

Minireviews provides an opportunity to summarize existing knowledge of selected ecological areas, with special emphasis on current topics where rapid and significant advances are occurring. Reviews should be concise and not too wide-ranging. All key references should be cited. A summary is required.

Dispersal and the metapopulation paradigm in amphibian ecology and conservation: are all amphibian populations metapopulations?

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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.

Amphibians are frequently characterized as having limited dispersal abilities, strong site fidelity and spatially disjunct breeding habitat. As such, pond-breeding species are often alleged to form metapopulations. Amphibian species worldwide appear to be suffering population level declines caused, at least in part, by the degradation and fragmentation of habitat and the intervening areas between habitat patches. If the simplification of amphibians occupying metapopulations is accurate, then a regionally based conservation strategy, informed by metapopulation theory, is a powerful tool to estimate the isolation and extinction risk of ponds or populations. However, to date no attempt to assess the class-wide generalization of amphibian populations as metapopulations has been made. We reviewed the literature on amphibians as metapopulations (53 journal articles or theses) and amphibian dispersal (166 journal articles or theses for 53 anuran species and 37 salamander species) to evaluate whether the conditions for metapopulation structure had been tested, whether pond isolation was based only on the assumption of limited dispersal, and whether amphibian dispersal was uniformly limited. We found that in the majority of cases (74%) the assumptions of the metapopulation paradigm were not tested. Breeding patch isolation via limited dispersal and/or strong site fidelity was the most frequently implicated or tested metapopulation condition, however we found strong evidence that amphibian dispersal is not as uniformly limited as is often thought. The frequency distribution of maximum movements for anurans and salamanders was well described by an inverse power law. This relationship predicts that distances beneath 11–13 and 8–9 km, respectively, are in a range that they may receive one emigrating individual. Populations isolated by distances approaching this range are perhaps more likely to exhibit metapopulation structure than less isolated populations. Those studies that covered larger areas also tended to report longer maximum movement distances – a pattern with implications for the design of mark-recapture studies. Caution should be exercised in the application of the metapopulation approach to amphibian population conservation. Some amphibian populations are structured as metapopulations – but not all.

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The importance of the spatial element in ecology has long been recognized (Andrewartha and Birch 1954), but its consideration has undergone a period of distinct

growth in the past thirty years (Hanski 1999) with increased emphasis paid to concepts such as the spatial nature of population dynamics and the spatial

Accepted 27 September 2004

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ISSN 0906-7590

partitioning of populations' genetic variability. The metapopulation approach, first outlined by Levins (1969, 1970), has been especially insightful for the development of spatial ecology and its application to conservation. In simple terms, a metapopulation is a collection of partially isolated breeding habitat patches, connected by occasionally dispersing individuals whereby each patch exists with a substantial extinction probability. Thus, long-term persistence occurs only at the regional level of the metapopulation. There are currently many variants of the metapopulation concept ranging from very simple models utilizing a minimum of data (Levins 1969) to much more complex models which incorporate many environmental variables (Sjögren Gulve and Ray 1996, Harrison and Taylor 1997, Hanski 1999). The most useful function of this continuum of metapopulation theory has been to integrate spatially structured interactions between local populations with processes occurring within populations and thereby enable better assessment of population viability.

Models more realistic than the initial Levins approach consider the effects of patch area, shape and isolation, and the effect of the non-habitat between patches on the likelihood of patch extinction or colonization (Hanski 1999). This addition of realism has been accompanied by an exponential increase in the number of biological systems examined for metapopulation structure (Hanski 1999). However, rapidly increasing empirical use of metapopulation concepts, without clear tests of the theory's applicability, may reduce the precision with which the term metapopulation is used (Freckleton and Watkinson 2003, Pannell and Obbard 2003). For instance, conservation strategies may be misdirected if similar species are considered a priori to exhibit similar population structure and dynamics in the absence of evidence to the contrary or if departures from simple metapopulation models are not clearly detailed (Hanski and Simberloff 1997). It has been stated that because metapopulation dynamics are concerned mostly with the presence or absence of species in local populations, the sampling of any specific local populations would not need to be as intense (Alford and Richards 1999). Clearly this will be a decision with dire consequences if there is no true metapopulation structure at all. Such a conclusion is only valid for a simple metapopulation and therefore it would also be a mistake if a more extended, complex metapopulation was actually modeled (Harrison and Taylor 1997). Therefore, the issue of whether or not populations of amphibians, or any taxa, form a metapopulation is not merely semantic but is relevant to their conservation and management.

Certainly, where disjunct breeding patches contain individual populations that exist in a shifting balance between extinctions and recolonisations via dispersing individuals the metapopulation approach is an attractive theoretical construct (Hanski 1999). Many temperate

amphibians do use spatially disjunct breeding habitat (Duellman and Trueb 1986), and are often regarded as poor-dispersers with high site fidelity (Duellman and Trueb 1986, Sinsch 1990, Blaustein et al. 1994, Beebee 1996, Berry 2001). In light of these observations, it appears highly probable that amphibian populations likely do operate as metapopulations (Harrison 1991, Alford and Richards 1999, Marsh and Trenham 2001). "...Our review of the literature suggests that many if not most amphibians exist in metapopulations" (Alford and Richards 1999). Yet the assumptions of limited dispersal, high site fidelity and evident metapopulation structure in amphibians have not been stringently tested, and we do so here.

We examined the literature for all references to amphibians as metapopulations using Current Contents, Scientific Citation Index, and other published reference lists. We tested whether the published literature for amphibians had addressed the four conditions deemed necessary for the existence of simple metapopulation structure (Hanski et al. 1995, Hanski 1999), and whether amphibians are indeed of low vagility and high site loyalty. Although the metapopulation concept has been extended to include population structures not described by these conditions (Harrison and Taylor 1997, Hanski 1999), our analysis is restricted to these simple conditions for the single reason that simple, stochastic metapopulations are likely good models for real populations living in highly fragmented landscapes (Ovaskainen and Hanski 2004) – a situation which includes many temperate, pond-breeding amphibians (Marsh and Trenham 2001). If populations inhabiting habitat patches are best described by simple metapopulation models that are described by Hanski's four conditions, then the collection of empirical data, advantageous to conservation and management, is relatively simple. Thus, to review the applicability of the four conditions of a simple metapopulation to amphibian ecology is timely and necessary.

Our secondary focus is upon Hanski's 3rd condition of limited dispersal ability. Previous reviews of amphibians and the metapopulation concept (Alford and Richards 1999, Marsh and Trenham 2001) focused primarily on the Hanski's 1st condition – that breeding ponds constitute separate and individual breeding populations. While both reviews identified the importance of dispersal for determining the range of recolonisation – a comprehensive review of dispersal abilities in relation to the metapopulation concept was not completed and our review is therefore complementary. It is also timely, for most metapopulation models assume that metapopulation dynamics are dominated by short distance movements (Hanski 1999, Bagnette 2003), and if we underestimate the likelihood of long distance dispersal we risk either incorrectly estimating the scale of a metapopulation effect, or incorrectly attributing

metapopulation structure to a system where local dynamics are more important than regional (i.e. not a metapopulation). Thus, correctly estimating long-distance dispersal lies at the heart of determining the appropriate scale of a metapopulation approach.

We compiled a comprehensive list of the longest distances moved by amphibians in both mark-recapture and displacement studies (Tables 3 and 4). To test whether the low-vagility hypothesis was caused by a lack of long-distance dispersal data in amphibians caused by small study areas we subsequently compared these movement distances to the maximum distance covered by the field site. If not recorded directly by the author, the maximum observable distance was most frequently entered as the diagonal of the figure documenting the study site – likely a liberal interpretation of maximum distance measurable.

The title of our review was inspired by that of Freckleton and Watkinson (2003) who have asked a similar question of the utility of the metapopulation concept to plant ecology.

Amphibians and Hanski's four metapopulation conditions

Hanski outlines four conditions necessary to demonstrate the existence of a metapopulation effect (Hanski and Kuussaari 1995, Hanski et al. 1995, Hanski 1999): 1) habitat patches support local breeding populations, 2) no single population is large enough to ensure long-term survival, 3) patches are not too isolated to prevent recolonisation, and 4) local dynamics are sufficiently asynchronous to make simultaneous extinction of all local populations unlikely. Someone who observes a species with high site-fidelity, limited dispersal and apparently disjunct breeding patches, may frequently and implicitly, evaluate (or accept) these assumptions a priori. Through an examination of studies in the literature involving amphibians where the term metapopulation or population subdivision was used, we examined whether these studies had tested, not tested or assumed the importance of each of these conditions (Appendix 1). In some cases, it was unclear whether a study had "not tested" a Hanski Condition or whether it had been "assumed" to be accurate. Examples of two common differences occurred where a study involved a genetic analysis of metapopulation structure, (Rowe et al. 2000), or where a study was dependant on the assumption of limited dispersal. In the first scenario of a genetic metapopulation Condition 1 (that habitat patches support local breeding populations) is mathematically necessary to support the existence of a metapopulation, and was therefore considered as assumed, rather than not tested. In the second scenario of limited dispersal, Condition 3 (limited dispersal with the

potential for recolonisation), was coded as assumed if there was an implication in the manuscript text that dispersal beyond a certain distance was expected to be impossible (Conroy and Brook 2003, Woodford and Meyer 2003).

Clearly there are a wide range of population conditions that have been called, "metapopulations" (Harrison and Taylor 1997), and we never suggest that the simple, stochastic type of metapopulation described by Hanski's four conditions is the only type of metapopulation that exists. Rather, our goal was to investigate the frequency with which these simple models were actually tested by using a diverse taxa for which it has been suggested that the simple metapopulation was likely the predominant population condition (Harrison 1991, Alford and Richards 1999). Additionally, it was our hope to focus attention on the increasingly extended definition of the term metapopulation. We agree with Pannell and Obbard (2003) that the term, metapopulation should not be extended to include every instance where a species inhabits discrete habitat patches that may or may not be involved in population structure. If the term is extended until it includes practically all situations then it's utility is compromised as it is no longer falsifiable.

In our review we examined all instances where metapopulation was used in the title, abstract or keywords of journal articles or theses that studied amphibians. We included those articles that did not explicitly test a Hanski style metapopulation – because this manner of untested, a priori, defining of metapopulations is part of the trend we examine, and wish to draw attention to. In the instance where authors relied on previously published material we considered that condition to have been tested.

The majority (73.6%) of the possible 212 Hanski metapopulation conditions (53 articles \times four conditions) were assumed or untested in the amphibian as metapopulation literature (Table 1). The most frequently tested condition was of isolation, although the dispersal ability of the amphibian species was rarely tested directly. Even though dispersal was indirectly estimated with genetics in 45% of the cases, the a priori assumption was that the amphibian was of low vagility. Any distance larger than one kilometre (Berven and Grudzien 1990, Sjögren 1991, Waldick 1997, Vos and Chardon 1998, Newman and Squire 2001, Conroy and Brook 2003), two kilometres (Hranitz and Diehl 2000), or several hundred meters (Reading et al. 1991, Skelly, et al. 1999) were referred to as critical distances beyond which amphibian dispersal would not penetrate. In fact, of the 53-amphibian/metapopulation studies, all explicitly tested or assumed that ponds were isolated due to the limited dispersal and/or high site fidelity of amphibians. 42 of 53 studies (79%) implicated this limited dispersal as the, or one of the, primary rationales behind the utility of the

Table 1. Literature review of the metapopulation paradigm in amphibian ecology. Fifty-three studies regarding amphibians and population sub-division were examined regarding their explicit or implicit testing of the four conditions necessary for a metapopulation effect (Hanski et al. 1995).

| | Habitat patches support local breeding population | No single population is large enough to ensure long-term survival | Patches are not too isolated to prevent recolonisation: isolation due to limited dispersal | Local dynamics are sufficiently asynchronous to make simultaneous extinction of all local population unlikely |
|------------|---|---|--|---|
| Not tested | 20 | 37 | 0 | 45 |
| Tested | 11 | 10 | 32 | 3 |
| Assumed | 22 | 6 | 21 | 5 |

metapopulation process. Interestingly, studies that rejected the metapopulation paradigm (10/53) did so because there was judged to be too much dispersal among patches.

Amphibian site loyalty and movement

The literature contains many references that explain the poor dispersal ability of amphibians as being a consequence of their physiology and behavior (Duellman and Trueb 1986, Sinsch 1990, Blaustein et al. 1994). Amphibian skin is highly permeable and amphibians therefore have a stringent dependence on moisture (Duellman and Trueb 1986). Additionally, amphibians can show extreme site loyalty (Blaustein et al. 1994). Many individual studies have demonstrated that amphibians are found at the same location between census years and, where individuals have been followed through time, their movement is limited (Sinsch 1990) (Table 2).

Nevertheless, in our review we found that while the view of limited amphibian dispersal may be true for some species, it clearly does not hold for all. Among 166 journal articles concerning 90 species recording the maximum distance moved, while 44% of the amphibian species moved no farther than 400 m (Tables 3 and 4), 5% were capable of movements greater than 10 km (Table 5). This literature review sampled much more of total salamander diversity (37 species of 352 worldwide, 10.5%) than anuran diversity (53 species of 3848 worldwide, 1.5%) (Duellman and Trueb 1986), and there were evident differences between these groups. Nearly one half (44%) of the anuran species displayed maximum dispersal distances greater than one kilometre, and 7% of frogs were observed to have maximum dispersal distances greater than 10 km (Table 4). This is surprising considering that one kilometre has appeared independently in the literature as a magic number beyond which amphibian populations would be isolated from dispersal events (Berven and Grudzien 1990, Sjögren 1991, Waldick 1997, Vos and Chardon 1998, Newman and Squire 2001, Conroy and Brook 2003); and 15 km has been defined as the maximum migratory range (Sinsch 1990). Amphibian species truly do appear to be site-loyal

on average, yet the frequency histogram of maximum distances moved is better fit by a power law than an exponential distribution (power (log-log) $R^2 = 0.67$, exponential (log-normal) $R^2 = 0.25$) (Figs 1–3). In the power relationship, a proportion of the individuals are not described by that average and move long distances. This proportion is larger in the power relationship than in one described by an exponential function. If these long-distance-dispersers were frequent it would reduce the likelihood of support for the paradigm of metapopulation structure through isolation. Such a high rate of dispersal would effectively unite disjunct populations into a single unit – or patchy population ((Harrison 1991, Harrison and Taylor 1997) and not as Freckleton and Watkinson (2003)). If any metapopulation structure were to exist in this case, it would more likely be at a larger spatial scale than predicted by an exponentially distributed frequency distribution. Thus, it is incorrect to infer isolation from observed philopatry.

Although 94% of the maximum dispersal distances for salamanders are less than 1 km (Table 3), the frequency distribution of distances was also an inverse power function (Fig. 2). Therefore, although most may not move very far, there is a strong likelihood that some individuals may complete long-distance movements. For example, *Plethodon glutinosus* is a remarkably site loyal animal across ages and sexes (Wells and Wells 1976). Using data provided in the paper for this species, we found that an inverse power law explained 74% of the variation in movement frequency for males (from Wells and Wells (1976) Fig. 1). In this case, although it is clear that most individuals are unlikely to move >10 m, according to this relationship there is an appreciable chance (~0.4%) that an individual could move one kilometre. Indeed, recent findings document that for some pond-breeding salamanders, rates of inter-pond migration are high enough to suggest that the fit of the metapopulation paradigm to this particular species was less than was expected (Trenham 1998).

Clearly, most amphibian species do not move very far, but surprisingly, greater than 7% of anurans we surveyed were capable of movements of greater than 10 km. This leptokurtic, inverse-power relationship neither supports nor rejects the model of the poorly

Table 2. Examples of site fidelity in amphibians.

| Species | Fidelity | Source |
|---|---|--|
| <i>Triturus vulgaris</i> | Not a single one of 2500 marked individuals changed breeding ponds between seasons. | Bell 1977 |
| <i>Plethodon cinereus</i> | Philopatric to the same cover object between years. | Placyk and Graves 2001 |
| <i>Triturus vulgaris</i> | Philopatric to the same cover object between years. | Dolmen 1981 |
| <i>Bufo bufo</i> | 93% of females and 96% of males that survived between years, returned to the same breeding ponds. | Reading et al. 1991 |
| <i>Bufo marinus</i> | No significant homing effect. | Seebacher and Alford 1999 |
| <i>Bufo marinus</i> | Return to their home site with 100% accuracy when displaced up to 70 m, or 165 m. | Brattstrom 1962, Carpenter and Gillingham 1987 |
| <i>Bufo americanus</i> | Returned to within 5 m of their original site after a 235 m translocation. | Dole 1972 |
| <i>Pseudacris triseriata triseriata</i> | The majority of recaptures were within 100 m of the initial capture site. | Kramer 1973 |
| <i>Pseudacris maculata</i> | The maximum distance moved is only 250 m. | Spencer 1964 |
| <i>Hyla regilla</i> | 71% of males were found in the same portion of the same pond when recaptured the following year. | Jameson 1957 |
| <i>Mixophyes iteratus</i> | 89% of individuals were recaptured 5 m or less away from where they were marked. | Lemckert and Brassil 2000 |
| <i>Rana sylvatica</i> | 100% of adults and 82% of juvenile are faithful to their first breeding pond or natal pond respectively. | Berven and Grudzien 1990 |
| <i>Rana sylvatica</i> | The mean distance between captures was only 11.25 m for 298 individuals. | Bellis 1965 |
| <i>Rana pipiens</i> | 98% of returned to their home pond after a one-kilometer displacement. | Dole 1968 |
| <i>Rana muscosa</i> | 89% percent of were recaptured at the same pond between breeding seasons. | Pope and Matthews 2001 |
| <i>Rana muscosa</i> | 50% of translocated individuals returned to their initial site within 20 days after a 630 m translocation. | Matthews 2003 |
| <i>Rana lessonae and Rana ridibunda</i> | 88% of individuals monitored between years did not move from their capture pond. | Holenweg Peter 2001 |
| <i>Rana aurora draytonii</i> | 75% did not move from their site over the course of a year and 90% of these philopatric individuals were never more than 60 m from the water. | Bulger et al. 2003 |

dispersing amphibian. Concluding all amphibians are poor dispersers is as incorrect as stating that all mammals move long distances. Rather, the power relationship demonstrates that, as a group, amphibians exhibit a wide range of dispersal strategies. As has been demonstrated (Stumpel and Hanekamp 1986, Platx et al. 1990, Tunner 1992, Vos et al. 2000, Hayes et al. 2001, Smith 2003), some amphibian species are capable of movements that are surprising for presumably poorly dispersing animals. Our review suggests that anurans have an average maximum movement recorded (2.02 km) that is two times as large as the distance commonly reported as wide enough to result in population isolation. The diversity of maximum movement recorded is apparent in the wide variance (2.40 E +07). Indeed, the anuran average and variance are an order of magnitude larger than the same patterns in salamanders (Table 5). Fitting an inverse power law to the movement frequency patterns for anurans and salamanders results in the explanation of 70% and 55% of the variance. Specific expectations for an individual species should not be based on a pattern demonstrated using many species and independent studies. However, note that our analysis makes a general prediction regarding the spatial scale at which one should expect local population differentiation: that distance where the inverse power law predicts a number of migrants equal to one. Genetically, populations tend to be locally differentiated when $N_e m \ll 1$ (Kimura and Maruyama 1971). For salamanders, the

inverse power law predicts that at least one individual is likely to move distances <8–9 km and for anurans at least one individual is likely to move 11–13 km. When pond networks are separated by these approximate distances – where dispersal is possible, but not common – is more likely to be a scale where the simple, stochastic metapopulation approach is applicable for amphibians. Such a rule will obviously not hold for all species all of the time (the environment between habitat patches, the species, the condition of individuals will all affect dispersal abilities and will differ), but our generalization is a hypothesis informed by the literature that invites further testing.

Others have noted that the perception of limited amphibian dispersal may reflect the scale at which amphibian-researchers operate, rather than the scale at which amphibians disperse (Turner 1960, Dole 1971, Staub et al. 1995, Marsh et al. 1999, Pope et al. 2000). Among those studies where there was enough data reported to estimate the longest axis of the study area, that distance was therefore the longest possible distance that could have been recorded. A regression of maximum distance dispersed on the size of the studies long axis resulted in a significant positive relationship where 72.65% of the observed variance in maximum dispersal distance is explained by having a larger study site (Fig. 4). This relationship suggests that our understanding of the maximum distances amphibians can move is being underestimated by the site size where we

Table 3. Maximum dispersal distance recorded, longest distance able to be measured in the reported study site, methodology used for distance estimate and sex and age of dispersing individual for 37 salamander species from 64 reports. Methodological abbreviations for capture techniques are as follows (Mark-recapture (MRR), toelcip (TOE), elastomer implant (ELAS), radio telemetry (RAD), passive integrated transponder (PIT), Radioactively tagged with Cobalt 60 (Co60), radioactively tagged with Tantalum 182 (Ta182), freeze branded (BRAND), distance to nearest wetland (DIST to WETLAND), microtagged (MICROTAG), individually specific skin pattern (PATTERN), displacement (DISP), tattoo (TAT), yearly rate of movement from introduction (RATE), jaw tag (JAW), spool of thread attached to animal and followed (SPOOL). When the largest reported dispersal distance is larger than the reported, or measured, longest axis of the study the ratio of study site long axis: maximum distance may exceed one. Such a situation might occur when an animal was recaptured during an occasional survey outside the study area as in Griffiths (1984), and Dole (1971). Thus values greater than one can be understood to support our hypothesis that animals are currently being located at the maximum distances being searched.

| Species | Max distance recorded (m) | Longest measure of study site (m) | Ratio study site to max distance | Method | Age | Reference |
|---|---------------------------|-----------------------------------|----------------------------------|--------------|--------------|-----------------------------|
| <i>Ambystoma californiense</i> | 670.00 | 3000.00 | 0.22 | MRR(PIT/TOE) | Adult | Trenham et al. 2001 |
| <i>Ambystoma californiense</i> | 129.00 | | | UNMARK | Adult | Loredo et al. 1997 |
| <i>Ambystoma jeffersonianum</i> | 250.00 | 567.00 | 0.44 | MRR(Co60) | Adult | Douglas and Monroe 1981 |
| <i>Ambystoma jeffersonianum</i> | 1610.00 | | | UNKNOWN | Unknown | Bishops 1941 |
| <i>Ambystoma jeffersonianum</i> | 625.00 | | | MRR(Ta182) | Adult | Williams 1973 |
| <i>Ambystoma jeffersonianum</i> | 231.00 | 692.00 | 0.59 | UNMARK | Unknown | Wacasey 1961 |
| <i>Ambystoma laterale</i> | 405.00 | 39000.00 | 0.03 | RAD | Adult | Faccio 2003 |
| <i>Ambystoma macrodactylum</i> | 1170.00 | 567.00 | 0.39 | UNMARK | Adult | Funk and Dunlap 1999 |
| <i>Ambystoma maculatum</i> | 220.00 | | | MRR(Co60) | Adult | Douglas and Monroe 1981 |
| <i>Ambystoma maculatum</i> | 125.00 | | | MRR(Ta182) | Adult | Williams 1973 |
| <i>Ambystoma maculatum</i> | 500.00 | 500.00 | 1.00 | MRR(TOE) | Adult female | Shoop 1968 |
| <i>Ambystoma maculatum</i> | 402.00 | | | UNMARK | Adult | Gordon 1968 |
| <i>Ambystoma maculatum</i> | 756.00 | 711.00 | 1.06 | RAD | Adult male | Madison 1997 |
| <i>Ambystoma maculatum</i> | 200.00 | | | UNMARK | Unknown | Wacasey 1961 |
| <i>Ambystoma maculatum</i> | 249.00 | 567.00 | 0.05 | MRR(Co60) | Unknown | Kleeberger and Werner 1983 |
| <i>Ambystoma opacum</i> | 30.00 | | | MRR(Co60) | Adult | Douglas and Monroe 1981 |
| <i>Ambystoma opacum</i> | 450.00 | | | MRR(Ta182) | Adult | Williams 1973 |
| <i>Ambystoma opacum</i> | 1000.00 | | | MRR | Juvenile | Pechmann et al. 2001 |
| <i>Ambystoma talpoideum</i> | 280.00 | 600.00 | 1.67 | MRR(Ta182) | Adult male | Semlitsch 1981 |
| <i>Ambystoma talpoideum</i> | 1000.00 | 600.00 | 1.67 | MRR | Juvenile | Pechmann et al. 2001 |
| <i>Ambystoma texanum</i> | 125.00 | 600.00 | 1.00 | MRR(Ta182) | Adult | Williams 1973 |
| <i>Ambystoma tigrinum</i> | 600.00 | | | MRR | Unknown | Pechmann et al. 2001 |
| <i>Ambystoma tigrinum</i> | 12.40 | | | MRR(TOE) | Adult | Semlitsch 1983 |
| <i>Ambystoma tigrinum</i> | 485.20 | | | MRR(RAD) | Adult male | Madison and Farrand 1997 |
| <i>Amphiuma tridactylum</i> | 297.00 | | | MRR(TAG) | Adult | Cagle 1948 |
| <i>Aneides aeneus</i> | 106.00 | | | MRR(TOE) | Adult female | Gordon 1961 |
| <i>Aneides aeneus</i> | 15.24 | | | UNMARK | Adult | Williams and Gordon 1961 |
| <i>Aneides vagrans</i> | 20.30 | 1300.00 | 0.02 | MRR(TOE) | Unknown | Davis 2002 |
| <i>Cryptobranchus alleganiensis</i> | 990.00 | | | MRR(TAG) | Adult | Nickerson and Mays 1973 |
| <i>Cryptobranchus alleganiensis</i> | 85.00 | 100.00 | 0.85 | MRR(BRAND) | Adult male | Peterson 1987 |
| <i>Cryptobranchus alleganiensis</i> | 900.00 | | | UNKNOWN | Unknown | Wiggs 1977 |
| <i>Desmognathus fuscus</i> | 19.80 | 50.00 | 0.40 | MRR(Co60) | Adult | Ashton 1975 |
| <i>Desmognathus fuscus</i> | 17.20 | | | MRR(Co60) | Adult | Barbour et al. 1969 |
| <i>Desmognathus fuscus</i> | 40.00 | | | MRR(TOE) | Adult | Barthalamus and Bellis 1972 |
| <i>Desmognathus quadromaculatus</i> | 25.00 | 40.00 | 1.00 | MRR(ELAST) | Larvae | Freeman 2003 |
| <i>Dicamptodon tenebrosus</i> | 66.25 | 180.00 | 0.14 | RAD | Adult | Johnston and Frid 2002 |
| <i>Dicamptodon tenebrosus</i> | 63.00 | 120.00 | 0.53 | MRR(TOE/PIT) | Larvae | Ferguson 2000 |
| <i>Eusatina eschscholtzii platensis</i> | 150.40 | | | MARK(SPOT) | Adult male | Staub et al. 1995 |
| <i>Eurycea bislineata</i> | 420.00 | 600.00 | 1.00 | UNMARK | Larvae | Johnson and Goldberg 1975 |
| <i>Eurycea quadridigitata</i> | 490.00 | 1000.00 | 0.49 | MRR | Juvenile | Pechmann et al. 2001 |
| <i>Gyrinophilus porphyriticus</i> | 490.00 | 332.00 | 0.27 | MRR(ELAS) | Unknown | Lowe 2003 |
| <i>Hynobius nebulosus tokyoensis</i> | 90.00 | | | MRR(TOE) | Adult | Kusano and Miyashita 1984 |

Table 3. (Continued).

| Species | Max distance recorded (m) | Longest measure of study site (m) | Ratio study site to max distance | Method | Age | Reference |
|----------------------------------|---------------------------|-----------------------------------|----------------------------------|-----------------|------------------------|----------------------------|
| <i>Necturus beyeri</i> | 65.00 | | | MRR(TOE) | Juvenile | Shoop and Gunning 1967 |
| <i>Necturus maculosus</i> | 256.00 | | | MRR(TOE) | Adult female | Shoop and Gunning 1967 |
| <i>Notophthalmus perstriatus</i> | 709.00 | | | DIST to WETLAND | Unknown | Dodd 1996 |
| <i>Notophthalmus viridescens</i> | 1000.00 | 6522.00 | 0.15 | MRR(SPOT) | Adult female | Gill 1978 |
| <i>Plethodon cinereus</i> | 90.00 | 90.00 | 1.00 | MRR(Co60) | Adult | Kleeberger and Werner 1982 |
| <i>Plethodon glutinosus</i> | 91.50 | 32.00 | 2.86 | MRR(TOE) | Adult male and female | Wells and Wells 1976 |
| <i>Plethodon jordani</i> | 60.00 | | | MRR(Ta182) | Adult female | Madison and Shoop 1970 |
| <i>Plethodon jordani</i> | 300.00 | 300.00 | 1.00 | MRR(TOE/DISP) | Adult | Madison 1969 |
| <i>Plethodon kentucki</i> | 13.95 | 15.00 | 0.93 | MRR(PATTERN) | Adult female | Marvin 1998 |
| <i>Plethodon vehiculatum</i> | 8.50 | 14.00 | 0.61 | MRR(TOE) | Adult male | Ovaska 1988 |
| <i>Rhyacotriton cascade</i> | 6.09 | 11.66 | 0.52 | MRR(PATTERN) | Adult female | Nijhuia and Kaplan 1998 |
| <i>Salamandra atra aurorae</i> | 30.00 | 933.00 | 0.03 | MRR(PATTERN) | Adult | Bonato and Fracasso 2003 |
| <i>Salamandra salamandra</i> | 30.00 | | | MRR(PATTERN) | Adult males and female | Rebello and Leclair 2003 |
| <i>Taricha rivularis</i> | 12874.75 | 12874.00 | 1.00 | MRR(AMP) | Adult | Twitty et al. 1967 |
| <i>Taricha rivularis</i> | 4023.36 | 4023.36 | 1.00 | MRR(AMP) | Adult | Twitty et al. 1964 |
| <i>Triturus alpestris</i> | 500.00 | | | MRR(PIT/TAT) | Adult | Perret et al. 2003 |
| <i>Triturus alpestris</i> | 200.00 | | | MRR(TOE) | Adult male and female | Joly and Grolet 1996 |
| <i>Triturus carnifex</i> | 299.00 | 637.00 | 0.47 | MRR(RAD) | Adult male and female | Schabetsberger et al. 2004 |
| <i>Triturus vulgaris</i> | 80.00 | 30.90 | 2.59 | MRR(TOE) | Adult female | Griffiths 1984 |
| <i>Triturus vulgaris</i> | 182.00 | 400.00 | 0.46 | UNMARK | Unknown | Warwick 1949 |
| <i>Triturus vulgaris</i> | 50.00 | | | MRR | Juvenile | Bell 1977 |
| <i>Triturus vulgaris</i> | 123.00 | | | MRR(TOE) | Adult female | Dolmen 1981 |

Table 4. Maximum dispersal distance recorded, longest distance able to be measured in the reported study site, methodology used for distance estimate and sex and age of dispersing individual for 53 anuran species from 102 reports. Abbreviations for capture methodology are as in Table 3.

| Species | Max distance recorded (m) | Longest measure of study site (m) | Ratio study site to max distance | Method | Age | Reference |
|-------------------------------------|---------------------------|-----------------------------------|----------------------------------|-----------------|--------------|------------------------------|
| <i>Aspaphus truei</i> | 360.00 | 2800.00 | 0.13 | MRR (TOE) | Juvenile | Daugherty and Sheldon 1982 |
| <i>Atelopus oxyrrhynchus</i> | 55.00 | | | MRR (TOE) | Adult male | Dole and Durant 1974 |
| <i>Atelopus varius</i> | 20.00 | 20.00 | 1.00 | MRR (TOE) | Adult male | Crump 1986 |
| <i>Bombina variegata</i> | 312.80 | 1000.00 | 0.31 | MRR (TOE) | Adult male | Beshkov and Jameson 1980 |
| <i>Bufo americanus</i> | 6437.38 | | | UNMARKED | Not reported | Hamilton 1934 |
| <i>Bufo americanus</i> | 235.00 | 235.00 | 1.00 | MRR (TOE/DISP) | Adult | Dole 1972 |
| <i>Bufo americanus</i> | 1000.00 | | | RATE/INTRO | Unknown | Maunder 1983 |
| <i>Bufo americanus</i> | 548.64 | 1254.03 | 0.44 | MRR (TOE) | Adult male | Blair 1943 |
| <i>Bufo americanus</i> | 594.00 | | | MRR (TOE/DISP) | Adult | Oldham 1966 |
| <i>Bufo americanus</i> | 4023.36 | | | UNMARKED | Not reported | Maynard 1934 |
| <i>Bufo baxteri</i> | 99.97 | | | MRR (TOE) | Adult male | Carpenter 1954 |
| <i>Bufo baxteri</i> | 423.80 | | | MRR (RAD) | Adult male | Parker and Anderson 2003 |
| <i>Bufo boreas</i> | 2440.00 | | | MRR (RAD) | Adult male | Bartlet 2000 |
| <i>Bufo boreas</i> | 6000.00 | | | MRR (RAD) | Unreported | Muths et al. 2003 |
| <i>Bufo boreas</i> | 2324.20 | 15000.00 | 0.40 | UNREPORTED | Adult female | Muths 2003 |
| <i>Bufo boreas</i> | 200.00 | 200.00 | 1.00 | MRR (TOE/DISP) | Adult | Tracy and Dole 1969 |
| <i>Bufo bufo</i> | 3000.00 | | | MRR (DISP) | Adult | Heusser 1969 |
| <i>Bufo bufo</i> | 3621.02 | | | MRR (TOE) | Unknown | Moore 1954 |
| <i>Bufo bufo</i> | 985.00 | 8485.28 | | MRR (RAD) | Adult female | Sinsch 1988 |
| <i>Bufo bufo</i> | 118.00 | | | MRR (TOE) | Not reported | Parker and Grittins 1979 |
| <i>Bufo bufo</i> | 500.00 | | | MRR (TOE) | Not reported | Haapanen 1974 |
| <i>Bufo bufo</i> | 1760.00 | | | MRR | Adult | Sinsch 1989 |
| <i>Bufo calamita</i> | 4411.00 | 3605.55 | | MRR (RAD) | Adult female | Miaud et al. 2000 |
| <i>Bufo calamita</i> | 400.00 | 2828.43 | | MRR (MICROTAG) | Juvenile | Sinsch 1997 |
| <i>Bufo calamita</i> | 2600.00 | | | MRR (RAD) | Adult | Sinsch 1992 |
| <i>Bufo fowleri</i> | 1650.00 | 2000.00 | | MRR (TOE) | Juvenile | Breden 1987 |
| <i>Bufo fowleri</i> | 312.00 | 1770.00 | | MRR (TOE) | Adult | Clarke 1974 |
| <i>Bufo fowleri</i> | 335.28 | 1254.03 | | MRR (TOE) | Adult male | Blair 1943 |
| <i>Bufo fowleri</i> | 1600.00 | | | MRR (TAG) | Adult | Stulle 1952 |
| <i>Bufo fowleri</i> | 1280.16 | | | UNKNOWN | Unreported | Nichols 1937 |
| <i>Bufo fowleri</i> | 34000.00 | 34000.00 | | MRR (TOE) | Adult Female | Smith and Green (unpubl.) |
| <i>Bufo fowleri</i> | 100.00 | | | MRR (TOE) | Adult | Ferguson 1960 |
| <i>Bufo hemiophrys</i> | 342.00 | | | MRR (TOE/Ta182) | Adult | Breckenridge and Tester 1961 |
| <i>Bufo japonicus formosus</i> | 260.00 | 500.00 | | MRR (RAD) | Adult | Kusano et al. 1995 |
| <i>Bufo marinus</i> | 15100.00 | | | RATE | Unknown | Eastal and Floyd 1986 |
| <i>Bufo marinus</i> | 35000.00 | | | RATE | Unknown | Freedland and Martin 1985 |
| <i>Bufo marinus</i> | 1300.00 | | | MRR (RAD) | Adult | Schwarzkopf and Alford 2002 |
| <i>Bufo punctatus</i> | 365.76 | 1105.30 | 0.33 | MRR (RAD) | Adult | Turner 1959 |
| <i>Bufo punctatus</i> | 822.96 | | | MRR (TOE) | Adult | Tewis 1966 |
| <i>Bufo punctatus</i> | 900.00 | 900.00 | 1.00 | MRR (TOE/DISP) | Adult female | Weintraub 1974 |
| <i>Bufo terrestris</i> | 1609.34 | 2449.29 | 0.66 | MRR (TOE) | Adult | Bogert 1947 |
| <i>Bufo variceps</i> | 800.00 | | | MRR (TOE) | Adult male | Blair 1943 |
| <i>Dendrobates pumilio</i> | 20.00 | 20.00 | 1.00 | MRR (TOE/DISP) | Adult female | McVey et al. 1981 |
| <i>Eleutherodactylus coqui</i> | 6.68 | | | MRR (ELASTOMER) | Adults | Woolbright 1985 |
| <i>Eleutherodactylus fitzingeri</i> | 35.00 | | | MRR (PATTERN) | Unreported | Hobel 1999 |
| <i>Gastrophryne olivacea</i> | 609.60 | | | UNKNOWN | Unknown | Fitch 1956 |
| <i>Gastrophryne carolinensis</i> | 914.00 | | | DIST to WETLAND | Unknown | Dodd 1996 |
| <i>Geococina alba</i> | 39.00 | 150.00 | 0.26 | MRR (TOE) | Adult male | Driscoll 1997 |
| <i>Geococina vitellina</i> | 49.00 | 150.00 | 0.33 | MRR (TOE) | Adult male | Driscoll 1997 |

Table 4. (Continued).

| Species | Max distance recorded (m) | Longest measure of study site (m) | Ratio study site to max distance | Method | Age | Reference |
|---------------------------------|---------------------------|-----------------------------------|----------------------------------|----------------------------|-----------------------|----------------------------------|
| <i>Helicoporus australiacus</i> | 463.00 | | | MRR (RAD) | Adult male | Lemckert and Brassil 2003 |
| <i>Helicoporus eyrei</i> | 2500.00 | | | DIST to WETLAND UNREPORTED | Unknown | Bamford 1992 |
| <i>Hyla arborea</i> | 12600.00 | 18000.00 | 0.70 | MRR | Unreported | Stumpel and Hanekamp 1986 |
| <i>Hyla arborea</i> | 12570.00 | | | UNREPORTED | Unreported | Vos et al. 2000 |
| <i>Hyla arborea</i> | 1500.00 | | | UNREPORTED | Unreported | Carlson and Edenhamm 2000 |
| <i>Hyla arborea</i> | 3750.00 | | | UNKNOWN | Unknown | Clausnitzer and Clausnitzer 1984 |
| <i>Hyla regilla</i> | 1000.00 | | 1.00 | MRR (TOE/DISP) | Adult male | Jameson 1957 |
| <i>Hyla regilla</i> | 1900.00 | | | RATE/INTRO | Unreported | Reimchen 1990 |
| <i>Hyla versicolor</i> | 125.00 | | 0.96 | MRR (TOE) | Juvenile | Roble 1979 |
| <i>Leiopelma hochstetteri</i> | 12.65 | | 0.11 | MRR (TOE) | Adult | Tessier et al. 1991 |
| <i>Mixophyes iteratus</i> | 2000.00 | | 0.05 | MRR (RAD) | Adult female | Lemckert and Brassil 2000 |
| <i>Pelobates fuscus</i> | 500.00 | | | MRR (PIT) | Adult male and female | Hels 2002 |
| <i>Phyllomedusa bicolor</i> | 46.60 | | | MRR (SPOOL) | Adult male | Neckel de Oliveira 1996 |
| <i>Physalaemus pustulosus</i> | 820.00 | | 0.27 | MRR (TOE) | Adult | Marsh et al. 1999 |
| <i>Pseudacris triseriata</i> | 213.00 | | 1.58 | MRR (Co60) | Adult | Kramer 1973 |
| <i>Pseudacris maculata</i> | 685.80 | | | UNKNOWN | Unknown | Spencer 1964 |
| <i>Rana arvalis</i> | 7600.00 | | 0.38 | RATE (GENETIC) | Nuclear marker | Vos et al. 2001 |
| <i>Rana aurora</i> | 300.00 | | | MRR (TOE) | Adult male | Calef 1973 |
| <i>Rana aurora aurora</i> | 24000.00 | | | MRR (PIT) | Adult female | Hayes et al. 2001 |
| <i>Rana aurora aurora</i> | 914.40 | | | UNMARKED | Adult | Dumas 1966 |
| <i>Rana aurora aurora</i> | 3600.00 | | 0.72 | MRR (RAD) | Adult | Bulger et al. 2003 |
| <i>Rana berlandieri</i> | 16000.00 | | | RATE | Adult male | Platz et al. 1990 |
| <i>Rana catesbeiana</i> | 1600.20 | | | MRR (JAW) | Adult | Ingram and Raney 1943 |
| <i>Rana catesbeiana</i> | 914.40 | 1363.76 | 0.67 | MRR (JAW) | Unreported | Raney 1940 |
| <i>Rana catesbeiana</i> | 966.00 | | | MRR (JAW) | Adult | Willis et al. 1956 |
| <i>Rana clamitans</i> | 600.0 | | | MRR (TOE) | Adult female | Martof 1953 |
| <i>Rana clamitans</i> | 560.00 | | | MRR (RAD) | Adult | Lamoureux and Madison 1999 |
| <i>Rana clamitans</i> | 4800.00 | | | MRR (TOE) | Juvenile | Schroeder 1976 |
| <i>Rana clamitans</i> | 300.00 | | | UNMARK | Adult | Ponsero and Joly 1998 |
| <i>Rana clamitans</i> | 1200.00 | 1000.00 | 1.20 | MRR (TOE) | Juvenile | Sjögren Gulve 1988 |
| <i>Rana lessonae</i> | 1760.00 | 2830.00 | 0.62 | MRR (PIT) | Adult | Holenweg Peter 2001 |
| <i>Rana lessonae</i> | 15000.00 | | | MRR | Unknown | Turner 1992 |
| <i>Rana lutiventris</i> | 6500.00 | | | MRR | Adult | Engle 2001 |
| <i>Rana lutiventris</i> | 2066.00 | 3905.00 | 0.53 | MRR (TOE/RAD) | Adult female | Pilliod et al. 2002 |
| <i>Rana lutiventris</i> | 560.00 | | | MRR (RAD) | Adult female | Bull and Hayes 2001 |
| <i>Rana mucosa</i> | 1020.00 | 1414.21 | 0.72 | MRR (PIT) | Adult female | Pope and Matthews 2001 |
| <i>Rana pipiens</i> | 3218.69 | | | MRR (TOE) | Adult | Merrell 1970 |
| <i>Rana pipiens</i> | 160.00 | 720.00 | 0.22 | MRR (TOE) | Adult female | Dole 1965 |
| <i>Rana pipiens</i> | 1744.00 | | | MRR (TOE) | Adult | Dole 1968 |
| <i>Rana pipiens</i> | 8000.00 | 8000.00 | 1.00 | MRR (TOE) | Juvenile | Seburn et al. 1997 |
| <i>Rana pipiens</i> | 5200.00 | 720.00 | 7.22 | MRR (TOE) | Juvenile male | Dole 1971 |
| <i>Rana pretiosa</i> | 1280.16 | 2133.60 | 0.60 | MRR (TOE) | Adult | Turner 1960 |
| <i>Rana pretiosa</i> | 45.11 | | | MRR (TOE) | Adult male | Carpenter 1954 |
| <i>Rana ridibunda</i> | 1760.00 | 2830.00 | 0.62 | MRR (PIT) | Adult | Holenweg Peter 2001 |
| <i>Rana sevosia</i> | 299.00 | 1202.00 | 0.25 | MRR (RAD) | Adult | Richter et al. 2001 |
| <i>Rana sevosia</i> | 2000.00 | | | MRR | Adult female | Franz et al. 1988 |
| <i>Rana sevosia</i> | 1600.00 | | | UNMARKED | Not reported | Carr 1940 |
| <i>Rana sylvatica</i> | 60.00 | 186.00 | 0.32 | UNMARKED | Not reported | Regosin et al. 2003 |

Table 4. (Continued).

| Species | Max distance recorded (m) | Longest measure of study site (m) | Ratio study site to max distance | Method | Age | Reference |
|------------------------------|---------------------------|-----------------------------------|----------------------------------|----------|----------|--------------------------|
| <i>Rana sylvatica</i> | 500.00 | | | MRR(TOE) | Adult | Howard and Kluge 1985 |
| <i>Rana sylvatica</i> | 2530.00 | 2287.00 | 1.11 | MRR(TOE) | Juvenile | Berven and Grudzien 1990 |
| <i>Rana sylvatica</i> | 89.61 | 65.84 | 1.36 | MRR(TOE) | Adult | Bellis 1965 |
| <i>Rana temporaria</i> | 460.00 | | | MRR(RAD) | Adult | Seitz et al. 1992 |
| <i>Syrriophus marmorati</i> | 380.39 | | | MRR(TOE) | Adult | Jameson 1955 |
| <i>Scaphiopus holbrookii</i> | 825.00 | | | MRR(TOE) | Adult | Pearson 1955 |

study such movement. Our review makes a simple prediction that monitoring larger areas in the future will result in the discovery of longer distance movements for both anurans and salamanders.

Case study

Some amphibians do function as metapopulations (Gill 1978, Sjögren 1991, Sjögren Gulve and Ray 1996, Vos et al. 2000). However, examining the amphibian-as-metapopulation literature indicates that the generalization that all amphibians will operate as metapopulations (Alford and Richards 1999) is not supported. The majority of the metapopulation conditions are either not tested or are assumed to hold in the amphibian as metapopulation literature. Instead, it is often taken as a foregone conclusion that amphibians operate as metapopulations. Bulger et al. (2003), for example, invoke metapopulation structure without having tested any of the related (Hanski and Kuussaari 1995, Hanski et al. 1995, Hanski 1999) hypotheses. For species we have examined ourselves (*Bufo americanus*, *Bufo fowleri*, *Pseudacris crucifer*, *Rana sylvatica*, *Rana pipiens*, *Rana clamitans* and *Rana catesbeiana*), both locally (on a scale of ≤ 10 km) and regionally (for *B. fowleri* ≤ 300 km), we found no evidence of metapopulation structure at either scale, and concluded that while there was not enough movement between populations separated by many tens of kilometres to support a metapopulation effect, there was likely too much dispersal occurring between the habitat patches separated by 10 km or less (Smith 2003). Most of these species are common to the area we investigated, but *B. fowleri* is currently listed as Threatened by the Committee on the Status of Endangered Species (COSEWIC) in Canada largely due to its isolated and fragmented habitat. Indeed, a metapopulation based conservation approach was intuitively appealing for this species, as, prior to our analysis, it qualitatively appeared to meet all of Hanski's four conditions.

To reconcile the acceptance of the metapopulation approach in amphibian conservation and ecology with the lack of stringent testing of hypotheses we compared those characteristics common to amphibians as metapopulations (Marsh and Trenham 2001), 1) population dynamics determined by pond-based-processes, 2) common local extinction and colonisation, 3) local extinction occurring in suitable habitat, 4) limited dispersal causing isolation) to the studies we have reviewed and the species for which we have data.

The majority (33/53) of the studies we examined had either implicitly assumed, or had tested, that the "ponds as patches" view was an accurate depiction of an amphibian population. Recently, Skelly and Meir (1997), Pope et al. (2000) and Marsh and Trenham

Table 5. Summary table for the analysis of maximum reported distance moved for 164 studies of 90 species of amphibians.

| | Amphibians | Frogs | Salamanders |
|--|------------|----------|-------------|
| Number of species in dispersal studies | 90 | 53 | 37 |
| Number of dispersal studies | 166 | 102 | 64 |
| % max dispersal ≤ 1 km | 70 | 56 | 94 |
| % max dispersal ≤ 400 m | 44 | 31 | 64 |
| % max dispersal ≥ 10 km | 5 | 7 | 2 |
| Average (m) | 2023.54 | 2922.51 | 576.75 |
| Standard deviation (m) | 4895.61 | 5929.89 | 1664.92 |
| Variance (m ²) | 2.40E+07 | 3.52E+07 | 2.77E+06 |

(2001) have criticized the assumed primacy of the pond. For instance, with *Rana pipiens*, any apparent metapopulation structure was removed when the non-pond variable of “summer habitat” was removed from the analysis (Pope et al. 2000). In our own work with *B. fowleri*, we know that the number of non-reproductive one year olds at year (t) explains nearly 80% of the variation in captured adults in year (t+1) (Green and Smith unpubl.). Although strong, this relationship was derived using only 5 yr worth of data and excludes one year where it was suspected that migration boosted the observed number of reproductive animals in year (t+1). Thus while population processes occurring in the pond are clearly important, there is strong evidence that events occurring outside the pond (migration, over-wintering success) also contribute the observed population dynamics. Therefore, instead of asking is the pond a patch (~Hanski Condition 1), we should ask is the patch only the pond? Stated another way; perhaps the easily spatially delineated feature “pond” is not the disjunct habitat one should model. The application to amphibian conservation is clear, for if one adopted a metapopulation based conservation approach on the hypothesis of ponds as metapopulation patches – and summarily protected those patches – without testing whether the habitat critical to the species survival was actually described by pond boundaries it is possible that the truly important habitat would not be protected.

Forty-five out of 53 articles in the literature (85%) did not examine the frequency of local extinction and colonization. A limited number of between-year occupancy transitions severely restrict the researcher’s ability to determine whether extinctions and colonizations are actually common features of the network of breeding assemblages (Thomas et al. 2002). For instance, within the local habitat patch assemblage we monitor in Ontario, there have been 38 observed colonisation and 31 extinction events for *B. fowleri* measured over 15 yr at Long Point, resulting in average colonisation and extinction rates of 0.2798 and 0.2481 respectively. Compared to values for other amphibian species (Table 2 of Marsh and Trenham (2001)), the values for *B. fowleri* are amongst the highest and yet there is no evident metapopulation effect involved in *B. fowleri* population dynamics (Smith 2003). Due to relatively high rates of local extinction and colonisation in *B. fowleri*, a conservation strategy might be based on the faulty notion that these toads occupy local and regional metapopulations when they are actually more intimately connected by regular dispersal (i.e. a patchy population).

One finding recorded regularly in the literature was that local amphibian extinctions were deterministic, not stochastic, as habitats underwent succession (Sjögren 1991, Skelly et al. 1999, Marsh and Trenham 2001, Bradford et al. 2003). Indeed, at Long Point the environment is constantly undergoing succession, and

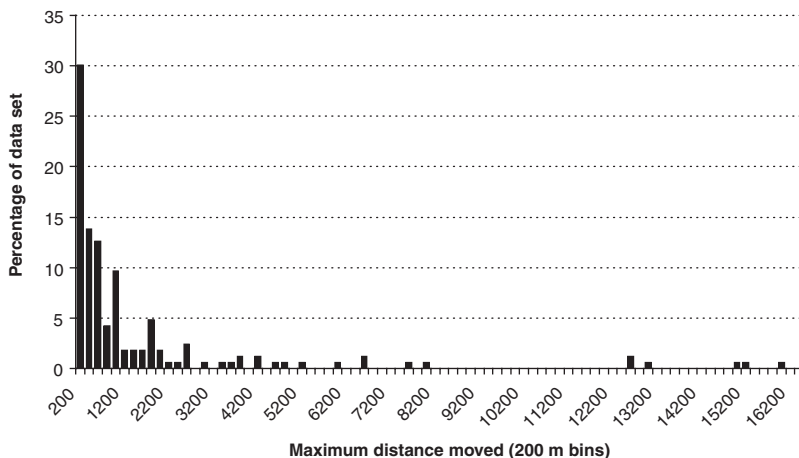
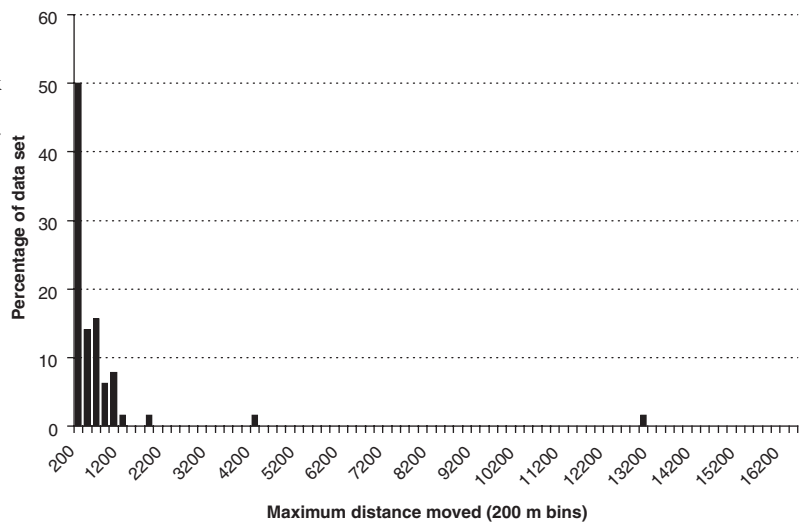


Fig. 1. Frequency histogram of the maximum distance moved by amphibians from 166 journal articles (90 species). 200 m size bins. 30% of the reviewed studies had maximum movement distances > 1 km. $y = 22.39x^{-0.7653}$, $R^2 = 0.7031$.

Fig. 2. Frequency histogram of the maximum distance moved by salamander species from 62 journal articles (37 species). 200 m size bins. Six percent of the reviewed studies had maximum movement distances >1 km. $y = 6.23x^{-0.4823}$, $R^2 = 0.544$.



ponds are likely to be exposed to deterministic degradation (as *B. fowleri* breeding habitat) as they go through succession. We suspected that at least several of the observed extinctions at Long Point were due to succession reducing habitat quality to such an extent as to cause extinction. Perhaps the effects of this deterministic change are predominant over any stochastic changes we have measured (Skelly et al. 1999), but a quantitative analysis of this question is beyond the scope of this investigation. Clearly though it remains important to do so (Ellner and Fussmann 2003), as differentiating between the importance of stochastic and deterministic changes will inform conservation decisions regarding whether management should focus on landscape factors or local habitat conditions.

The supposition of limited dispersal causing isolation was the most frequently implicated reason for evident, or assumed, metapopulation structure in amphibians. In

our own work with *B. fowleri*, we concluded that dispersal was likely the primary factor implicated in the lack of metapopulation structure we demonstrated – both too little and too frequent (Smith 2003). At a local scale of ≤ 10 km, individuals dispersed over a distance and at a rate that made even isolated populations connected to the whole. Regionally (≤ 300 km), populations were too isolated for even occasional migrants to recolonise habitat following local extinction. We suspect that the generalization of limited amphibian dispersal causing population isolation, and therefore metapopulation structure, may not be warranted as frequently as the literature implies (Alford and Richards 1999). This is especially true for pond-breeding anurans species with a high turnover of local populations and dependent upon dispersal for its persistence, for without the effect of rescue from neighboring populations, they will suffer greater cumulative local extinctions (Green 2003). We

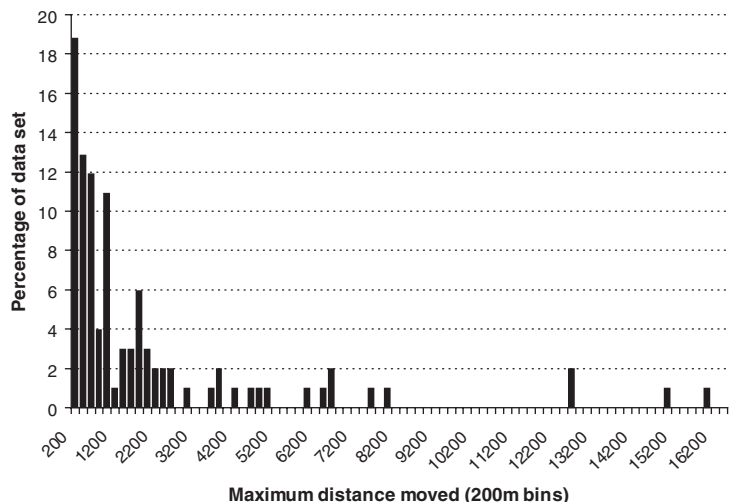


Fig. 3. Frequency histogram of the maximum distance moved by anurans from 102 journal articles (53 species). 200 m size bins. Forty-four percent of the reviewed studies had maximum movement distances >1 km. $y = 13.749x^{-0.6396}$, $R^2 = 0.6797$.

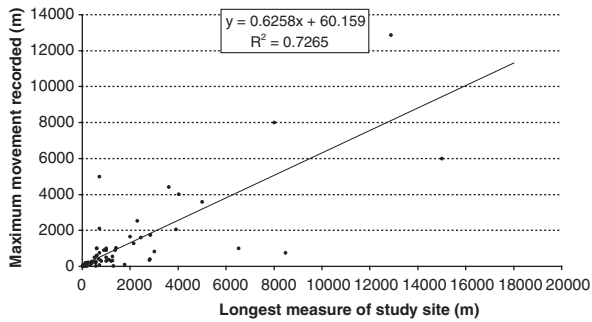


Fig. 4. Relating the maximum movement recorded with the maximum size of the study area.

find that movement distances for anurans are an order of magnitude greater (~ 10 km) than has previously been thought.

Conclusions

Our review demonstrates that the applicability of the metapopulation paradigm to amphibian species is largely dependant on the hypothesis of limited dispersal. As there are a wide range of dispersal abilities within amphibian species, we should be cautious with the indiscriminant application of the metapopulation approach to amphibians – especially where conservation decisions are to be based on the assumptions of isolation and metapopulation structure though limited dispersal. Although amphibians are predominantly site-loyal and of low vagility, they can move distances much greater than previously anticipated. Their dispersal capabilities suggest that occasional migrants may connect populations separated by tens of kilometers. Although it is clear that type and quality of the landscape occurring between habitat patches will affect the number of successful immigrants (Ray et al. 2002); we make the general suggestion that for salamanders and anurans, population differentiation is most likely to occur at scales upward of 10 km. If somewhat regular movement of individuals can connect populations separated by distances smaller than this, then the effective number of populations is reduced. If reduced to one, then simple patch occupancy models are ineffective tools for research or conservation as they ignore local dynamics (Hanski 1998). All amphibians are not metapopulations and not all amphibians are dispersal poor. The paradigm of pond-breeding amphibian populations as metapopulations has been adopted before there have been sufficient data available to evaluate it (Hanski and Simberloff 1997). If the meaning of the term “metapopulation” has lost clarity (Smedbol et al. 2002), researchers would do well to test the elementary predictions of a simple metapopulation prior to announcing that their particular study organism/population constitutes one. If a researcher were encour-

aged to use the term metapopulation without even simple tests of whether necessary conditions were met, then the metapopulation would no longer be a falsifiable hypothesis. We feel that the metapopulation concept has much greater utility, and scientific integrity, when it is phrased as a hypothesis.

It is not our intent to summarily reject the positive influence the development of the metapopulation concept has had on ecology and conservation. Undoubtedly there are amphibian species for which the metapopulation assumption of pond isolation due to limited dispersal is valid. However, the generality of this assumption is not supported by data. The metapopulation approach – especially regarding habitat patch isolation due to limited dispersal – must be more stringently tested and more clearly reported.

Acknowledgements – We gratefully acknowledge the support of the Natural Sciences and Engineering Council (NSERC) and the World Wildlife Fund Canada Endangered Species Recovery Fund for grants to DMG and the Mountain Equipment Co-op Environment Fund, McGill Univ., NSERC and Fonds Nature et Technologies for grants and scholarships to MAS. Comments from T. Hels helped improve this manuscript. M.A.S. gives special thanks to Elaine Bazinet Smith, Clark Smith and Alison Judd for support and encouragement.

References

- Alford, R. A. and Richards, S. J. 1999. Global amphibian declines: a problem in applied ecology. – *Annu. Rev. Ecol. Syst.* 30: 133–165.
- Andrewartha, H. G. and Birch, I. C. 1954. The distribution and abundance of animals. – Chicago Univ. Press.
- Ashton, R. E. Jr 1975. A study of movement, home range, and winter behaviour of *Desmognathus fuscus*. – *J. Herpetol.* 9: 85–91.
- Baguette, M. 2003. Long distance dispersal and landscape occupancy in a metapopulation of the cranberry fritillary butterfly. – *Ecography* 26: 153–160.
- Bamford, M. J. 1992. The impact of fire and increasing time after fire upon *Heleioporus eyrei*, *Limnodynastes dorsalis* and *Myobatrachus gouldii* (Anura: Leptodactylidae) in Banksia woodland near Perth, western Australia. – *Wildl. Res.* 19: 169–178.
- Barbour, R. W. et al. 1969. Home range, movements, and activity of the dusky salamander, *Desmognathus fuscus*. – *Copeia* 1969: 293–297.
- Barthlamus, G. T. and Bellis, E. D. 1972. Home range, homing and homing mechanism of the salamander, *Desmognathus fuscus*. – *Copeia* 1972: 632–642.
- Bartlett, P. E. 2000. A biophysical analysis of habitat selection in western toads (*Bufo boreas*) in southeastern Idaho. – Ph.D. thesis, Idaho State Univ.
- Beebee, T. J. C. 1996. Ecology and conservation of amphibians. – Chapman and Hall.
- Bell, G. 1977. The life of the smooth newt (*Triturus vulgaris*) after metamorphosis. – *Ecol. Monogr.* 47: 279–299.
- Bellis, E. D. 1965. Home range and movements of the wood frog in a northern bog. – *Ecology* 6: 90–98.
- Berry, O. 2001. Genetic evidence for wide dispersal by the sand frog, *Heleioporus psammophilus* (Anura: Myobatrachidae), in western Australia. – *J. Herpetol.* 35: 136–141.
- 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.
- Bishops, S. C. 1941. The salamanders of New York. – New York State Museum Bulletin.
- 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.
- Bogert, C. M. 1947. Results of the Archbold Expeditions. No 57. A field study of homing in the Carolina toad. – *Am. Mus. Nov.* 1355: 1–24.
- Bonato, L. and Fracasso, G. 2003. Movements, distribution pattern and density in a population of *Salamandra atra aurorae* (Caudata: Salamandridae). – *Amphib.-Reptilia* 24: 251–260.
- Bradford, D. F. et al. 2003. Habitat patch occupancy by toads (*Bufo punctatus*) in a naturally fragmented desert landscape. – *Ecology* 84: 1012–1023.
- Brattstrom, B. H. 1962. Homing in the giant toad, *Bufo marinus*. – *Herpetologica* 18: 176–180.
- Breckenridge, W. J. and Tester, J. R. 1961. Growth, local movements and hibernation of the Manitoba toad, *Bufo hemiophrys*. – *Ecology* 42: 637–646.
- Breden, F. 1987. The effects of post-metamorphic dispersal on the population genetic structure of Fowler's toad *Bufo fowleri*. – *Copeia* 1987: 386–395.
- 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.
- Bull, E. L. and Hayes, M. P. 2001. Post-breeding season movements of Columbia spotted frogs (*Rana luteiventris*) in northeastern Oregon. – *West N. Am. Nat.* 61: 119–123.
- Cagle, F. R. 1948. Observations of a population of the salamander, *Amphiuma tridactylum* (Cuvier). – *Ecology* 29: 479–491.
- 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.
- Call, D. R. 1997. Microsatellite characteristics and population structure for two anurans (*Rana luteiventris* and *Hyla regilla*). – Ph.D. thesis, Washington State Univ.
- Carlson, A. and Edenhamn, P. 2000. Extinction dynamics and the regional persistence of a tree frog metapopulation. – *Proc. R. Soc. Lond. B Biol. Sci.* 267: 1311–1313.
- Carpenter, C. C. 1954. A study of amphibian movement in the Jackson's Hole Wildlife Park. – *Copeia* 1954: 197–200.
- Carpenter, C. C. and Gillingham, J. C. 1987. Water hole fidelity in the marine toad, *Bufo marinus*. – *J. Herpetol.* 21: 158–161.
- Carr, A. F. Jr 1940. A contribution to the herpetology of Florida. – *Univ. of Florida Publ. Biol. Sci. Ser.* 3: 1–18.
- Clarke, R. D. 1974. Activity and movement patterns in a population of Fowler's toad, *Bufo woodhousei fowleri*. – *Am. Midl. Nat.* 92: 257–274.
- Clausnitzer, C. and Clausnitzer, H. J. 1984. First results of a repopulation of the tree frog *Hyla arborea* in the district of Celle, Lower Saxony, West Germany. – *Salamandra* 20: 50–55.
- 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.
- Corser, J. D. 2001. Decline of disjunct green salamander (*Aneides aeneus*) populations in the southern Appalachians. – *Biol. Conserv.* 97: 119–126.
- Crump, M. L. 1986. Homing and site fidelity in a neotropical frog, *Atelopus varius*, (Bufonidae). – *Copeia* 1986: 438–444.
- Daugherty, C. H. and Sheldon, A. L. 1982. Age-specific movement patterns of the frog *Ascaphus truei*. – *Herpetologica* 38: 468–474.
- Davis, T. M. 2002. Microhabitat use and movements of the wandering salamander, *Aneides vagrans*, on Vancouver Island, British Columbia, Canada. – *J. Herpetol.* 36: 699–703.
- Dodd, C. K. Jr 1996. Use of terrestrial habitats by amphibians in the sandhill uplands of north-central Florida. – *Alytes* 14: 42–52.
- Dole, J. W. 1965. Summer movements of adult leopard frog, *Rana pipiens* Schreber, in northern Michigan. – *Ecology* 46: 236–255.
- 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. 1972. Homing and orientation of displaced toads, *Bufo americanus*, to their home sites. – *Copeia* 1972: 151–158.
- 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.
- Dolmen, D. 1981. Local migration, rheotaxis and philopatry by *Triturus vulgaris* within a locality in central Norway. – *Br. J. Herpetol.* 6: 151–158.
- Douglas, M. E. and Monroe, B. L. 1981. A comparative study of topographical orientation in *Ambystoma* (Amphibia: Caudata). – *Copeia* 1981: 460–463.
- Driscoll, D. 1997. Mobility and metapopulation structure of *Geocrinia alba* and *Geocrinia vitellina*, two endangered frog species from southwestern Australia. – *Aust. J. Ecol.* 22: 185–195.
- Duellman, W. E. and Trueb, L. 1986. Biology of amphibians. – McGraw-Hill.
- Dumas, P. C. 1966. Studies of the *Rana* species complex in the Pacific Northwest. – *Copeia* 1966: 60–74.
- Easteal, S. and Floyd, R. B. 1986. The ecological genetics of introduced populations of the giant toad, *Bufo marinus*: dispersal and neighborhood size. – *Biol. J. Linn. Soc.* 27: 17–45.
- Ebisuno, M. and Gentili, A. 2002. Reproductive site selection and characteristics of sources and sinks in an Italian tree frog metapopulation (*Hyla intermedia*, Boulenger 1882). – *Revue d'ecologie-la terre et la vie* 57: 263–278.
- Ellner, S. P. and Fussmann, G. 2003. Effects of successional dynamics on metapopulation persistence. – *Ecology* 84: 882–889.
- 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.Sc. thesis, Boise State Univ.
- Faccio, S. D. 2003. Postbreeding emigration and habitat use by Jefferson and spotted salamanders in Vermont. – *J. Herpetol.* 37: 479–489.
- Ferguson, D. E. 1960. Observations on movements and behavior of *Bufo fowleri* in residential areas. – *Herpetologica* 16: 112–114.
- Ferguson, H. M. 2000. Larval colonisation and recruitment in the Pacific giant salamander (*Dicamptodon tenebrosus*) in British Columbia. – *Can. J. Zool.* 78: 1238–1242.
- Fitch, H. S. 1956. A field study of the Kansas ant-eating frog *Gastrophryne olivacea*. – *Univ. Kans. Publ. Mus. Nat. Hist.* 8: 275–307.
- Franz, R. et al. 1988. *Rana aerolata aesopus*: movement. – *Herpetol. Rev.* 19: 33.
- Freckleton, R. P. and Watkinson, A. R. 2003. Are all plant populations metapopulations? – *J. Ecol.* 91: 321–324.
- Freeland, W. J. and Martin, K. C. 1985. The rate of range expansion by *Bufo marinus* in northern Australia, 1980–1984. – *Aust. Wildl. Res.* 12: 555–559.
- Freeman, S. L. 2003. Movement of larval *Desmognathus quadramaculatus* in linear and connected habitats. – Ph.D. thesis, Univ. of Virginia.
- Funk, W. C. and Dunlap, W. W. 1999. Colonization of high-elevation lakes by long-toed salamanders (*Ambystoma*

- macrodactylum*) after the extinction of introduced trout populations. – *Can. J. Zool.* 77: 1759–1767.
- Gill, D. E. 1978. The metapopulation ecology of the red-spotted newt, *Notophthalmus viridescens*, (Rafinesque). – *Ecol. Monogr.* 48: 145–166.
- Goldber, C. S. 2002. Habitat, spatial population structure, and methods for monitoring barking frogs (*Eleutherodactylus augusti*) in southern Arizona. – M.Sc. thesis, Univ. of Arizona.
- Gordon, R. E. 1961. The movement of displaced green salamanders. – *Ecology* 42: 200–202.
- Gordon, R. E. 1968. Terrestrial activity of the spotted salamander, *Ambystoma maculatum*. – *Copeia* 1968: 879–880.
- Green, D. M. 2003. The ecology of extinction: population fluctuation and decline in amphibians. – *Biol. Conserv.* 111: 331–343.
- Griffiths, R. A. 1984. Seasonal behaviour and intrahabitat movements in an urban population of smooth newts, *Triturus vulgaris* (Amphibia: Salamandridae). – *J. Zool. Lond.* 203: 241–251.
- Haapanen, A. 1974. Site tenacity of the common toad, *Bufo bufo* (L.). – *Ann. Zool. Fenn.* 11: 251–252.
- Halley, J. M. et al. 1996. Predicting the persistence of amphibian populations with the help of a spatial model. – *J. Appl. Ecol.* 33: 455–470.
- Hamilton 1934. The rate of growth of the toad (*Bufo americanus*) under natural conditions. – *Copeia* 1934: 88–90.
- Hanski, I. 1998. Metapopulation dynamics. – *Nature* 396: 41–49.
- Hanski, I. 1999. Metapopulation ecology. – Oxford Univ. Press.
- Hanski, I. and Kuussaari, M. 1995. Butterfly metapopulation dynamics. – In: Cappuccino, N. and Price, P. W. (eds), *Population dynamics: new approaches and synthesis*. Academic Press, pp. 149–171.
- Hanski, I. and Simberloff, D. 1997. The metapopulation approach, its history, conceptual domain, and application to conservation. – In: Hanski, I. and Gilpin, M. (eds), *Metapopulation biology: ecology, genetics and evolution*. Academic Press, pp. 2–26.
- Hanski, I. et al. 1995. Metapopulation persistence of an endangered butterfly in a fragmented landscape. – *Oikos* 72: 21–28.
- Harrison, S. 1991. Local extinction in a metapopulation context: an empirical evaluation. – *Biol. J. Linn. Soc.* 42: 73–88.
- Harrison, S. and Taylor, A. D. 1997. Empirical evidence for metapopulation dynamics. – In: Hanski, I. and Gilpin, M. (eds), *Metapopulation biology: ecology, genetics and evolution*. Academic Press, p. 512.
- Hartwell, H. H. 1990. Relictual amphibians and old-growth forests. – *Conserv. Biol.* 4: 309–319.
- Hayes, M. P. Jr et al. 2001. *Rana aurora aurora*: movement. – *Herpetol. Rev.* 32: 35–36.
- Hecnar, S. J. and M'Closkey, R. T. 1996. Regional dynamics and the status of amphibians. – *Ecology* 77: 2091–2097.
- Hels, T. 2002. Population dynamics in a Danish metapopulation of spadefoot toads *Pelobates fuscus*. – *Ecography* 25: 303–313.
- Heusser, H. 1969. Die lebensweise der erdkrote (*Bufo bufo* L.). Das orientierungsproblem. – *Rev. Suisse Zool.* 76: 444–517.
- Hobel, G. 1999. Notes on the natural history and habitat use of *Eleutherodactylus fitzingeri* (Anura: Leptodactylidae). – *Amphib.-Reptilia* 20: 65–72.
- 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. and Kluge, A. G. 1985. Proximate mechanisms of sexual selection in wood frogs. – *Evolution* 39: 260–277.
- Hranitz, J. M. and Diehl, W. J. 2000. Allozyme variation and population genetic structure during the life history of *Bufo woodhousii fowleri* (Amphibia: Anura). – *Biochem. Syst. Ecol.* 28: 15–27.
- Ingram, W. M. and Raney, E. C. 1943. Additional studies on the movement of tagged bullfrogs. – *Am. Midl. Nat.* 29: 239–241.
- Jameson, D. L. 1955. The population dynamics of the cliff frog *Syrrophus marnocki*. – *Am. Midl. Nat.* 54: 342–382.
- Jameson, D. L. 1957. Population structure and homing responses in the pacific tree frog. – *Copeia* 1957: 221–228.
- 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, J. R. and Semlitsch, R. D. 2003. Defining core habitat of local populations of the gray treefrog (*Hyla versicolor*) based on choice of oviposition site. – *Oecologia* 137: 205–210.
- Johnston, B. and Frid, L. 2002. Clearcut logging restricts the movements of terrestrial Pacific giant salamanders (*Dicamptodon tenebrosus* Godd.). – *Can. J. Zool.* 80: 2170–2177.
- Joly, P. and Grolet, O. 1996. Colonization dynamics of new ponds, and the age structure of colonizing Alpine newts, *Triturus alpestris*. – *Conserv. Biol.* 15: 239–248.
- Joly, P. et al. 2001. Habitat matrix effects on pond occupancy in newts. – *Conserv. Biol.* 15: 239–248.
- Kimura, M. and Maruyama, T. 1971. Patterns of neutral variation in a geographically structure population. – *Gen. Res.* 18: 125–131.
- Kleeberger, S. R. and Werner, J. K. 1982. Home range and homing behavior of *Plethodon cinereus* in northern Michigan. – *Copeia* 1982: 409–415.
- Kleeberger, S. R. and Werner, J. K. 1983. Post-breeding migration and summer movement of *Ambystoma maculatum*. – *J. Herpetol.* 17: 176–177.
- Knapp, R. A. et al. 2003. Developing probabilistic models to predict amphibian site occupancy in a patchy landscape. – *Ecol. Appl.* 13: 1069–1082.
- Kramer, D. C. 1973. Movements of western chorus frogs (*Pseudacris triseriata triseriata*) tagged with Co⁶⁰. – *J. Herpetol.* 7: 231–235.
- Kusano, T. and Miyashita, K. 1984. Dispersal of the salamander, *Hynobius nebulosus tokyoensis*. – *J. Herpetol.* 18: 349–353.
- Kusano, T. et al. 1995. Post-breeding dispersal of the Japanese toad, *Bufo japonicus formosus*. – *J. Herpetol.* 29: 633–638.
- Laan, R. and Verboom, B. 1990. Effects of pool size and isolation on amphibian communities. – *Biol. Conserv.* 54: 251–262.
- Lamoureux, V. S. and Madison, D. M. 1999. Overwintering habitats of radio-implanted green frogs, *Rana clamitans*. – *J. Herpetol.* 33: 430–435.
- Lemckert, F. and Brassil, T. 2000. Movements and habitat use of the endangered giant barred river frog (*Mixophyes iteratus*) and the implications for its conservation in timber production forests. – *Biol. Conserv.* 96: 177–184.
- Lemckert, F. and Brassil, T. 2003. Movements and habitat use by the giant burrowing frog, *Heleioporus australiacus*. – *Amphib.-Reptilia* 24: 207–211.
- Levins, R. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. – *Bull. Entomol. Soc. Am.* 15: 237–240.
- Levins, R. 1970. Extinction. – In: Gerstenhaber, M. (ed.), *Some mathematical problems in biology*. American Mathematical Society, pp. 75–107.
- Loredo, I. et al. 1997. Habitat use and migration behaviour of the California tiger salamander. – *J. Herpetol.* 282: 285.
- Lowe, W. H. 2003. Linking dispersal to local population dynamics: a case study using a headwater salamander system. – *Ecology* 84: 2145–2154.
- Madison, D. M. 1969. Homing behaviour of the red-cheeked salamander, *Plethodon jordani*. – *Anim. Behav.* 17: 25–39.

- Madison, D. M. 1997. The emigration of radio-implanted spotted salamanders, *Ambystoma maculatum*. – J. Herpetol. 31: 542–551.
- Madison, D. M. and Shoop, C. R. 1970. Homing behaviour, orientation, and home range of salamanders tagged with Tantalum-182. – Science 168: 1484–1487.
- Madison, D. M. and Farrand, L. 1997. Habitat use during breeding and emigration in radio-implanted tiger salamanders, *Ambystoma tigrinum*. – Copeia 1997: 402–410.
- 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.
- Marvin, G. A. 1998. Territorial behavior of the plethodontid salamander, *Plethodon kentucki*: influence of habitat structure and population density. – Oecologia 114: 133–144.
- Matthews, K. R. 2003. Response of mountain yellow-legged frogs, *Rana muscosa* to short distance translocation. – J. Herpetol. 37: 621–626.
- Maunders, J. E. 1983. Amphibians of the province of Newfoundland. – Can. Field-Nat. 97: 33–46.
- Maynard, E. A. 1934. The aquatic migration of the toad, *Bufo americanus* Le Conte. – Copeia 1934: 174–177.
- 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.
- Miaud, C. et al. 2000. Terrestrial movements of the natterjack toad *Bufo calamita* (Amphibia, Anura) in a semi-arid, agricultural landscape. – Amphib.-Reptilia 21: 357–369.
- Monsen, K. J. 2002. Population and conservation genetic structure of the cascades frog, *Rana cascade* throughout the species' range. – Ph.D. thesis, Oregon State Univ.
- Moore, H. J. 1954. Some observations on the migration of the toad, (*Bufo b. bufo*). – Br. J. Herpetol. 1: 194–224.
- Muths, E. 2003. Home range and movements of boreal toads in undisturbed habitat. – Copeia 2003: 160–165.
- Muths, E. et al. 2003. Evidence for disease-related amphibian decline in Colorado. – Biol. Conserv. 110: 357–365.
- Neckel de Oliveira, S. 1996. Daily movements of male *Phyllomedusa bicolor* in Brazil. – Herpetol. Rev. 27: 180–181.
- 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.
- Nickerson, M. A. and Mays, C. E. 1973. A study of the ozark hellbender *Cryptobranchus alleganiensis bishopi*. – Ecology 54: 1164–1165.
- Nijhuita, M. J. and Kaplan, R. H. 1998. Movement patterns and life history characteristics in a population of the cascade torrent salamander (*Rhyacotriton cascade*) in the Columbia River gorge, Oregon. – J. Herpetol. 32: 301–304.
- Oldham, R. S. 1966. Spring movements in the american toad, *Bufo americanus*. – Can. J. Zool. 44: 63–100.
- Osborne, W. S. and Norman, J. A. 1991. Conservation genetics of corroboree frogs, *Pseudophryne corroboree* Moore (Anura: Myobatrachidae): population subdivision and genetic divergence. – Aust. J. Zool. 39: 285–297.
- Ovaska, K. 1988. Spacing and movements of the salamander, *Plethodon vehiculum*. – Herpetologica 44: 377–386.
- Ovaskainen, O. and Hanski, I. 2004. Metapopulation dynamics in highly fragmented landscapes. – In: Hanski, I. and Gaggiotti, O. (eds), Ecology, genetics, and evolution in metapopulations. Academic Press, pp. 73–104.
- Pannell, J. R. and Obbard, D. J. 2003. Probing the primacy of the patch: what makes a metapopulation? – J. Anim. Ecol. 91: 485–488.
- Parker, A. G. and Gittins, S. P. 1979. A note on home range in the common toad in mid-Wales and a method for tracking toads for behavioural observation. – Br. J. Herpetol. 6: 7–8.
- Parker, J. M. and Anderson, S. H. 2003. Habitat use and movements of repatriated Wyoming toads. – J. Wildl. Manage. 67: 439–446.
- Pearson, P. G. 1955. Population ecology of the spadefoot toad, *Scaphiopus h. holbrookii* (Harlan). – Ecol. Mongr. 25: 233–267.
- Pechmann, J. H. K. et al. 2001. Amphibian colonization and use of ponds created for trial mitigation of wetland loss. – Wetlands 21: 93–111.
- Perret, N. et al. 2003. Transience, dispersal and survival rates in new patchy populations. – J. Anim. Ecol. 72: 567–575.
- Peterson, C. L. 1987. Movement and catchability of the hellbender, *Cryptobranchus alleganiensis*. – J. Herpetol. 21: 197–204.
- 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.
- Placyk, J. S. Jr and Graves, B. M. 2001. *Plethodon cinereus* (red-backed salamander): site attachment. – Herpetol. Rev. 32: 246.
- Platx, J. E. et al. 1990. *Rana berlandieri*: recently introduced populations in Arizona and southeastern California. – Copeia 1990: 324–333.
- Ponsero, A. and Joly, P. 1998. Clutch size, egg survival and migration distances in the agile frog (*Rana dalmatina*) in a floodplain. – Arch. Hydrobiol. 142: 343–352.
- 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.
- Pope, S. E. et al. 2000. Landscape complementation and metapopulation effects on leopard frog populations. – Ecology 81: 2498–2508.
- 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.
- Ray, N. et al. 2002. Modeling spatial distribution of amphibian populations: a GIS approach based on habitat matrix permeability. – Biol. Conserv. 11: 2143–2165.
- Reading, C. J. et al. 1991. Breeding pond fidelity in common toads, *Bufo bufo*. – J. Zool. Lond. 225: 201–211.
- Rebelo, R. and Leclair, M. H. 2003. Site tenacity in the terrestrial salamandrid *Salamandra salamandra*. – J. Herpetol. 37: 440–445.
- Regosin, J. V. et al. 2003. Terrestrial habitat use and winter densities of the wood frog (*Rana sylvatica*). – J. Herpetol. 37: 342–353.
- Reh, W. and Seitz, A. 1990. The influence of land use on the genetic structure of populations of the common frog *Rana temporaria*. – Biol. Conserv. 54: 239–249.
- 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.
- Richter, S. C. et al. 2001. Postbreeding movements of the dark gopher frog, *Rana sevosa* Goins and Netting: implications for conservation and management. – J. Herpetol. 35: 316–321.
- Ritland, K. et al. 2000. Phylogeography of the tailed frog (*Ascaphus truei*) in British Columbia. – Can. J. Zool. 78: 1749–1758.
- Roble, S. M. 1979. Dispersal movements and plant associations of juvenile gray tree frogs, *Hyla versicolor* Le Conte. – Trans. Kans. Acad. Sci. 82: 235–245.
- Routman, E. 1993. Population structure and genetic diversity of metamorphic and paedomorphic populations of the tiger

- salamander *Ambystoma tigrinum*. – J. Evol. Biol. 6: 329–357.
- Rowe, G. et al. 2000. A microsatellite analysis of natterjack toad, *Bufo calamita*, metapopulations. – Oikos 88: 641–651.
- Schabetsberger, R. et al. 2004. Delineation of terrestrial reserves for amphibians: post-breeding migrations of Italian crested newts (*Triturus c. carnifex*) at high altitude. – Biol. Conserv. 117: 95–104.
- Schroeder, E. E. 1976. Dispersal and movement of newly transformed green frogs, *Rana clamitans*. – Am. Midl. Nat. 95: 471–474.
- Schwarzkopf, L. and Alford, R. A. 2002. Nomadic movement in tropical toads. – Oikos 94: 492–506.
- Scribner, K. T. et al. 1994. Comparative analysis of intra- and interpopulation genetic diversity in *Bufo bufo*, using allozymes, single-locus microsatellite, minisatellite, and multilocus minisatellite data. – Mol. Biol. Evol. 11: 737–748.
- Scribner, K. T. et al. 2001. Environmental correlates of toad abundance and population genetic diversity. – Biol. Conserv. 98: 201–210.
- Seburn, C. N. L. et al. 1997. Northern leopard frog (*Rana pipiens*) dispersal in relation to habitat. – In: Green, D. M. (ed.), Amphibians in decline: Canadian studies of a global problem. Society for the study of amphibians and reptiles, pp. 72–64.
- Seebacher, F. and Alford, R. A. 1999. Movement and microhabitat use of a terrestrial amphibian (*Bufo marinus*), on a tropical island: seasonal variation and environmental correlates. – J. Herpetol. 33: 208–214.
- Seitz, A. et al. 1992. Radio-tracking of the common frog, *Rana temporaria*. – In: Priede, I. G. and Swift, S. M. (eds), Wildlife telemetry: remote monitoring and tracking of animals. Ellis Horwood, pp. 484–489.
- Semlitsch, R. D. 1981. Terrestrial activity and summer home range of the mole salamander (*Ambystoma talpoideum*). – Can. J. Zool. 59: 315–322.
- Semlitsch, R. D. 1983. Terrestrial movements of an eastern tiger salamander, *Ambystoma tigrinum*. – Herpetol. Rev. 14: 112–113.
- Semlitsch, R. D. and Bodie, J. R. 1998. Are small, isolated wetlands expendable? – Conserv. Biol. 12: 1129–1133.
- Semlitsch, R. D. et al. 1996. Structure and dynamics of an amphibian community: evidence from a 16-year study of a natural pond. – In: Cody, M. L. and Smallwood, J. A. (eds), Long-term studies of vertebrate communities. Academic Press, pp. 217–247.
- Seppa, P. and Laurila, A. 1999. Genetic structure of island populations of the anurans *Rana temporaria* and *Bufo bufo*. – Heredity 82: 309–317.
- Shaffer, H. B. et al. 2000. The genetics of amphibian declines: population substructure and molecular differentiation in the Yosemite toad, *Bufo canorus* (Anura, Bufonidae) based on single-strand conformation polymorphism analysis (SSCP) and mitochondrial DNA sequence data. – Mol. Ecol. 9: 245–257.
- Shoop, C. R. 1968. Migratory orientation of *Ambystoma maculatum*: movements near breeding ponds and displacements of migrating individuals. – Biol. Bull. 7: 230–238.
- Shoop, C. R. and Gunning, G. E. 1967. Seasonal activity and movements of *Necturus* in Louisiana. – Copeia 1967: 732–737.
- Sinsch, U. 1988. Temporal spacing of breeding activity in the natterjack toad, *Bufo calamita*. – Oecologia 76: 399–407.
- Sinsch, U. 1989. Migratory behaviour of the common toad *Bufo bufo* and the natterjack toad *Bufo calamita*. – In: Langton, T. E. S. (ed.), Amphibians and roads, proceedings of the toad tunnel conference. ACO Polymer Products, Bedfordshire, U.K., pp. 113–125.
- Sinsch, U. 1990. Migration and orientation in anuran amphibians. – Ethol. Ecol. Evol. 2: 65–79.
- Sinsch, U. 1992. Structure and dynamic of a natterjack toad metapopulation (*Bufo calamita*). – Oecologia 112: 42–47.
- Sinsch, U. 1997. Postmetamorphic dispersal and recruitment of first breeders in a *Bufo calamita* metapopulation. – Oecologia 112: 42–47.
- 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. 1988. Metapopulation biology of *Rana lessonae* Camerano on the northern periphery of its range. – Ph.D. thesis, Uppsala Univ. no. 35.
- 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. and Ray, C. 1996. Using logistic regression to model metapopulation dynamics: large scale forestry extirpates the pool frog. – In: McCullough, D. R. (ed.), Metapopulations and wildlife conservation. Island Press, pp. 111–128.
- Skelly, D. K. and Meir, E. 1997. Rule-based models for evaluating mechanisms of distributional change. – Conserv. Biol. 11: 531–538.
- Skelly, D. K. et al. 1999. Long-term distributional dynamics of a Michigan amphibian assemblage. – Ecology 80: 2326–2337.
- Smedbol, R. K. et al. 2002. Myths and moderation in marine “metapopulations”? – Fish and Fisheries 3: 20–35.
- Smith, M. A. 2003. Spatial ecology of *Bufo fowleri*. – Ph.D. thesis, McGill Univ. no. 200.
- Spencer, A. W. 1964. The relationship of dispersal and migration to gene flow in the boreal chorus frog. – Ph.D. thesis, Colorado State Univ.
- Staub, N. L. et al. 1995. Patterns of growth and movements in a population of *Ensatina eschscholtzii platensis* (Caudata: Plethodontidae) in the Sierra Nevada, California. – J. Herpetol. 29: 593–599.
- Stille, W. T. 1952. The nocturnal amphibian fauna of the southern Lake Michigan Beach. – Ecology 33: 149–162.
- 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., pp. 409–412.
- Tallmon, D. A. et al. 2000. Genetic differentiation among long-toed salamander (*Ambystoma macrodactylum*) populations. – Copeia 2000: 27–35.
- Ter Braak, C. J. and Etienne, R. S. 2003. Improved Bayesian analysis of metapopulation data with an application to a tree frog metapopulation. – Ecology 84: 231–241.
- Tessier, C. et al. 1991. Population density and daily movement patterns of Hochstetter’s frogs, *Leiopelma hochstetteri*, in a New Zealand Mountain Stream. – J. Herpetol. 25: 213–214.
- 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. 2002. Short-term studies underestimate 30-generation changes in a butterfly metapopulation. – Proc. R. Soc. Lond. B. Biol. Sci. 269: 563–569.
- Tracy, C. R. and Dole, J. W. 1969. Orientation of displaced California toads, *Bufo boreas*, to their breeding sites. – Copeia 1969: 693–700.
- Trenham, P. C. 1998. Demography, migration and metapopulation structure of pond breeding salamanders. – Ph.D. thesis, Univ. of California, Davis.
- Trenham, P. C. et al. 2001. Spatially autocorrelated demography and interpond dispersal in the salamander, *Ambystoma californiense*. – Ecology 82: 3519–3530.
- 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. 1959. Some features of the ecology of *Bufo punctatus* in Death Valley, California. – Ecology 40: 175–181.

- Turner, F. B. 1960. Population structure and dynamics of the western spotted frog, *Rana pretiosa* Baird and Girard, in Yellowstone Park, Wyoming. – *Ecol. Monogr.* 30: 251–278.
- Twitty, V. et al. 1964. Long distance homing in the newt, *Taricha rivularis*. – *Proc. Natl. Acad. Sci. USA* 51: 51–58.
- Twitty, V. et al. 1967. Initial homeward orientation after long-distance displacements in the newt, *Taricha rivularis*. – *Proc. Natl. Acad. Sci. USA* 57: 342–348.
- 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.
- Vos, C. C. et al. 2001. Genetic similarity as a measure for connectivity between fragmented populations of the moor frog (*Rana arvalis*). – *Heredity* 86: 598–608.
- Wacasey, J. W. 1961. An ecological study of two sympatric species of salamanders, *Ambystoma maculatum* and *Ambystoma jeffersonium* in southern Michigan. – Ph.D. thesis, Michigan State Univ.
- 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.
- Warwick, T. 1949. The colonization of bomb-crater ponds at Marlow, Buckinghamshire. – *J. Anim. Ecol.* 18: 137–141.
- Weintraub, J. D. 1974. Movement patterns of the red-spotted toad, *Bufo punctatus*. – *Herpetologica* 30: 212–215.
- 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.
- Wiggs, R. L. 1977. Movement and homing in the hellbender, *Cryptobranchus alleganiensis*, in the Niangua River, Missouri. – M.Sc. thesis, Southwest Missouri State Univ.
- Williams, K. L. and Gordon, R. E. 1961. Natural dispersal of the salamander *Aneides aeneus*. – *Copeia* 1961: 353.
- Williams, P. K. 1973. Seasonal movements and population dynamics of four sympatric mold salamanders, genus *Ambystoma*. – Ph.D. thesis, Indiana Univ.
- Willis, Y. L. et al. 1956. Emergence, breeding, hibernation, movements and transformation of the bullfrog, *Rana catesbeiana*, in Missouri. – *Copeia* 1956: 30–41.
- Woodford, J. E. and Meyer, M. W. 2003. Impact of lakeshore development on green frog abundance. – *Biol. Conserv.* 110: 277–284.
- Woolbright, L. L. 1985. Patterns of nocturnal movement and calling by the tropical frog *Eleutherodactylus coqui*. – *Herpetologica* 41: 1–9.

Appendix 1. Testing of metapopulation conditions. 0 = not tested, 1 = tested, and 2 = assumed.

| Condition 1: habitat patches support local breeding populations | Condition 2: no single population is large enough to ensure long-term survival | Condition 3: patches are not too isolated to prevent recolonisation (i.e. limited dispersal allows isolation with potential recolonisation) | Condition 4: local dynamics are sufficiently asynchronous to make simultaneous extinction of all local populations unlikely | Source |
|---|--|---|---|----------------------------|
| 2 | 2 | 2 | 2 | Alford and Richards 1999 |
| 1 | 1 | 1 | 0 | Berven and Grudzien 1990 |
| 2 | 1 | 2 | 0 | Blaustein et al. 1994 |
| 2 | 1 | 1 | 0 | Bradford et al. 2003 |
| 2 | 0 | 1 | 0 | Call 1997 |
| 2 | 0 | 2 | 0 | Carlson and Edenhamn 2000 |
| 2 | 2 | 2 | 0 | Corser 2001 |
| 0 | 0 | 1 | 0 | Driscoll 1997 |
| 1 | 0 | 1 | 0 | Gill 1978 |
| 2 | 0 | 2 | 0 | Goldber 2002 |
| 2 | 0 | 2 | 0 | Halley et al. 1996 |
| 1 | 1 | 2 | 0 | Hartwell 1990 |
| 2 | 0 | 2 | 0 | Hecnar and M'Closkey 1996 |
| 0 | 0 | 1 | 0 | Hels 2002 |
| 2 | 0 | 2 | 0 | Hranitz and Diehl 2000 |
| 0 | 0 | 1 | 0 | Johnson and Semlitsch 2003 |
| 2 | 0 | 1 | 0 | Knapp et al. 2003 |
| 2 | 2 | 2 | 2 | Laan and Verboom 1990 |
| 0 | 2 | 1 | 0 | Marsh et al. 1999 |
| 0 | 0 | 2 | 0 | Marsh and Trenham 2001 |
| 2 | 0 | 1 | 0 | Monsen 2002 |
| 0 | 0 | 1 | 0 | Muths et al. 2003 |
| 2 | 2 | 1 | 2 | Newman and Squire 2001 |
| 0 | 0 | 1 | 0 | Osborne and Norman 1991 |
| 1 | 0 | 2 | 0 | Perret et al. 2003 |
| 0 | 0 | 2 | 0 | Pope et al. 2000 |
| 0 | 0 | 1 | 0 | Reading et al. 1991 |
| 2 | 2 | 1 | 2 | Reh and Seitz 1990 |
| 2 | 0 | 1 | 0 | Ritland et al. 2000 |
| 0 | 0 | 2 | 0 | Routman 1993 |
| 2 | 0 | 1 | 2 | Rowe et al. 2000 |
| 0 | 0 | 1 | 0 | Scribner et al. 1994 |
| 0 | 0 | 1 | 0 | Scribner et al. 2001 |
| 0 | 0 | 2 | 0 | Semlitsch and Bodie 1998 |
| 0 | 0 | 2 | 0 | Semlitsch et al. 1996 |
| 2 | 0 | 1 | 0 | Seppa and Laurila 1999 |
| 0 | 0 | 1 | 0 | Shaffer et al. 2000 |
| 0 | 0 | 1 | 0 | Sinsch 1992 |
| 1 | 1 | 1 | 0 | Sjögren 1991 |
| 1 | 1 | 1 | 0 | Sjögren Gulve 1994 |
| 0 | 0 | 1 | 1 | Skelly and Meir 1997 |
| 2 | 0 | 1 | 0 | Skelly et al. 1999 |
| 0 | 0 | 1 | 0 | Tallmon et al. 2000 |
| 1 | 1 | 1 | 1 | Ter Braak and Etienne 2003 |
| 1 | 1 | 1 | 0 | Trenham 1998 |
| 2 | 0 | 1 | 0 | Vos et al. 2001 |
| 2 | 0 | 1 | 0 | Vos and Chardon 1998 |
| 1 | 1 | 1 | 1 | Vos et al. 2000 |
| 0 | 0 | 2 | 0 | Woodford and Meyer 2003 |
| 2 | 0 | 2 | 0 | Conroy and Brook 2003 |
| 0 | 0 | 2 | 0 | Ebisuno and Gentili 2002 |
| 1 | 0 | 2 | 0 | Joly et al. 2001 |