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THE EFFECTS OF KINSHIP ON INTERACTIONS BETWEEN TADPOLES OF *RANA CASCADAE*

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Abstract. In a series of four field and mesocosm studies, we examined the effects of kinship on growth, survival, and aggregation behavior in tadpoles of the Cascades frog (*Rana cascadae*) under different ecological conditions. (1) Field observations of tadpole aggregations revealed ecological factors that may interact with kinship to influence tadpole interactions. (2) In an experiment conducted in mesocosms, food distribution, predator presence, thermal heterogeneity, and kinship all interacted to influence tadpole dispersion. (3) In a field experiment conducted in natural ponds, kinship significantly influenced group size at artificially established food patches. (4) In a field enclosure experiment, density, access to the substrate, and kinship all interacted to significantly influence growth and survivorship of tadpoles. Subsequent analysis revealed that kinship affected the distribution of individual tadpole body size: mass was more skewed (i.e., more small individuals) in groups of mixed relatedness than in kin groups. The interaction among kinship, density, and substrate factors resulted in context-dependent effects on tadpole size distribution and survivorship. Our results demonstrate that kinship factors can influence competitive interactions between tadpoles depending upon the ecological conditions, and they provide a functional explanation for kin-discriminating behavior observed in tadpoles of *R. cascadae*. Kinship-mediated competition may be particularly important for recruitment in size-structured populations.

Key words: anuran; competition; growth and development; kinship; ontogeny; Rana cascadae; *size structure; tadpole behavior.*

INTRODUCTION

Population- and community-level phenomena are ultimately the result of interactions between individuals and their environment. Consequently, individual variation is an important component in many population- and community-level models (e.g., Lomnicki 1978, 1980, Hassell and May 1985). In particular, variability in behavior among individuals may greatly influence population and community dynamics (e.g., Gilliam 1987, Rosenzweig 1987, Abrams 1991, 1992, Chesson and Rosenzweig 1991, Gordon 1991, Werner 1992). Variability in behavior is affected by many factors, including genetic relatedness or kinship (Hamilton 1964*a*, *b*). Thus, kinship may potentially affect important ecological processes such as competition, predation, cannibalism, habitat selection, and mate choice (e.g., Bateson 1983, Blaustein et al. 1987*a*, *b*, Blaustein 1988, Waldman 1988, 1991, Reeve 1989).

For example, when resources are limiting and all else is equal, Hamilton's Rule (Hamilton 1964*a*, *b*) predicts that individuals should direct intraspecific competition away from kin. Similarly, individuals should benefit by directing intraspecific predation toward non-kin (Walls and Roudebush 1991, Pfennig et al. 1993, Pfennig et al. 1994, but see also Walls and Blaustein 1995). In gregarious species, aggregations may be composed primarily of kin or of numerous individuals of mixed relatedness, depending upon ecological conditions and the kin-discriminating ability of the organism (Blaustein et al. 1987*b*, Beecher 1988, Reeve 1989, Waldman 1991, Hokit et al. 1996). Consequently, elucidating the importance of kinship to ecological phenomena may substantially alter the way ecological processes are viewed and understood.

We explored the ecological aspects of kin-biased behavior in anuran larvae. Tadpoles of several anuran species discriminate between kin and non-kin (reviewed by Blaustein and Waldman 1992, Blaustein and Walls 1995), although the adaptive value of this behavior is poorly understood (Waldman 1991, Blaustein and Waldman 1992). One hypothesis is that kinship may enhance growth and development for tadpoles living in kin groups. Kin discrimination may allow tadpoles to direct competitive interactions away from kin, perhaps by altering behavioral interference or by selectively releasing chemical growth inhibitors (Waldman 1986, Blaustein 1988, Waldman 1991, Blaustein and Waldman 1992). Tadpoles of the Cascades frog (*Rana cascadae*) discriminate between kin and non-kin and preferentially associate with kin in aggregations in laboratory and field experiments (e.g., O'Hara and Blaustein 1981, Blaustein and O'Hara 1982, O'Hara

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and Blaustein 1985, Blaustein and O'Hara 1987). For this species, rapid metamorphosis from small, ephemeral breeding sites combined with the tendency to form larval aggregations in nature (O'Hara 1981, Blaustein 1988), may lead to intense intraspecific competition among tadpoles of *R. cascadae.*

Anuran larvae have often been used in studies of intraspecific competition (e.g., Wilbur and Collins 1973, Wilbur 1977, 1980, 1984, Steinwascher 1978, Semlitsch and Caldwell 1982, Alford and Harris 1988, Smith 1990). Characteristically, these studies show that individual tadpole body size decreases with increasing tadpole density and tadpole populations become size structured. The distribution of individual tadpole body size becomes positively skewed (i.e., more small individuals) in proportion to initial densities. Similar studies have assessed the effects of kinship on growth and development (Shvarts and Pyastolova 1970, Travis 1980, Waldman 1986, 1991, Jasienski 1988, Smith 1990, Blaustein and Waldman 1992, Hokit and Blaustein 1994) although conclusions remain controversial. Kinship effects appear to depend upon the species examined and the experimental conditions. A previous laboratory study (Hokit and Blaustein 1994) suggested that tadpoles of *R. cascadae* reared in sibling groups have smaller mass at metamorphosis than tadpoles reared in mixed groups of sibling and nonsiblings. Given that body size is known to be positively correlated with fitness in several amphibians (e.g., Berven and Gill 1983, Smith 1987, Semlitsch et al. 1988), these results appear to contradict the predictions of kinship theory.

In a series of four field and mesocosm studies, we assessed the effects of kinship on growth, survival, and aggregation behavior in tadpoles of *R. cascadae* under different ecological conditions. We initially observed natural aggregations of tadpoles to assess factors that were most likely to affect aggregation behavior. We chose a subset of factors to manipulate in a mesocosm experiment and field experiment to assess further the contribution of each factor to aggregation formation and the extent to which they interact with kinship. Finally, we examined the effects of kinship on growth and survival in a multifactorial field experiment using ecological factors found important in the previous studies.

METHODS

Study site

Our study site was a subalpine meadow (elevation = 2300 m) located 40 km west of Bend, Oregon, USA, 3 km north of Todd Lake in the Deschutes National Forest. This meadow (200 by 100 m in size) contains 38 individual potholes or small pools, a permanent stream, and several ephemeral springs. Although most of the pools are too small and ephemeral to sustain tadpoles (average volume = 5.22 m^3), adults of *R. cascadae* were observed breeding in 12 of the larger pools (average volume of pools containing *R. cascadae* tadpoles = 14 m^3).

With the exception of an occasional boreal toad (*Bufo boreas*), the Pacific treefrog (*Pseudacris regilla*) was the only other anuran found in the meadow. Other amphibians included salamanders that are potential predators of tadpoles (roughskinned newt, *Taricha granulosa*; long-toed salamander, *Ambystoma macrodactylum,* Peterson and Blaustein 1991). No other vertebrates were found in the potholes. However, there were aquatic invertebrates that may prey on tadpoles (adult and larval dytiscids, notonectids, and odonate larvae; Hews 1988, Peterson and Blaustein 1992).

Field observations

Tadpole aggregation behavior was observed from 25 June to 23 July 1991. All potholes were surveyed on the same day at 2–3 d intervals. Adults of *R. cascadae* are explosive breeders, with breeding often completed within 2–3 d (Nussbaum et al. 1983). Female *R. cascadae* lay one clutch per year and appear to mate with one male (O'Hara and Blaustein 1981), reducing the chance of half-sib relationships within clutches. Thus, the offspring from within a clutch are probably full siblings. During breeding, multiple egg masses were oviposited in the two largest pools (12 in one and four in the other). Oviposition in six other pools included only one clutch each. Therefore, after hatching, it was possible to observe tadpole aggregation behavior in potholes containing only siblings and in potholes containing tadpoles of mixed relatedness.

We measured the following pothole variables: pool volume, substrate type, temperature, the number of potential predators (salamanders and invertebrate predators), the number of potential competitors (larval *P. regilla*), and the number of conspecifics. Volume (cubic meters) was estimated by averaging several diameter measures combined with depth measures taken every 0.5 m. We categorized substrate type at each depth measure as dominated by silt, sand, moss, gravel, or sedge. Potential predators, competitors, and conspecifics were counted after trapping in minnow traps and during visual surveys. We measured temperature (degrees Celsius) in the middle of each pool at a depth of 10 cm.

The larvae of many anurans form aggregations in nature (Bragg 1965, Wassersug 1973, Beiswenger 1975, Caldwell 1989, reviewed by Blaustein and Walls 1995). Tadpole aggregations of *R. cascadae* may be described as loose, nonpolar, stationary, and much smaller than the average clutch size (O'Hara 1981, Blaustein and O'Hara 1982). They usually consist of <40 individuals resting or feeding on the substrate, either in contact with one another or within 5 cm of one another (category D2 to D3 of Beiswenger 1975). Because individuals are attracted to other conspecifics (O'Hara 1981, Blaustein and O'Hara 1982), aggregations of *R. cascadae* tadpoles can be influenced by social factors (Bragg 1965, Wassersug 1973, Blaustein and Walls 1995). For our observations, a minimum aggregation was arbitrarily defined as five or more individuals within a 15-cm^2 area. Aggregations >15 cm^2 were defined such that the greatest distance between any tadpole and its closest neighbor was not >5 cm.

We performed an exploratory analysis to assess which pothole variables were correlated with the frequency of aggregations and how these correlations may be influenced by kinship factors. First, Pearson rank correlation was used to assess the association between the number of aggregations found within a pothole and the pool volume, proportion of silty substrate type, the number of potential predators, potential competitors, and conspecifics within a pothole. To extend this analysis such that kinship effects could be assessed, we constructed two regression models (one including and one excluding data points from the mixed relatedness pools) relating aggregation frequency with the pothole factors found to be strongly correlated with aggregation frequency. Because of large differences between pools in the number of predators and the number of conspecifics, these two data sets were log-transformed.

When a tadpole aggregation was found, we measured the following aggregation variables: the number of tadpoles, temperature at the aggregation site, substrate type at the aggregation, depth of water at the aggregation site, and the location of the aggregation within each pool. Aggregation location was mapped for each pool by taking a compass bearing along a line that intersected a permanent central stake and the location of the aggregation. The compass bearing was combined with a measure of the distance from shore for each aggregation, measured along the same intersection line.

Having mapped the location of each aggregation within each pothole, we assessed whether or not there were preferred aggregation sites within each pothole. We used nearest neighbor analysis (Krebs 1989) to test if aggregations were clumped in distribution or randomly distributed across a pothole. This analysis was not performed on potholes with fewer than five aggregations due to potential sample size bias (Krebs 1989).

Mesocosm experiment

From our field observations, we hypothesized that the distribution of food, thermal gradients, and predator abundance were particularly influential in the formation of tadpole aggregations. These three factors and a kinship factor were manipulated in plastic wading pools in a completely orthogonal design to test for their effects on tadpole dispersion.

We collected 10 newly oviposited clutches of *R. cascadae* from the field site on 26 May 1992. We kept the clutches separate while transporting them to our laboratory where they were placed into aerated 38-L aquaria filled with dechlorinated tap water. Egg masses were divided and equal portions were placed into sibling-only aquaria ($n = 10$) and mixed-sibling and nonsibling aquaria ($n = 10$). After hatching (developmental stage 22, Gosner 1960), tadpoles were transported to an outdoor site for the duration of the experiment. We introduced tadpoles into wading pools (1.5 m in diameter, filled to a depth of 15 cm with spring water), 100 individuals to a pool. This density was comparable to densities observed in similar-sized natural pools at the field site (D. G. Hokit, *personal observation*). Water and food levels were equilibrated across all pools.

Manipulations consisted of tadpoles reared in (1) groups of all siblings vs. a mixture of all 10 egg masses; (2) pools with homogeneously vs. patchily distributed food (rabbit chow); (3) pools with vs. without predators; (4) pools with vs. without a thermal gradient, and every possible combination of these four factors. This resulted in 16 treatments, which we replicated four times, requiring a total of 64 pools. The four replicates were randomly arranged within four spatial blocks.

Pools with predators each contained one predatory newt (*T. granulosa*) housed in a plastic mesh cage (9 cm in diameter). Thus, all potential predator effects were nonlethal. We placed plastic mesh cages in all pools to control for potential thigmotactic responses from the tadpoles. Thermal gradients were established within pools by mounting submersible heating elements inside 1-L glass jars filled with cooking oil and water (equal ratio of oil to water), and placing these ‘‘heating units’’ inside the pools. The heaters created warm water pockets (2–5 cm in diameter), up to 5°C warmer than the surrounding water mass. Although the amount of food was equivalent for all pools, it was deposited in haphazardly located patches in some pools and broadcast evenly across others.

We sampled each pool five times, allowing ample time between trial sampling periods (2–4 d) maximizing the likelihood that each trial was independent. Sampling of tadpole dispersion began 2 wk after introduction to the wading pools (to allow tadpoles to equilibrate to their rearing environment) and continued for 17 d. During this period, we photographed each pool on five different, randomly chosen days. A camera was suspended over the pools on a sliding rail system that allowed the pools to be photographed remotely, thus minimizing disturbance to the tadpoles.

We projected each resulting slide image onto a grid and recorded the number of tadpoles within each grid cell. Using the total number of tadpoles, the number of tadpoles per cell, and the total number of cells, we calculated Morisita’s standardized index of dispersion (Krebs 1989) for each slide image. This index ranges from -1.0 to $+1.0$. Random dispersion patterns give an index of 0.0, aggregated patterns are positive, and uniform patterns are negative. Additionally, this index has 95% confidence limits at $+0.5$ and -0.5. Therefore, any population with a dispersion index >0.5 is significantly more aggregated than a randomly distributed population.

We combined the five trial samples from each pool to obtain a mean tadpole dispersion index for each pool. The index data were transformed by the Box-Cox method (Sokal and Rohlf 1981) to meet the parametric assumption of normality. Before testing for treatment effects, we used analysis of variance (ANOVA) to test for spatial block effects and for interactions between spatial blocks and individual treatments. We then used ANOVA to test for treatment effects on tadpole dispersion.

Field experiment one: Kinship and predator effects on group size

We manipulated kinship and predator abundance under natural conditions to test for their effects on the size of tadpole aggregations. We collected nine newly oviposited egg masses from our field site on 9 July 1993 and redistributed them into 12 pools chosen for their similarity in volume and substrate type. Portions of the egg masses were allotted to each pool such that all pools received an approximately equal number of eggs. Egg masses were distributed such that six pools contained only sibling tadpoles and six pools contained a mixture of siblings and nonsiblings. Sibling and mixed pools were chosen randomly.

We sampled all pools two times each week and recorded the number of *R. cascadae* tadpoles and the number of predators in each pool. We removed predators with a dip net from three of the sibling pools and three of the mixed pools. To control for the potentially disruptive effect of sampling, we used dip nets to count predators in the remaining pools and then returned the predators.

All possible combinations of our manipulations of kinship and predators resulted in four treatments, each replicated in three different potholes. Two artificial food patches were established within each pool by sinking plastic cups (volume = 200 mL) into the substrate. We established and sampled all 24 food patches on five different days from 27 July to 13 August 1993. Food patches were placed a minimum of 1 m apart to minimize activity at one patch influencing another, and each patch was placed in a different location within each pothole at each sampling period.

To begin a sampling trial, we created a food patch by filling each cup with 3 g of rabbit chow pellets. After establishment, food patches were left undisturbed for 1 h, at which time we counted the number of tadpoles at each patch.

We combined the five trial samples from each pool to obtain the mean number of tadpoles per patch per pool. Transformation of data was not necessary. Several uncontrolled factors in the natural potholes may have potentially affected the number of tadpoles per pothole. Because tadpole abundance may be positively associated with aggregation frequency (see *Results: Field observations*), we used analysis of covariance (ANCOVA) to test for treatment effects, using the number of tadpoles per pool as a covariate. ANCOVA adjusted the means to account for differences in the number of tadpoles per pool.

Field experiment two: Kinship effects on growth and development

We chose one pothole (volume = 35 m^3) for this experiment that had a consistent history of breeding adults and was relatively homogeneous with respect to depth (average depth = 20.63 cm) and substrate type. We placed eight newly oviposited (<8 h old) clutches of *R. cascadae* into separate incubation enclosures on 5 July 1993. Only tadpoles that hatched by 15 July were used in this study. Hatchlings were transferred from incubation enclosures to experimental enclosures on 15 July. All enclosures used in this study consisted of fiberglass mesh (mesh size = 2 mm) supported by a 0.5-m^3 wood frame.

Our behavioral observations suggested that tadpoles in aggregations may benefit by foraging in pits dug into the silty substrate by tadpole swimming activity (see *Results*). To test this hypothesis, we attached fiberglass mesh across the bottoms of half of the enclosures to prevent tadpoles from digging into the substrate. We nailed 8 cm wide vinyl molding around the bottom of the remaining enclosures and sunk them into the substrate to keep tadpoles from escaping. We shoveled silty, flocculent substrate from the same pothole into the closed-bottomed enclosures to a depth of ≈3 cm. Thus, tadpoles in both open and closed-bottomed enclosures were reared on the same substrate. However, tadpoles in the closed-bottom substrate could only ‘‘dig’’ pits to a depth of 3 cm. We stirred the substrate inside the open-bottomed enclosures so that both types of enclosures were equally disturbed.

We randomly assigned hatchlings to (1) low vs. high density enclosures; (2) enclosures with vs. without access to the substrate; (3) enclosures containing kin (sibling tadpoles from the same clutch) vs. mixed siblings and nonsiblings (an equal number of tadpoles from each of the eight clutches); and every possible combination of these three factors. This resulted in eight treatments, which we replicated four times, thus producing a total of 32 enclosures. We placed 48 animals per enclosure in the low density treatments (6 tadpoles per clutch in the mixed groups) resulting in ≈0.91 tadpoles per L, and 104 animals per enclosure in the high density treatments (13 tadpoles per clutch in the mixed groups) resulting in ≈1.98 tadpoles per L. The small size and ephemeral nature of breeding sites for *R. cascadae* can produce density levels within this range (O’Hara 1981; D. G. Hokit, *personal observation*). We spatially blocked each of the four replicates within the pothole and randomly determined the position of treatments within each block.

An unusually warm and dry summer caused potholes at our study site to dry prematurely. With the pothole containing our enclosures in danger of drying, we collected all surviving tadpoles on 12 September. At this point only six individuals had reached metamorphosis (forelimb emergence, stage 42, Gosner 1960). Thus, we measured the mass of all surviving tadpoles to the nearest 0.001 g on an electronic scale. However, tadpole survivorship does not always correlate with survival through metamorphosis and is often not significantly affected by density-related factors (Wilbur 1977). Small, stunted tadpoles may persist for indefinite periods of time without ever metamorphosing. We assumed that these stunted individuals would not survive and removed them from our initial analysis. We utilized the mass of the smallest metamorph (0.200 g) in our previous laboratory study (Hokit and Blaustein 1994) to determine a cutoff for including individuals in our analysis. Because tadpoles often lose ≈0.050 g before metamorphosis (Wilbur and Collins 1973, Wilbur 1977, Dash and Hota 1980, Alford and Harris 1988) we defined all tadpoles >0.250 g as ''survivors.'' Thus, we assumed that all individuals collected on 12 September with a mass ≥0.250 g would have reached metamorphosis had the pothole not prematurely dried.

We used multivariate analysis of variance (MANOVA) to test for density, substrate, and kinship effects on the proportion (calculated from initial densities) and mean mass of individuals per enclosure projected to metamorphose. Mass measures were analyzed as enclosure means because individuals within enclosures may not be independent of one another. We performed univariate analysis of variance (ANOVA) on both response variables within each main effect to help assess which variables were responsible for significant main effects. However, because there was a strong pooled, within-cell correlation (>0.40) between mean mass and proportion projected to metamorphose, it was likely that the two response variables were correlated in their response to the treatments (Tabachnick and Fidell 1989). This correlation was expected given that mass was used to define the cutoff for survivors. Therefore, we performed a more conservative stepdown *F* test for the proportion projected to metamorphose to assess better the response of the dependent variables to the main effects (Tabachnick and Fidell 1989). This test analyzes the combined response of both dependent variables corrected for their lack of independence (Tabachnick and Fidell 1989).

To meet parametric assumptions of normality, measurements of the proportion of individuals projected to metamorphose were arcsine-transformed (Zar 1984). Three enclosures were dislodged during a wind storm on 27 July and, thus, were eliminated from the experiment. These three enclosures were evenly distributed across the replicates and no treatment lost more than one enclosure. However, to correct for unequal sample sizes within cells, we applied the regression method (method 1 of Overall and Spiegel 1969) to assess treatment effects. This method assesses each treatment effect after adjusting for all other effects and is the recommended correction for unequal sample sizes for experimental research (Tabachnick and Fidell 1989).

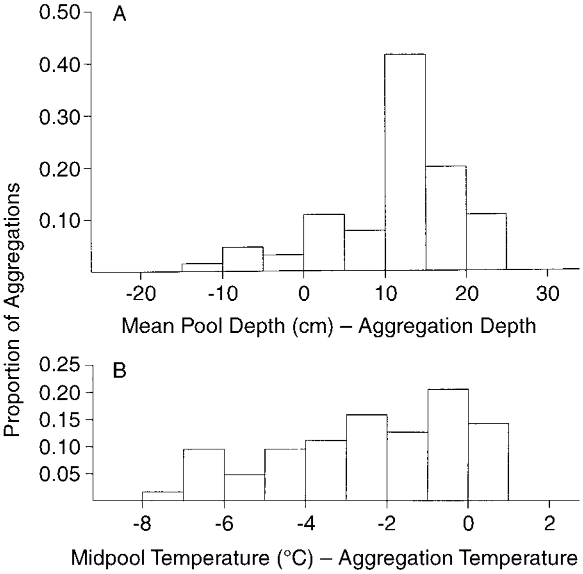

FIG. 1. The distributions of (A) the difference between mean pool depth and aggregation depth and (B) the difference between the temperature at the middle of the pool and temperature at the aggregation site, for all pools.

To assess further the source of treatment effects, we constructed paired histograms of the mass of all surviving individuals (i.e., including those <0.250 g) in kin vs. mixed enclosures within each of the other four treatments (low density substrate open, low density substrate closed, high density substrate open, high density substrate closed). These four treatments were ranked from least to most harsh in terms of the magnitude of their effects upon the mean mass of individual tadpoles (i.e., the smaller the mean tadpole mass the more harsh the environment). Such graphical representation helped to visualize the effects of treatments on the distribution of individual tadpole mass. Additionally, to statistically assess such effects, we used ANOVA to test for the effects of kinship and environmental harshness on the coefficient of variation of tadpole mass calculated for each enclosure. All analyses were conducted using SYSTAT version 5.1 (Wilkinson 1986).

RESULTS

Field observations

Sixty-five tadpole aggregations were observed ranging in size from 5 to 25 tadpoles (9.22 ± 4.04 tadpoles, mean ± 1 SE). The majority of aggregations were observed in shallow, warm water on silty substrates. Seventy-five percent of the aggregations occurred over silty, flocculent substrates. The difference between the mean depth of a pool and the depth at aggregations within the same pool was positively skewed (Fig. 1A). The mean depth of a pool was, on average, 12 cm

TABLE 1. Results of nearest neighbor analysis of aggregations for each pool with five or more aggregations; including the number of aggregations (n), the observed mean distance (in meters) to the nearest aggregation, the expected mean distance (in meters), and z tests for significantly aggregated distribution.

Pothole	n	Observed distance	Expected distance	z statistic	P
1	13	1.07	1.79	−2.48	0.013
2	20	0.89	1.41	−2.86	0.004
3	5	1.36	3.14	−2.16	0.031
4	6	1.80	2.81	−1.50	0.134
5	9	0.95	2.37	−2.89	0.004
6	6	0.60	3.14	−3.07	0.002

deeper than the mean depth of aggregations. Likewise, the mean temperature of aggregation sites was, on average, 3°C warmer than the temperature at the middle of the pool (Fig. 1B).

Aggregations were repeatedly observed at or near the same location within a pool. Nearest neighbor analysis of mapped aggregations revealed that, for the majority of the pools, the aggregations were not randomly distributed (Table 1). Many aggregations occurred in the same areas of silty substrate. Tadpoles within aggregations were observed ''digging'' small pits (4–8 cm in diameter and 4–6 cm deep) through repeated swimming and feeding behavior. Much of the silty, flocculent substrate is composed of organic detritus, providing a potentially rich food resource for the tadpoles (O'Hara 1981). Aggregations were often observed over several days in the same pit.

Pearson rank correlation revealed strong correlations (0.5 or greater) between aggregation frequency and the proportion of silty substrate, the number of predators, and the number of conspecifics in a pothole (Table 2). However, the effects of the proportion of silty substrate and the number of conspecifics may be confounded due to their strong correlation with each other. The number of competitors and pool volume had considerably weaker correlations with aggregation frequency (Table 2).

Regression analysis indicated that both the proportion of silty substrate and the log of the number of conspecifics were positively associated with aggregation frequency but were only significantly associated after the elimination of the mixed pothole data points (Fig. 2a, c, Table 3). Such a relationship may be expected of silty substrates if such substrates are a common food resource. Additionally, a greater number of conspecifics may increase the probability of finding aggregations. The log of the number of predators was significantly negatively associated with aggregation frequency (Fig. 2b, Table 3). Thus, predators appear to disrupt aggregation behavior in *R. cascadae.*

The elimination of the data points for mixed pools in the regression analysis improved the model fit for all three pothole variables (Fig. 2, Table 3). The influence of each data point is generally greater in regressions with small sample sizes and, thus, the removal of any data point was likely to improve the fit of the regression model. However, for the regression models that included all data, data points for mixed pools consistently influenced the model in the same direction and often to a considerable degree (Fig. 2, and e.g., a Cook's statistic >1.0 suggests an outlier, Tabachnick and Fidell 1989). These patterns at least suggest that pure sibling and mixed populations are potentially different with regard to aggregation behavior.

Mesocosm experiment

ANOVA revealed no significant spatial block effect or interaction between blocks and treatments. Therefore, we pooled the blocks for the remaining tests and treated them as replicates (Zar 1984). In a four-way interaction, kinship, thermal heterogeneity, presence of predators, and the distribution of food all influenced significantly tadpole dispersion behavior (Table 4, Fig. 3). Therefore, kin-biased aggregation behavior in tadpoles of *R. cascadae* depends upon the ecological conditions.

Sibling groups responded to ecological factors as would be predicted from field observations if ecological effects are additive. Mean dispersion indices for sibling pools were lowest when heaters were absent, predators were present, and food was homogeneously distributed, and were highest when heaters were present, predators were absent, and food was patchily distributed (Fig. 3). Mean dispersion indices for mixed

TABLE 2. Pearson rank correlation analysis between pothole variables and the frequency of observed aggregations.

Variables	Aggregations	Silt	Predators	Competitors	Conspecifics
Aggregations	1.00				
Silt	0.66 (0.07)	1.00			
Predators	−0.80 (0.01)	−0.21 (0.62)	1.00		
Competitors	−0.35 (0.39)	0.10 (0.81)	0.56 (0.14)	1.00	
Conspecifics	0.62 (0.10)	0.91 (0.01)	−0.22 (0.59)	0.15 (0.72)	1.00
Volume	−0.24 (0.56)	0.52 (0.18)	0.64 (0.08)	−0.72 (0.04)	0.52 (0.18)

Notes: Pothole variables include the volume of potholes, the proportion of silt per pothole, the number of predators per pothole (salamanders and invertebrate predators), the number of competitors per pothole (*P. regilla*), and the number of conspecifics. Numbers in parentheses are probability values.

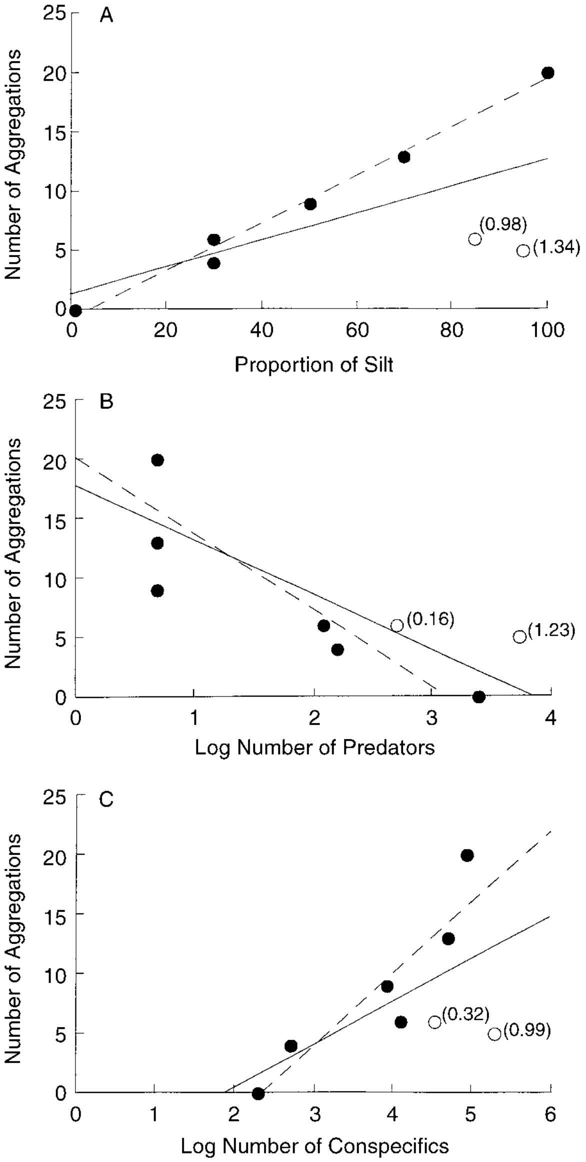

FIG. 2. (A) Regression analysis of the number of aggregations against the proportion of silt per pool, (B) the log number of predators per pool, and (C) the log number of conspecifics per pool. Regression statistics are included in Table 3. Solid lines represent the best fit model including both the mixed pool data (○) and the sibling pool data (●). Dashed lines represent the best fit model including only the sibling pool data. The numbers in parentheses next to mixed pool data points represent Cook's statistic, which is a measure of the influence these data points have on the model.

pools were higher than would be expected for the heater absent, predator present, homogeneous food treatment. Three other treatments for mixed pools had lower dispersion indices than the expected low treatment.

All 16 treatments had a positive index of dispersion, which indicates a tendency to aggregate. However, only six of the treatments had mean dispersion indices that were significantly aggregated (i.e., indices >0.5). Of these six, half were sibling and half were mixed treatments, half were homogeneous food and half were patchy food treatments, four were heater present and two were heater absent treatments, and all six were in predator absent treatments. Thus, it appears that temperature and predators had disproportionate effects, at least in the significantly aggregated treatments.

Field experiment one: Kinship and predator effects on group size

Kinship significantly influenced the number of tadpoles per food patch (ANCOVA, Table 5). The mean number of tadpoles per food patch, adjusted for the covariate (number of tadpoles per pool), was significantly greater in sibling pools than in mixed pools (sibling mean = 17.25 ± 0.91, mixed mean = 11.01 ± 0.58). Predator abundance and interactions between the factors did not significantly influence the number of tadpoles per food patch.

Field experiment two: Kinship effects on growth and development

Preliminary MANOVA revealed no significant spatial block effect or interaction between blocks and treatments. Therefore, we pooled the blocks for the remaining tests and treated them as replicates (Zar 1984). In a three-way interaction, density, access to substrate, and kinship affected significantly tadpole growth and development (MANOVA, Table 6A). The source of the interaction was a combined effect on the two response variables (Stepdown *F*, Table 6B,C). Mean mass and the proportion projected to metamorphose were both lower for tadpoles in sibling enclosures in the high-density, closed-substrate treatment (Fig. 4). Tadpoles reared in sibling groups had lower mass than tadpoles reared in mixed groups, but more were projected to reach metamorphosis in the high-density, open-substrate and low-density, closed-substrate treatments (Fig. 4). There was little difference in mean mass and the proportion projected to metamorphose for tadpoles reared in sibling vs. mixed groups in the low-density, open-substrate treatment (Fig. 4). Thus, the effect of each factor depended upon the other factors.

Paired histograms revealed increased skewness of tadpole mass for both kin and mixed treatments as environmental harshness increased (Fig. 5). However, the degree of skewness was not symmetrical across the kinship treatment, resulting in differences in the proportion projected to metamorphose. Because of differences in the distributions, kin enclosures produced more individuals >0.250 g than did mixed enclosures in the low-density, closed-substrate and high-density, open-substrate treatments, and fewer individuals >0.250 g in the high-density, closed-substrate treatment. There was little difference between kin and mixed enclosures in the low-density, open-substrate treatment. These differences in distribution were reflected in the coefficient of variation for each enclosure.

TABLE 3. Results of regression analysis to assess the influence of the proportion of silt, the (log) number of predators, and the (log) number of conspecifics per pool on aggregation frequency (y).

x factor	Equation	R	P
Proportion of silt			
with mixed	$y = 0.11x + 1.29$	0.659	0.076
without mixed	$y = 0.20x - 0.83$	0.994	<0.001
Log no. predators			
with mixed	$y = -4.61x + 17.75$	0.845	0.008
without mixed	$y = -6.41x + 20.07$	0.930	0.007
Log no. conspecifics			
with mixed	$y = 3.59x - 6.74$	0.618	0.102
without mixed	$y = 6.01x - 14.10$	0.905	0.013

Note: Regressions were performed with and without the data points from pools of mixed relatedness.

Both environmental harshness and kinship significantly influenced the coefficient of variation (Table 7). The coefficient of variation increased with environmental harshness and mixed enclosures had higher coefficients than did kin enclosures (Fig. 6).

DISCUSSION

Our study suggests that kinship may interact with ecological factors to influence aggregation behavior. Consistent with other studies of tadpole aggregation behavior (e.g., Wassersug 1973, Beiswenger 1972; reviewed by Blaustein and Walls 1995), thermal gradients and food patches enhanced aggregation behavior in larval *R. cascadae*. In the field, aggregations were most often observed in warm shallow water over silty substrates (potential food) and, in mesocosms, the aggregation index was generally greater with a heater present or patchily distributed food. Conversely, the presence of predators tended to disrupt aggregation behavior in larval *R. cascadae*. In natural pools, aggregation frequency was negatively associated with the number of predators and, in mesocosms, the aggregation index was generally lower when newt predators were present. Kinship is known to influence the aggregation behavior of larval *R. cascadae*. Tadpoles of *R. cascadae* preferentially associate with kin in aggregations in the laboratory and field (e.g., O'Hara and Blaustein 1981, Blaustein and O'Hara 1982, O'Hara and Blaustein 1985, Blaustein and O'Hara 1987). However, kinship, the distribution of food resources, presence of predators, and thermal heterogeneity all interacted to affect tadpole dispersion in our mesocosm experiment. Thus, the effect of each factor must be considered within the context of the other factors.

TABLE 4. Results of ANOVA testing for treatment effects on tadpole dispersion (Morisita's index of dispersion) in the mesocosm experiment.

Source	df	MS	F	P
Food	1	230.59	5.26	0.026
Predator	1	1011.21	3.09	<0.001
Heater	1	123.64	2.82	0.099
Kinship	1	1.72	0.04	0.844
Food × Predator	1	76.56	1.75	0.192
Food × Heater	1	24.79	0.57	0.455
Food × Kinship	1	133.56	3.05	0.087
Predator × Heater	1	127.68	2.97	0.094
Predator × Kinship	1	50.17	1.15	0.290
Heater × Kinship	1	170.04	3.88	0.055
Food × Predator × Heater	1	86.58	1.98	0.166
Food × Predator × Kinship	1	0.74	0.02	0.897
Food × Heater × Kinship	1	44.34	1.01	0.319
Predator × Heater × Kinship	1	396.26	9.05	0.004
Food × Predator × Heater × Kinship	1	319.64	7.30	0.010
Error	48	43.78		

Note: Treatments include food distribution (either homogeneous or patchy), presence or absence of predators, presence or absence of heaters, and kinship (either siblings or mixed siblings and nonsiblings).

In field experiment one, kinship influenced group size without interacting with predator abundance. The number of tadpoles per food patch was significantly greater in sibling pools than in mixed pools, but there was no detectable predator effect. It is likely that predator abundance was unsuccessfully manipulated in field experiment one. Invertebrate predator numbers were low in 1993, probably due to a late spring thaw. Experimental pools with predators had substantially fewer predators (9.33 ± 4.30 predators, mean ± 1 SE) than pools from the previous year (28.50 ± 13.50 predators). Thus, predators may not have been at a sufficient density to have significantly affected group size.

Tadpoles of *R. cascadae* may form kin-biased aggregations for several reasons. First, groups of tadpoles (regardless of kinship), by virtue of their dark color, may form thermal sinks, which elevate body temperatures more than a solitary individual can achieve and increase growth rates (e.g., Beiswenger 1972, O'Hara 1981, Guilford 1988). Individuals may accrue additional benefits through increased inclusive fitness if they preferentially associate with kin in such thermal aggregations. Our study is at least compatible with this hypothesis in that tadpole aggregations were often associated with thermal gradients.

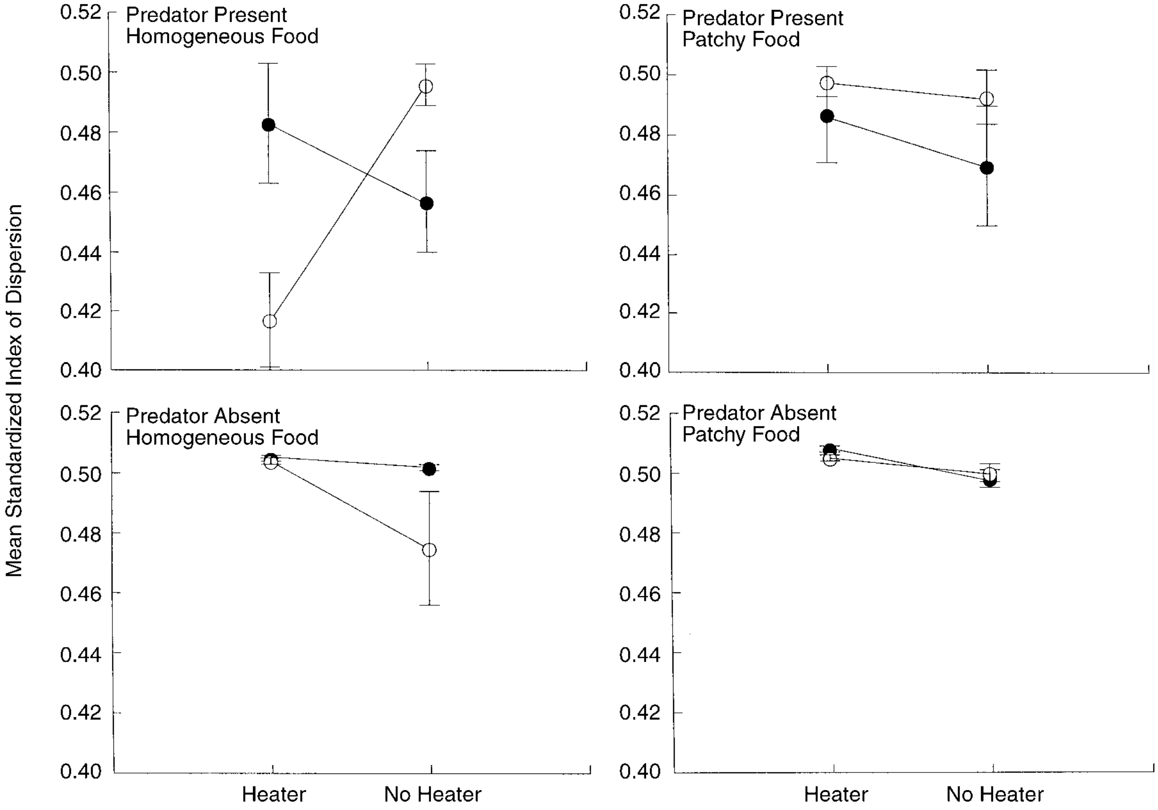

FIG. 3. Interaction diagram of the mean Morisita's index of dispersion for all 16 treatments in the mesocosm experiment. Filled circles represent tadpoles reared in sibling groups, and open circles represent tadpoles reared in a mixture of siblings and nonsiblings.

Second, groups of tadpoles may be able to detect and to avoid predators more efficiently than solitary individuals (Hamilton 1971, Bertram 1978, Pulliam and Caraco 1984). Individuals that preferentially associate with kin may accrue additional inclusive fitness benefits through cooperative predator vigilance or "warning" behavior. When captured by a predator, many tadpoles release an alarm substance (Hrbacek 1950, Hews and Blaustein 1985, Waldman 1986, Hews 1988), which could warn relatives in kin-biased aggregations (Hews and Blaustein 1985, Blaustein and Waldman 1992). However, our field observations and mesocosm results indicate that predators increase tadpole dispersion (i.e., reduce aggregation), which might limit the opportunity for such an alarm mechanism. Furthermore, a laboratory study (Hokit and Blaustein 1995) did not reveal alarm response behavior in tadpoles of *R. cascadae* and, although tadpoles did respond to the presence of a predator by reducing swimming activity, this behavior was not kin-biased.

Finally, groups of tadpoles are known to stir up the substrate, which may increase foraging efficiency and body size (Beiswenger 1972, 1975, Wilbur 1977). We similarly observed groups of larval *R. cascadae* stirring up the substrate in our field observations, resulting in pits in suitable (silty flocculent substrate) locations. Furthermore, kin groups had more individuals than mixed groups at artificial food patches (field experiment one), patchily distributed food generally enhanced aggregation behavior (mesocosm study), and access to silty substrate resulted in larger tadpole mass (field experiment two). Thus, kin-biased aggregations may form in response to foraging opportunities.

Kinship effects on growth and development may result from, or be enhanced by, such kin-biased behavior. Small initial differences in competitive ability between individuals may result from such processes as differential maternal investment (Kaplan 1980, 1989), priority effects (Bryant 1978, Prado et al. 1993), and/or

TABLE 5. Results of ANCOVA testing for treatment effects on group size at food pits in the field experiment.

Source	df	MS	*F*	*P*
Kinship	1	177.40	5.61	0.032
Predator	1	38.42	1.06	0.320
Kinship × Predator	1	0.12	0.01	0.952
No. tadpoles (covariate)	1	468.36	14.81	0.002
Error	15	31.62		

Note: Treatments include kinship (either siblings or a mixture of siblings and nonsiblings) and presence or absence of predators, with the number of tadpoles per pool as the covariate.

TABLE 6. Results of MANOVA for overall effects of density, access to substrate, kinship, and all possible interactions, and univariate analysis (ANOVAs and Stepdown *F*s) of each response variable within each main effect. Response variables are the mean mass and proportion projected to metamorphose per enclosure.

A) MANOVA for overall effects

Source	Wilks' Lambda	*F*	df	*P*
Density	0.325	19.73	2,19	<0.001
Substrate	0.734	3.44	2,19	0.053
Kinship	0.868	1.45	2,19	0.260
Density × Substrate	0.895	1.11	2,19	0.350
Density × Kinship	0.971	0.28	2,19	0.757
Substrate × Kinship	0.949	0.51	2,19	0.608
Density × Substrate × Kinship	0.650	5.11	2,19	0.017

B) Univariate analysis (ANOVA) of mean mass

Source	df	MS	*F*	*P*†
Density	1	2.038	14.13	0.001
Substrate	1	0.273	1.89	0.184
Kinship	1	0.333	2.31	0.144
Density × Substrate	1	0.096	0.67	0.423
Density × Kinship	1	0.028	0.19	0.662
Substrate × Kinship	1	0.084	0.58	0.454
Density × Substrate × Kinship	1	0.289	2.01	0.172
Error	20	0.144		

C) Univariate analysis (ANOVA and stepdown *F* test) of mean proportion projected to metamorphose

Source	df	MS	*F*	*P*†	Step *F*	*P*†
Density	1	8.162	41.52	<0.001	15.26	0.001
Substrate	1	1.419	7.22	0.014	4.64	0.044
Kinship	1	0.004	0.03	0.882	0.63	0.438
Density × Substrate	1	0.458	2.33	0.142	1.53	0.231
Density × Kinship	1	0.117	0.59	0.449	0.38	0.548
Substrate × Kinship	1	0.004	0.02	0.882	0.46	0.508
Density × Substrate × Kinship	1	0.529	2.69	0.117	7.55	0.013
Error (ANOVA)	20	0.197				
Mean mass (stepdown covariate)					8.89	0.008
Error (stepdown)	19	0.014				

† Significant at $P = 0.025$, Bonferroni-adjusted for two response variables.

genetic factors (Lomnicki 1978, 1980, Travis 1980). Any of these initial sources of variation may be greatly enhanced by intraspecific competition, resulting in the asymmetric distribution of resources and the performance of individuals (Wilbur and Collins 1973, Rubenstein 1981, Begon 1984). Both exploitative and interference mechanisms of competition have been observed in tadpoles (Steinwascher 1978). Larger tadpoles may exploit food resources better due to their larger feeding structures (Wassersug 1975) and/or agonistic behavior (Savage 1952, John and Fenster 1975). Also, larger tadpoles may release chemically based growth inhibitors (Richards 1958, Steinwascher 1978) although this mechanism may be mostly a laboratory phenomenon (Biesterfeldt et al. 1993). Any of these mechanisms may enhance initial differences in competitive ability and result in increasingly skewed distributions of mass with increases in density (Wilbur and Collins 1973, Rubenstein 1981, Begon 1984). Because tadpoles of *R. cascadae* can discriminate between kin and non-kin (e.g., O'Hara and Blaustein 1981, Blaustein and O'Hara 1982, O'Hara and Blaustein 1985, Blaustein and O'Hara 1987), individual tadpoles may direct competitive interactions away from kin (Waldman 1986, Blaustein 1988, Waldman 1991, Blaustein and Waldman 1992).

In our study, density-dependent effects were consistent with previous studies of other anuran species (e.g., Wilbur and Collins 1973, Wilbur 1977, Steinwascher 1978, Wilbur 1980, Semlitsch and Caldwell 1982, Alford and Harris 1988, Smith 1990). We found both a decrease in mass and increasingly skewed distributions of mass at higher densities, resulting in fewer individuals projected to metamorphose (field experiment two). However, the magnitude of this density-dependent effect depended upon kinship and substrate access. Kinship, density, and access to substrate interacted in their effects on growth and development of larval *R. cascadae.*

The distribution of individual tadpole mass was less skewed for tadpoles reared in sibling vs. mixed enclosures. This kin-bias in distribution resulted in differ-

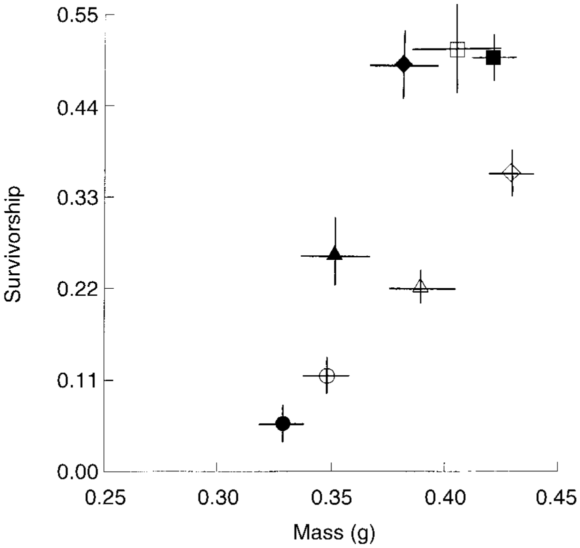

FIG. 4. The mean proportion projected to reach metamorphosis (±1 SE vertical) vs. mean tadpole mass per enclosure (±1 SE horizontal) coded for kinship (kin enclosures, filled symbols; mixed enclosures, open symbols) and subdivided into high-density closed-substrate, circles; high-density, open-substrate, triangles; low-density, closed-substrate, diamonds; and low-density, open-substrate treatments, squares.

TABLE 7. Results of ANOVA for the effects of environmental harshness and kinship on the coefficient of variation of mass.

Source	df	MS	*F*	*P*
Environment	3	0.037	6.60	0.003
Kinship	1	0.184	32.46	<0.001
Environment × Kinship	3	0.010	1.74	0.191
Error	20	0.006		

ences in mean tadpole mass and the number projected to metamorphose depending upon the density and substrate factors. There was little difference between tadpoles reared in sibling vs. mixed groups in the low-density, open-substrate treatment. Tadpoles reared in sibling groups had lower mass but more were projected to survive through metamorphosis in the low-density, closed-substrate and high-density, open-substrate treatments. Tadpoles in sibling groups had lower mass and fewer were projected to survive through metamorphosis in the high-density, closed substrate treatment.

The results of our previous laboratory study (Hokit and Blaustein 1994) revealed that size at metamorphosis was smaller for larval *R. cascadae* reared in sibling groups than tadpoles reared in groups of mixed relatedness. This closely matches the results observed in the high-density, closed-substrate treatment in this study, suggesting that the laboratory conditions of the previous experiment closely mimicked the most harsh environmental conditions of field experiment two.

Several studies suggest that kinship factors influence growth and development in tadpoles (Shvarts and Pyastolova 1970, Waldman 1986, Jasienski 1988, Smith 1990, Hokit and Blaustein 1994), although not always to the advantage of kin groups (Shvarts and Pyastolova 1970, Waldman 1991, Hokit and Blaustein 1994). Our results provide a possible explanation for the disparate findings of previous studies of kinship effects on tadpole growth and development. We suggest that kinship

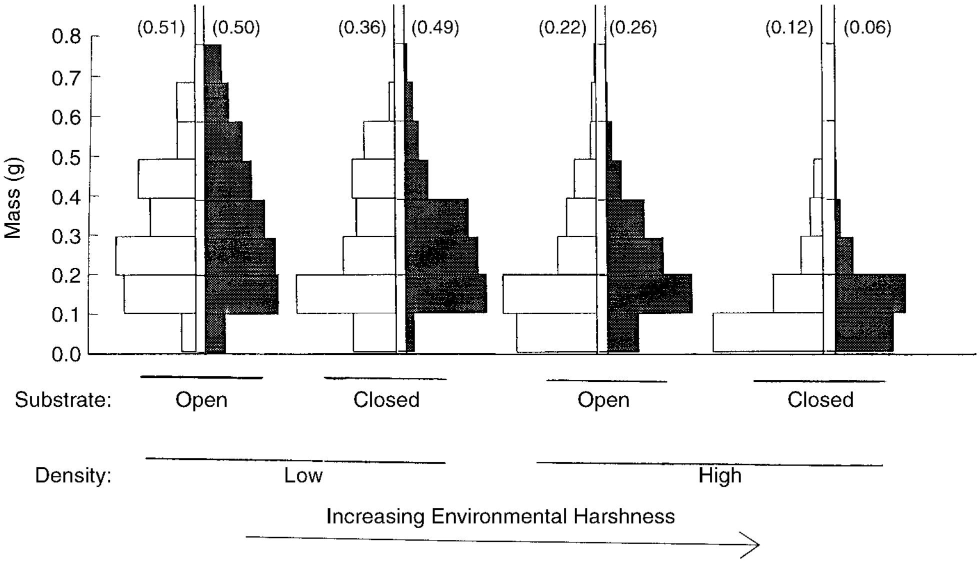

FIG. 5. Frequency histograms of individual tadpole mass for each treatment type pooled across replicates. Kin groups (filled) and mixed groups (open) are paired for each density/substrate treatment. Density/substrate treatments are ranked from least to most harsh by their effects on mean tadpole mass. Numbers in parentheses are the proportions (of the initial density) projected to reach metamorphosis (i.e., all those >0.250 g).

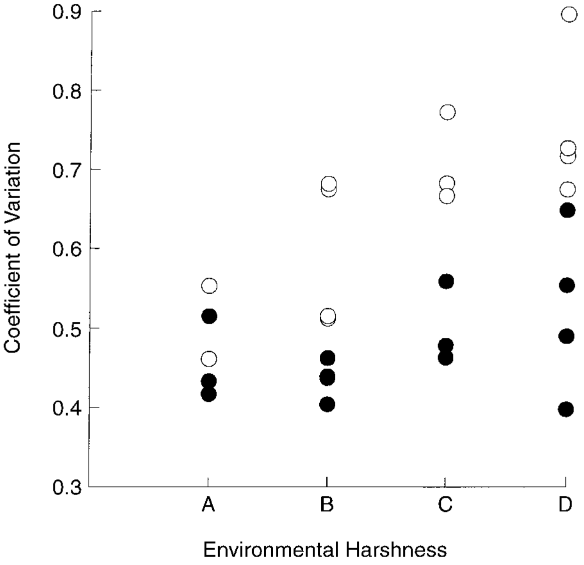

FIG. 6. Coefficient of variation of mean tadpole mass vs. environmental harshness, coded for kin groups (filled symbols) and mixed groups (open symbols). Environments from least to most harsh include (A) low-density, open-substrate, (B) low-density, closed-substrate, (C) high-density, open-substrate, and (D) high-density, closed-substrate treatments.

effects are highly dependent upon ecological (and thus, experimental) conditions and may simultaneously affect multiple correlates of fitness in a manner not detected by independent analyses of each fitness correlate. Tadpoles of *R. cascadae* reared in sibling groups had higher survivorship (at some cost to mass) depending upon the density and substrate factors (field experiment two). Similar contextual kinship effects have been observed in other tadpoles. For example, Smith (1990) found that growth rates and the proportion of tadpoles that attained metamorphosis were greater in sibling groups of *Pseudacris triseriata* than in mixed groups, but only at higher densities.

Regardless of the specific mechanism, kinship effects have important implications for size-structured populations. Size-structured populations are common (Werner and Gilliam 1984) and most dramatic in organisms that undergo metamorphosis (Wilbur 1980, Blakley 1981, Policansky 1983, Werner and Gilliam 1984). Furthermore, size structure can greatly affect population dynamics and species interactions (e.g., Wilbur 1980, Begon 1984, Werner and Gilliam 1984, Werner 1986, 1994, Mittelbach and Osenberg 1993, Wootton 1993). As our results demonstrate, kinship factors can influence the number and size of individuals recruited into higher size classes and, thus, may influence the dynamics of size-structured populations. However, any kin advantage will depend upon ecological conditions and tadpoles may form kin-biased aggregations accordingly.

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