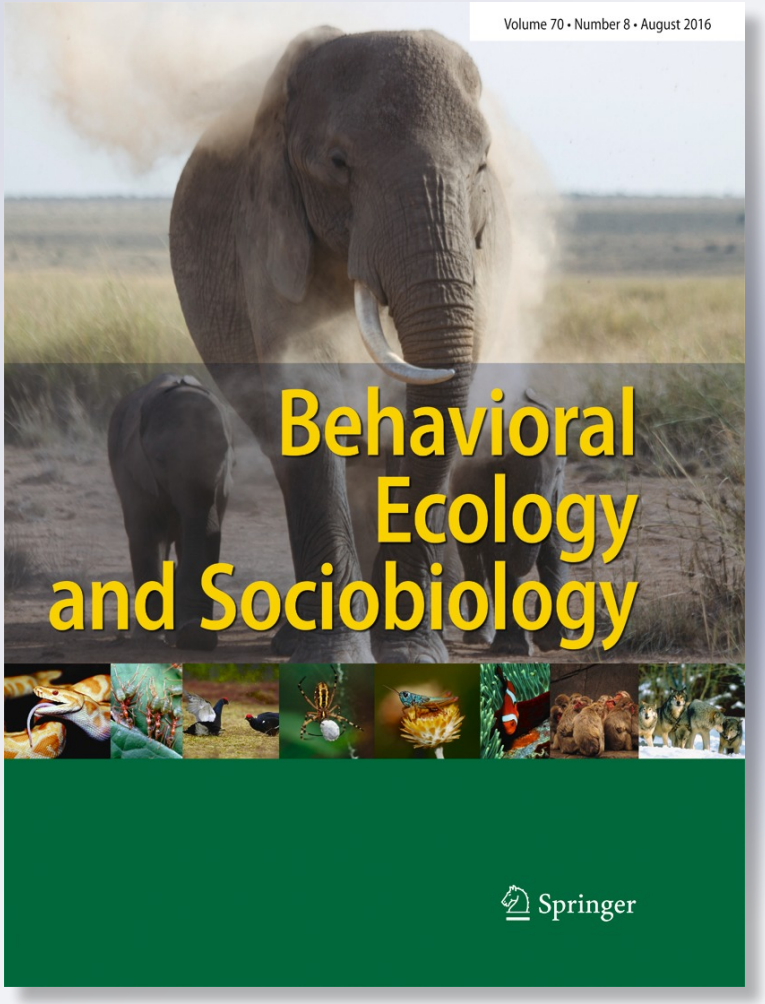
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ORIGINAL ARTICLE

Natal philopatry varies with larval condition in salamanders

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Abstract
An individual's physiological condition early in ontogeny often regulates natal dispersal and philopatry decisions; however, increased condition promotes dispersal in some organisms and philopatry in others. These disparate findings likely arise from interactions among an individual's early life stage physiological condition, its likelihood of surviving a dispersal event (i.e., dispersal capacity), and its motivation to leave its natal site (i.e., dispersal propensity). Due to the broad importance of reproductive site selection to population structure and dynamics, studies disentangling these various phenotype-dependent effects are critical. We evaluated the relationships between two aspects of larval physiological condition and natal philopatry in Arizona tiger salamanders (*Ambystoma tigrinum nebulosum*) in an isolated pond system. In this population, geographic distance between ponds is small, adult survivorship is very high, and thus the likelihood of a successful breeding event should mediate reproductive site selection as opposed to the likelihood of surviving the dispersal event. We found that natal philopatry increased with an estimate of long-term body condition in males, but there was no relationship in females. However, natal philopatry decreased with an estimate of short-term body condition. We also found that an individual's natal pond had effects on philopatry that influenced both sexes and were independent of the pond's direct effects on body condition. Together, these findings strongly support the importance of an individual's early developmental experience in the natal environment to its reproductive behaviors across its lifespan, and further highlight the value of considering how phenotype-dependent dispersal mechanisms may vary between the sexes.

Significance statement
Previous research has not discerned a generalizable relationship between larval physiological condition and natal philopatry, likely because of the complex interaction between an individual's ability (dispersal capacity) and its motivation (dispersal propensity) to reproduce in its natal habitat. Using a salamander population with small inter-pond distances and high adult survival, we isolated the effects of two aspects of physiological condition on dispersal propensity. We found that increased long-term larval physiological condition was associated with natal philopatry in male, but not female, tiger salamanders, as well as differences in philopatry based on natal pond. In contrast, short-term larval physiological condition was negatively associated with philopatry. Our findings suggest an important, long-lasting role of the natal environment on reproductive site selection, and further implicate that the conditions experienced in early development can strongly affect reproductive behaviors across the life cycle.

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Keywords Natal habitat effects · Reproductive site selection · Phenotype-dependent dispersal · Informed dispersal

Introduction

An individual's fitness can be strongly affected by where it reproduces (e.g., Howard 1978; Tarwater and Beissinger 2012). As many organisms are able to actively disperse, the decision to reproduce in the natal environment (i.e., natal philopatry) or a new environment (i.e., natal dispersal) may have especially important fitness implications (Benard and McCauley 2008; Clobert et al. 2009). The fitness payoffs of such decisions result from a complex array of factors including the probability of surviving emigration and resettlement (Calsbeek 2009; Chaput-Bardy et al. 2010; Cote and Clobert 2010), the suitability of a new environment for offspring (e.g., Sinervo et al. 2006), and the likelihood of potentially costly matings with closely related individuals (e.g., Szulkin and Sheldon 2008). Accordingly, natural selection is likely to act strongly on the behavioral and morphological factors that influence the decision between philopatry and dispersal (Clobert et al. 2009).

The environment experienced in the natal habitat may have an important effect on natal dispersal or philopatry decisions (Benard and McCauley 2008; Clobert et al. 2009). Often, such environmental variation may indirectly influence reproductive site selection through its direct effects on phenotypes, such as early life stage size and body condition (Clobert et al. 2009). For example, initial resource availability may affect these traits, which then influence whether an individual reproduces in its natal or a non-natal habitat (e.g., Baines et al. 2015). Size or condition may then act as a conduit through which the natal environment mediates dispersal and philopatry behavior (Benard and McCauley 2008), and, indeed, such traits have been shown to influence natal philopatry in many organisms (e.g., lizards: Meylan et al. 2002; birds: Barbraud et al. 2003; odonates: Chaput-Bardy et al. 2010; ungulates: Debeffe et al. 2012). However, support for a generalizable relationship between early life stage size or condition and philopatry remains equivocal, as high body condition facilitates dispersal in some organisms (Anholt 1990; Meylan et al. 2002; Baines et al. 2015) but philopatry in others (McPeek and Holt 1992; Cote and Clobert 2010). It is thus likely that early life stage condition does not regulate this decision alone. Instead, it may interact with the individual's probability of surviving a dispersal event (i.e., dispersal capacity) versus its motivation to leave its natal site (i.e., dispersal propensity; Benard and McCauley 2008; Bonte and de la Peña 2009). For instance, individuals in low body condition may be motivated to leave the natal habitat because they are unlikely to have high reproductive success there, but may not have the capacity to survive the dispersal event. The relative importance of dispersal capacity versus propensity consequently must be disentangled in order to elucidate the relationship between early life stage body condition and natal philopatry.

Natal philopatry decisions may also have sex-specific fitness consequences (Forero et al. 2002; Calsbeek 2009; Tarwater and Beissinger 2012), and any relationship between body condition or size and natal philopatry may differ between males and females (Sinervo et al. 2006; Chaput-Bardy et al. 2010). For instance, while male reproductive success tends to vary primarily with the number of matings, female reproductive success may be particularly sensitive to the effects of environmental variation on the success of offspring at each reproductive event (Trivers 1972; Howard 1983; Champan et al. 2003; but see Byers and Dunn 2012). Because the variance in offspring success will also be closely tied to the location where a female reproduces, the use of cues about the suitability of the environment for offspring may be under especially strong selection in females (e.g., Howard 1978; Resetarits 1996). Consequently, the cues used for reproductive site selection may vary between the sexes according to the likelihood of such reproductive payoffs (Bowler and Benton 2005). As an individual's condition in the natal habitat may convey more information about the likelihood of future offspring success than about the likelihood of obtaining mates (e.g., Sinervo et al. 2006; Cote and Clobert 2010), the strength and/or direction of its relationship with natal philopatry may not be the same for both males and females.

In amphibians, the environment experienced during the aquatic larval stage may be especially important to natal philopatry. An individual's larval size and condition reflect the environment experienced during the aquatic stage (Scott et al. 2007; Doyle and Whiteman 2008; Whiteman et al. 2012) and are often associated with important adult fitness components, such as post-metamorphic survival and size at maturity (Earl and Whiteman 2015). Larval size and condition may then reflect the suitability of the natal pond for offspring, and thus could have a critical impact on natal philopatry (Wilbur 1980; Benard and McCauley 2008). We investigated the relationship between larval condition and natal philopatry in a natural population of the Arizona tiger salamander (*Ambystoma tigrinum nebulosum*) that has been the focus of a long-term monitoring program. This population provides an excellent system for exploring the relationship between larval condition and natal philopatry for at least two reasons. First, the maximum distance between breeding ponds is less than 170 m (Fig. 1), well within the dispersal distance of this species (Whiteman et al. 1995b; Whiteman and Wissinger 2005) and other similar species (reviewed in Smith and Green 2005). Second, long-term mark-recapture estimates indicate that adult survivorship is very high (>75 %: HHW, unpublished data). Thus, neither the distance between ponds nor an individual's ability to survive such movement strongly limits reproductive site selection. Our study system therefore isolates the relationship between an individual's larval size

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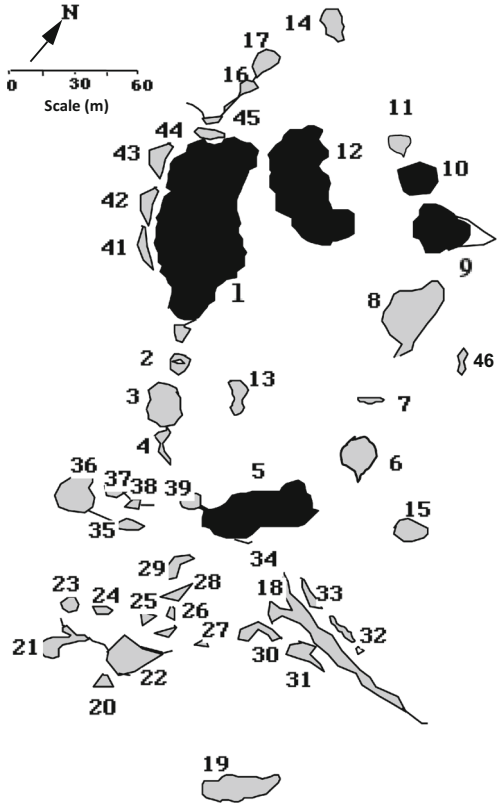


Fig. 1 Map of the Mexican Cut Nature Preserve; *numbers* indicate unique ponds. Ponds shaded with *black* are focal ponds, and ponds shaded with *gray* were not included in this study due to no or few total metamorphs (<5). Modified from Wissinger et al. (2003)

and condition and its propensity for natal philopatry. As the dispersal capacity with respect to larval condition should not limit movement in this system, we predicted that individuals with low larval condition would be more likely to breed in non-natal ponds. We also predicted that, because natural selection is expected to act more intensely on cues used by females, the relationship between larval condition and philopatry would be stronger in females.

Methods

Study site and study organism

The Mexican Cut Nature Preserve (MCNP) is a high-elevation (3640 m) property owned by The Nature Conservancy in western Colorado, USA (39.02° N, 107.06° W). The elevation of the study site enables growth and activity periods that are limited to only a few months from early or mid-June to mid-September (Whiteman and Wissinger 2005). The ponds at MCNP (Fig. 1) vary in numerous environmental parameters, including hydroperiod, prey densities, and water chemistry (Wissinger and Whiteman 1992; Wissinger et al. 1999; Whiteman and Wissinger 2005). The population used in this study has been the subject of continuous monitoring since 1988. Individuals at MCNP are facultatively paedomorphic, expressing either a terrestrial or aquatic adult phenotype (Whiteman 1994: Whiteman et al. 2012). Here, we consider the philopatric reproductive behavior of only terrestrial (metamorphic) adults, as aquatic (paedomorphic) adults forfeit their ability to disperse through the expression of this alternate life history. Although life cycle expression depends on larval condition in this population (Whiteman et al. 2012), theoretical and empirical work indicates that the metamorphic life cycle occurs in individuals that represent the middle and right-hand tail of the body condition distribution (Whiteman 1994; Denoël et al. 2005; Whiteman et al. 2012). Thus, the exclusion of paedomorphs primarily eliminates only the very smallest individuals from the population and should not bias our results significantly. Larvae in this population typically undergo metamorphosis by the end of their third summer (83.3 %; Whiteman et al. 2012), and reach sexual maturity approximately 4 and 6 years after metamorphosis, for males and females, respectively. As mating occurs aquatically, both males and females must enter ponds to reproduce. In ponds, males both compete with other males and actively court females (Whiteman et al. 1999), and mated females produce large clutches of eggs (observed range 64–666).

Monitoring

We captured salamanders of all life stages from ponds by hand and using long-handled dip nets, and identified individuals using unique toe clips or passive integrated transponder (PIT) tags (Whiteman et al. 2016). At each capture, we measured several characteristics of each individual, including mass (g) and snout-vent length (SVL; mm). During the breeding season (late June–mid July), we considered adults to be in breeding condition if they exhibited a swollen cloaca (males and females) or extruded eggs (females). Though an individual (particularly males) in breeding condition may not successfully reproduce in a given year, it is assumed that individuals in breeding condition are selecting ponds that give themselves the best chance at successful reproduction.

As the length of the larval period is typically over 2 years in this population (~65 % of individuals; HHW, unpublished data), long-term (i.e., across years) and short-term (i.e., within a year) aspects of an individual's physiological condition may provide different information for reproductive site selection (Feder and Burggren 1992; Rose 2005). Consequently, we quantified two indices of larval physiological condition that reflect a larva's long-term and short-term experience of the environment. We first characterized an individual's size-specific mass by dividing its mass by its SVL when it was last captured as a larva. In this and other salamander populations (e.g., Denoël et al. 2002; Whiteman et al. 2012), this metric reflects aspects of physiological condition that are associated

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with an individual's long-term larval growth history and post-metamorphic fitness prospects (Earl and Whiteman 2015). As a consequence, this estimate of condition intentionally incorporates the variation in physiological state that is correlated with structural size differences. To assess body condition related to short-term resource accumulation at the end of the larval period, we also calculated body condition from the residuals of log-transformed body mass regressed on log-transformed SVL (hereafter "residual body condition"; Jakob et al. 1996; Schulte-Hostedde et al. 2005). This body condition metric accounts for mass differences among individuals that are independent of the covariation between mass and SVL. These mass differences therefore reflect variation that is associated with short-term aspects of physiological condition (e.g., gut fullness, fat content) that may be used by salamanders for the assessment of recent environmental quality (Feder and Burggren 1992; Rose 2005). Quantifying both metrics of condition enables us to directly compare the relative influence of short-term versus long-term physiological state on reproductive site selection.

Additionally, because we monitored this population closely on a cohort-specific basis, the date of metamorphosis could be accurately estimated (see also Whiteman et al. 2012). Analyses indicated that the age of individuals at metamorphosis was not related to either size-specific mass or residual body condition (generalized linear model: both $\chi^2 < 1.7$, $P > 0.194$), and thus, these metrics are not biased by individuals with longer or shorter larval periods. Because all individuals were captured and uniquely marked as larvae, and because larvae cannot move between ponds, we know the pond of origin for each individual used in this study without error.

Analyses

We began by exploring relationships among our potential explanatory variables. First, we considered how sex and natal pond might have influenced variation in larval condition using two-way analyses of variance on the two condition metrics, with each individual's condition included as the response variable. Additionally, because natal philopatry may be mediated by the time spent in the terrestrial environment, we used Pearson product-moment correlation coefficients to evaluate the relationships between an individual's post-metamorphic juvenile duration, the time (years) between metamorphosis and first reproduction, and each of the larval body condition metrics. Lastly, we assessed the correlation between our two condition metrics.

To analyze natal philopatry, we used two separate methods. First, we used multiple regression to analyze the proportion of times an individual was captured in breeding condition in its natal pond versus any non-natal pond (degree of philopatry). In this analysis, an increase in the proportion of times an individual breeds in its natal pond corresponds to an increase in philopatric breeding behavior over its reproductive lifespan. We specifically evaluated the effects of an individual's sex, size-specific mass, residual body condition, and natal pond. Because of the low sample sizes in several ponds relative to the number of terms in the model (Table 1), we did not fit three- or four-way interactions to avoid overfitting. We calculated the partial R^2 of each effect by comparing the change in R^2 between models with and without the effect. Second, because any potential relationship between either short-term or long-term larval condition and philopatry may be strongest at the first reproductive event, philopatry at the first reproductive event was analyzed using a generalized linear model with a binomial error distribution (i.e., 1 = philopatric, 0 = not philopatric). The explanatory variables included in this model were the same as described above. We did not include an individual's cohort for either of these analyses, as cohort was strongly confounded with pond in many cases, and data visualization indicated that observed patterns were qualitatively similar among cohorts within ponds. For both analyses of natal philopatry, we also initially included several covariates that may be affected by short-term and long-term body condition or natal pond and could in turn affect reproductive site selection: an individual's juvenile duration (the time [years] between metamorphosis and first reproduction), its age at metamorphosis, and its total number of breeding events. However, these additional covariates were never significant (all $P > 0.389$) and were not considered further. All two-way interactions between natal pond and other terms were also non-significant ($P > 0.368$), likely because of the small sample sizes within some ponds (Table 1), and we removed these interactive effects to further avoid overfitting. For comparing philopatric behavior within and between analyses across the expressed ranges of size-specific mass and residual body condition, we predicted the degree of philopatry and the likelihood of philopatry during the first reproductive event from the final models at the 25th, 50th, and 75th quantiles of the each condition metric.

Because some variables in the models were found to be significantly associated, we assessed the degree of multicollinearity among individual terms in the multiple regression model with variance inflation factors (VIF; Petraitis et al. 1996). Multicollinearity was initially high in some cases (>10),

Table 1 Number of male and female metamorphs originating from each pond at the Mexican Cut Nature Preserve that were included in analyses

	Pond				
	1	5	9	10	12
No. of females	7	4	8	4	31
No. of males	12	19	19	4	49

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and thus, we *z*-transformed variables (Schielzeth 2010). After transformation, all VIF in the final models were less than 2.4, indicating that multicollinearity among explanatory variables does not bias our results. We logit-transformed dependent proportion variables to improve the normality of the residuals of our linear models (Warton and Hui 2011). All analyses were conducted using R version 3.1.2 (R Development Core 2014). To reduce observer bias, compiling and organizing data were completed blindly with respect to an individual's natal pond.

Results

In total, 157 metamorphs from five natal ponds were used in these analyses (Table 1). Males and females were captured in breeding condition 2.15 ± 1.80 and 1.48 ± 0.88 times (mean ± SD), respectively. Evaluating the relationships between explanatory variables revealed several significant associations. Size-specific mass varied among natal ponds ($F_{4,147} = 10.6$, $P < 0.001$; Fig. 2a), and males had higher larval size-specific mass than females ($F_{1,147} = 4.6$, $P = 0.034$), but there was no interaction between pond and sex ($F_{4,147} = 0.50$, $P = 0.74$). Residual body condition also varied among ponds ($F_{4,147} = 9.4$, $P < 0.001$; Fig. 2b), and males had greater residual body condition than females ($F_{1,147} = 4.3$, $P = 0.040$), but there was no interaction ($F_{4,147} = 1.3$, $P = 0.267$). An individual's post-metamorphic juvenile duration decreased with its size-specific mass ($r = -0.269$, $t_{1,148} = -3.4$, $P < 0.001$), but not with its residual body condition ($r = -0.011$, $t_{1,148} = -0.1$, $P = 0.889$). Lastly, residual body condition and size-specific mass were positively associated ($r = 0.611$, $t_{1,155} = 9.6$, $P < 0.001$).

We first considered natal philopatry across all reproductive events. Degree of philopatry varied among natal ponds ($F_{4,146} = 2.5$, $P = 0.047$, partial $R^2 = 0.053$). Although no pairwise differences were significant (Tukey post hoc, all $P > 0.068$), individuals from ponds 1 and 12 tended to have a higher degree of philopatry than individuals from other ponds (Fig. 2c). An individual's degree of philopatry depended on the interaction between its larval size-specific mass and its sex ($F_{1,146} = 10.4$, $P = 0.002$), whereby philopatry increased with size-specific mass in males ($F_{1,96} = 14.4$, $P < 0.001$, partial $R^2 = 0.108$) but not females ($F_{1,47} = 0.03$, $P = 0.857$, partial $R^2 = 0.005$). For males, size-specific mass at the 25th, 50th, and 75th quantiles was associated with degrees of philopatry of 11.9, 30.3, and 60.0 %, respectively (Fig. 3a). Conversely, females returned to their natal ponds in 38.3 % of breeding events irrespective of their larval size-specific mass (Fig. 3b). Degree of philopatry tended to weakly decrease with residual body condition ($F_{1,146} = 3.4$, $P = 0.067$, partial $R^2 = 0.018$), and there was no effect of the interaction with sex ($F_{1,146} = 0.13$, $P = 0.252$) or with size-specific mass ($F_{1,146} = 0.2$, $P = 0.627$).

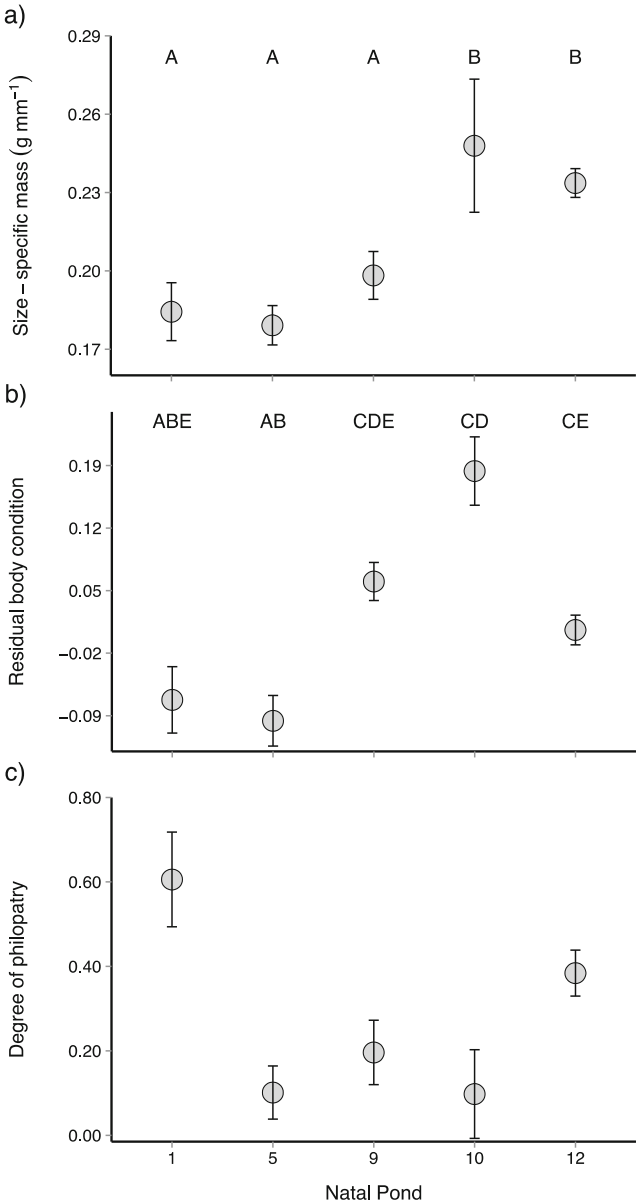


Fig. 2 **a** Mean larval size-specific mass and **b** residual body condition of individuals differed among natal ponds ($P < 0.001$). **c** Degree of philopatry (proportion of times an individual returned to breed in its natal pond) of individuals from each pond as predicted by the full multiple regression model. Philopatry differed among ponds ($P = 0.047$, partial $R^2 = 0.053$), although no pairwise comparisons were significant (Tukey post hoc, all $P > 0.068$). Sample sizes can be found in Table 1. All *points* are pond means ± SE, and *letters* indicate significant Tukey post hoc differences

Across both sexes, the predicted degree of philopatry was 31.5, 22.6, and 16.7 % at the 25th, 50th, and 75th quantiles of residual body condition, respectively. However, a linear regression including only residual body condition as an explanatory variable of degree of philopatry was not significant ($F_{1,155} = 0.09$, $P = 0.766$), indicating the weak observed relationship between residual body condition and natal philopatry occurs only when size-specific mass is taken into account.

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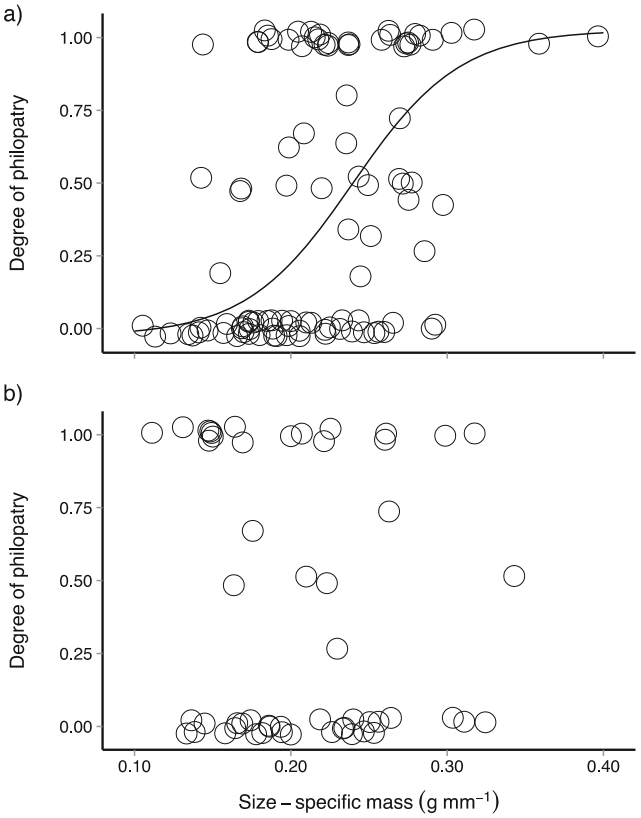


Fig. 3 Degree of philopatry of metamorphic individuals at the Mexican Cut Nature Preserve for males (**a**) and females (**b**). Each *point* represents the proportion of times an individual returned to reproduce in its natal pond. There is an overall significant larval body condition × sex interaction ($P = 0.002$), where the relationship is significant for males ($P < 0.001$), but not females ($P > 0.857$). For visual clarity of effects, untransformed values are presented, and points are jittered vertically by 0.02

Results were qualitatively similar when only focusing on an individual's first reproductive event (Table S1). In males, the likelihood of philopatry at the first reproductive event was 20.5, 35.2, and 54.9 % at the 25th, 50th, and 75th quantiles of size-specific mass, respectively. The likelihood of philopatry at the first reproductive event was 37.0 % in females irrespective of size-specific mass. Lastly, comparing across the 25th, 50th, and 75th quantiles of residual body condition, the likelihood of philopatry at the first reproductive event decreased from 39.5 to 30.8 to 24.6 %, respectively.

Discussion

Early life stage body condition is widely predicted to modulate decisions between philopatry and dispersal (Clobert et al. 2009). However, a generalizable relationship between natal philopatry and early ontogenetic size or condition is lacking, likely because these traits can simultaneously improve an individual's capacity for surviving a dispersal event and provide cues that the natal habitat is favorable for reproduction (Bowler and Benton 2005; Benard and McCauley 2008). This study assessed reproductive site selection in metamorphic salamanders in a pond system where dispersal capacity was not limited by distance among ponds or high mortality risk. We were thus able to isolate the effects of an individual's propensity to reproduce in a natal versus non-natal pond. We found that natal philopatry increased with size-specific mass (long-term body condition) in male, but not female, salamanders (Fig. 3a). Additionally, after controlling for variation in size-specific mass, natal philopatry weakly decreased with residual body condition (short-term body condition). These findings are contrary to our predictions, but provide important insight into the sex-specific influence of the early life stage environment on reproductive site selection.

As our data are observational, we cannot say definitively that larval physiological condition causally affects natal philopatry. For example, some natal environmental factor may simultaneously increase larval condition and the propensity for natal philopatry (e.g., resource availability, predators; Baines et al. 2015). However, if the natal environment directly affected larval condition and independently affected natal philopatry, and the association between condition and philopatry was spurious, then we would have been unlikely to observe significant effects of pond and larval condition when all terms were included in our analyses. Additionally, while other environmental factors may confer information about the suitability of the environment for future reproduction (e.g., Tarwater and Beissinger 2012; Auillon and Duckworth 2015; Baines et al. 2015), the extent of the information provided by general resource availability should be largely integrated via larval condition (e.g., Wilbur and Collins 1973; Clobert et al. 2009; Cote and Clobert 2010), and even experimental manipulations of resource availability would be unable to disentangle any direct effects on philopatry from indirect effects mediated through condition. It is also unlikely that larval condition indirectly affected natal philopatry via a direct effect on some additional, post-metamorphic trait (e.g., juvenile duration), as such traits were never significantly associated with natal philopatry. Consequently, our results are strongly consistent with direct, biological relationships between larval physiological condition and natal philopatry in salamanders.

The various physiological factors contributing to an individual's body condition may provide information about different aspects of the environment, and may therefore differentially affect complex behaviors like reproductive site selection (Sinervo et al. 2006; Clobert et al. 2009; Saastamoinen et al. 2010). Due to the prolonged larval period of *A. t. nebulosum*, size-specific mass may provide more reliable information about the fitness payoffs of reproducing in the natal pond than do other, more transient features of physiological condition such as gut fullness or fat reserves. Consistent with this hypothesis, size-specific mass, at least in males, had a stronger influence on

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natal philopatry than did residual body condition. Intriguingly, the two estimates influenced natal philopatry in opposite ways, further suggesting that they encode different information. In this population, the ponds with the greatest access to nutrient-rich resources, such as fairy shrimp, are primarily semi-permanent (Bohanak and Whiteman 1999), which will produce larvae with very high residual body condition, but also may be extremely unreliable for reproduction. Such information may not be provided by size-specific mass, and selection may then favor the use of high residual body condition as a cue that their natal pond may dry. Indeed, larvae from pond 10, which is semi-permanent and supports the greatest densities of nutrient-rich fairy shrimp among the focal ponds, had the highest residual body condition but also the lowest philopatry (Fig. 2b, c). Future work remains necessary to test this hypothesis explicitly. Importantly, however, the effects of both indices of larval condition on natal philopatry were modest in absolute terms (partial R^2: male size-specific mass = 0.11; residual body condition = 0.02). Despite this, comparable strengths are found in many studies of phenotype-dependent dispersal (e.g., Anholt 1990; Calsbeek 2009; McCauley 2010; Auillon and Duckworth 2015), and such findings ultimately underscore the diversity of cues, including different features of physiological condition, that modulate complex behaviors such as natal philopatry.

Males with higher size-specific mass exhibited greater natal philopatry. Importantly, as the slope of the relationship between size-specific mass and philopatry actually became slightly steeper when all of the reproductive events were included as opposed to only the first event, the information conveyed by size-specific mass is likely persistent across the reproductive lifespan. Currently, mechanisms linking larval size-specific mass to male reproductive success in natal versus non-natal ponds are unknown. Males with low size-specific mass presumably had a relatively unfavorable experience in their natal environment (Doyle and Whiteman 2008; Whiteman et al. 2012). In a variety of systems, the dispersal of males with lower condition or smaller body size has been linked to a poor position in the social breeding hierarchy (e.g., Sinervo et al. 2006; McCauley 2010). Males with low size-specific mass may become adults that also perform poorly in competition for mates, and move to other ponds where their chances of obtaining mates could be higher (Pulliam 1988). A weak correlation between larval size-specific mass and an individual's position in the social breeding hierarchy may then be sufficient for maintaining the observed relationship between size-specific mass and natal philopatry. Alternatively, low size-specific mass may indicate to males that the environment experienced was unfavorable for their genotype, and offspring sired in that pond may perform similarly poorly. While the underlying mechanism linking larval size-specific mass to natal philopatry in males merits future consideration, the findings of this study add to the growing list of research implicating the importance of the early ontogenetic environment to male reproductive success (Cornwallis and Uller 2010).

Opposite to our expectations, natal philopatry was not associated with larval size-specific mass in females. Because of the high energetic investment that females allocate towards each clutch relative to males (Trivers 1972; Howard 1983), selection on females should favor the use of only the most reliable cues when choosing ponds for reproduction (Bowler and Benton 2005). In our system, most individuals develop in permanent ponds where large paedomorphs and older cohorts of conspecific larvae simultaneously dominate the availability of prey (Wissinger et al. 1999, 2010; Whiteman and Wissinger 2005) and pose a substantial predation risk to hatchlings (Wissinger et al. 2010; MPM and HHW, unpublished data). As densities of these aquatic individuals fluctuate through time within ponds (Whiteman and Wissinger 2005), larval size-specific mass may not provide reliable enough information to females about the suitability of the natal pond for future offspring. Amphibians are known to adaptively choose oviposition sites depending on selective pressures that offspring may face, such as predators (Resetarits and Wilbur 1989; Sadeh et al. 2009), parasites (Kiesecker and Skelly 2000), competitors (Resetarits and Wilbur 1989), and acidity (Whiteman et al. 1995a). Furthermore, physiological condition at the time of yolk provisioning will have strong, environment-dependent fitness consequences for offspring through adulthood (Moore et al. 2015). Females thus may also have to choose oviposition sites in the context of their current condition and the range of likely offspring phenotypes they will produce. Investigations of the complex interactions between external and internal cues used by females for reproductive site selection remain necessary.

For organisms with high annual adult survivorship, the decision to breed in their natal versus a non-natal environment is expected to largely depend on the suitability of the natal environment for reproductive success. We found strong evidence that information conveyed about the natal environment through long-term and short-term aspects of physiological condition influenced natal philopatry. Independent of these phenotype-dependent effects, natal philopatry also differed among ponds (Fig. 2). Future work should determine if the abiotic (e.g., permanence, pH) or biotic (e.g., invertebrate prey assemblages) features of the natal ponds that exhibit strong enough temporal correlations influence philopatry independent of their direct effects on physiological condition (Whiteman et al. 1995a; Wissinger et al. 1999, 2010; Whiteman and Wissinger 2005). Importantly, the factors associated with the natal environment together explained about 28 % of the variation in male philopatry across the reproductive lifespan. Given that we found this relationship in a species with a relatively long duration between metamorphosis and sexual maturity, an individual's experience of the natal

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environment might be even more important for reproductive site selection in organisms that reach maturity more rapidly. However, in the many organisms with comparably high adult survivorship and late onset of reproductive maturity (e.g., Jones et al. 2014), this study supports predictions that conditions in early life stages may have crucial effects on an individual's propensity to breed in its natal or non-natal environment.

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Compliance with ethical standards

Ethical approval All protocols were approved by the Murray State and RMBL Institutional Animal Care and Use Committees, and all animals were captured under Colorado Parks and Wildlife Permit HP-0339.

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