decline of breeding amphibians at an isolated pond in marginal land, 1954-1967. *British Journal of Herpetology* **4**, 93-96.
- Sinsch, U. (1991). Mini-review: the orientation behaviour of amphibians. *The Herpetological Journal* **1**, 541-544.
- Sjögren-Gulve, P. (1994). Distribution and extinction patterns within a northern metapopulation of the pool frog, *Rana lessonae*. *Ecology* **75**, 1357-1367.
- Sjögren-Gulve, P. & Ray, C. (1996). Using logistic regression to model metapopulation dynamics: large-scale forestry extirpates the pool frog. In *Metapopulations and Wildlife Conservation*, McCullough (Ed). Washington DC: Island Press.
- Stott, A. P., Parr, T. W., Barr, C. J., Bunce, R. G. H., Fuller, R. M. & Furse, M. (1993). *Countryside Survey 1990 Summary Report*. London: Department of the Environment.
- Stumpel, A. H. P. & van der Voet, H. (1998). Characterizing the suitability of new ponds for amphibians. *Amphibia-Reptilia* **19**, 125-142.
- Swan, M. J. S. & Oldham, R. S. (1993). *Herptile Sites, Volume 1: National Amphibian Survey Final Report*. Research Reports No. 38. Peterborough: English Nature.
- Warwick, T. (1949). The colonisation of bomb-crater ponds at Marlow, Buckinghamshire. *Journal of Animal Ecology* **18**, 137-141.
- Watt, P. J., Nottingham, S. F. & Young, S. (1997). Toad tadpole aggregation behaviour: evidence for a predator avoidance function. *Animal Behaviour* **54**, 865-872.
- Wilkinson, D. M. & Slater, F. M. (1995). Relationship between plant and invertebrate richness in upland ponds in Mid Wales. *Naturalist* **120**, 103-108.
- Williams, P., Biggs, J., Corfield, A., Fox, G., Walker, D. & Whitfield, M. (1997). Designing new ponds for wildlife. *British Wildlife* **8**, 137-150.

Accepted: 28.10.98