BEHAVIORAL AND DEMOGRAPHIC RESPONSES
OF TÚNGARA FROGS TO VARIATION IN POND DENSITY

David M. Marsh[1]

*Department of Environmental Science and Policy and Center for Population Biology, University of California,
Davis, California 95616 USA*

Abstract. Population responses to variable environments can result from individual behavior (i.e., dispersal and habitat selection) or demography (i.e., changes in birth and death rates). Distinguishing behavioral from demographic responses to environmental variability has important implications for interpretation of spatial patterns and projections of population persistence. I studied the behavioral and demographic responses of túngara frogs, *Physalaemus pustulosus,* to experimental variation in the density of breeding ponds over two years. At natural spatiotemporal scales of variation in pond density, behavioral responses predominated over demographic responses. In the first year of the experiment, when plots varied in pond density, túngara frogs were proportionally more abundant in plots that contained higher densities of ponds. This behavioral response appeared to be due to increased ability to find plots with high pond densities and reduced effects of pond saturation (i.e., availability of unused ponds) within these plots. In the second year of the experiment, when plots had equal pond densities, there was a detectable demographic response to breeding-pond density early in the season, with fewer frogs in plots that had contained no ponds in the previous year. This response was short-lived, however, and by the end of the second year there was no detectable demographic effect. These results demonstrate that behavioral responses may predominate over demographic responses even on relatively large scales. Thus, studies demonstrating changes in patterns of abundance and distribution must be cautious in interpreting these results in the context of metapopulation dynamics without a detailed understanding of species-specific dispersal behavior.

Key words: Barro Colorado Island, Panama; dispersal behavior; metapopulations; Physalaemus pustulosus; *pond density and frogs; ponds, temporary; population dynamics; recruitment; spatial patterns; tadpoles; túngara frogs; variation.*

INTRODUCTION

Patterns of animal abundance and distribution vary over time. A number of recent studies have recorded pronounced year-to-year changes in patterns of abundance (Berven 1995, Nuernberger 1996, Sutcliffe et al. 1996, Bjornstad et al. 1999) or in patterns of habitat occupancy (Schoener and Spiller 1987, Sjögren 1991, Thomas and Harrison 1992, Hanski et al. 1995, Hecnar and M'Closkey 1996, Skelly and Meir 1997). Because these changes have important implications for population regulation (Levins 1970, Pulliam 1988, Hanski and Gilpin 1991) and interspecific interactions (Huffaker 1958, Kareiva 1987, Bengtsson 1989), understanding them is a priority for ecologists. This can be difficult, however, because changes in patterns of abundance and occupancy can result from a variety of ecological processes, many of which cannot be distinguished with survey data alone. At one extreme, spatial patterns may vary as a result of individual behavior; i.e., dispersal and habitat selection. At the other ex-treme, patterns of abundance may change largely as a result of demography; i.e., fluctuations in birth and death rates among relatively independent subpopulations. Whether responses to environmental variation are primarily behavioral or demographic likely depends on the spatial scale of individual dispersal relative to the scale at which the environment varies (Harrison and Taylor 1997). However, these scales have rarely been documented in studies of spatial patterns in patchy environments (but see Hanski et al. 1994, Lewis et al. 1997).

Knowing whether spatial patterns vary due to behavior or demography is important in several respects. First, such an understanding is necessary for proper interpretation of existing data. For example, spatial pattern data can be used to develop models either for habitat selection (Morris 1995, Arthur et al. 1996) or for metapopulation dynamics (Hanski 1994*a*). However, which approach is relevant depends on a priori assumptions about which processes are actually operating. Second, the relative strength of behavioral vs. demographic responses may have important implications for population persistence in variable environments. When habitat quality fluctuates, populations that are able to track fluctuations by moving to better patches are at an advantage compared to populations that

[1] Present address: Department of Biology, Washington and Lee University, Lexington, Virginia 24550 USA.
E-mail: marshd@wlu.edu

only track habitat quality through changes in birth or death rates (Pulliam and Danielson 1991).

Pond-breeding amphibians provide an excellent system for investigating behavioral and demographic responses to environmental variability. Ponds form discretely patchy habitats, and pond quality is both variable and crucial for successful recruitment and population persistence (Sjögren-Gulve 1994, Semlitsch et al. 1996, Skelly and Meir 1997). Furthermore, the use of artificial ponds allows for experimental manipulation of habitat patchiness at ecologically relevant scales (Marsh et al. 1999). Finally, amphibian distributions may be highly dynamic (Edenhamn 1996, Hecnar and M'Closkey 1996, Skelly and Meir 1997), though, as with other taxa, the processes underlying these changes are often unclear. However, because amphibians may be able to detect changes in habitat quality (Resetarits and Wilbur 1989, Crump 1991, Spieler and Linsenmair 1997), and because the local demography of amphibians may fluctuate widely between years (Pechmann et al. 1991, Semlitsch et al. 1996), both behavioral and demographic responses are indeed possible in most systems.

I conducted a two-year experiment to test the behavioral and demographic responses of túngara frogs, *Physalaemus pustulosus,* to variability in the local density of breeding ponds. I used an experimental design that varied breeding-pond density both within and between years, and that mimicked the natural spatial and temporal scales of variation in breeding-pond density. I used this experiment to ask the following questions: (1) Do túngara frogs respond behaviorally to variation in the local density of breeding ponds? If so, what aspects of dispersal behavior produce these responses? (2) Do túngara frogs respond demographically to variation in breeding-pond density? If so, what aspects of demography are affected? I then synthesize these data to examine the relative importance of behavioral vs. demographic responses for túngara frogs and to comment on the relevance of these results to spatial dynamics and population persistence in this and other species.

Methods

Study species and site

I conducted all experimental work on Barro Colorado Island, Panama (BCI). BCI is located in the canal zone of central Panama and is composed of primary and secondary tropical moist forest (Leigh et al. 1996). Rainfall on BCI is highly seasonal, with most rainfall occurring between the months of May and December. Túngara frogs, *Physalaemus pustulosus,* are common on BCI and the surrounding mainland. They are a small (SVL 24–34 mm), neotropical species with a prolonged breeding season lasting from April or May until October or November (Rand 1983). Males may breed nightly, while females may breed every 2–4 wk (D. M.

Marsh, *unpublished data*). Túngara frogs breed in a variety of ephemeral ponds and pools, including stream pools, forest puddles, and tree holes. The density of suitable túngara frog breeding sites is highly variable, both within and between years. Groups of stream pools are often used early in the wet season but are abandoned as streams fill completely and begin to flow (Marsh et al. 1999). Forest depressions often fill later in the wet season, but the density of these sites varies greatly from year to year depending on seasonal and yearly rainfall. Of 14 natural sites monitored between 1997 and 1999, four remained dry in at least one year, and only six showed signs of use in all three years.

The túngara frog's breeding system has been described extensively elsewhere (Ryan 1985). Briefly, females select males from nightly choruses. The pair leaves the breeding pond and, several hours later, deposits a foam nest containing the fertilized eggs at the chosen oviposition site. Each pair makes only one nest, and these nests can be easily distinguished. Ovipositing túngara frogs generally avoid conspecific foam nests (Dillon and Fiaño 2000) and tadpoles (D. M. Marsh, *unpublished data*), at least within controlled artificial ponds. Tadpoles hatch and leave the nests within 3–5 d, and tadpoles generally metamorphose in 3–5 wk. In laboratory colonies, túngara frogs developed to reproductive maturity in 8–12 wk (Davidson and Hough 1969), though somewhat longer development times are likely in the field.

Adult túngara frogs appear to rarely live longer than a single breeding season in the field. In the course of extensive work on breeding behavior, A. S. Rand and M. J. Ryan have toe-clipped thousands of adult túngara frogs at a nearby site, and marked frogs have only very rarely been recaptured in the following year (A. S. Rand, *personal communication*). I recorded similarly low recapture rates from 1997 to 1998 (0.3%) and from 1998 to 1999. In addition, I kept toe-clipped túngara frogs over one year and observed no regrowth of clipped toes. An annual life-history is also consistent with the extremely high rates of predation observed on breeding túngara frogs (Ryan et al. 1981), and annual life-histories have been suggested for ecologically similar frogs both in the neotropics (Kluge 1981) and in the temperate zone (Caldwell 1987).

Experimental design

To decouple behavioral and demographic responses to pond density, I used the experimental design illustrated in Fig. 1. In the first year of the experiment (i.e., 1998), I selected 18 experimental plots and randomly assigned them to three treatments: no ponds, four ponds, or 25 ponds, with six replicates per treatment. No more than two plots of the same treatment were adjacent, so treatments were not spatially clumped. Within each plot, ponds were separated by 5 m. All ponds were removed ~3 mo after establishment. At the beginning of the second rainy season, nine ponds were
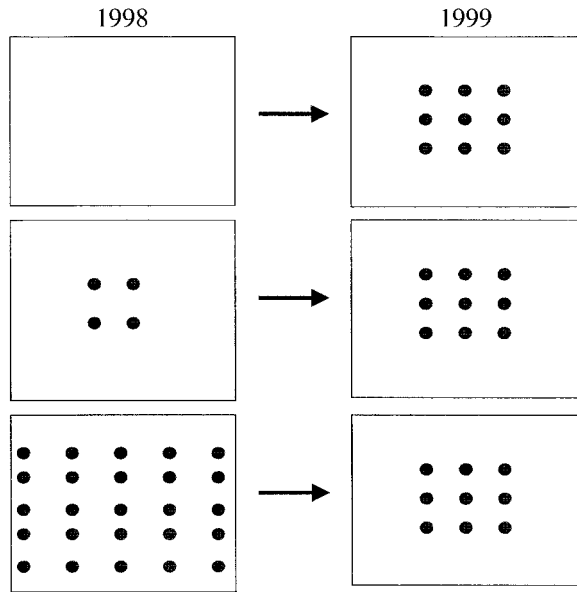
FIG. 1. Design for the pond-density experiment on *Physalaemus pustulosus* breeding in the forest on BCI. In 1998, six plots contained 0 ponds, six plots contained four ponds, and six plots contained 25 ponds. In 1999, each of these plots contained nine ponds.

added to each plot (Fig. 1) and data collection began immediately after ponds filled.

If responses to pond density are largely behavioral, frogs should track the local density of breeding ponds in each year. Thus in 1998, plots with higher pond densities should have more breeding frogs, while in 1999, with pond densities being equal, all plots should have similar numbers of frogs. In contrast, if responses to pond density are largely demographic, pond density should have no effect on 1998 frog abundance, at least between the four- and 25-pond plots. However, due to increased tadpole survival (reduced density dependence) in the 25-pond plots as compared to the four-pond plots, the 25-pond plots should have greater recruitment and therefore more breeding frogs in 1999. Similarly, under this scenario, the four-pond plots should have higher frog abundance in 1999 than the plots that had no ponds in the previous year.

In order to minimize background variation in frog density, all plots were located in relatively flat areas of the forest in which there were no natural túngara frog breeding sites within 200 m. In addition, experimental plots were themselves separated by ≥200 m, which is well within the range of intersite distances observed for natural breeding sites (50–800 m). I have previously shown that spatial patterns of breeding pond use are highly correlated at scales <200 m, presumably due to dispersal, but appear to be uncorrelated at greater scales (Marsh et al. 1999). Thus the scale of the experiment is similar to the scale of natural variation in breeding-pond density, and is a scale at which it is not

obvious whether responses to habitat change will be primarily behavioral or demographic.

Data collection

For experimental ponds, I used small (diameter = 30 cm, depth = 10 cm), plastic basins sunk in the ground and containing a layer of leaf litter to provide a food source for tadpoles. In 1998, I established all plots on 1 and 2 June (equal numbers of each treatment on each day). These plots filled from rainfall within four to eight days and were naturally colonized by breeding túngara frogs. From 6 June to 8 August 1998, all ponds were censused daily for foam nests. In addition, I conducted regular nightly frog censuses, in which breeding frogs were captured and marked with individual toe-clips (Donnelly et al. 1994). To estimate the number of frogs metamorphosing from each pond, I counted the numbers of tadpoles that reached Gosner stage 40–44 (Gosner 1960). Because these tadpoles were 1–3 d from metamorphosis, I repeated counts every 4–5 d to avoid double-counting individuals. Because some individuals may die before metamorphosis, this method is probably not reliable for determining the exact number of metamorphs emerging from each pond. However it should provide a good relative estimate of metamorphosis between plots. The number of metamorphs was estimated through 5 September, when all experimental ponds were removed from the plots. Holes remaining after removal did not retain water and were not used by túngara frogs (D. M. Marsh, *personal observation*).

On 3 May 1999, I re-established the 18-pond plots with nine ponds in each plot. Rainfall filled the ponds within 24 h, and plots were surveyed for foam nests on 3 May and from 5 May to 5 July. As in 1998, I also conducted nightly mark–recapture of adults. Due to time constraints, I could not count late-stage tadpoles in 1999; however, I did use 1998 estimates for metamorphosis relative to the number of nests per pond to project the expected number of metamorphs per plot in 1999. This projection can be used to determine whether any effects of 1998 pond density might carry over into the year following the experiment.

Statistical analysis

Estimating relative frog abundances from mark–recapture data proved difficult because capture rate was likely biased by treatment. Because it took longer to search 25-pond plots, a greater proportion of frogs escaped capture in these plots. Thus, I used the mark–recapture data only to make rough estimates of dispersal rates between plots and survival between years. For estimates of relative frog abundance, I used the number of foam nests deposited. The number of foam nests is unlikely to be affected by any similar observation bias and can be measured without error. Furthermore, foam-nest abundance has the advantage of

contributing directly to the demographic responses of interest.

For the 1998 data, I used one-way MANOVA to analyze the effects of pond density treatment on the total number of foam nests, the number of foam nests per pond, and the estimated number of metamorphs in each plot. In this analysis, I compared only the four-pond plots and the 25-pond plots, since it is trivial that plots with no ponds will not contain breeding frogs of this species.

I also used nest accumulation data to test two potential hypotheses for a positive effect of pond density on foam nest abundance. The first hypothesis was that frogs find 25-pond plots more easily than they find four-pond plots. The second hypothesis was that plot saturation (i.e., avoidance of oviposition in plots containing high densities of conspecific eggs and larvae) is less of a factor in the 25-pond plots than in the four-pond plots. I tested the first hypothesis by analyzing the effects of pond density treatment on time to colonization (i.e., time when the first nest appears within the plot), which should be correlated with ease of finding a plot. I tested the second hypothesis by analyzing the effects of pond density treatment on the time from first use of a plot to the time at which 90% of the total number of nests had been deposited. If nests accumulate at a constant rate that depends on pond density, treatments will not differ with respect to this response variable. Conversely, if saturation causes nest accumulation rate to decline over time in any pond-density treatment, that treatment will reach time to 90% of total nests more quickly. I carried out both these analysis with a nonparametric logrank test for analysis of survival data. This test is suitable for analyzing treatment effects on time to an event, with minimal assumptions about the underlying survival function (Abacus Concepts 1996).

I analyzed the effects of the 1998 pond density treatment on the number of foam nests in 1999 using repeated-measures ANOVA. These demographic effects would be expected to be strongest early in the rainy season but then diminish later due to dispersal. I thus considered the number of foam nests deposited in five intervals (1–10 d, 11–20 d, 21–30 d, 31–40 d, and 41–50 d), rather than just the cumulative number of foam nests for the year. Although the use of five intervals was somewhat arbitrary, using four or six intervals had no substantial influence on the results. I used the repeated-measures model to test for an interaction between pond density and time that would indicate a demographic response that occurred only early in the breeding season. I also tested for a significant overall effect of 1998 pond density on 1999 foam nests deposition. In each of these tests, I transformed the number of nests deposited as $\ln(\text{nests} + 1)$ because the variance in nest deposition tended to increase with the mean number of nests for each time interval.

Due to time constraints, I could not record the number of metamorphs emerging from each pond in 1999. This information is potentially important because it addresses the question of whether any differences in frog density in 1999 would likely carry over into the following year. However, because the number of successful metamorphs per nest is a function of the number of nests in a pond ($r = -0.47$, $P < 0.0001$ in 1998), the number of nests per pond can be used to project the number of expected metamorphs per pond (and thus also the number of metamorphs per plot) and to place confidence intervals on these expectations. To project the number of metamorphs per plot in 1999, I first assembled a matrix of 1998 values for metamorphs per pond given a particular number of nests deposited in a pond. I also calculated the number of nests deposited within each pond in 1999. I then bootstrapped the 1998 estimates for metamorphs onto the 1999 data for nests per pond. I used these bootstrapped data to project mean metamorphosis per plot for 1999 and to compare the effect size for metamorphs (measured as ln ([mean metamorphs from 25-pond plots]/[mean metamorphs from 0 pond plots]) to the effect size observed for total foam nests deposited (measured as ln [mean no. foam nests in 25-pond plots]/[mean foam nests in 0 pond plots]). This comparison of effect size can be used to ask whether density-dependence in tadpole survival is likely to reduce the strength of demographic responses to pond density in the second year of the experiment. I used the above measure of effect size for this comparison because it is independent of differences in means and variances between the two response variables.

RESULTS

1998 results: behavioral responses to pond density

In 1998, plots contained variable numbers of ponds, and effects on túngara frog abundance should reflect behavioral responses to pond density. The overall model for the effect of pond density on 1998 frog abundance was highly significant ($F_{3,7} = 161.6$, Wilks' lambda = 0.014, $P = 0.0001$). The total number of nests deposited in 25-pond plots was significantly greater than the number of nests deposited in the four-pond plots ($F_{1,9} = 21.6$, $R^2 = 0.70$, $P = 0.0012$, Fig. 2A). This increase in nest deposition was roughly proportional to the difference in pond density. Thus, the number of nests deposited per pond was only slightly higher in the four-pond plots than in the 25-pond plots ($F_{1,9} = 0.11$, $R^2 = 0.012$, $P = 0.75$, Fig. 2B). The total estimate for metamorphs emerging was also significantly greater in the 25-pond plots than in the four-pond plots ($F_{1,9} = 294.4$, $R^2 = 0.97$, $P = 0.0001$, Fig. 2C). The strong outlier here was a plot in which most ponds contained larvae of the poison-arrow frog *Dendrobates auratus,* which consumed most of the túngara larvae. This outlier was not included in the MANOVA model in order to maintain normality and homogeneity of variances.
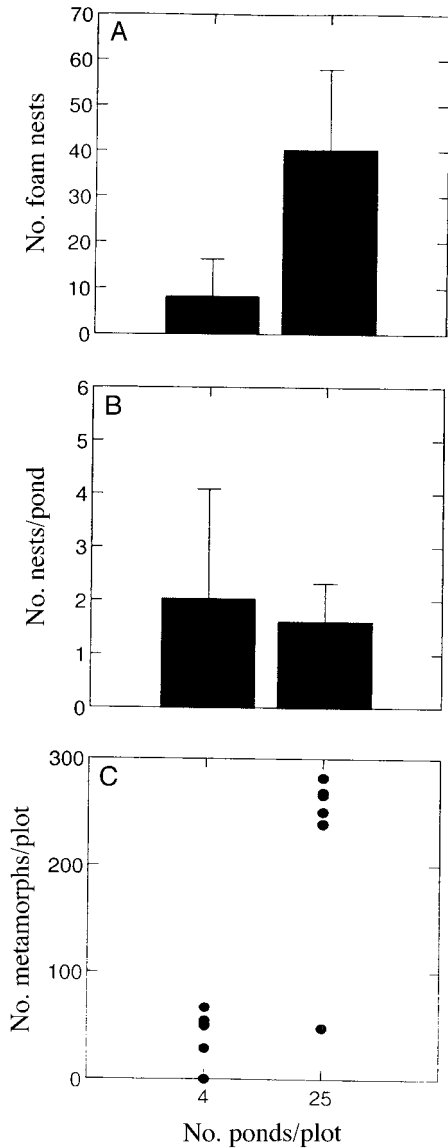
FIG. 2. Responses of *Physalaemus pustulosus* frogs to pond density in 1998. The number of nests per plot (A) was significantly higher in 25-pond plots than in four-pond plots, but the number of nests per pond (B) was not significantly different among the pond-density treatments. Error bars in these graphs indicate 95% confidence intervals. The number of metamorphs per plot (C) was also significantly higher in the 25-pond plots, though there was one outlier caused by a high abundance of tadpole predators within one of the 25-pond plots.

However, with this outlier included in a univariate analysis based on randomization (which makes no assumptions about distributions or variances [see Manly 1991]), the number of metamorphs was still significantly higher in the 25-pond plots than in the four-pond plots (randomization test, $P = 0.008$).

Because these results indicated strong behavioral responses to breeding-pond density, I also tested the hy-

potheses that túngara frogs find 25-pond plots more easily and that pond saturation effects are less important in these plots than in the four-pond plots. Time to colonization was significantly lower in 25-pond plots than in four-pond plots (mean time for 25-pond plots = 5.8 d vs. mean time for four-pond plots = 15.5 d, $\chi^2 = 4.58$, df = 1, $P = 0.032$), which supports the hypothesis that the high density plots are more easily found. In addition, time from colonization to 90% of total nest deposition was significantly higher in 25-pond plots than in four-pond plots (mean time for 25-pond plots = 42.0 d vs. mean time for four-pond plots = 20.6 d, $\chi^2 = 10.55$, df = 1, $P = 0.001$). This result was essentially unchanged using 80% of total nest deposition instead of 90% saturation (mean time for 25-pond plots = 36.3 d vs. mean time for four-pond plots = 15.4 d, $\chi^2 = 10.06$, df = 1, $P = 0.002$). Thus, the hypothesis that plot saturation contributes to reduced use of the four-pond plots was also supported.

1999 results: demographic responses to pond density

In 1999, plots contained equal numbers of ponds, and the effects of 1998 pond density on 1999 frog abundance should represent demographic effects. There was a significant interaction between 1998 pond density and time for the 1999 nests accumulation data ($F_{8,24} = 2.67$, $P = 0.03$), which corresponded to a significant effect of pond density on nest deposition for the first time interval ($F_{2,15} = 6.58$, $R^2 = 0.47$, $P = 0.009$, Fig. 3), but no significant effect for any later time intervals ($P > 0.50$ for all intervals, Fig. 3).

The overall effect of 1998 pond density on 1999 nest deposition was nonsignificant for the repeated-measures model ($F_{2,15} = 1.70$, $P = 0.22$), though it was in the predicted direction (i.e., 25 ponds > 4 ponds > 0 ponds). A simple one-way ANOVA with 1998 pond density as a fixed effect yielded a similar result for total nest deposition in 1999 ($F_{2,15} = 1.08$, $R^2 = 0.13$, $P = 0.366$). To determine how large of an effect could have been detected for total nest deposition, I performed a post hoc power analysis on this one-way ANOVA (Neter et al. 1996). I proportionally increased the ratio of the difference between the treatments, keeping both the standard deviation within treatments and the total number of nests constant. The results are shown in Fig. 4. Eighty percent power would be achieved with ratio of number of nests in four-pond plots to number of nests in 0-pond plots ≅1.45 and a ratio of nests in 25-pond plots to nests in four-pond plots ≅1.36. A true difference of <1.30 for four ponds vs. 0 ponds and <1.20 for 25 ponds vs. four ponds would likely not have been detected. Thus, the results for cumulative foam nest deposition are consistent with either no effect or with a small to moderate effect of 1998 pond density.

When metamorphosis was projected for 1999, any differences in abundance among plots were reduced even further. The mean effect size for metamorphs, measured as ln ([mean no. metamorphs from 25-pond
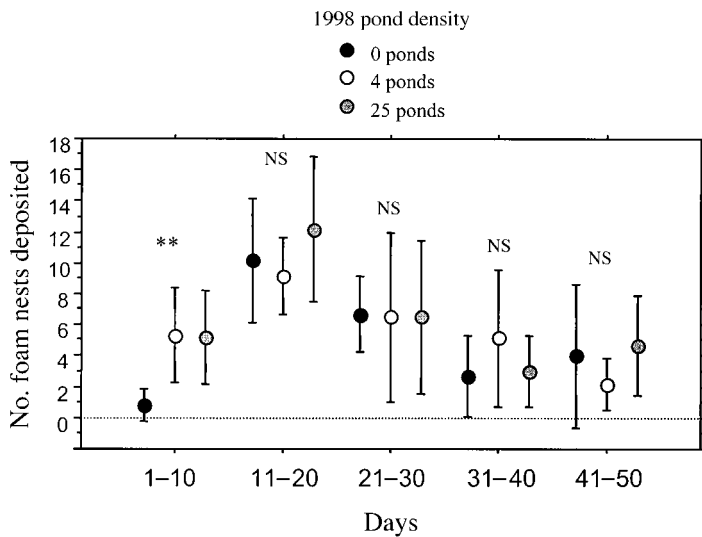
FIG. 3. Deposition of foam nests in the artificial ponds in 1999. Nest deposition was divided into five intervals of 10 d. Pond density in 1998 significantly affected 1999 nest deposition only for the first time interval ($P < 0.01$), with few nests deposited in plots that had contained no ponds in the previous year.

plots]/[mean no. metamorphs from 0-pond plots]) was 0.13 (95% confidence interval -0.03 to 0.29), compared to an effect size for 1999 foam nest deposition of 0.27. The effect size was reduced here because the plots containing more nests (i.e., the 25- and four-pond plots) also had comparatively higher densities of tadpoles. Because the number of successful recruits per nest declined with the number of nests ($r = -0.47$, $P < 0.001$; Fig. 5), density dependence tended to wash out any remaining effects of 1998 pond density on frog abundance.

Mark–recapture data

In 1998, I captured 59 frogs a total of 100 times. In 1999, I captured 121 frogs a total 165 times. None of the frogs marked in 1998 were recaptured in 1999, supporting the hypotheses that túngara frogs are primarily annuals and that the early responses in 1999 do indeed represent demographic responses and not returning frogs from the previous year. Of the 41 recaptures in 1998 and the 44 recaptures in 1999, only one and two recaptures respectively included movements between plots. Thus, frequency of movement between plots, or at least frequency of breeding in multiple plots, was low.

While frogs rarely moved between plots, they did move regularly between ponds in the same plot. In 1998, 28 of the 41 recaptures (68%) included movements between ponds, and in 1999, 33 of 44 recaptures (75%) included movements between ponds. In 1998, these interpond movements were marginally shorter
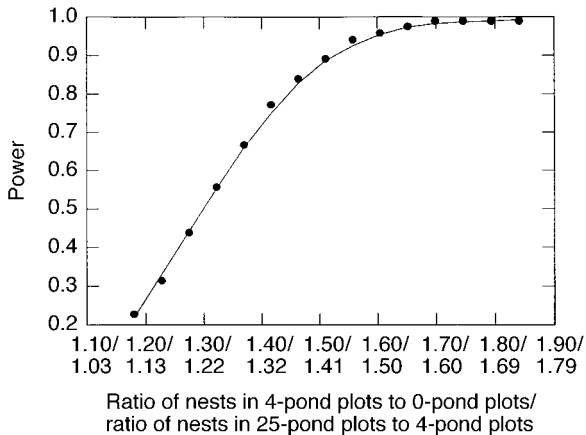

FIG. 4. Power analysis for the effect of 1998 pond density on cumulative nest deposition in 1999, based on a one-way ANOVA with $\alpha = 0.05$. The recorded effect for cumulative number of nests was not signficant, though it was in the predicted direction. Thus, power (i.e., probability that a true effect would be detected) was calculated for a range of differences in nest deposition among treatments to determine how large a difference could have been detected.
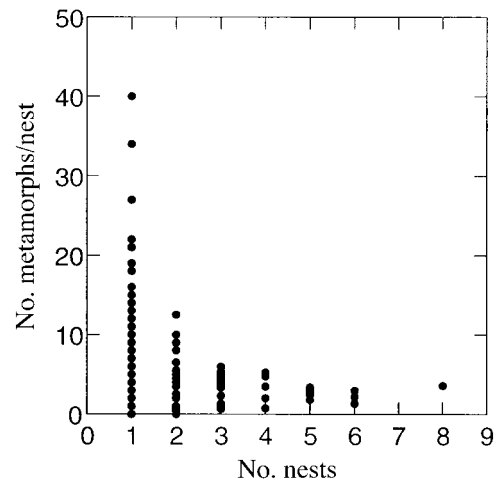

FIG. 5. The number of metamorphs per nest as a function of the number of nests within each pond in 1998. The negative correlation here ($r = -0.47$, $P < 0.01$) indicates density dependence in larval survival.

than would be expected if frogs moved randomly between ponds within a plot (mean distance = 11.7 m vs. 13.4 m for random movement, $P = 0.055$). In 1999, interpond movements were also shorter than random (mean distance = 7.8 m vs. 8.3 m for random movement, $P = 0.12$), though this difference was not statistically significant.

DISCUSSION

Túngara frogs exhibited strong behavioral responses to variation in breeding-pond density. In 1998, frog abundance was approximately proportional to pond density, indicating that frogs tracked the density of breeding ponds almost perfectly. In 1999, demographic effects of pond density in the previous year were evident only early in the breeding season. By the end of the experiment, overall demographic effects were weak and not statistically significant, which is also consistent with behavioral tracking of pond density. Below, I first suggest how túngara frogs may be able to track changes in breeding-pond density, and I then comment on the implications of these abilities for population dynamics and conservation.

The proportional effect of breeding-pond density on 1998 frog abundance is analogous to an ideal free distribution of frogs among ponds (Fretwell 1972). This ideal free distribution did not, however, likely result from anything approaching ideal free habitat selection, in which individuals sample all available habitats and make an accurate comparison of habitat quality (Fretwell 1972). Although recapture data were somewhat sparse, frequencies of movements among plots were nevertheless low. For both years combined, only three of 85 recaptures (3.5%) represented movements between plots. Previous mark–recapture work on túngara frogs has also demonstrated that dispersal frequencies are probably low at distances >200 m (Marsh et al. 1999). Thus, behavioral tracking of breeding-pond density apparently occurred even though most individuals did not breed in multiple plots. Instead, responses to breeding-pond density seem have been a function of ease of finding high-density plots and reduced saturation effects within these plots. These responses are similar to those proposed in Root's ''resource concentration hypotheses'' (Root 1973), which sought to explain the high densities of herbivores observed in patches containing high densities of host plants. It is important to note that both ease in finding high-density resource patches and reduced saturation effects in these patches potentially allow organisms to track changes in resource densities over larger scales than would be possible through sampling multiple patches. As these local effects of behavior can produce patterns of abundance on a between-patch scale, it may often be difficult to distinguish a smaller behavioral scale from a larger demographic scale (e.g., Hanski 1994b).

Exactly how túngara frogs find pond plots is not known. For many amphibian species, olfaction may be a primary mechanism of orientation (Savage 1961, Oldham 1967, Sinsch 1990, Joly and Miaud 1993). If an olfaction stimulus were proportional to the number of breeding ponds, this could explain the increased colonization rates of the 25-pond plots; however, without better data on túngara frog olfactory abilities, this hypothesis remains speculative. Previous results for túngara frogs do suggest that attraction to conspecific calls may not be of great importance to pond colonization. In a laboratory experiment, attraction of females to the calls of single males was not detected at distances >5 m (Marsh et al. 2000). In general, this would make calls of limited use in finding ponds, though attraction to choruses could potentially occur over greater distances (D. M. Marsh, *unpublished data*). In addition, females were often found at ponds that contained no males, suggesting that these females may find breeding sites without conspecific cues.

Because the experiment described here was similar to a traditional resource addition experiment (e.g., Stewart and Pough 1983, Krebs et al. 1995), the results can be used to comment upon the proposition that the density of breeding ponds limits túngara frog population density. Because tadpole growth and survival are often density dependent (see Wilbur [1997] for review), pond availability is sometimes assumed to limit the size of amphibian populations. Evidence for pond limitation has been largely correlative, however (Beebee et al. 1996, Beebee 1997), and may be complicated by the fact that little is generally known about population regulation in terrestrial stages (Wilbur 1984). For amphibians that do not oviposit in aquatic habitats, experimental additions of oviposition sites (Stewart and Pough 1983) and tadpole-rearing sites (Donnelly 1989) have resulted in significant demographic responses. The demographic responses to pond additions observed in this experiment, though short-lived, provide some of the first experimental evidence of breeding-site limitation in pond-breeding amphibians. As some natural túngara frog breeding sites may be isolated by distances much larger than the 200 m used in this experiment, breeding site density could cause more lasting demographic effects at these more isolated sites. However, the presence of demographic response to pond density would not rule out potential interacting effects of predation or competition in limiting adult population size. For example, some predators and competitors of túngara frogs may also respond to variation in pond density. In addition, species with complex life cycles may be limited by different factors at each stage (Wilbur 1996) and, as with many other amphibians, the terrestrial ecology of túngara frogs is largely unknown.

The amphibian ecology literature has stressed the low vagility of amphibians and their consequent vulnerability to landscape change (Sinsch 1990, Bradford et al. 1993, Blaustein et al. 1994b, Sjögren-Gulve and Ray 1996, Driscoll 1997, Marsh and Pearman 1997). Given this prevalent view of amphibians, the strong

behavioral responses of túngara frogs to pond density are initially surprising. However, unlike many amphibians, túngara frogs use breeding ponds with densities that are highly variable in space and time. Adaptation to this natural variation in pond density may therefore explain the capacity of túngara frogs to track the pronounced changes in pond density in this experiment (see Harrison and Fahrig 1995). This interpretation of amphibian dispersal behavior is similar to that of Gill (1978), who suggested that dispersal by red-spotted newts was adaptive in the context of turnover of beaver ponds, their natural breeding habitats. Although the breeding sites used by many other species may vary less in density and distribution, they may vary highly in quality due to changes in the distributions of predators, competitors, or abiotic factors. Thus, changes in patterns of abundance on a between-pond scale may represent behavioral responses to these factors, and not necessarily metapopulation dynamics. One should therefore exercise caution in interpreting data on spatial patterns without a detailed understanding of species-specific dispersal behavior.

It is interesting to note that túngara frogs are very common in disturbed habitats throughout Central America (Rand 1983, Ryan 1985). In these human-dominated landscapes, túngara frogs breed in roadside ditches, garden pools, and even glasses of water (Rand 1983). The persistence of túngara frogs in disturbed landscapes may be related to their capacity to track rapid changes in the distribution of available breeding habitat. For most organisms, colonization ability is understood as a major correlate of invasiveness or ''weediness'' (e.g., Rejmanek and Richardson 1996). For amphibians, however, previous studies of among-species variation in population trends have tended to focus on habitat relationships (Williams and Hero 1998), and relative susceptibility to environmental hazards such as UV-B (Blaustein et al. 1994a, Van Den Mortel et al. 1998) and introduced predators (Drost and Fellers 1996). Few studies have attempted to examine the role of colonization ability in determining which amphibian species are declining and which are persisting in any given region (but see Beebee 1997). Ultimately, though, this sort of information may be crucial to questions of persistence. It may also be necessary for predicting species-specific responses to changes in landscape spatial structure and designing appropriate strategies for conservation and recovery.

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