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# Breeding pond fidelity in the common toad, *Bufo bufo*

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(With 2 figures in the text)

Two independent studies of adult common toad, *Bufo bufo*, movements between different spawning ponds/populations both within and between years were made in England and Sweden during the spring breeding periods of 1987–1990. The results of the two studies were subsequently combined since they were found to be complementary. In addition, in England during 1984 and 1985, large numbers of 'toadlets' were marked so that they could be identified if recaptured as breeding adults.

The degree of relocation between ponds was negatively correlated to the distance between ponds. The proportion of both males and females that moved between ponds within a particular year was significantly less than the proportion relocating between years. In any year, between 79% and 96% of adults that survived to breed the following year, returned to the original pond. Similarly, of the toadlets marked during 1984–85, 81% of the males that subsequently returned as breeding adults were captured in their pond of origin.

Isolation, in relation to both population dynamics and population genetics, is defined and its implications for the management of common toad populations discussed.

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## Introduction

Although adult common toads (*Bufo bufo*) have been shown to be relatively sedentary during the summer months and also to return, after hibernation and spawning, to within a few metres of a



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previous summer territory (Haapanen, 1974) nothing, other than anecdotal accounts, is known about their apparent fidelity to a particular spawning pond. Similarly, nothing is known about the dispersion from, or loyalty to, any particular 'natal' pond.

In an attempt to investigate the within and between year movements (immigration and emigration) of adult common toads between different spawning ponds/populations, two independent studies were made in England and Sweden during the spring breeding periods of 1987–1990.

The aim of both studies was to quantify the between pond movement of adult toads and to relate this to the distance between ponds so that a definition of what constitutes an isolated pond/population could be found. Such a definition of isolation, with respect to common toads, would then be of use in explaining and/or predicting how their potential for geographical range expansion in response to, for example, climate change might be affected. The following is a joint report of both studies.

## Study sites and methods

We only became aware of each other's research in September 1989 when it became clear that the 2 studies were complementary and so we agreed to combine our results. The methods used to collect the data at each site were not the same and therefore they had to be analysed in a way that would allow for this discrepancy but still produce results that were comparable.

The 2 study areas each contained 4 or 5 ponds of different sizes that were used as breeding sites by common toads. The habitats surrounding the ponds in each area were similar, consisting of mixed coniferous and deciduous woodland and pasture.

In England, the study ponds were located in south Dorset (50° 39′ N, 2° 07′ W) approximately 13 km north of Swanage. All 4 ponds were flooded old clay pits in which the spawning sites were 225–830 m apart (Fig. 1a). Although, at all 4 ponds, the toads were captured by hand during the day, more effort was put into searching for toads in pond LP because this was the site of a long-term study (1980–present) of toad population dynamics. The toads at this site were marked (toe-clipped) to denote the year of capture, whilst those in the remaining 3 ponds were given a pond-specific toe-clip with only the new arrivals each year being identified and counted. All toe-clipping was carried out under licence from the Home Office.

At pond LP in 1984 and 1985, 5158 and 2101 toadlets, respectively, were captured from along the pond edge and toe-clipped, using fine watch-makers' forceps, to denote the year of hatching (and pond of origin) and released. It was not possible to determine the sex of the marked toadlets. During subsequent years all adults captured at all 4 of the study ponds were checked for these specific marks.

The study area in southern Sweden was situated 10 km east of Lund (55° 40′ N, 13° 30′ E) and consisted of 4 ponds connected by a stream and separated by deciduous forest (Fig. 1b). The distance between ponds ranged from 60–300 m. A fifth pond, that was only investigated in 1990, was situated approximately 2 km from the other 4.

The toads were captured by hand at night and were each given a unique combination of toe-clips allowing the movements of every recaptured toad to be determined over the 3 years of the study.

### *Indices of relocation*

In order to compare within-area and between-year movements of toads, a measure of toad movement, or 'index of relocation' (IR) was required, that could be estimated for any pair of ponds and that preferably compensated for pond size.

Therefore, if the assumption is made that the likelihood of a toad moving from a source pond to a recipient pond is independent of recipient pond size, then:

$$IR_1 = M_{sr}/N_s \cdot S \qquad (1)$$

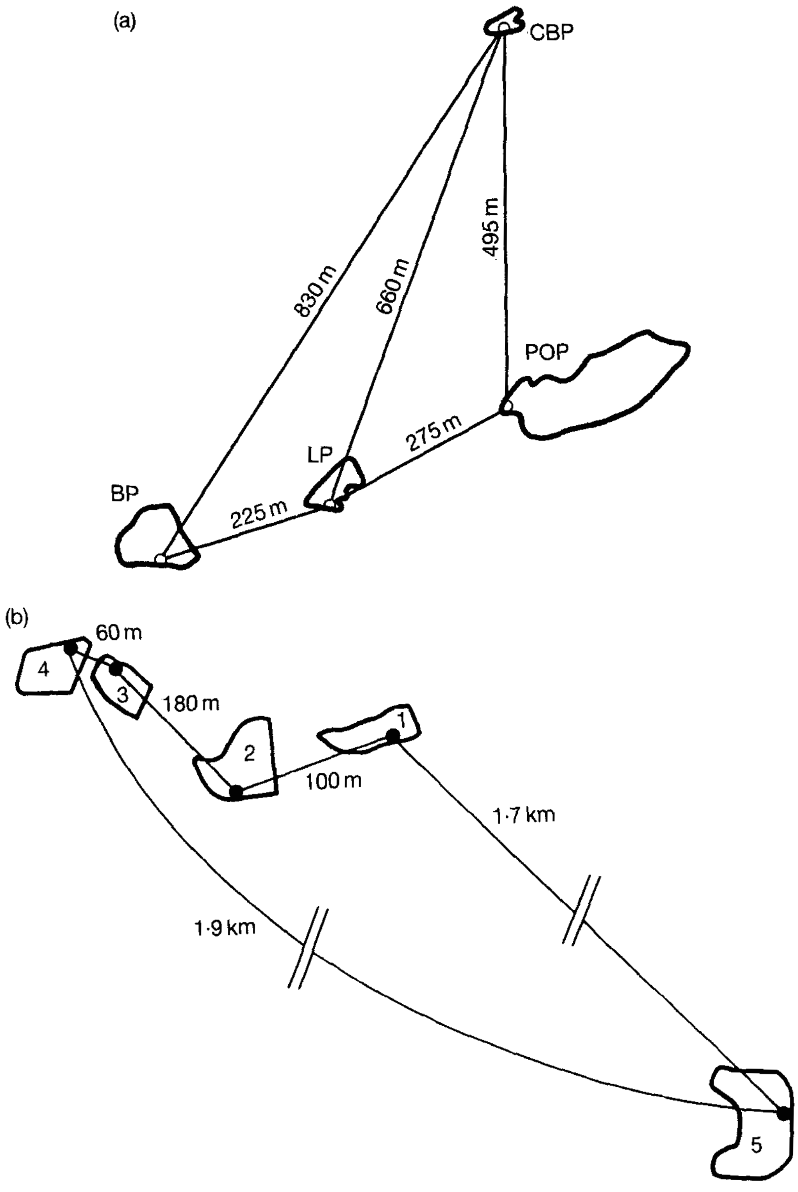


FIG. 1. Diagrammatic maps showing the distances between each of the study ponds at the (a) English and (b) Swedish sites.

is a suitable index of relocation (IR), where $M_{sr}$ is the number of toads that were present in the source pond in year t and that moved to the recipient pond in year t+1; $N_s$ is the total number of toads present in the source pond in year t and S is the survival rate of toads from the source pond between year t and t+1. The index therefore gives the proportion of survivors in the source pond that moved to the recipient pond.

If the assumption is also made that more toads are likely to move to a large pond than to a small pond, then another index of relocation is required that compensates for this, so that only the effect of distance between ponds is measured. One measure of pond size is pond area. However, in this case, it is not an appropriate measure because toads are unlikely to be attracted by overall pond area but rather to the size and suitability of its spawn sites. The best available measure of this is the number of toads that are present in a pond. Thus, for the recipient pond in year t+1:

$$IR_2 = M_{sr}/N_s \cdot N_r \cdot S \tag{2}$$

where $N_r$ is the total number of toads present in the recipient pond in year t+1.

Although it is not usually possible to measure $M_{sr}$ directly, it can be estimated if toads are marked in the source pond in year t and a sample of toads is then captured in the recipient pond in year t+1. Recaptures from the source pond can then be identified:

$$m'sr = n_s \cdot M_{sr}/N_s \tag{3}$$

where m'sr is the number of toads moving from the source pond to the recipient pond that were marked in the *source pond* in year t; $n_s$ is the total number of toads marked in the source pond in year t. In these equations capital letters refer to population values whilst lower case letters refer to sample values. Also:

$$m_{sr} = m'sr \cdot n_r/N_r \tag{4}$$

where $m_{sr}$ is the observed number of toads that moved from the source pond in year t to the recipient pond in year t+1; $n_r$ is the number of toads captured in the recipient pond in year t+1. Thus, from equations 3 and 4:

$$M_{sr} = m_{sr} \cdot N_s \cdot N_r / n_s \cdot n_r \tag{5}$$

Therefore the two indices of relocation are:

From equations 1 and 5:

$$IR_1 = m_{sr} \cdot N_r / n_s \cdot n_r \cdot S \tag{6}$$

From equations 2 and 5:

$$IR_2 = m_{sr} / n_s \cdot n_r \cdot S \tag{7}$$

If the objective is to compare the effects of distance between ponds in the same area in a particular year, then it is reasonable to assume that the adult toad survival rates for each pond are equal and therefore the survival term S can be disregarded in such cases.

If, as in the present study, the objective is to compare the number of adult toads moving between different sites and/or between pairs of years, then it is necessary to include an estimate of site and year specific survival rates. In this case, no information about source pond size is necessary ($IR_2$). The alternative index of relocation, ($IR_1$), requires information about recipient pond/population size.

### *Survival and population sizes*

In Sweden, the $N_r$ and S values used in estimating $IR_1$ and $IR_2$ were obtained from the capture-mark-recapture data. Population sizes (for $N_r$) were obtained separately for each pond, year and sex using a subprogram, of program 'CAPTURE', that corrects for time specific variation in capture rate (White *et al.*, 1982). This results in an algorithm that is corrected for differences in any individual's capture probability between different days. Survival (S) was assumed to be the same for toads in all ponds during one year but assumed to vary between years and sexes. The same program was used to estimate the combined number of toads in ponds 1, 2 and 3 (that were searched in all years) for each sex and year separately. Survival was then estimated as:

Survival = (surviving marked toads/all marked toads in 1st year),

where:

Surviving marked toads = (recaptured marked toads/proportion of toads marked in 2nd year), where:

Proportion of marked toads in 2nd year =
(number of toads captured in 2nd year/estimated number of toads present in 2nd year)

Annual survival rates for the English toads were estimated using the data from pond LP where all toads were marked each year. As in Sweden, survival was assumed to be constant between ponds in any one year but to vary between years and sexes.

## Results

### *Adults*

With the exception of the three English ponds BP, POP and CBP in 1988 and 1989, where only the number of captured new arrivals to each of the ponds could be recognized and counted, the total number of individuals captured per pond was known (Table I). An excess of males over females was found in all ponds in all years, with the English ponds having the largest numbers of toads.

During the three-year study in England, only one toad was captured at more than one pond in the same year. In Sweden, on the other hand, a relatively large number of toads were both captured more than once at different ponds in a particular year and at different ponds during successive years. It was, therefore, important to determine the degree of movement between ponds within a year compared with that occurring between years (Table II).

In Sweden, the mean proportion of males, that, within a year, were captured in more than one

TABLE I

*Total number of adult male and female common toads captured between 1987 and 1990 in England and Sweden at each of the study ponds*

| | Number of toads captured | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | 1987 | | 1988 | | 1989 | | 1990 | |
| Pond | M | F | M | F | M | F | M | F |
| England | | | | | | | | |
| LP | 502 | 264 | 903 | 286 | 687 | 203 | — | — |
| BP | 317 | 122 | 182* | 57* | 197* | 104* | — | — |
| POP | 161 | 73 | 121* | 43* | 133* | 56* | — | — |
| CBP | 204 | 93 | 65* | 59* | 175* | 133* | — | — |
| Sweden | | | | | | | | |
| 1 | 258 | 58 | 204 | 56 | 209 | 35 | — | — |
| 2 | 161 | 46 | 159 | 32 | 150 | 31 | — | — |
| 3 | 73 | 10 | 33 | 3 | 5 | 5 | — | — |
| 4 | — | — | — | — | 175 | 23 | — | — |
| 5 | — | — | — | — | — | — | 96 | 27 |

M male; F female

* These represent the total number of captured new arrivals to a pond and not the overall total number of individuals captured

TABLE II

*Within and between year recaptures of adult toads at ponds 1–3 in Sweden*

| | Within a year | | Between two years | |
|---|---|---|---|---|
| Total number of captures | N | Proportion from different ponds (%) | N | Proportion from different ponds (%) |
| Males | | | | |
| 2 | 247 | 9 | 90 | 17 |
| 3 | 80 | 14 | 94 | 21 |
| 4 | 20 | 10 | 70 | 24 |
| <4 | 9 | 11 | 79 | 26 |
| Females | | | | |
| 2 | 51 | 10 | 15 | 13 |
| 3 | 12 | 0 | 13 | 38 |
| >3 | 4 | 0 | 7 | 26 |

TABLE III

*England: Number of adult toads marked in each pond each year and the annual number of recaptures of marked toads from each of the study ponds*

| | Numbers recaptured/pond | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | LP | | BP | | POP | | CBP | | Numbers not recaptured | |
| Marking pond | 88 | 89 | 88 | 89 | 88 | 89 | 88 | 89 | 87–88 | 88–89 |
| (a) Males | | | | | | | | | | |
| LP | 161 | 223 | 3 | 5 | 2 | 2 | 0 | 0 | 336 | 673 |
| BP | 5 | 3 | * | * | 0 | 0 | 0 | 0 | * | * |
| POP | 6 | 0 | 0 | 0 | * | * | 0 | 0 | * | * |
| CBP | 0 | 1 | 0 | 0 | 1 | 0 | * | * | * | * |
| (b) Females | | | | | | | | | | |
| LP | 51 | 41 | 0 | 2 | 1 | 0 | 0 | 1 | 212 | 242 |
| BP | 2 | 2 | * | * | 0 | 0 | 0 | 0 | * | * |
| POP | 1 | 1 | 0 | 0 | * | * | 0 | 0 | * | * |
| CBP | 2 | 0 | 0 | 0 | 0 | 0 | * | * | * | * |

* In ponds BP, POP and CBP the number of marked toads returning to breed in the same pond were not recorded. In these ponds only the numbers of new arrivals each year were recorded.

pond (10·1%; N = 356; S.E. = 1·6) was significantly lower ($P < 0{\cdot}001$) than the mean proportion that were captured in more than one pond between years (20·1%; N = 333; S.E. = 2·2). Similarly, significantly fewer ($P < 0{\cdot}02$) females were captured from more than one pond within a year than between years. The mean within and between year proportions for females were 7·5% (N = 67;

TABLE IV

*Sweden: Number of adult toads marked in each pond each year and the annual number of recaptures of marked toads from each of the study ponds. None of the 123 toads captured in pond 5 in 1990 (Table V) had been previously marked in any other pond*

| | Numbers recaptured/pond | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | 1 | | 2 | | 3 | | 4 | | Numbers not recaptured | |
| Marking pond | 88 | 89 | 88 | 89 | 88 | 89 | 88 | 89 | 87–88 | 88–89 |
| (a) Males | | | | | | | | | | |
| 1 | 94 | 65 | 5 | 6 | 1 | 0 | * | 1 | 158 | 132 |
| 2 | 4 | 3 | 63 | 52 | 3 | 3 | * | 1 | 91 | 100 |
| 3 | 3 | 1 | 2 | 1 | 4 | 3 | * | 0 | 64 | 28 |
| (b) Females | | | | | | | | | | |
| 1 | 8 | 7 | 1 | 1 | 0 | 0 | * | 0 | 49 | 49 |
| 2 | 3 | 1 | 3 | 7 | 0 | 0 | * | 1 | 36 | 23 |
| 3 | 0 | 0 | 0 | 0 | 0 | 0 | * | 0 | 10 | 3 |

* Not determined

S.E. = 3·2) and 25·7% (N = 35; S.E. = 7·4), respectively. The difference is also clear if the number of captures per toad is controlled for (Table II).

At the four ponds (LP, 1, 2, 3) where data were available, it is clear that by far the highest proportion of both males (England: >96%; Sweden: >89%) and females (England: >93%; Sweden: >79%), that survived to breed the following year, returned to the pond from which they were first caught (Tables III and IV). The data from these ponds also suggested that the number of toads that were subsequently recaptured, from a pond other than their original pond, declined as the distance between the original and recipient pond increased. This is illustrated in Fig. 2 where the two indices of relocation ($IR_1$ and $IR_2$) are plotted against the distance between ponds.

A statistical comparison between male and female relocation rates could only be made using the pooled samples. This was due to the small sample sizes of females from the individual ponds, leading to a bimodal distribution of $IR_1$s and $IR_2$s; zero if no relocating toads were found and comparatively high values if only one or a few were found (Fig. 2). However, the total proportion of toads relocating was similar for both males and females ($\chi^2 = 0{\cdot}32$ and 0·24 for England and Sweden, respectively, Table V).

### *Juveniles*

Out of a total of 7259 toadlets marked over the two years, 83% of the males and 100% of the females that were subsequently recaptured as adults were found in pond LP, the 'natal' pond (Table VI). A small number of males were recaptured at the two ponds nearest to pond LP whilst none was found in the pond furthest from pond LP.

The proportion of the males, marked as juveniles (17%, N = 35), that moved to a pond other

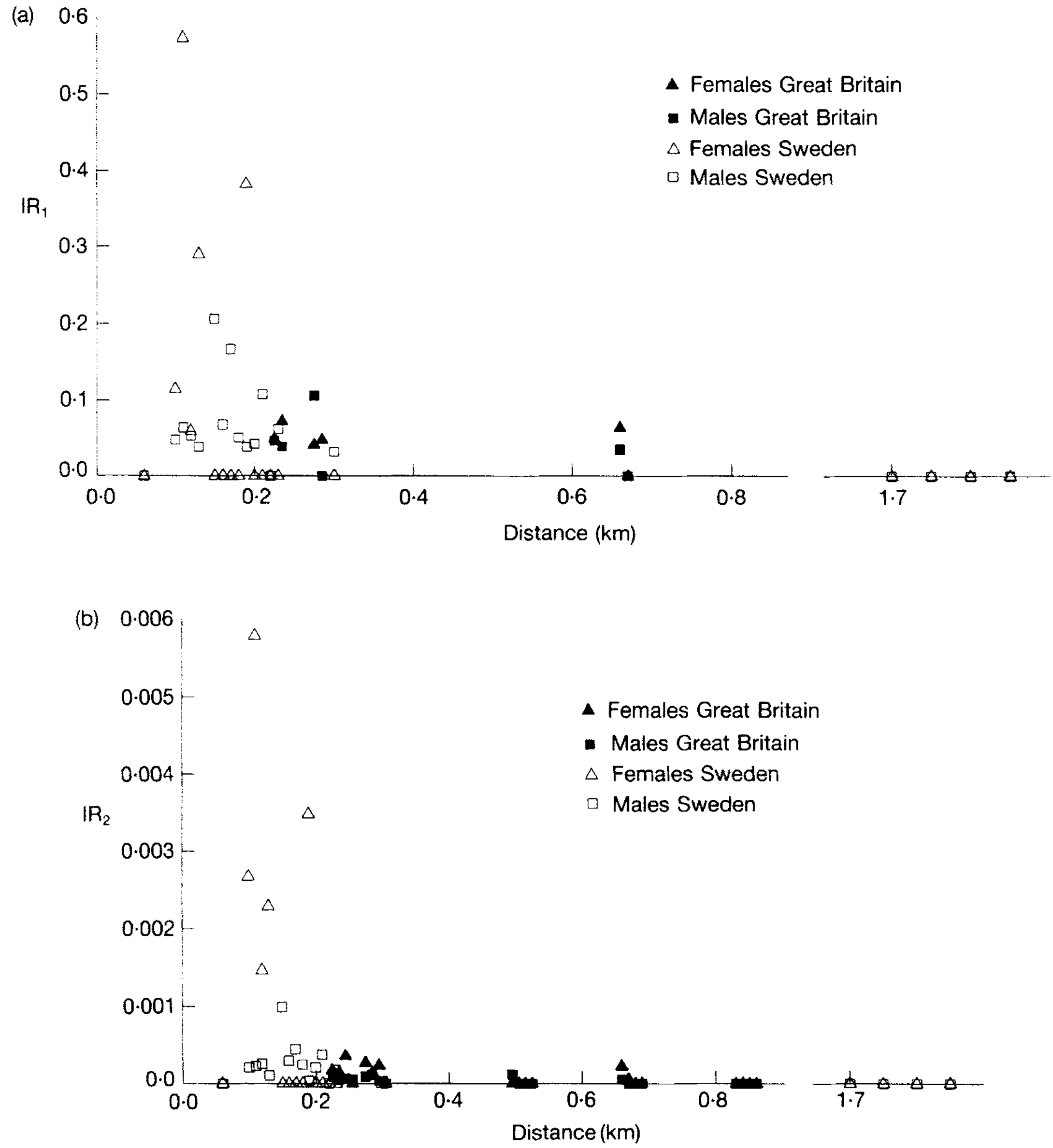


FIG. 2. Indices of relocation (a—$IR_1$; b—$IR_2$), calculated for males and females in England and Sweden, plotted against the distance between ponds.

than their natal pond was significantly higher than the proportion of adult males (3%, N = 396) that relocated ($\chi^2 = 16{\cdot}00$, $d.f. = 1$, $P < 0{\cdot}001$). Although no significant difference was found for females, the number of individuals that were recaptured was too small to allow a meaningful comparison to be made.

TABLE V

*Total proportion of males and females relocating from pond LP in England and ponds 1–3 inclusive in Sweden*

| | Pond | Year | Females % Relocating | Females N | Males % Relocating | Males N |
|---|---|---|---|---|---|---|
| England | LP | 1987–88 | 1·9 | 52 | 3·0 | 166 |
| | | 1988–89 | 6·8 | 44 | 3·0 | 230 |
| Sweden | 1–3 | 1987–88 | 21·1 | 19 | 10·1 | 179 |
| | | 1988–89 | 12·5 | 16 | 10·4 | 134 |

TABLE VI

*England: Number of emergent toadlets from pond LP marked in 1984 and 1985 that were subsequently recaptured as adults at ponds LP, BP, POP and CBP (1984–1989 inclusive)*

| | | No. of marked toadlets recaptured as adults | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | LP | | BP | | POP | | CBP | | Total | |
| Cohort marked | Total no. marked | M | F | M | F | M | F | M | F | M | F |
| 1984 | 5158 | 26 | 5 | 1 | 0 | 3 | 0 | 0 | 0 | 30 | 5 |
| 1985 | 2101 | 3 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 5 | 0 |
| Total | 7259 | 29 | 5 | 2 | 0 | 4 | 0 | 0 | 0 | 35 | 5 |
| % of total returning | | 83 | 100 | 6 | 0 | 11 | 0 | 0 | 0 | | |

M male; F female

## Discussion

### *The two indices*

Although the two indices used in this study were slightly different, the conclusions they each gave rise to remained similar. Index $IR_1$ is more easily interpreted directly since its value refers to the proportion of animals that relocate. However, if different sites are to be compared then it may be judged that not only those aspects related to relocating behaviour *per se* are important, but also those aspects relating to the suitability of the different ponds in an area. This is allowed for by index $IR_2$. The equation used in deriving this index also enables some factors to be cancelled, which in the present study allowed the use of less complete data (compared to $IR_1$). We, therefore, conclude that these indices may prove useful in other comparative studies of migration.

### *Nature of the movements*

Both within and between year movements of toads between ponds were detected. However, in most cases where toads were captured a number of times from different ponds in the same year, they were caught more in one pond than another. This suggests that they were moving through a less favoured pond on their way to a favoured pond when they were caught. Although within-year movements were detected, they were relatively small when compared with the movements that occurred between ponds between years in each of the study areas. This indicates a different cause for the relocations with the simplest explanation being that of a switch of favoured pond.

Our results show that the degree of movement between ponds is mainly related to the distance between them, the greater the distance the less interaction between breeding populations and hence the higher the degree of population isolation.

Although we have shown that adult toads do sometimes visit and breed in more than one pond during their life, the reasons for this are unclear. We suggest three possible explanations which would result in toads occurring in new ponds.

1. A toad, while on its spring migration to a known breeding pond, may encounter a new pond by chance (Moore, 1954).
2. If the conditions in a breeding pond deteriorate, some toads may actively leave and search for a new pond.
3. Some males pair with females on land before reaching the breeding pond (Reading & Clarke, 1983). If a male pairs with a female from a different pond to his own, then he will be passively taken to the female's pond.

### *Consequences of the movements*

The consequences resulting from individual toads moving to new ponds become more apparent if, within a particular habitat containing a number of toad breeding ponds, the toads found in any one pond are considered to represent sub-populations of a larger meta-population. Then, although a sub-population may be essentially self contained with respect to its population dynamics, through dispersal of juveniles or relocation of adults, it nevertheless has the potential to interact with other sub-populations within the meta-population.

An example of this is given by Gill (1978) whose study of the red-spotted newt (*Notophthalmus viridescens*) in the USA showed that adults were totally faithful to their particular breeding pond. In addition, he found that in any one pond breeding adults were not replaced by their own progeny but by individuals from other ponds (sub-populations), and that recolonization of existing ponds, or colonization of new ponds, within the meta-population, was solely the result of juvenile dispersal.

Individual sub-populations may disappear as a result of:

1. Permanent habitat deterioration or
2. Temporary catastrophic events.

In the first case, the sub-population will be lost. In the second case, if the sub-population is part of a meta-population then recolonization of the original pond may occur. It has been shown that a meta-population is more likely to survive for a specified length of time than are an equivalent number of individual isolated populations (Lefkovitch & Fahrig, 1985). Hence, it is important to understand what constitutes either a sub-population or an isolated population.

For the common toad we have shown that sub-population interaction of both adults and juveniles decreases as the distance between ponds increases such that no interaction was found between ponds BP and CBP, a distance of 830 m. With a pond separation of only 300 m, the level of interaction was small enough to reduce significantly the mutual support of sub-populations. Therefore, from a population dynamics point of view, the ponds in this study that were separated by more than 300 m can be considered to be isolated and, therefore, particularly vulnerable.

However, in terms of population genetics, genetic diversity will be maintained if only one individual per sub-population per generation interacts with another sub-population (Maynard Smith, 1989). Therefore, extrapolating from the data shown in Fig. 2 for adults and Table V for juveniles, it is predicted that only ponds/populations separated by more than 830 m do not interact and can therefore be considered to be genetically isolated.

The relevance of these two definitions of isolation can be appreciated when they are viewed in the context of either amphibian conservation management following habitat deterioration/loss, or the potential for geographical range expansion resulting from, for example, beneficial changes in climate or habitat.

If toads are reliant on a combination of both suitable terrestrial conditions for feeding and hibernating and also a habitat that contains a mosaic of suitably spaced breeding ponds, then the deterioration or loss of patches/ponds may result in areas that effectively form barriers to toads in terms of range expansion or sub-population interaction. The eventual loss of the resulting fragmented small meta-populations is, therefore, more likely than is the loss of the larger unfragmented meta-population (Lefkovitch & Fahrig, 1985).

Similarly, if as a result of an improvement in environmental conditions, the area of suitable terrestrial habitat increases, then unless this also includes the formation of suitably spaced breeding ponds, the species will not be able to expand its geographical range.

Common toads are a widely distributed boreal species (Arnold & Burton, 1978) whose habitat is particularly diverse. In this paper, we have attempted to quantify dispersion and define population isolation for toads occurring in mixed coniferous and deciduous woodland in England and Sweden. Although it is likely that both these parameters will vary according to habitat type, the methods given in this paper for measuring the interactions between ponds/populations should nevertheless be relevant to common toads throughout their habitat range.

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