NRC Research Press

ARTICLE

Positive correlation between dispersal and body size in Green Frogs (*Rana clamitans*) naturally colonizing an experimental landscape

C.A. Searcy, B. Gilbert, M. Krkošek, L. Rowe, and S.J. McCauley

Abstract: Dispersers are often assumed to have the mean phenotype observed across the entire metapopulation, despite growing evidence of dispersal–phenotype correlations. We examined three dispersal–phenotype correlations in Green Frogs (*Rana clamitans* Latreille, 1801 = *Lithobates clamitans* (Latreille, 1801)). Two were in traits that have been previously tied to fitness (body size and body condition), while a third (relative hindlimb length) has been linked to movement performance. We constructed a spatially dispersed array of experimental ponds in close proximity to source ponds known to support Green Frog breeding populations. Over the course of two breeding seasons (four sampling periods), we measured phenotypes of all Green Frogs that had colonized the experimental ponds and a sample of individuals from the source ponds. After only 1 month, a positive correlation was detected between dispersal and body size within the population of dispersers occupying the experimental ponds. After a 2nd month, this positive dispersal – body size correlation was also present when comparing the population of dispersers to the population of nondispersers remaining at the source ponds. Even if generated solely by plasticity, a positive correlation between dispersal and body size (a trait tightly linked to fitness) has the ability to alter metapopulation capacity and thus the probability of regional species persistence.

Key words: body condition, body size, Green Frog, hindlimb length, metapopulation, *Rana clamitans*.

Résumé : Il est souvent tenu pour acquis que les individus qui se dispersent ont le phénotype moyen observé à l'échelle de toute la métapopulation, malgré l'accumulation de données indiquant des corrélations entre dispersion et phénotype. Nous avons examiné trois corrélations entre dispersion et phénotype chez les grenouilles vertes (*Rana clamitans* Latreille, 1801 = *Lithobates clamitans* (Latreille, 1801)), dont deux portent sur des caractères déjà reliés à l'aptitude (taille du corps et embonpoint), alors que la troisième (longueur relative des membres postérieurs) a été reliée à la performance de déplacement. Nous avons construit un réseau dispersé dans l'espace d'étangs expérimentaux situés très près d'étangs sources qui supportent des populations reproductrices de grenouilles vertes. Au cours de deux saisons de reproduction (quatre périodes d'échantillonnage), nous avons mesuré les phénotypes de toutes les grenouilles vertes qui avaient colonisé les étangs expérimentaux et un échantillon d'individus des étangs sources. Après un seul mois, une corrélation positive était décelée entre la dispersion et la taille du corps au sein de la population d'individus s'étant dispersés dans les étangs expérimentaux. Au bout d'un deuxième mois, cette corrélation positive entre la dispersion et la taille du corps était aussi observée en comparant la population de spécimens dispersés à la population de spécimens non dispersés demeurant dans les étangs sources. Même si elle n'était le seul fait de la plasticité, une corrélation positive entre la dispersion et la taille du corps (un caractère étroitement relié à l'aptitude) pourrait modifier la capacité de la métapopulation et ainsi la probabilité de persistance régionale de l'espèce. [Traduit par la Rédaction]

Mots-clés : embonpoint, taille du corps, grenouille verte, longueur des membres postérieurs, métapopulation, *Rana clamitans*.

Introduction

Many models in ecology and evolutionary biology assume that dispersal propensity is uncorrelated with other phenotypic characters (e.g., Hadfield 2016; Edelaar et al. 2017). However, a comprehensive review has shown correlations between dispersal propensity and physiological, behavioral, morphological, and life-history characters (Clobert et al. 2009). Out of 24 reviewed studies, 6 showed dispersal correlations with physiology, 9 found correlations with behavior, 9 observed correlations with morphology, and 3 detected correlations with life-history traits. Only the life-history traits (fecundity and survival) are directly tied to fitness, but many of the other traits are potential proxies for fitness as well. In particular, body size is positively correlated with fitness in many taxa (Kingsolver and Huey 2008), and there are also reasons to expect larger bodied individuals to disperse farther. For example, a meta-analysis of dispersal syndromes across 15 animal orders demonstrates that larger species tend to disperse farther (Stevens et al. 2014), perhaps because of decreased locomotion costs (Hein et al. 2012). These patterns from interspecific comparisons suggest that intraspecific comparisons might also reveal positive body size – dispersal correlations. Body condition (mass for a given structural size) is another morphological trait often used to represent fitness (Jakob et al. 1996). Together, body

---

Received 23 March 2018. Accepted 25 June 2018.

C.A. Searcy* and S.J. McCauley. Department of Biology, University of Toronto Mississauga, 3359 Mississauga Road, Mississauga, ON L5L 1C6, Canada.
B. Gilbert, M. Krkošek, and L. Rowe. Department of Ecology and Evolutionary Biology, University of Toronto, 25 Willcocks Street, Toronto, ON M5S 3B2, Canada.

Corresponding author: C.A. Searcy (email: casearcy@bio.miami.edu).
*Present address: Department of Biology, University of Miami, 1301 Memorial Drive, Coral Gables, FL 33146, USA.

Can. J. Zool. **96**: 1378–1384 (2018) dx.doi.org/10.1139/cjz-2018-0069

size and body condition account for all nine of the morphology–dispersal correlations mentioned above, suggesting that dispersal–fitness correlations may actually be more common than a first-pass review of the literature would suggest.

Among potential dispersal–phenotype correlations, correlations between dispersal and fitness-related traits are particularly important, as these will affect both demographic outcomes (e.g., metapopulation viability) and evolutionary processes (e.g., potential for genetic differentiation) (Benard and McCauley 2008). For example, there is a common rule of thumb that a single migrant per generation between two subpopulations is sufficient to maintain genetic diversity within each (Mills and Allendorf 1996). However, this assumes that migrants have the mean fitness observed in the entire population. If migrants have above-average fitness, then a lower migration rate may be sufficient to maintain genetic diversity, whereas the opposite may be true if migrants have below-average fitness. From a demographic perspective, the assumption that migrants have the mean fitness observed in the entire population may either overestimate or underestimate patch connectivity, which will in turn overestimate or underestimate metapopulation capacity and the probability of regional persistence (Ovaskainen and Hanski 2003; Moilanen and Hanski 2006).

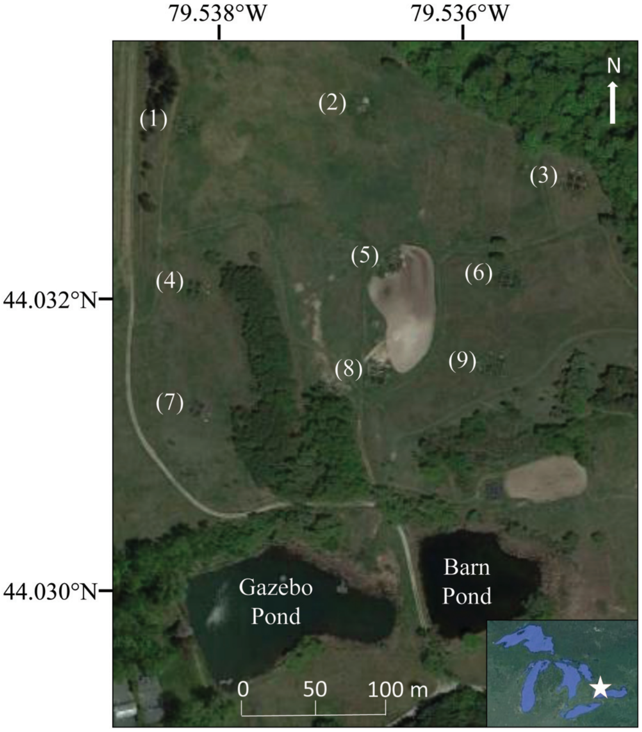
Correlations between dispersal and nonfitness-related traits do not have the same consequences for demography and overall genetic differentiation, but such correlations can alter dynamics along invasion fronts and across regions of varying patch connectivity. One classic example of this is the invasion of Australia by Cane Toads (*Rhinella marina* (Linnaeus, 1758)), in which there is a positive correlation between dispersal and residual hindlimb length (Phillips et al. 2006). This leads to toads at the invasion front having longer hindlimbs than those a few generations behind the invasion front (Hudson et al. 2016). Numerous generations of the most dispersive toads breeding with each other along this front has caused a rapid increase in range expansion (Shine et al. 2011). This type of dynamic can be expected whenever dispersal–phenotype correlations encounter landscapes with a continuous supply of unoccupied habitat patches such as during the invasion process (Renault et al. 2018). In a more static landscape where the majority of patches are already occupied, patch neighborhoods with higher mean patch isolation can still select for more dispersive phenotypes. This has been observed in both amphibians and odonates (McCauley et al. 2010; Brodin et al. 2013).

In amphibians, body size is considered a good proxy for fitness, as larger individuals have higher survivorship, lower mean age at maturity, and larger clutch sizes (Scott 1994; Berven 2009; Searcy et al. 2014). This high fitness may be heritable, or it may be generated by phenotypic plasticity based on environmental conditions experienced in the larval stage (Semlitsch 1987; Tejedo and Reques 1994; Searcy et al. 2015). Either way, a positive fitness–dispersal correlation will increase demographic connectivity and decrease rates of local adaptation due to dispersers making up a larger proportion of the gene pool in their destination pond than would be expected just based on the fraction of individuals immigrating. Our study assessed whether there was a correlation between body size and dispersal in Green Frogs (*Rana clamitans* Latreille, 1801 = *Lithobates clamitans* (Latreille, 1801)) colonizing a newly created pond array and whether this pattern changed through time as animals continued to disperse across the landscape. We also examined correlations between dispersal and two other traits hypothesized to affect dispersal capacity, body condition, and residual hindlimb length.

Materials and methods

We constructed an array of 36 experimental ponds at the Koffler Scientific Reserve (King City, Ontario, Canada; 44.03°N, 79.54°W) during summer 2014. The reserve had three natural ponds: two only 25 m apart at the base of the field where we constructed the experimental ponds (Fig. 1) and the other 580 m from the nearest experimental ponds. This latter, more distant pond does not support Green Frog breeding, and there are no ponds off the reserve that are closer. Thus, we consider the two nearest ponds to form the source of all migrants to our pond array.

Fig. 1. Map of the experimental pond array. Each cluster of four experimental ponds is labeled 1–9. The two source ponds (Barn and Gazebo) are labeled to the south. Map data from Google. Color version online.



We constructed the experimental ponds along three transects (100 m apart) running north from the source ponds. Along these transects, the experimental ponds were located at distances of 100, 200, and 300 m from the source ponds, with four experimental ponds (one pond cluster) at each distance. The elevation of the experimental ponds relative to the source ponds ranged from 6 to 25 m. Experimental ponds within the same cluster were 2 m apart from each other. Each experimental pond had a square surface area of 11–17 m^2. All ponds were shallowest at their southern edge, gradually sloped to a depth of 0.32–0.52 m, and then dropped at a 90° angle to a depth of 0.54–0.90 m. The pond bottoms were lined with EPDM, a rubberized water-impermeable barrier. There is a thin strip of woodland along the shorelines of the source ponds and they are otherwise separated from the experimental ponds by open fields. The experimental ponds were filled between 29 June and 4 July 2014 with water pumped from the source ponds and strained through a 30 μm filter.

We used hand nets to capture all Green Frogs residing in the experimental ponds at four time points: 31 July and 1 September 2014 and 6 June and 30–31 July 2015. When we approached the experimental ponds, all Green Frogs that were sitting on the bank jumped into the water, and we collected these animals as well as animals in the water already. We counted the number of individuals as we approached the ponds, and due to the small size of the experimental ponds, we were able to wait until all individuals resurfaced and could be netted. Associated with the first two of these capture efforts, we also caught a sample of Green Frogs from the source ponds (5 and 7 August and 1 and 6 September 2014). At the source ponds, we captured the first 18–30 Green Frogs encountered while making a circuit of the pond perimeter. At both experimental and source ponds, we measured the snout–vent length (SVL) and hindlimb length of each frog using digital calipers (±0.01 mm) and the mass of each frog using a hand-held digital scale (±0.1 g), after which they were released into their pond of origin. For morphological measurements see Supplementary Table S1.[1] This work was carried out under Institutional Animal Care and Use Protocol 20010749.

Green Frogs in this area breed in early-mid July (Walpole et al. 2012). Tadpoles overwinter in the breeding ponds and usually emerge the following year in late June to early August (C.A. Searcy, B. Gilbert, M. Krkošek, L. Rowe, and S.J. McCauley, unpublished data). Most dispersal in this species occurs within 1 month of emergence (Schroeder 1976). This means that our first and fourth samplings occurred during the dispersal period in their respective years, while the second sampling occurred after the dispersal period in 2014 and the third sampling occurred before the dispersal period in 2015. Green Frogs grow rapidly as juveniles, and most attained breeding size (60 mm SVL in males and 65 mm SVL in females) within 1 year during a study in Ithaca, New York, USA (similar latitude and summer temperatures; Ryan 1953). Thus, in newly available habitat patches, a dispersal–phenotype correlation that is present in the dispersing juveniles can be passed on to the next generation after only a single year, assuming the phenotype is heritable. Adults generally breed in the same ponds that they occupy during the nonbreeding season, so breeding migrations are rare (Pauley 2005). The fact that nonbreeding adults occupy ponds rather than upland burrows (as some amphibians do) indicates that all Green Frogs colonizing our newly created ponds must have migrated from an existing pond rather than already being in the terrestrial habitat adjacent to the newly created ponds. Most individuals breed every year and some females are known to breed twice in the same year (Pauley 2005). Longevity is estimated to be 5–6 years (Cortwright 1998).

To estimate the functional isolation of each experimental pond, we measured each pond's elevation and distance from the closest point on either of the source ponds. We then performed a principal components analysis on these two measurements and retained the first principal component (PC) axis as our metric of functional isolation. This PC axis explained more of the variance in the number of frogs at each pond cluster than did distance alone (26% vs. 8%). Our three morphometric variables were SVL (ln-transformed), residual hindlimb length, and body condition. Residual hindlimb length was calculated as the residuals from a linear regression of ln(hindlimb length) vs. ln(SVL) (Supplementary Fig. S1),[1] and body condition was calculated as the residuals from a linear regression of ln(mass) vs. ln(SVL) (Supplementary Fig. S2).[1] This body condition index is often used due to its complete orthogonality to body size (Jakob et al. 1996; but see Peig and Green 2010).

We used linear mixed models to examine (*i*) the relationship between each of these morphometric variables and our functional isolation metric (main effect of functional isolation) and (*ii*) whether any of these relationships changed through time (functional isolation × time interaction). Each mixed model included functional isolation, sampling period, and their interaction, plus a random factor of sampling period nested within pond cluster. This analysis treats all four ponds in the same cluster as a single experimental unit. We tried a second model with sampling period nested within pond nested within cluster as a random effect and compared the two models using Akaike's information criterion (AIC) and by testing for autocorrelation within the residuals. The model using only sampling period and cluster performed better in all analyses, with lower AIC and no significant temporal autocorrelation in the residuals. This finding matched our observations of Green Frogs moving freely among ponds within a cluster. We therefore report results from the analyses that include only sampling period nested within pond cluster as a random effect. We also used mixed models to compare the morphology of frogs in the experimental ponds to those in the source ponds. Each of these comparisons included fixed effects of pond type (source vs. experimental), sampling period (first vs. second), and their interaction, as well as a random effect of pond cluster or source pond. As the source ponds were only sampled in 2014, these latter analyses only used the data from the first two sampling periods.

Both these sets of analyses are potentially confounded by pseudoreplication, as we do not know whether the same individual frogs were measured during multiple sampling periods. We therefore examined whether each of the morphometric variables varied significantly over the functional isolation gradient (or between the source and experimental ponds) during individual sampling periods as well. For these examinations, we employed mixed models that included functional isolation or pond type (source vs. experimental) as a fixed effect and pond cluster or source pond as a random effect. If these single sampling period analyses are significant, then it ensures that any main effects of functional isolation or pond type detected using all sampling periods are not due to pseudoreplication inflating our degrees of freedom, but instead represent a dispersal–phenotype correlation that was present at a single time point. The interaction terms from the models including all sampling periods can then be used to determine whether this correlation changed significantly through time or generally maintained the same magnitude as individual frogs reshuffled themselves across the landscape. All mixed effects models were estimated using maximum likelihood and P values were determined using likelihood ratio tests. These analyses were conducted using the nlme package in R (R Core Team 2013).

One potential explanation for a positive dispersal – body size correlation is that Green Frogs undergo an ontogenetic niche shift in which juveniles remain directly adjacent to the aquatic habitat, while adults occupy more terrestrial habitat. To check whether such a pattern could be driving our results, we removed all of the adult frogs (SVL > 62.5 mm; Ryan 1953) from the data set and reran the analyses. Adult frogs accounted for 8% of our total sample and removing them did not qualitatively alter any of our results. Another possible explanation for a positive dispersal – body size correlation is that one sex is both larger and more dispersive. To check for such a pattern of sexual dimorphism, we used another data set collected at the same location in 2012 with more adult frogs that could be sexed (Joksimovic 2015) and employed Student's t tests to compare male and female measurements for each of our three morphological variables. None of the three variables exhibited significant sexual dimorphism.

Results

During the first sampling, we captured 45 frogs from the experimental ponds and 56 from the source ponds (30 from Gazebo and 26 from Barn). During the second sampling period, we captured 64 frogs from the experimental ponds and 36 from the source ponds (equal numbers from each pond). During the third and fourth samplings, we collected 21 and 116 frogs from the experimental ponds, respectively.

The PC representing functional isolation explained 81% of the variation in distance and elevation of the experimental ponds, and both had equal positive loadings on this axis. None of the residuals of the linear mixed models showed significant autocor-

---

[1] Supplementary figures and table are available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/cjz-2018-0069.

relation across the four sampling periods ($P \geq 0.34$ for all three morphological traits). This suggests that our degrees of freedom were not inflated by taking multiple measurements from the same ponds through time. Nonetheless, we also addressed the issue of pseudoreplication by reanalyzing our data with only single sampling periods included (see the Materials and methods) and report the additional single-sample results below.

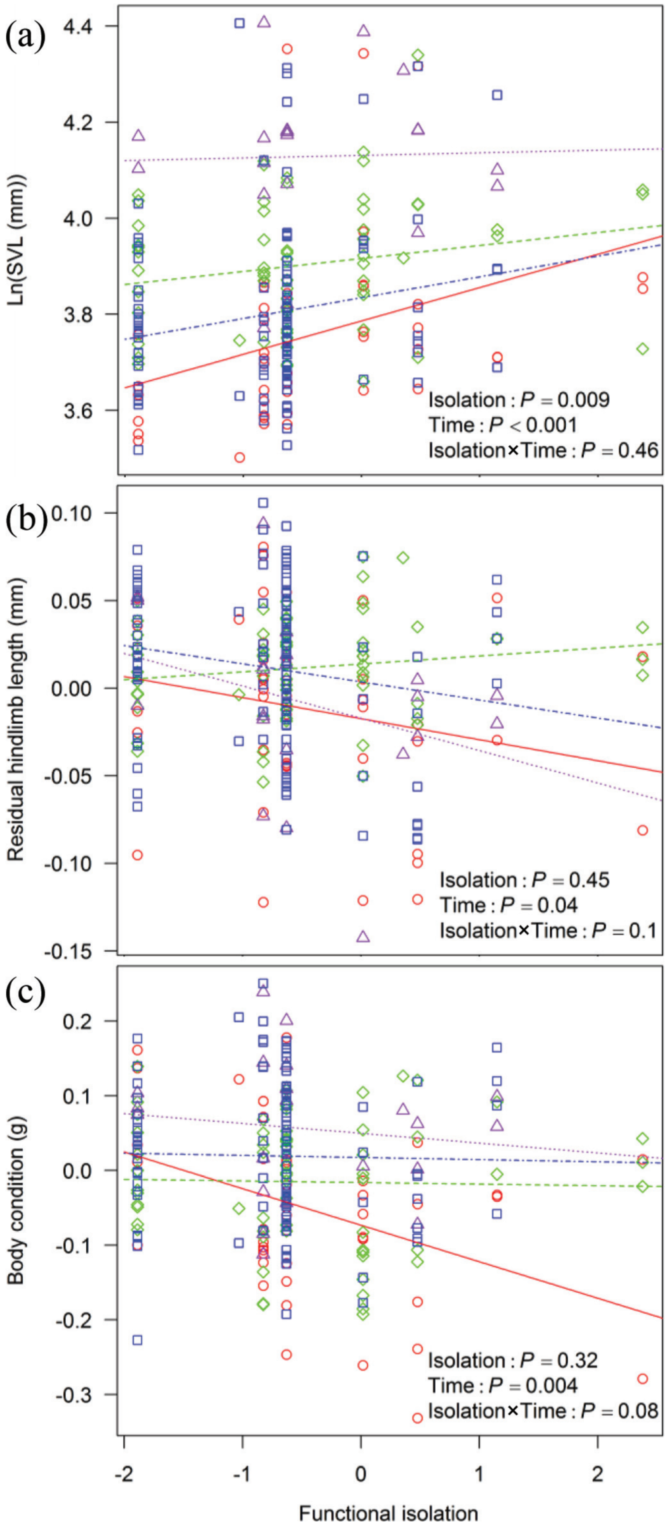
Across all four sampling periods, the most isolated ponds tended to have the largest frogs ($\chi^2_{[1]} = 6.8$, $P = 0.009$; Fig. 2*a*). This result did not vary significantly across the four sampling periods (interaction of isolation × time: $\chi^2_{[3]} = 2.6$, $P = 0.46$). The result was also present in the first sampling period alone ($\chi^2_{[1]} = 6.8$, $P = 0.024$). Together, these results indicate that the positive correlation between dispersal and body size was rapidly established (within 1 month of the ponds being created) and did not vary significantly through time as individual frogs continued to move around the landscape. However, the trend was for the slope of the body size and functional isolation relationship to be largest during the July samples ($\beta_1 = 0.069 \pm 0.028$ (±SE) and $\beta_4 = 0.043 \pm 0.021$ (±SE) for the 2014 and 2015 samples, respectively) and smallest during the June sample ($\beta_3 = 0.0054 \pm 0.039$ (±SE)). July is the time of year during which juvenile dispersal occurs, suggesting that these first-year dispersers played a major role in driving the positive dispersal – body size correlation. In contrast, early June is pre-emergence, when the majority of captured frogs were adults.

Within the population of dispersers, there was no overall correlation between isolation and body condition ($\chi^2_{[1]} = 1.0$, $P = 0.32$; Fig. 2*c*), but there was a marginally significant isolation × time effect ($\chi^2_{[3]} = 6.8$, $P = 0.08$). The size of the body condition – isolation correlation was most pronounced during the first sample ($\beta_1 = -0.049 \pm 0.017$ (±SE)), with frogs in the most isolated ponds exhibiting the lowest body condition. No significant effects were identified in the relationship between isolation and residual hindlimb length (Fig. 2*b*).

The comparison between the experimental and source ponds also demonstrated a significant body size difference between dispersers and residents ($\chi^2_{[1]} = 5.3$, $P = 0.021$; Fig. 3*a*), with frogs in the experimental ponds being larger than those in the source ponds. Again, there was no significant variation in this effect across the sampling periods ($\chi^2_{[1]} = 0.84$, $P = 0.36$). When considered alone, the effect in the first sampling period was only marginally significant ($\chi^2_{[1]} = 2.9$, $P = 0.086$), whereas the effect in the second sampling period was significant ($\chi^2_{[1]} = 6.2$, $P = 0.013$). Thus, a body size differential between the population of dispersers and the population of residents was present and detectable within a single time period (i.e., without being confounded by repeated measurements of individual frogs), but it was not established quite as rapidly as the phenotypic gradient within the population of dispersers. It is also important to note that the difference in mean body size between source and experimental ponds increased between the first and the second sampling periods, not just the significance of the relationship ($\delta_1 = -0.10 \pm 0.045$ (±SE) and $\delta_2 = -0.15 \pm 0.042$ (±SE) for the first and second samples, respectively).

Body condition did not vary significantly between dispersers and residents ($\chi^2_{[1]} = 1.9$, $P = 0.17$; Fig. 3*c*), but there was significant variation in this effect across the sampling periods ($\chi^2_{[1]} = 3.9$, $P = 0.048$). As with body size, the mean difference in body condition between residents and dispersers increased between first and second sampling periods ($\delta_1 = 0.015 \pm 0.021$ (±SE) and $\delta_2 = 0.070 \pm 0.019$ (±SE) for the first and second samples, respectively). In this case, however, frogs in the experimental ponds had lower, rather than higher, body condition compared with frogs in the source ponds. Again, no significant effects were identified in the comparison of residual hindlimb length between residents and dispersers (Fig. 3*b*).

Fig. 2. Linear mixed models between Green Frog (*Rana clamitans*) morphology and functional isolation. First sampling = solid red line, red circles; second sampling = dashed green line, green diamonds; third sampling = dotted purple line, purple triangles; fourth sampling = dot-and-dash blue line, blue squares. (*a*) Natural logarithm of snout–vent length (SVL); (*b*) residual hindlimb length; (*c*) body condition. Color version online.



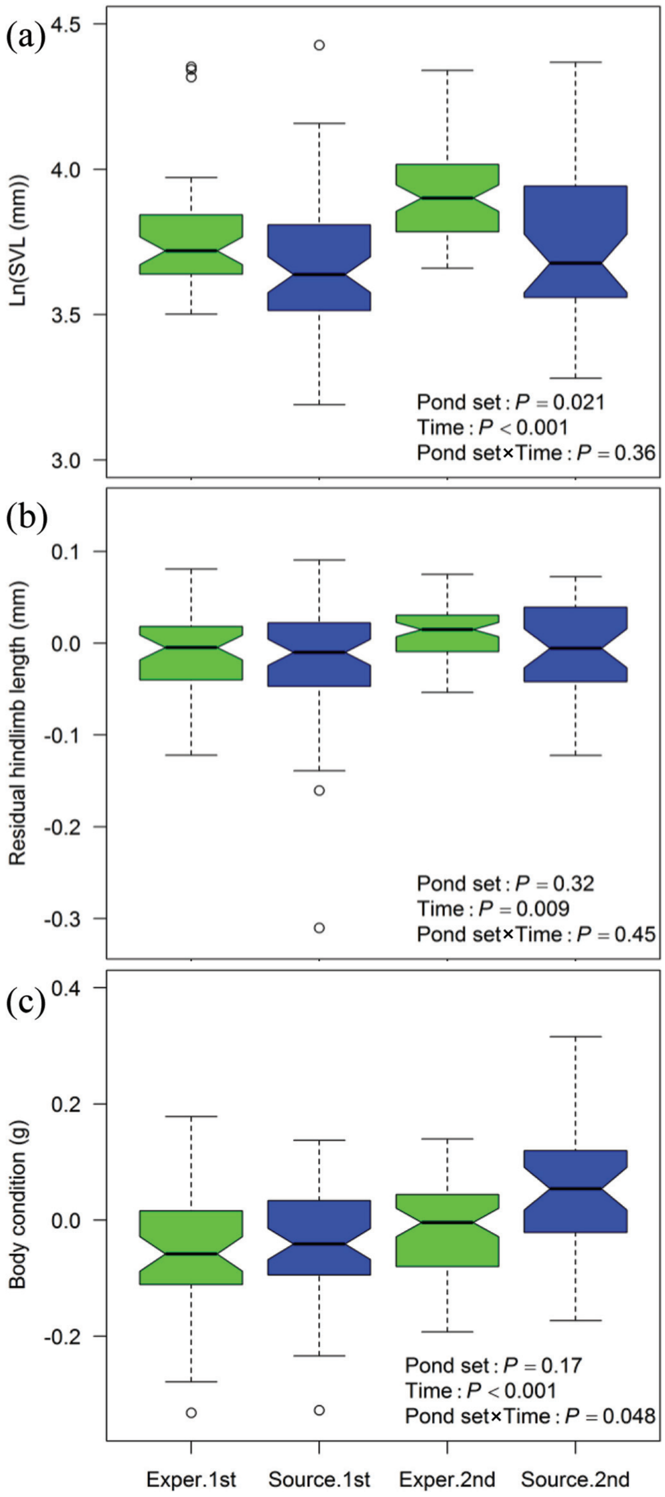


Fig. 3. Comparison of Green Frog (*Rana clamitans*) morphology between experimental ponds (green online and light gray in print) and source ponds (blue online and dark gray in print) across the first and second sampling periods. Black horizontal bands are medians; boxes show first and third quartiles; notches illustrate 95% confidence interval; whisker bars show 1.5 times the interquartile range of the data (or maximum value, if smaller); open circles are outliers. *P* values are from factorial ANOVAs including main effects of pond set (experimental vs. source), time, and their interaction. (*a*) Natural logarithm of snout–vent length (SVL); (*b*) residual hindlimb length; (*c*) body condition. Color version online.

Discussion

Our results indicate that there is a positive correlation between dispersal and body size for Green Frogs colonizing experimental ponds at our study site. This is true both when comparing the population of dispersers in the experimental ponds with the population of residents in the source ponds (Fig. 3*a*), as well as when looking at the distribution of dispersers across the isolation gradient in the experimental ponds (Fig. 2*a*). This positive correlation between functional isolation and body size was established very quickly (within 1 or 2 months) after our experimental ponds were constructed and may be driven by larger frogs taking longer foraging forays and thus being more likely to encounter the newly created ponds (Martof 1953). The strength of the dispersal–phenotype correlation did not vary significantly over the course of the 2-year study, although the trend was for it to be weakest when only older frogs were present in the terrestrial landscape (early June) and strongest when young-of-the-year frogs were dispersing (July).

When the ponds were first constructed, all Green Frogs inhabiting them were new colonizers that presumably dispersed from the source ponds, since Green Frogs mainly inhabit the margins of water bodies and do not occupy dry terrestrial habitat (Pauley 2005). Between 2014 and 2015, however, some Green Frogs overwintered in the experimental ponds such that by the third sampling period (June 2015), the majority of individuals detected may have occupied the ponds for almost a year. At this time, the dispersal–phenotype correlation was at its weakest, perhaps because the population of dispersers had continued to reshuffle themselves across the experimental landscape until they approximated an equilibrium distribution, perhaps because of elevated growth rates of the smallest individuals narrowing initial size differentials, or perhaps because of elevated mortality of the smallest individuals over the winter (Martof 1956; Boone 2005). However, over the course of the following 2 months, the next cohort of dispersing juveniles re-strengthened the dispersal–phenotype correlation.

Having established the pattern of dispersal – body size correlations across this landscape, we explore the factors generating this pattern. One potential explanation is that this pattern arises from increased growth rates of dispersing frogs arriving at these newly created sites, compared with growth rates of residents at natural ponds. We can address this using the data on body condition. Although we did not find any significant relationships between dispersal and body condition, all trends were in the direction of more dispersive individuals having lower body condition (Figs. 2*c* and 3*c*). This is in sharp contrast to all previous studies, which have shown a positive correlation between these traits (Clobert et al. 2009). There are many possible explanations for this pattern. First, we measured body condition after dispersal, whereas other studies measured it before dispersal. Thus, our negative correlation could reflect the energetic cost of dispersing (Benard and McCauley 2008). A second possibility is that frogs with initially lower body condition were most likely to disperse, perhaps because they would have been poor competitors in the already saturated source ponds (Hanski et al. 1991). A third explanation is that scarcity of prey items in the newly created ponds caused the body condition of frogs occupying these ponds to decrease relative to individuals remaining in the source ponds. Whichever of these explanations is correct, the important thing with regards to the dispersal – body size correlation is that frogs in the experimental ponds were not growing rapidly due to lower competition for resources. Instead, they had lower body condition than frogs that remained in the source ponds. This indicates that larger frogs being present in the experimental ponds is not the result of increased growth rates of those individuals after dispersal.

Another potential driver that we would like to consider is time. Do larger frogs simply have a head start that allows them to reach the farther ponds first? As mentioned in the Materials and methods, the vast majority (92%) of frogs captured in this study were juveniles. Eliminating the 8% of individuals that were adults did not qualitatively alter any of our results. This allows us to focus on a single age class — the juveniles. Since most Green Frogs mature in a single year (Ryan 1953), most juveniles are probably young of the year that emerged from the source ponds that same summer. We are thus looking primarily at a single cohort. Within this single cohort, there is still potential for temporal variation in size, as mean size at metamorphosis often decreases through time (Morey and Reznick 2000; Day and Rowe 2002; Searcy et al. 2014). This means that larger juveniles that emerged earlier would have had more time to disperse to the more isolated ponds, potentially generating the positive correlation between body size and functional isolation observed during the first sampling period. In turn, this could explain why the correlation became weaker after the juvenile dispersal period, at which point the later emerging, smaller individuals would have had time to reach the more isolated ponds as well. However, this interpretation is contradicted by the fact that over this same period, the body size differential between the population of residents in the source ponds and the population of dispersers in the experimental ponds trended in the opposite direction. If the observed patterns were driven by smaller individuals continuing to disperse from the source ponds, then this size differential should have decreased in magnitude after the end of the emergence period rather than increasing in magnitude. This indicates that larger frogs being present in the most isolated ponds is not due to them simply having more time to reach those ponds.

Although it would have been ideal to mark individual frogs before dispersal and recapture them after dispersal, we feel that by using our full data set (e.g., body condition, multiple sampling periods) in the arguments above, we can eliminate all reasonable alternate hypotheses for why a positive dispersal – body size correlation would be observed and can conclude that frogs that are larger (whether measured before or after dispersal) are those most likely to reach the most isolated ponds. We still do not know whether this pattern is due to larger frogs being more likely to attempt dispersal, or if it is due to differential mortality of smaller frogs during the dispersal process, for instance due to elevated desiccation risk for smaller frogs when crossing a dry terrestrial matrix (Mazerolle 2001; Child et al. 2008). We also do not know whether these differences in body size are heritable or generated solely by phenotypic plasticity. However, even if the differences in body size are generated by plasticity, a positive correlation between dispersal and body size, a well-established proxy for fitness among amphibians (Scott 1994; Berven 2009; Searcy et al. 2014), alters the effective connectivity of metapopulations and ultimately their viability.

In summary, our results demonstrate that the dispersers arriving at these newly created ponds are not a random sample from the source population of Green Frogs at the natural ponds, but instead that body size is positively related to dispersal. Colonists of these new ponds were larger than the mean resident of the source ponds, and among these colonists, the largest individuals were those most likely to settle in the most isolated of the newly constructed ponds. These results suggest that demographic connectivity between habitat patches is greater than if dispersers had the same fitness as the mean member of the metapopulation. Taking this into account may change which patches are classified as sources and sinks, and thus how the metapopulation should be managed to ensure long-term persistence (Runge et al. 2006). It also suggests that gene flow is higher than would be expected based on the fraction of individuals that disperse, which has the potential to limit local adaptation and possibly affect the ability of species to persist in a habitat (Slatkin 1987; Ronce and Kirkpatrick 2001). Finally, from a metacommunity perspective that considers multiple species in addition to individual metapopulations, accounting for phenotype–dispersal correlations within species will create a more nuanced view of competition–colonization trade-offs and other processes that favor coexistence (Lowe and McPeek 2014).

Acknowledgements

We thank S. Catania, J. Phillips, D. Przelicki, and A. Rego for help catching frogs. Research was supported by Natural Sciences and Engineering Research Council of Canada (NSERC) grants 402355, 435614, and 454124 and funding from the University of Toronto Mississauga.

References

Benard, M.F., and McCauley, S.J. 2008. Integrating across life-history stages: consequences of natal habitat effects on dispersal. Am. Nat. **171**(5): 553–567. doi:10.1086/587072. PMID:18419566.

Berven, K.A. 2009. Density dependence in the terrestrial stage of wood frogs: evidence from a 21-year population study. Copeia, **2009**(2): 328–338. doi:10.1643/CH-08-052.

Boone, M.D. 2005. Juvenile frogs compensate for small metamorph size with terrestrial growth: overcoming the effects of larval density and insecticide exposure. J. Herpetol. **39**(3): 416–423. doi:10.1670/187-04A.1.

Brodin, T., Lind, M.I., Wiberg, M.K., and Johansson, F. 2013. Personality trait differences between mainland and island populations in the common frog (*Rana temporaria*). Behav. Ecol. Sociobiol. **67**(1): 135–143. doi:10.1007/s00265-012-1433-1.

Child, T., Phillips, B.L., and Shine, R. 2008. Abiotic and biotic influences on the dispersal behavior of metamorph cane toads (*Bufo marinus*) in tropical Australia. J. Exp. Zool. **309A**(4): 215–224. doi:10.1002/jez.450. PMID:18288694.

Clobert, J., Le Galliard, J., Cote, J., Meylan, S., and Massot, M. 2009. Informed dispersal, heterogeneity in animal dispersal syndromes and the dynamics of spatially structured populations. Ecol. Lett. **12**(3): 197–209. doi:10.1111/j.1461-0248.2008.01267.x. PMID:19170731.

Cortwright, S.A. 1998. Ten to eleven-year population trends of two pond-breeding amphibian species, red-spotted newt and green frogs. *In* Status and conservation of midwestern amphibians. *Edited by* M.J. Lannoo. University of Iowa Press, Iowa City. pp. 61–71.

Day, T., and Rowe, L. 2002. Developmental thresholds and the evolution of reaction norms for age and size at life-history transitions. Am. Nat. **159**(4): 338–350. doi:10.1086/338989. PMID:18707419.

Edelaar, P., Jovani, R., and Gomez-Mestre, I. 2017. Should I change or should I go? Phenotypic plasticity and matching habitat choice in the adaptation to environmental heterogeneity. Am. Nat. **190**(4): 506–520. doi:10.1086/693345. PMID:28937819.

Hadfield, J.D. 2016. The spatial scale of local adaptation in a stochastic environment. Ecol. Lett. **19**(7): 780–788. doi:10.1111/ele.12614. PMID:27188689.

Hanski, I., Peltonen, A., and Kaski, L. 1991. Natal dispersal and social dominance in the common shrew *Sorex araneus*. Oikos, **62**(1): 48–58. doi:10.2307/3545445.

Hein, A.M., Hou, C., and Gillooly, J.F. 2012. Energetic and biomechanical constraints on animal migration distance. Ecol. Lett. **15**(2): 104–110. doi:10.1111/j.1461-0248.2011.01714.x. PMID:22093885.

Hudson, C.M., Brown, G.P., and Shine, R. 2016. It is lonely at the front: contrasting evolutionary trajectories in male and female invaders. R. Soc. Open Sci. **3**(12): 160687. doi:10.1098/rsos.160687. PMID:28083108.

Jakob, E.M., Marshall, S.D., and Uetz, G.W. 1996. Estimating fitness: a comparison of body condition indices. Oikos, **77**(1): 61–67. doi:10.2307/3545585.

Joksimovic, O. 2015. The evolution of sexual dimorphism: resource investment in Anura and a case of sexual selection in a scramble breeder (*Lithobates sylvaticus*). M.Sc. thesis, Department of Ecology and Evolutionary Biology, University of Toronto, Toronto, Ont.

Kingsolver, J.G., and Huey, R.B. 2008. Size, temperature, and fitness: three rules. Evol. Ecol. Res. **10**: 251–268.

Lowe, W.H., and McPeek, M.A. 2014. Is dispersal neutral? Trends Ecol. Evol. **29**(8): 444–450. doi:10.1016/j.tree.2014.05.009. PMID:24962790.

Martof, B. 1953. Home range and movements of the green frog, *Rana clamitans*. Ecology, **34**(3): 529–543. doi:10.2307/1929725.

Martof, B. 1956. Factors influencing size and composition of populations of *Rana clamitans*. Am. Midl. Nat. **56**(1): 224–245. doi:10.2307/2422457.

Mazerolle, M.J. 2001. Amphibian activity, movement patterns, and body size in fragmented peat bogs. J. Herpetol. **35**(1): 13–20. doi:10.2307/1566017.

McCauley, S.J., Brodin, T., and Hammond, J. 2010. Foraging rates of larval dragonfly colonists are positively related to habitat isolation: results from a landscape-level experiment. Am. Nat. **175**(3): E66–E73. doi:10.1086/650444. PMID:20109064.

Mills, L.S., and Allendorf, F.W. 1996. The one-migrant-per-generation rule in conservation and management. Conserv. Biol. **10**(6): 1509–1518. doi:10.1046/j.1523-1739.1996.10061509.x.

Moilanen, A., and Hanski, I. 2006. Conectivity and metapopulation dynamics in highly fragmented landscapes. *In* Connectivity conservation. *Edited by* K.R. Crook and M. Sanjayan. Cambridge University Press, Cambridge. pp. 44–71.

Morey, S., and Reznick, D. 2000. A comparative analysis of plasticity in larval development in three species of spadefoot toads. Ecology, **81**(6): 1736–1749. doi:10.1890/0012-9658(2000)081[1736:ACAOPI]2.0.CO;2.

Ovaskainen, O., and Hanski, I. 2003. Extinction threshold in metapopulation models. Ann. Zool. Fenn. **40**(2): 81–97.

Pauley, T.K. 2005. *Rana clamitans* Latreille, 1801: green frog. *In* Amphibian declines: the conservation status of United States species. *Edited by* M.J. Lannoo. University of California Press, Berkeley. pp. 549–552.

Peig, J., and Green, A.J. 2010. The paradigm of body condition: a critical reappraisal of current methods based on mass and length. Funct. Ecol. **24**(6): 1323–1332. doi:10.1111/j.1365-2435.2010.01751.x.

Phillips, B.L., Brown, G.P., Webb, J.K., and Shine, R. 2006. Invasion and the evolution of speed in toads. Nature, **439**: 803. doi:10.1038/439803a. PMID:16482148.

R Core Team. 2013. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available from https://www.r-project.org/.

Renault, D., Laparie, M., McCauley, S.J., and Bonte, D. 2018. Environmental adaptations, ecological filtering, and dispersal central to insect invasions. Annu. Rev. Entomol. **63**: 345–368. doi:10.1146/annurev-ento-020117-043315. PMID:29029589.

Ronce, O., and Kirkpatrick, M. 2001. When sources become sinks: migration meltdown in heterogeneous habitats. Evolution, **55**(8): 1520–1531. doi:10.1111/j.0014-3820.2001.tb00672.x. PMID:11580012.

Runge, J.P., Runge, M.C., and Nichols, J.D. 2006. The role of local populations within a landscape context: defining and classifying sources and sinks. Am. Nat. **167**(6): 925–938. doi:10.1086/503531. PMID:16615034.

Ryan, R.A. 1953. Growth rates of some ranids under natural conditions. Copeia, **1953**(2): 73–80. doi:10.2307/1440128.

Schroeder, E.E. 1976. Dispersal and movement of newly transformed green frogs, *Rana clamitans*. Am. Midl. Nat. **95**(2): 471–474. doi:10.2307/2424413.

Scott, D.E. 1994. The effect of larval density on adult demographic traits in *Ambystoma opacum*. Ecology, **75**(5): 1383–1396. doi:10.2307/1937462.

Searcy, C.A., Gray, L.N., Trenham, P.C., and Shaffer, H.B. 2014. Delayed life history effects, multilevel selection, and evolutionary trade-offs in the California tiger salamander. Ecology, **95**(1): 68–77. doi:10.1890/13-0120.1. PMID: 24649647.

Searcy, C.A., Snaas, H., and Shaffer, H.B. 2015. Determinants of size at metamorphosis in an endangered amphibian and their projected effects on population stability. Oikos, **124**(6): 724–731. doi:10.1111/oik.01775.

Semlitsch, R.D. 1987. Paedomorphosis in *Ambystoma talpoideum*: effects of density, food, and pond drying. Ecology, **68**(4): 994–1002. doi:10.2307/1938370.

Shine, R., Brown, G.P., and Phillips, B.L. 2011. An evolutionary process that assembles phenotypes through space rather than through time. Proc. Natl. Acad. Sci. U.S.A. **108**(14): 5708–5711. doi:10.1073/pnas.1018989108. PMID: 21436040.

Slatkin, M. 1987. Gene flow and the geographic structure of natural populations. Science, **236**(4803): 787–792. doi:10.1126/science.3576198. PMID:3576198.

Stevens, V.M., Whitmee, S., Le Galliard, J., Clobert, J., Böhning-Gaese, K., Bonte, D., Brändle, M., Dehling, D.M., Hof, C., Trochet, A., and Baguette, M. 2014. A comparative analysis of dispersal syndromes in terrestrial and semi-terrestrial animals. Ecol. Lett. **17**(8): 1039–1052. doi:10.1111/ele.12303. PMID: 24915998.

Tejedo, M., and Reques, R. 1994. Plasticity in metamorphic traits of natterjack tadpoles: the interactive effects of density and pond duration. Oikos, **71**(2): 295–304. doi:10.2307/3546278.

Walpole, A.A., Bowman, J., Tozer, D.C., and Badzinski, D.S. 2012. Community-level response to climate change: shifts in anuran calling phenology. Herpetol. Conserv. Biol. **7**(2): 249–257.