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Sex, isolation and fidelity: unbiased long-distance dispersal in a terrestrial amphibian

M. Alex Smith and David M. Green

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Amphibians in general are considered poor dispersers and thus their dispersal curve should be dominated by short movements. Additionally, as male toads do not compete for females and sexual selection is by female choice, dispersal should be male-biased. Furthermore, since adults are site-loyal and polygynous, juveniles should move farther and faster than adults. We tested the hypotheses that dispersal would be limited and both sex- and age-biased in a population of Fowler's toads *Bufo fowleri* at Lake Erie, Ontario, Canada. Based on a mark-recapture study of 2816 toads, 1326 recaptured at least once, we found that although the toads did show high site fidelity, the dispersal curve was highly skewed with a significant "tail" where the maximum distance moved by an adult was 34 km. Dispersal was neither sex-biased nor age-biased despite clear theoretical predictions that dispersal should be biased towards males and juveniles. We conclude that the resource competition hypothesis of sex-biased dispersal does not predict dispersal tendencies as readily for amphibians as for mammals and birds. Toad dispersal only appears to be juvenile-biased because the juveniles are more abundant than the adults, not because they are the more active dispersers.

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Habitat destruction, fragmentation, and deterioration have resulted in populations of many species becoming patchily distributed across the landscape (Saunders et al. 1991). When a set of populations is patchily distributed over a landscape with significant environmental stochasticity, we expect variance in population persistence in the local habitat patches (Thomas et al. 1996, Green 2003). Yet, species in such landscapes do not simply become extinct. This is because immigrants may rescue populations that have gone locally extinct, or are on the verge of local extinction. Thus, the rate and extent of movement over the landscape is an important predictor of the persistence of the species overall and consequently extinctions cannot be predicted without understanding the movement characteristics and resultant population

size and population level genetic relationships for the animal in question (Petit et al. 2001). For many species, such as plethodontid salamanders (Welsh and Droege 2001), with low variance in demographic characteristics, this "rescue effect" (Brown and Kodric-Brown 1977) may not be noticeable (Green 2003). However, when there is high variance in reproductive success and resources, as in many species of amphibians, the importance of dispersal for population persistence may be high. Indeed, at the population level, dispersal is the source of novelty and resilience that mutation is to the individual, and thus studies of dispersal are as crucial to ecology as estimates of mutation are to genetics. Temperate anuran amphibians often utilize patchily distributed breeding habitat and tend to breed in the

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same ponds year after year (Duellman and Trueb 1986, Sinsch 1990) and thus when there is variation in reproductive success dispersal ability is a critical population parameter. Although the literature for amphibians in general (Sinsch 1990, Blaustein et al. 1994) suggests that any movement is limited and occasional, the dispersal range and frequency of specific amphibian species often is poorly known. Because breeding ponds are both ephemeral and a potentially limiting resource for pond-breeding amphibians (both the aquatic (breeding, feeding etc.) and the terrestrial (hibernation, feeding etc.) aspects of "pond" habitat (Skelly et al. 1999, Marsh and Trenham 2001)), dispersal should in theory be both male- and juvenile-biased (Lomnicki 1988). Indeed, the individual frogs and toads observed to have dispersed the greatest distances often are juveniles (Berven and Grudzien 1990, Bulger et al. 2003).

It is notoriously difficult to track large numbers of individuals accurately enough to determine a dispersal curve (Nathan et al. 2001, Largier 2003, Cain et al. 2003, Gaines et al. 2003). Fowler's toad (*Bufo fowleri* – a medium-sized toad whose adults are 50 to 80 mm from snout to vent, with females slightly larger than males) exists in a landscape with near ideal conditions for measuring dispersal. At Long Point, Ontario, the toads occur along 35 km of virtually uninterrupted beach. Aside from small-scale daily movements between the water's edge and retreats to foreshore dunes, dispersal is one-dimensional, confined to east-west movements parallel to the shoreline. With global positioning system technology, marked and recaptured individuals can be located with great accuracy, enabling movement distances to be determined at both small and large scales.

Although common in the eastern United States, populations of Fowler's toads within Canada are limited to the sandy beaches on the northern shoreline of Lake Erie-isolated from one another by uninhabitable stretches of shoreline development and by the lake itself. As with many pond-breeding amphibians their abundance fluctuates wildly (Green 1997), and we would expect them to be incapable of the long-distance movements necessary to recolonise isolated populations. Thus, estimating extinction risk is intrinsically tied to estimating dispersal potential. Although maximum movements from the literature for *B. fowleri* exist (ranging between 100 and 2000 m (Nichols 1937, Blair 1943, Stille 1952, Ferguson 1960, Clarke 1974, Breden 1987, 1988)), the pattern of movement has not been rigorously quantified for this species. As with many amphibian species, previous measures likely were underestimates of potential movement (Smith and Green 2005).

To date, there is little empirical work regarding the theoretical prediction of sex-biased dispersal in amphibians. Indeed, there is limited evidence to support a recent statement that amphibian dispersal is female-

biased (Palo et al. 2004). Differential competition for resources between the sexes has been implicated in the evolution of dispersal and the maintenance of a sex bias in dispersal. If it is solely inbreeding avoidance that selects for dispersal there should be no sex-bias in dispersal capabilities (Johnson and Gaines 1990). Female-biased dispersal is to be expected when, prior to female selection of males, there is some kind of resource partitioning by males as in monogamously mating birds (resource competition hypothesis – Greenwood 1980). Male-biased dispersal is to be expected when the distribution of males is determined by the distribution of females, not by any a priori resource partitioning (Greenwood 1980). These predictions have been widely supported in birds and mammals, but testing these generalizations with amphibians has yet to be pursued. In general the *Bufo* mating system is polygynous (Wells 1977), and in *B. fowleri* males do not appear to compete for females (Laurin and Green 1990, Green 1992). Sexual selection likely is by female choice (Sullivan 1983, 1992) where females judge males and likely do not breed more than once a year. Therefore, we predicted that with no a priori partitioning of resources, *B. fowleri* would exhibit male-biased dispersal. To test the hypothesis of sex-biased dispersal we compared site-specific and known-point mark-recapture distance records for adult males and females as dispersal frequency distributions (dispersal curves i.e. Nathan et al. 2001).

Toad mortality rates, high at all life stages, are greatest during early life (Type III survivorship curve) predicting that pre-sexual animals should move farther, faster, and more frequently than adults, assuming resource limitations (Hamilton and May 1977). Indeed, dispersal in anurans, and in many vertebrates, is usually attributed to the young. Dole (1968, 1971) noted that the longest distances recorded by *Rana pipiens* were by juvenile frogs and that connections between populations likely were made by juveniles rather than adult frogs. Schroeder (1976) documented that most between-population movement is accomplished by immature *Rana clamitans*. Sjögren Gulve (1998) observed that while only 1% of adult *Rana lessonae* dispersed between localities, 35% of juveniles dispersed to neighboring ponds. Bulger et al. (2003) invoked the importance of juvenile dispersal, yet never observed this. We tested the hypothesis of age-biased dispersal by comparing dispersal distances of known-age animals and comparing the frequency distributions of movement rates for known-point mark-recapture distance records for adult males and females, pre-sexual animals (juveniles) and pre-hibernation toadlets (metamorphs).

Each hypothesis tested here is dependant on the assumption that we can accurately measure long-distance dispersal events on the scale of our study site. Yet, even if movement is limited, animals can emigrate outside the study site. Since such individuals cannot be

recaptured, the animal's capability of long-distance movement is not properly estimated. To determine whether our estimate of the kurtosis of the movement frequency distribution was biased by the size of our study site, and test that we had not underestimated the long-distance movements of *B. fowleri*, we considered three methods to correct for this bias – two analytical and one simulation.

Materials and methods

(a) Mark-recapture

We studied *B. fowleri* at Long Point, Ontario (Fig. 1), a 35 km long sand spit and dune formation that lies approximately east-west on the north shore of Lake Erie (42°34'37"N, 080°26'24"W). Each year, beginning in late April, adult toads in the study area were found, hand-captured, marked, and recorded. Estimates of total population size based on recaptures suggest that 70–100% of the adult male toads were captured each year (Green unpubl.). All study sites were inspected nightly from late April until late June (a period extending both earlier and later than the breeding season at our locality). The position of each individual was recorded by site (Fig. 1) from 1988 to 2000, by global positioning system (GPS –Garmin II+) in 2001, and using differentially corrected GPS in 2002–2003 (DGPS –Garmin II+ with GBR23 differential correction beacon). Toads were measured (snout-vent length), sexed, and a unique combination of toes was clipped to allow for the identification of individual animals (Green 1992). Phalanges were stored in 10% buffered formalin and were used in skeletochronological estimates of age on individuals captured in 1994, 1995, and 1997–1999 (Kellner and Green 1995). Although toe clipping can potentially

reduce the survivorship of individuals and therefore the recapture rate (Clarke 1972, Parris and McCarthy 2001, May 2004, McCarthy and Parris 2004, Funk et al. 2005), we observed no reduction in recapture rate between individuals with an increasing number of clipped toes (Smith and Green unpubl.). The movements of 227 known-age animals (23 females, 204 males) were grouped by sex and age classes (1–5 yr old). Female toads are inconspicuous and spend less time than males at breeding sites (Green 1997). Much of these data were generated while the animals were breeding so it is to be expected that the total number of females captured will be less than males. On the beach, foraging males and females have equivalent capture probabilities. For more specific details regarding field methodology see Green (1992, 1997).

In 2002, we individually marked 421 juveniles using only non-additive toe-clips (i.e. no more than one toe per appendage was clipped). Although some individuals may achieve sexual maturity in their first year, others may not do so until the age of 3. All juveniles were captured and released on the Thoroughfare Unit at Long Point, Ontario. In August of 2003, we similarly marked 70 recently transformed individuals at James N. Allan Provincial Park (42°50'27.6"N, 079°32'49.2"W). In each case, we calculated the distance and the movement rate between all captures, and between initial and final capture for each individual. The frequency distribution of these observations was transformed to a percentage and then compared to the equivalent data (DGPS recorded recaptures) for adult males and females collected in 2001 and 2002.

For each recaptured animal the distance, time, and direction between captures was calculated and the statistical properties of the movement frequency distributions were determined using a Kruskal-Wallis test (Sokal and Rohlf 1995). We tested the hypothesis that the movement distribution was normal using Lilliefors' test for normality, and estimated the kurtosis and symmetry of the distribution.

The movement frequency data were compared to exponential and power models. The significance of each model was calculated by regression analysis of $\ln(\text{frequency} + 1)$ vs distance and $\ln(\text{frequency} + 1)$ vs $\ln(\text{distance})$ respectively. Statistical comparisons were made using Systat (v 9), and Matlab (v 6.12).

(b) Testing limits of the study site

Habitat exists to the east and west of the study site, and it is possible that animals captured near the eastern and western perimeters were not recaptured because they had moved off the site. We have used three methods to estimate the effect that these missed individuals would have upon our measurement of the movement frequency

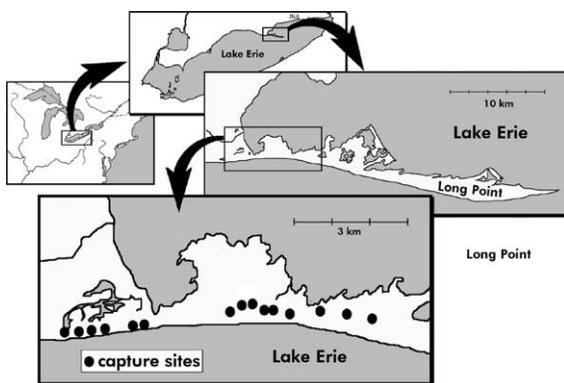


Fig. 1. Fowler's toad breeding localities (capture sites) monitored nightly at the base of Long Point, Ontario Canada. Location of James N. Allan Provincial Park (JNA) is also marked. The Thoroughfare Unit of the Canadian Wildlife Services is the area from the margin of the foremost box to the easternmost site.

distribution. The first was simply to restrict analysis to those animals first captured in the centre of the study site, thereby increasing the likelihood of recapture.

The second method adjusted the observed frequency distribution according to the probability that the dispersal was contained within the study site (Barrowclough 1978), defined for R (radius of study site), r (distance from site centre to capture point), and x (distance from capture to recapture). When $0 < r < R - x$, the probability is 1, and when $R > r > R - x$ the probability (p) is described by:

$$p = \frac{\left(\frac{\pi - \cos^{-1} [R^2 - x^2 - r^2]}{2xr} \right)}{\pi} \quad (1)$$

Each x has an associated correction. For each 100 m distance category, the total number of animals observed was divided by the average correction factor associated for movements in that category to give the corrected distribution.

The third method we developed was “idealized site” (IS), based on Baker et al. (1995) and written in Matlab (v 6.12). We considered the network of habitat patches described here (Fig. 1) which is roughly linear without habitat to the north or south but with habitat to the east and west. These areas were occasionally surveyed, but the study site was too large to allow frequent regular visits to all areas. We mirrored the observed landscape of toad breeding habitats to the east and west creating a hypothetical transect of 25 km with 56 habitat patches to estimate the dispersal events we might see if our study transect was extended in each direction. Within this new transect containing our actual and hypothetically added sites, we considered all actual dispersal events (of distance i), that originated from an actual site j . Around each event, we described a circle with radius i . In reality dispersal event i originating at j was observed in one direction (observed). Assuming that all endpoints are equi-probable, that movement event was equally likely to have occurred in the opposite direction (alternate). We let x represent the number of observed sites covered by distance i . For that same distance event, we let y equal the number of sites in the alternate direction. Thus, the probability of observing an equivalently sized dispersal event, in the direction opposite what actually occurred, is $y/(x+y)$. The average of these values grouped by equivalently sized dispersal events was the IS correction factor. Dividing the observed frequency of the dispersal event by this factor estimates the animals missed by the structure of the study site. The methodology assumes that all endpoints are equi-probable, and this allows the use of averages.

Results

(a) Mark-recapture

We marked 2200 adults and 410 juveniles at Long Point between 1990 and 2002; of these 986 and 260, respectively, were recaptured at least once. At James N. Allan Provincial Park, 101 adults and 70 metamorphs were marked with 38 and 42 recaptured at least once. Overall, 2816 toads were marked and of these 1326 were recaptured at least once.

While nearly 70% of recaptured toads (536 of 736 between site recaptures male and female combined) were within 100 m of their initial capture site, ca 2% of the animals marked (12) moved the maximum distance of the Long Point habitat patches (Fig. 1 and 2). The dispersal curves were highly skewed leptokurtic (kurtosis = 79.74, skewness = 8.81), and were neither normal (Lilliefors’ test = 1) nor exponential. An inverse power relationship explained 63% of the observed variation in the movement frequency when recaptures were measured for adults with DGPS (Table 1). There was no significant difference between the movement distance frequencies of adult males and females (Mann Whitney $U = 3939$, $DF = 1$, $p = 0.099$). Only 11% of

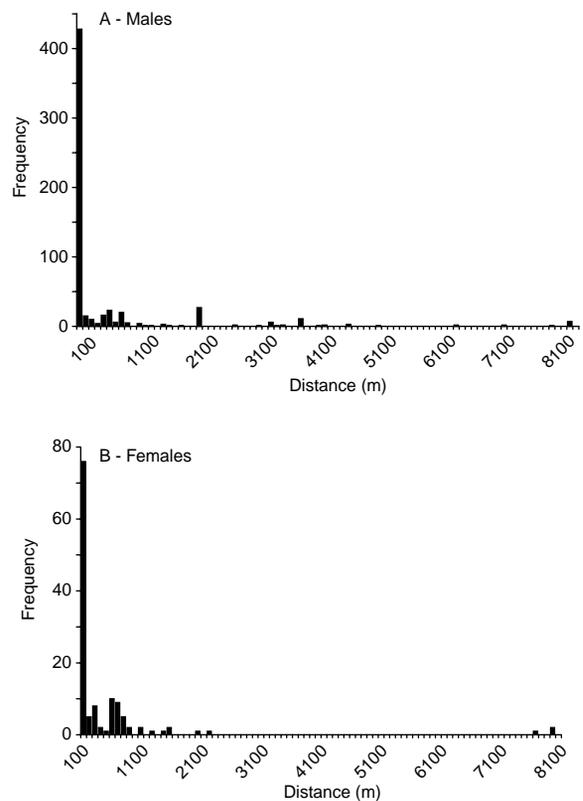


Fig. 2. Movement frequency distribution of between-capture distances made by 609 male (A) and 129 female (B) *Bufo fowleri* between 1991 and 2001. Movement bins along the x-axis are for 100 m. All captures were made the same year.

Table 1. Comparing movement estimates using movements measured among-sites with differentially corrected global positioning system (DGPS) to an exponential or power model. In the exponential model, DISTANCE is the untransformed distance (m), in the power model DISTANCE is the natural logarithm of the distance from the previous capture. The comparisons between male and female frequency distributions were made with distances measured among sites.

	Exponential		Power	
	R ²	Significance (p)	R ²	Significance (p)
All individuals, DGPS	0.081	0.005	0.633	<0.0001
Males among sites	0.245	<0.0001	0.577	<0.0001
Females among sites	0.247	<0.0001	0.703	<0.0001

either males or females had moved to another habitat patch upon recapture. The average between-site distance moved by male and female toads was 390 m and 385 m, respectively. The dispersal curves for both sexes were highly skewed leptokurtic (adult males kurtosis = 80.04, skewness = 8.84, adult females kurtosis = 74.25, skewness = 8.38). For both males and females, an inverse power relationship was a close description of the movement frequency data (Fig. 2, Table 1). Using three estimates of “long-distance” (1 km (a common value from the literature – Berven and Grudzien 1990, Sjögren 1991, Waldick 1997, Vos and Chardon 1998, Newman and Squire 2001, Conroy and Brook 2003), 4 km (roughly half the Long Point study site), and 7.5 km (a value slightly less than the maximum size of the study site)), it is clear that these long-distance events are not rare at any of these scales (Table 2).

On 24 May 2000 a juvenile Fowler’s toad was hand-captured and given a site-specific toe-clip in a breeding pond at the base of Long Point. On 28 August 2001, this toad (now distinguishable as a female) was recaptured near the tip of the peninsula, 34 km away. This is the longest recorded movement between captures for *B. fowleri* and may be the longest for any anuran (Sinsch 1990, Smith and Green 2005).

Table 2. The frequency of long distance dispersal events per year. The number of recaptures per year fluctuates in concordance with population size.

Year	≥1 km	≥4 km	≥7.5 km	Number of recaptures
1991	10	4	0	76
1992	27	6	3	123
1993	8	2	2	108
1994	14	2	2	62
1995	1	0	0	40
1996	2	1	0	16
1997	1	1	0	6
1998	15	4	2	162
1999	6	0	0	66
2000	5	2	2	34
2001	20	8	7	41
2002	6	5	3	19
2003	2	0	0	9
Mean	9	2.69	1.62	
Std. Dev.	8	2.53	2.02	
Years with no movers	0	3	6	

There was no significant relationship between age and distance moved between captures for either adult males (age classes 1–5, total n = 150, Kruskal-Wallis = 0.84, p = 0.993, DF = 4) or females (age classes 1–4, total n = 23, Kruskal-Wallis = 0.863, p = 0.834, DF = 3). The dispersal curve for all ages of toads was highly skewed leptokurtic (adult kurtosis = 29.70, p < 0.001, skewness = 5.15, juveniles kurtosis = 29.80, p < 0.001, skewness = 5.1680, metamorph kurtosis = 29.85, p < 0.001, skewness = 5.18). There was no significant difference between the resulting distributions of adult, juvenile and metamorph movement rates (Kruskal-Wallis = 4.286, p = 0.12, DF = 3) (Fig. 3).

(b) Testing limits of the study site

The study area was not closed. Marked animals moved off, unmarked animals moved in, and so we applied various methods to account for such movements. If the leptokurtic distribution of dispersal events seen over the entire data set were a function of recaptures missed at the edges (Baker et al. 1995), we would expect to see a

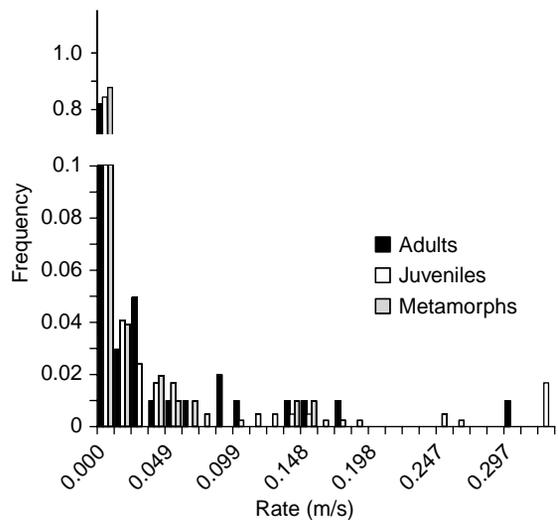


Fig. 3. Frequency distribution of rates for all observed movements for 101 adults, 410 juveniles, and 103 post-metamorphic individuals. The three distributions are not significantly different (Kruskal-Wallis 4.286, DF = 2, p = 0.117).

more normal distribution of movement events within the sub-sample of animals initially captured in the centre of the study site. However, the pattern in the subset was the same: a power relationship of the proportion of recaptures that moved a certain distance (Fig. 4). Additionally, although the Barrowclough and Ideal Site corrections increased the probability of an animal moving the maximum length of the study site, both corrections were still best described by an inverse power law and were not significantly different from the uncorrected distribution pattern (Fig. 5). Neither correction was significantly different from the uncorrected data (observed compared to ideal site correction Mann-Whitney U test statistic = 4073.000, $p=0.94$; observed compared to Barrowclough correction Mann-Whitney U test statistic = 3909.000, $p=0.74$). We therefore conclude that our study site was large enough to reliably measure the dispersal potential of this toad without underestimating the long-distance dispersal potential. The leptokurtic pattern demonstrated was not due to recaptures missed because of a spatially finite study site.

Discussion

Even though it is true that most toads did not move far, there is a significant tail to the *B. fowleri* dispersal curve where nearly 2% of recaptured animals completed long-distance dispersal events. Amphibians are not ordinarily considered to be capable of long-distance movements, although this may be due to a lack of data (Marsh et al. 1999) and an expression of the scale of investigation rather than the abilities of the animals (Turner 1960, Dole 1971, Smith and Green 2005). The previous mark-recapture estimate of the longest distance moved by an amphibian was 15 km (Tunner 1992), but

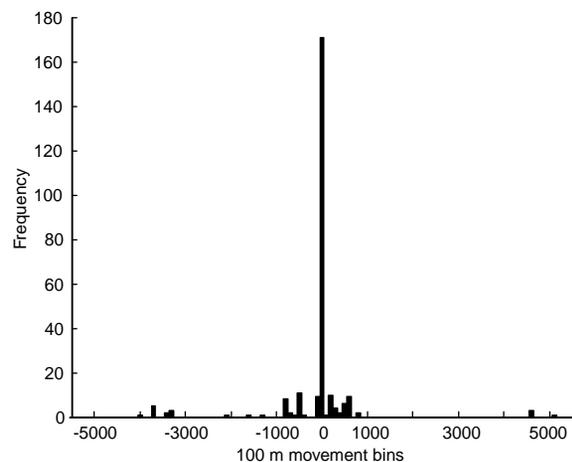


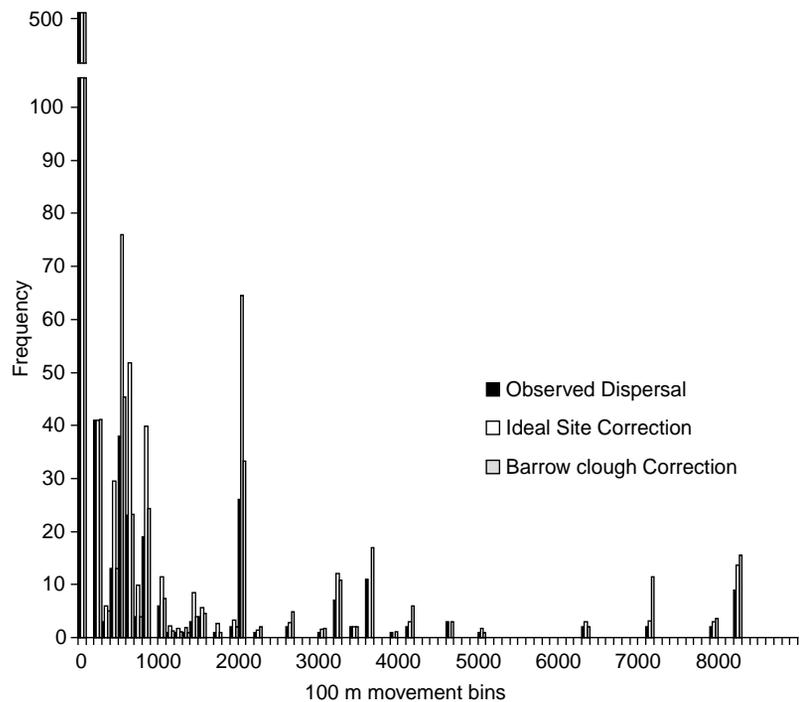
Fig. 4. Movement frequency distribution of adult (male and female combined) recaptures of 255 adults when first capture is restricted to sites in the centre of the study area. Movement west is negative, movement east is positive.

B. fowleri at Long Point appear able to move more than twice that distance. In fact, according to the power relationship detailed here, we should expect at least 0.15% of toads at Long Point to move at least 15 km. An inverse power function, which was the best description of movement frequency for this toad, is often a good description of movement as it does not under-represent long-distance dispersal events (Hill et al. 1996, Ricketts 2001, Baguette 2003).

We expected dispersal to be male-biased, as there is no resource partitioning by males in a polygynous mating system. However, we found movement in *B. fowleri* had no sex bias. Greenwood (1980) recognized that where there is any partitioning of resources by males, prior to the selection of males by females, there should be female-biased dispersal. Where males are highly territorial (Drewry 1970, Howard 1978, Wells 1978, Brzoska et al. 1982, Woolbright 1985, Radwan and Schneider 1988, Sjögren Gulve 1994, Davis and Verrell 2005) Greenwood's hypothesis predicts that dispersal should be female-biased. However, for many of these species their movement was not sex-biased (McVey et al. 1981, Woolbright 1985, Stumpel and Hanekamp 1986, Hohenweg Peter 2001, Lamoureux et al. 2002, Pilliod et al. 2002). Indeed, one species predicted to have female-biased dispersal actually exhibited male-biased dispersal (*Hyla arborea* – Vos et al. 2000). As females invest heavily in offspring, and can only breed once per year while males can breed more than once per breeding season – with a comparatively low metabolic investment – we expect selection for male-biased dispersal. However, for species which appear to meet these conditions, there was no sex bias to dispersal (Licht 1969, Calef 1973, Dole and Durant 1974, Howard 1988, Berven and Grudzien 1990, Bulger et al. 2003, Watson et al. 2003). The elegant generalities documented by Greenwood are occasionally supported by amphibians (Turner 1960, Weintraub 1974, Beshkov and Jameson 1980). Genetic evidence has indicated that dispersal in *Rana catesbeiana* is female-biased (Austin et al. 2003) which supports Greenwood's hypothesis (however, mark-recapture data from the 1930s indicates that male *R. catesbeiana* actually move larger distances than females (Raney 1940)). Thus, although there is occasional support for Greenwood's hypothesis with amphibians, they are not described as readily and uniformly as are birds and mammals. Either the hypothesis is wrong, or there are elements of anuran life history that invalidate similar applicability to anurans.

Our finding that juvenile Fowler's toads move neither faster nor farther than adults also appears to run counter to expectations (Dole 1968, 1971, Schroeder 1976, Sjögren Gulve 1998, Bulger et al. 2003) because juveniles generally are held to be the dispersing life history stage in amphibians. However, it is not difficult to find examples that contradict that assumption

Fig. 5. Movement frequency distribution of adult recaptures when corrected by the Barrowclough, and ideal site methodology. The first bins (0–100 m) are truncated for all distributions.



(Turner 1960, Wells and Wells 1976, Beshkov and Jameson 1980, Semlitsch 1981, Reading et al. 1991, Kusano et al. 1995, Holenweg Peter 2001). Conclusions concerning dispersal must be informed by knowledge of the population's overall age structure. If there is no bias to dispersal, the ages of dispersing individuals will be in direct proportion to the sizes of the various age classes. When juveniles outnumber adults, which is frequently but not inevitably the case among amphibians, no other explanation is needed for observations of greater numbers of juveniles than adults having dispersed long distances. Yet, such unbiased dispersal with respect to age and sex, as we have observed in *B. fowleri*, runs counter to certain theory. Species with very high juvenile mortality – the classic Type III survivorship curve (Deevey 1947, Breden 1988) – should have more highly dispersing juveniles than adults as any resource held by adults likely would be unavailable to juveniles.

How then do we explain the lack of age- or sex-bias in dispersal in Fowler's toad? Mortality is high for all age classes in this species and it varies from year to year in relation to a highly changeable environment (Green 2003). Demonstrated theoretically (Roff 1974a, b, Vepsäläinen 1974, Jarvinen 1976, Levin et al. 1984, McPeck and Holt 1992, Oliveri et al. 1995) and empirically (Peroni 1994), high dispersal frequencies can result from environmental variability even if there is a 99% chance of mortality during dispersal (Hamilton and May 1977, Motro 1982). Nevertheless, the shape of the dispersal curve, and its consistency in both sexes and all age classes, indicates that there may be more than one factor

driving dispersal movements that overrides other considerations. We propose that a stratified movement hypothesis where the long-distance movements we have observed are part of a multi-stage, mixed process, where much local movement is random diffusion, but long distance movement is due, at least in part to the passive dispersal of toads via the currents of the lake. This stratified movement may be due to differential behaviour between animals that disperse or do not disperse or be related to the operation of different dispersal vectors, as has been noted in many plants (Gomez 2003). Either or both may be true in the case of *B. fowleri* at Long Point. In particular, considering that the toads forage immediately beside the lakeshore and, like other bufonids, should be able to survive up to a week in fresh water (Czopek 1962, Schmid 1965), the long-distance movements we have observed may be due in part to surface currents in Lake Erie (Schwab and Bennett 1987, Beletsky et al. 1999) dispersing the toads. Such passive aquatic transmission of adult amphibians has been invoked previously for *B. fowleri* (Blair 1943) as well as for a variety of other species (Martof 1953, Carpenter 1954, Tevis 1966, Schroeder 1976, Crump 1986, Reimchen 1990, Dubois and Stoll 1995, Engle 2001, Pope and Matthews 2001). Water-borne dispersal has also been reported in amphibian larvae (Merrell 1970, Johnson and Goldberg 1975, Stoneburner 1978, Klewen 1986) and 9 species of amphibian have been observed passively dispersing on floating macrophyte mats in the Amazon River (Schiesari et al. 2003). Water-borne dispersal of this may be involved in connecting populations

otherwise isolated by intervening landscape structures (Smith and Green 2004).

In summary, we have shown that 1) although predominantly site loyal, *B. fowleri* can move surprising distances with unanticipated frequency. 2) There was no apparent sex bias to *B. fowleri* dispersal. Polygynous mating systems have been predicted to foster male-biased dispersal in other animals, and the absence of such a pattern here may reflect an apparently random nature of movement locally and vector-driven passive dispersal, possibly by lake currents, over longer distances regardless of sex. 3) The fact that younger toads do not move faster, nor farther, than adult toads does not support the dispersing juvenile hypothesis. However, there may be an order of magnitude more juveniles than adults and thus an equally large differential in the likelihood that any recaptured disperser will be a juvenile. The judgment that juvenile toads contribute differentially more than adults to a “dispersal pool” may be one biased by abundance. Since all life history stages seem to have the same dispersal characteristics, juvenile toads can comprise a large proportion of the dispersal pool simply because of their greater relative abundance. 4) Our study site was large enough in extent to enable reliable estimation of the long-distance dispersal characteristics of this toad and the highly leptokurtic shape of the dispersal curve. 5) We propose that for these toads, and perhaps for many amphibians, passive aquatic drift facilitates long-distance movement with currents in adjacent water bodies.

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References

- Austin, J. D. et al. 2003. Genetic evidence for female-biased dispersal in the bullfrog, *Rana catesbeiana* (Ranidae). – *Mol. Ecol.* 12: 3165–3172.
- Baguette, M. 2003. Long distance dispersal and landscape occupancy in a metapopulation of the cranberry fritillary butterfly. – *Ecography* 26: 153–160.
- Baker, A. M. et al. 1995. Correcting biased estimates of dispersal and survival due to limited study area: theory and an application using wren-tits. – *Condor* 97: 663–674.
- Barrowclough, G. F. 1978. Sampling bias in dispersal studies based on finite area. – *Bird Banding* 49: 333–341.
- Beletsky, D. et al. 1999. Mean circulation in the Great Lakes. – *J. Great Lakes Res.* 25: 78–93.
- Berven, K. A. and Grudzien, T. A. 1990. Dispersal in the wood frog (*Rana sylvatica*): implications for population structure. – *Evolution* 44: 2047–2056.
- Beshkov, V. A. and Jameson, D. L. 1980. Movement and abundance of the yellow-bellied toad *Bombina variegata*. – *Herpetologica* 36: 365–370.
- Blair, A. P. 1943. Population structure in toads. – *Am. Nat.* 127: 563–568.
- Blaustein, A. R. et al. 1994. Amphibian declines: judging stability, persistence and susceptibility of populations to local and global extinctions. – *Conserv. Biol.* 8: 60–71.
- Breden, F. 1987. The effects of post-metamorphic dispersal on the population genetic structure of Fowler's toad *Bufo fowleri*. – *Copeia* 1987: 386–395.
- Breden, F. 1988. Natural history and ecology of Fowler's toad, *Bufo woodhousei fowleri* (Amphibia: Bufonidae), in the Indiana Dunes National Lakeshore. – *Fieldian: Zoology* 49: 1–16.
- Brown, J. H. and Kodric-Brown, A. 1977. Turnover rates in insular biogeography: effect of immigration on extinction. – *Evolution* 58: 445–449.
- Brzoska, J. et al. 1982. Territorial behavior and vocal response in male *Hyla arborea savignyi* (Amphibia: Anura). – *Isr. J. Zool.* 31: 27–37.
- Bulger, J. B. et al. 2003. Terrestrial activity and conservation of adult California red-legged frogs *Rana aurora draytonii* in coastal forests and grasslands. – *Biol. Conserv.* 110: 85–95.
- Cain, M. L. et al. 2003. Long-distance dispersal. – *Ecology* 84: 1943–1944.
- Calef, G. W. 1973. Spatial distribution and “effective” breeding populations of red-legged frogs (*Rana aurora*) in Marion Lake, British Columbia. – *Can. Field-Nat.* 87: 279–284.
- Carpenter, C. C. 1954. A study of amphibian movement in the Jackson's Hole Wildlife Park. – *Copeia* 1954: 197–200.
- Clarke, R. D. 1972. The effect of toe-clipping on survival in Fowler's toad (*Bufo woodhousei fowleri*). – *Copeia* 1972: 182–185.
- Clarke, R. D. 1974. Activity and movement patterns in a population of Fowler's toad, *Bufo woodhousei fowleri*. – *Am. Midl. Nat.* 92: 257–274.
- Conroy, S. D. S. and Brook, B. W. 2003. Demographic sensitivity and persistence of the threatened white- and orange-bellied frogs of western Australia. – *Popul. Ecol.* 45: 105–114.
- Crump, M. L. 1986. Homing and site fidelity in a neotropical frog, *Atelopus varius*, (Bufonidae). – *Copeia* 1986: 438–444.
- Czopek, J. 1962. Tolerance to submersion in water in amphibians. – *Acta Biol. Cracov Ser. Zool.* 5: 241–251.
- Davis, A. B. and Verrell, P. A. 2005. Demography and reproductive ecology of the Columbia spotted frog (*Rana luteiventris*) across the Palouse. – *Can. J. Zool.* 83: 702–711.
- Deevey, E. S. 1947. Life tables for natural populations of animals. – *Q. Rev. Biol.* 22: 283–314.
- Dole, J. W. 1968. Homing in leopard frogs, *Rana pipiens*. – *Ecology* 49: 386–399.
- Dole, J. W. 1971. Dispersal of recently metamorphosed leopard frogs, *Rana pipiens*. – *Copeia* 1971: 221–228.
- Dole, J. W. and Durant, P. 1974. Movements and seasonal activity of *Atelopus oxyrhynchus* (Anura: Atelopodidae) in a Venezuelan cloud forest. – *Copeia* 1974: 230–235.
- Drewry, G. 1970. The role of amphibians in the ecology of the Puerto Rican rain forest. – In: Puerto Rico Nuclear Center Rain Forest Project Annual Report. Puerto Rico Nuclear Center, pp. 16–85.
- Dubois, R. B. and Stoll, F. M. 1995. Downstream movement of leopard frogs in a Lake Superior tributary exemplifies the concept of a lotic macrodrift. – *J. Freshwater Ecol.* 10: 135–139.
- Duellman, W. E. and Trueb, L. 1986. *Biology of Amphibians*. – McGraw-Hill.

- Engle, J. C. 2001. Population biology and natural history of Columbia spotted frogs (*Rana luteiventris*) in the Owyhee Uplands of southwest Idaho: implications for monitoring and management. – M.S. thesis, Boise State Univ.
- Ferguson, D. E. 1960. Observations on movements and behavior of *Bufo fowleri* in residential areas. – *Herpetologica* 16: 112–114.
- Funk, W. C. et al. 2005. Alternative views of amphibian toe-clipping. – *Nature* 433: 193.
- Gaines, S. D. et al. 2003. Avoiding current oversights in marine reserve design. – *Ecol. Appl.* 13: S32–S46.
- Gomez, J. M. 2003. Spatial patterns in long-distance dispersal of *Quercus ilex* acorns by jays in a heterogeneous landscape. – *Ecography* 26: 573–584.
- Green, D. M. 1992. Fowler's toads (*Bufo woodhousei fowleri*) at Long Point, Ontario: changing abundance and implications for conservation. – In: Bishop, C. A. and Petit, K. E. (eds), Declines in Canadian amphibian populations: designing a national monitoring strategy. Canadian Wildlife Service, pp. 37–43.
- Green, D. M. 1997. Temporal variation in abundance and age structure in Fowler's toads, *Bufo fowleri*, at Long Point, Ontario. – In: Green, D. M. (ed.), Amphibians in decline: Canadian studies of a global problem. Society for the Study of Amphibians and Reptiles, pp. 45–56.
- Green, D. M. 2003. The ecology of extinction: population fluctuation and decline in amphibians. – *Biol. Conserv.* 111: 331–343.
- Greenwood, P. J. 1980. Mating systems, philopatry and dispersal in birds and mammals. – *Anim. Behav.* 28: 1140–1162.
- Hamilton, W. D. and May, R. M. 1977. Dispersal in stable habitats. – *Nature* 269: 578–581.
- Hill, J. K. et al. 1996. Effects of habitat patch size and isolation on dispersal by *Hesperia comma* butterflies: implications for metapopulation structure. – *J. Appl. Ecol.* 65: 725–735.
- Holenweg Peter, A.-K. 2001. Dispersal rates and distances in adult water frogs, *Rana lessonae*, *R. ridibunda* and their hybridogenetic associate, *R. esculenta*. – *Herpetologica* 57: 449–460.
- Howard, R. D. 1978. The evolution of mating strategies in bullfrogs, *Rana catesbeiana*. – *Evolution* 32: 850–871.
- Howard, R. D. 1988. Reproductive success in two species of anurans. – In: Clutton-Brock, T. H. (ed.), Reproductive success. Univ. of Chicago Press, pp. 99–118.
- Jarvinen, O. 1976. Migration, extinction and alary morphism in water-strider. – *Ann. Acad. Sci. Fenn.* 206: 1–7.
- Johnson, J. E. and Goldberg, A. S. 1975. Movement of larval two lined salamanders (*Eurycea bislineata*) in the Mill River, Massachusetts. – *Copeia* 1975: 588–589.
- Johnson, M. J. and Gaines, M. S. 1990. Evolution of dispersal: theoretical models and empirical tests using birds and mammals. – *Annu. Rev. Ecol. Syst.* 21: 449–480.
- Kellner, A. and Green, D. M. 1995. Age structure and age at maturity in Fowler's toads, *Bufo woodhousii fowleri*, at their northern range limit. – *J. Herpetol.* 29: 485–489.
- Klewen, R. 1986. Population ecology of *Salamandra salamandra terrestris* in an isolated habitat. – In: Roček, Z. (ed.), Studies in Herpetology. Charles Univ., pp. 395–398.
- Kusano, T. et al. 1995. Post-breeding dispersal of the Japanese toad, *Bufo japonicus formosus*. – *J. Herpetol.* 29: 633–638.
- Lamoureux, V. S. et al. 2002. Premigratory autumn foraging forays in the green frog, *Rana clamitans*. – *J. Herpetol.* 36: 245–254.
- Largier, J. L. 2003. Considerations in estimating larval dispersal distances from oceanographic data. – *Ecol. Appl.* 13: S71–S89.
- Laurin, G. and Green, D. M. 1990. Spring emergence and male chorus behaviour in Fowler's toads, *Bufo woodhousii fowleri*, at Long Point, Ontario. – *Can. Field-Nat.* 104: 429–434.
- Levin, S. A. et al. 1984. Dispersal strategies in patchy environments. – *Theor. Popul. Biol.* 26: 165–191.
- Licht, L. E. 1969. Comparative breeding behavior of the red-legged frog (*Rana aurora aurora*) and the western spotted frog (*Rana pretiosa pretiosa*) in southwestern British Columbia. – *Can. J. Zool.* 47: 1287–1299.
- Lomnicki, A. 1988. Population ecology of individuals – Princeton Univ. Press.
- Marsh, D. M. and Trenham, P. C. 2001. Metapopulation dynamics and amphibian conservation. – *Conserv. Biol.* 15: 40–49.
- Marsh, D. M. et al. 1999. Effects of breeding pond isolation on the spatial and temporal dynamics of pond use by the tungara frog, *Physalaemus pustulosus*. – *J. Anim. Ecol.* 68: 804–814.
- Martof, B. 1953. Home range and movements of the green frog, *Rana clamitans*. – *Ecology* 34: 529–543.
- May, R. M. 2004. Ecology: ethics and amphibians. – *Nature* 431: 403.
- McCarthy, M. A. and Parris, K. M. 2004. Clarifying the effect of toe clipping on frogs with Bayesian statistics. – *J. Appl. Ecol.* 41: 780–786.
- McPeck, M. A. and Holt, R. D. 1992. The evolution of dispersal in spatially and temporally varying environments. – *Am. Nat.* 140: 1010–1027.
- McVey, M. E. et al. 1981. Territoriality and homing behavior in the poison dart frog (*Dendrobates pumilo*). – *Copeia* 1981: 1–8.
- Merrell, D. J. 1970. Migration and gene dispersal in *Rana pipiens*. – *Am. Zool.* 10: 47–52.
- Motro, O. 1982. Optimal rates of dispersal I. Haploid populations. – *Theor. Popul. Biol.* 21: 394–411.
- Nathan, R. et al. 2001. Field validation and sensitivity analysis of a mechanistic model for tree seed dispersal by wind. – *Ecology* 82: 374–388.
- Newman, R. A. and Squire, T. 2001. Microsatellite variation and fine-scale population structure in the wood frog (*Rana sylvatica*). – *Mol. Ecol.* 10: 1087–1110.
- Nichols, R. J. 1937. Preliminary studies on the movements of toads. – *Bull. Ecol. Soc. Am.* 18: 56.
- Oliveri, I. et al. 1995. Metapopulation genetics and the evolution of dispersal. – *Am. Nat.* 146: 202–228.
- Palo, J. U. et al. 2004. Microsatellite marker data suggest sex-biased dispersal in the common frog *Rana temporaria*. – *Mol. Ecol.* 13: 2865–2869.
- Parris, K. M. and McCarthy, M. A. 2001. Identifying effects of toe clipping on anuran return rates: the importance of statistical power. – *Amphib.-Reptilia* 22: 275–289.
- Peroni, P. A. 1994. Seed size and dispersal potential of *Acer rubrum* (Aceraceae) samaras produced by populations in early and late successional environments. – *Am. J. Bot.* 81: 1428–1434.
- Petit, S. et al. 2001. Metapopulation dynamics of the bog fritillary butterfly: movements between habitat patches. – *Oikos* 92: 491–500.
- Pilliod, D. S. et al. 2002. Seasonal migration of Columbia spotted frogs, (*Rana luteiventris*) among complementary resources in a high mountain basin. – *Can. J. Zool.* 80: 1849–1862.
- Pope, K. L. and Matthews, K. R. 2001. Movement ecology and seasonal distribution of mountain yellow-legged frogs, *Rana muscosa*, in a high-elevation Sierra Nevada Basin. – *Copeia* 2001: 787–793.
- Radwan, N. M. M. and Schneider, H. 1988. Social behaviour, call repertory and variation in the calls of the pool frog, *Rana lessonae* (Anura: Ranidae). – *Amphib.-Reptilia* 9: 329–351.
- Raney, E. C. 1940. Summer movements of the bullfrog, *Rana catesbeiana* Shaw, as determined by the jaw-tag method. – *Am. Midl. Nat.* 23: 733–745.
- Reading, C. J. et al. 1991. Breeding pond fidelity in common toads, *Bufo bufo*. – *J. Zool. Lond.* 225: 201–211.
- Reimchen, T. W. 1990. Introduction and dispersal of the Pacific treefrog, *Hyla regilla*, on the Queen Charlotte Islands, British Columbia. – *Can. Field-Nat.* 105: 288–290.

- Ricketts, T. H. 2001. The matrix matters: effective isolation in fragmented landscapes. – *Am. Nat.* 158: 87–99.
- Roff, D. A. 1974a. The analysis of a population model demonstrating the importance of dispersal in a heterogeneous environment. – *Oecologia* 15: 259–275.
- Roff, D. A. 1974b. Spatial heterogeneity and the persistence of populations. – *Oikos* 15: 245–258.
- Saunders, D. A. et al. 1991. Biological consequences of ecosystem fragmentation: a review. – *Conserv. Biol.* 5: 18–32.
- Schiesari, L. et al. 2003. Macrophyte rafts as dispersal vectors for fishes and amphibians in the Lower Solimoes River, central Amazon. – *J. Trop. Ecol.* 19: 333–336.
- Schmid, W. D. 1965. Some aspects of the water economies of nine species of amphibians. – *Ecology* 46: 261–269.
- Schroeder, E. E. 1976. Dispersal and movement of newly transformed green frogs, *Rana clamitans*. – *Am. Midl. Nat.* 95: 471–474.
- Schwab, D. J. and Bennett, J. R. 1987. Lagrangian comparison of objectively analyzed and dynamically modeled circulation patterns in Lake Erie. – *J. Great Lakes Res.* 13: 515–529.
- Semlitsch, R. D. 1981. Terrestrial activity and summer home range of the mole salamander (*Ambystoma talpoideum*). – *Can. J. Zool.* 59: 315–322.
- Sinsch, U. 1990. Migration and orientation in anuran amphibians. – *Ethol. Ecol. Evol.* 2: 65–79.
- Sjögren, P. 1991. Extinction and isolation gradients in metapopulations: the case of the pool frog (*Rana lessonae*). – *Biol. J. Linn. Soc.* 42: 135–147.
- 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. 1998. Spatial movement patterns in frogs: target-oriented dispersal in the pool frog, *Rana lessonae*. – *Ecoscience* 5: 31–38.
- Skelly, D. K. et al. 1999. Long-term distributional dynamics of a Michigan amphibian assemblage. – *Ecology* 80: 2326–2337.
- Smith, M. A. and Green, D. M. 2004. Phylogeography of *Bufo fowleri* at its northern range limit. – *Mol. Ecol.* 13: 3723–3733.
- Smith, M. A. and Green, D. M. 2005. Dispersal and the metapopulation paradigm in amphibian ecology and conservation: are all amphibian populations metapopulations? – *Ecography* 28: 110–128.
- Sokal, R. R. and Rohlf, F. J. 1995. *Biometry*. – W. H. Freeman.
- Stille, W. T. 1952. The nocturnal amphibian fauna of the southern Lake Michigan Beach. – *Ecology* 33: 149–162.
- Stoneburner, D. L. 1978. Salamander drift: observations on the two-lined salamander (*Eurycea bislineata*). – *Freshwater Biol.* 8: 291–293.
- Stumpel, A. H. P. and Hanekamp, G. 1986. Habitat and ecology of *Hyla arborea* in the Netherlands. – In: Roček, Z. (ed.), *Studies in Herpetology*. Charles Univ., Prague, Czech Republic, pp. 409–416.
- Sullivan, B. K. 1983. Sexual selection in Woodhouse's toad (*Bufo woodhousei*). II. Female choice. – *Anim. Behav.* 31: 1011–1017.
- Sullivan, B. K. 1992. Calling behavior of the southwestern toad (*Bufo microscaphus*). – *Herpetologica* 48: 383–389.
- Tevis, L., Jr 1966. Unsuccessful breeding by desert toads (*Bufo punctatus*) at the limit of their ecological tolerance. – *Ecology* 47: 766–775.
- Thomas, C. D. et al. 1996. Catastrophic extinction of population sources in a butterfly metapopulation. – *Am. Midl. Nat.* 146: 957–975.
- Tunner, H. T. 1992. Locomotion behaviour in water frogs from Neusiedlersee. – In: Koros, Z. and Kiss, I. (eds), *Proc. of the sixth ordinary general meeting of the Society for European Herpetologists*. Hungarian Natural History Museum, pp. 449–452.
- Turner, F. B. 1960. Population structure and dynamics of the western spotted frog, *Rana pretiosa* Baird and Girard, in Yellowstone Park, Wyoming. – *Ecol. Mongr.* 30: 251–278.
- Vepsäläinen, K. 1974. The life cycles and wing lengths of Finnish Gerris Fabr. species (Heteroptera: Gerridae). – *Acta Zool. Fenn.* 141: 1–73.
- Vos, C. C. and Chardon, J. P. 1998. Effects of habitat fragmentation and road density on the distribution pattern of the moor frog *Rana arvalis*. – *J. Appl. Ecol.* 35: 44–56.
- Vos, C. C. et al. 2000. Incidence function modeling and conservation of the tree frog *Hyla arborea* in the Netherlands. – *Ecol. Bull.* 48: 165–180.
- Waldick, R. 1997. Effects of forestry practices on amphibian populations in eastern North America. – In: Green, D. M. (ed.), *Amphibians in decline: Canadian studies of a global problem*. Society for the study of amphibians and reptiles, pp. 191–205.
- Watson, J. W. et al. 2003. Home ranges, movements and habitat selection of Oregon spotted frogs (*Rana pretiosa*). – *J. Herpetol.* 37: 292–300.
- Weintraub, J. D. 1974. Movement patterns of the red-spotted toad, *Bufo punctatus*. – *Herpetologica* 30: 212–215.
- Wells, K. D. 1977. The social behavior of anuran amphibians. – *Anim. Behav.* 25: 666–693.
- Wells, K. D. 1978. Territoriality in the green frog, (*Rana clamitans*): vocalizations and agnostic behaviour. – *Anim. Behav.* 26: 1051–1063.
- Wells, K. D. and Wells, R. A. 1976. Patterns of movement in a population of the slimy salamander, *Plethodon glutinosus*, with observations on aggregations. – *Herpetologica* 32: 156–162.
- Welsh, H. H. and Droege, S. 2001. A case for using plethodontid salamanders for monitoring biodiversity and ecosystem integrity of North American forests. – *Conserv. Biol.* 15: 558–569.
- Woolbright, L. L. 1985. Patterns of nocturnal movement and calling by the tropical frog *Eleutherodactylus coqui*. – *Herpetologica* 41: 1–9.

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