



The Effects of Kinship on Growth and Development in Tadpoles of *Rana cascadae*

D. Grant Hokit; Andrew R. Blaustein

Evolution, Volume 48, Issue 4 (Aug., 1994), 1383-1388.

Stable URL:

<http://links.jstor.org/sici?sici=0014-3820%28199408%2948%3A4%3C1383%3ATEOKOG%3E2.0.CO%3B2-A>

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at <http://www.jstor.org/about/terms.html>. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

Evolution is published by Society for the Study of Evolution. Please contact the publisher for further permissions regarding the use of this work. Publisher contact information may be obtained at <http://www.jstor.org/journals/ssevol.html>.

Evolution

©1994 Society for the Study of Evolution

JSTOR and the JSTOR logo are trademarks of JSTOR, and are Registered in the U.S. Patent and Trademark Office. For more information on JSTOR contact jstor-info@umich.edu.

©2003 JSTOR

THE EFFECTS OF KINSHIP ON GROWTH AND DEVELOPMENT IN TADPOLES OF *RANA CASCADAE*

D. GRANT HOKIT AND ANDREW R. BLAUSTEIN

Department of Zoology, Oregon State University, Corvallis, Oregon 97331-2914

Key words.—Anura, growth, intraspecific competition, kinship, metamorphosis, *Rana cascadae*.

Received November 23, 1992. Accepted November 16, 1993.

Tadpoles of the frog, *Rana cascadae* can discriminate between kin and nonkin (kin recognition) and preferentially associate with kin in laboratory and field experiments (e.g., O'Hara and Blaustein 1981, 1985; Blaustein and O'Hara 1982, 1987). Such association, combined with rapid metamorphosis from small, ephemeral breeding sites and the tendency to form aggregations in nature may lead to intense intraspecific competition among *R. cascadae* tadpoles (O'Hara 1981; Blaustein 1988). Kin recognition may allow tadpoles to direct competitive interactions away from kin, perhaps by altering behavioral interference or by selectively releasing chemical growth inhibitors (Waldman 1986, 1991; Blaustein 1988; Blaustein and Waldman 1992).

In tadpoles, the effects of kin association on growth and development remain controversial (Shvarts and Pyastolova 1970; Travis 1980; Waldman 1986, 1991; Jasienski 1988; Smith 1990; reviewed by Blaustein and Waldman 1992). In particular, the direction of the kinship effect (i.e., whether individuals in kin groups grow faster/larger or slower/smaller than those in mixed groups) appears to depend upon the species examined and the experimental conditions. For example, kinship effects vary for American toads (*Bufo americanus*). Some family groups show increased larval growth rate when reared with siblings, whereas the growth rate in other families is slower when reared with sibling competitors (Waldman 1986). Individual growth rate is greater in sibling groups of the chorus frog (*Pseudacris triseriata*) than in mixed groups but only at high density (Smith 1990). However, with the exception of *B. americanus* (Waldman 1986, 1991), none of the species previously examined for kinship effects on growth and development are known to discriminate kin from nonkin. Using *R. cascadae*, we examined whether individuals within groups of full-sibling tadpoles and groups

of tadpoles of mixed relatedness differ in several key components of reproductive success including the lengths of the larval period, proportions of metamorphs produced, and body lengths and masses at metamorphosis. These traits correlate with fitness in some amphibians (e.g., Berven and Gill 1983; Smith 1987; Semlitsch et al. 1988).

MATERIALS AND METHODS

We collected four newly oviposited (less than 8 h old) clutches of *Rana cascadae* eggs on March 28, 1992 from an ephemeral pond adjacent to Cache Lake in the Deschutes National Forest of central Oregon, United States (100 km east of Corvallis, Jefferson County). *Rana cascadae* adults 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 a half-sib relationship within clutches. Thus, the offspring from within a clutch were probably full siblings. We kept the clutches separate while transporting them to our laboratory where they were placed into aerated 38-liter aquaria filled with dechlorinated tap water. Only tadpoles that hatched on April 7 (developmental stage 18, Gosner 1960), were used in this study.

We randomly assigned tadpoles to low-density (48 animals per aquarium: 1.26 tadpoles per liter) and high-density (200 animals per aquarium: 5.26 tadpoles per liter) treatments. The small size and ephemeral nature of *R. cascadae* breeding sites can produce density levels within this range (Hokit and Blaustein unpubl. data). Within each density treatment, we assigned tadpoles to kin groups (sibling tadpoles from the same clutch) and mixed groups (an equal number of tadpoles from each of the four clutches). Thus, a factorial design resulted with four treatments: (1) low-density kin group, (2) low-density mixed group,

TABLE 1. Results of MANOVA for overall effects of density, kinship, and density \times kinship interaction, and of ANOVAs for each response variable within each of the main effects. Response variables are number of days to metamorphosis (days), body length (length), mass at metamorphosis, and the proportion of metamorphs produced per tank (mets).

| | Kinship | | | Density | | | Density \times kinship | | |
|---------------------------|---------|------|--------|---------|------|---------|--------------------------|------|-------|
| | F | df | P | F | df | P | F | df | P |
| MANOVA (Wilks' criterion) | 4.64 | 4, 9 | 0.026 | 265.58 | 4, 9 | <0.001 | 2.51 | 4, 9 | 0.116 |
| ANOVAs | | | | | | | | | |
| Days | 1.34 | 1 | 0.269 | 140.67 | 1 | <0.001* | 0.33 | 1 | 0.574 |
| Length | 3.13 | 1 | 0.102 | 145.72 | 1 | <0.001* | 3.27 | 1 | 0.096 |
| Mass | 10.20 | 1 | 0.008* | 302.63 | 1 | <0.001* | 7.08 | 1 | 0.021 |
| Mets | 1.90 | 1 | 0.193 | 714.46 | 1 | <0.001* | 1.90 | 1 | 0.193 |

* Significance level for univariate tests is 0.0125 (Bonferroni adjusted for four response variables).

(3) high-density kin group, and (4) high-density mixed group, with four replicates of each treatment (a total of 16 aquaria). We considered each sibling group as a replicate for the kin treatments.

We fed tadpoles ground rabbit chow daily, with high-density treatments receiving four times as much food as low-density treatments. We augmented food throughout the experiment to adjust for tadpole growth, with amounts ranging from 0.5 to 1.0 g per day for low-density treatments and 2.0 to 4.0 g per day for high-density treatments. On any given day all treatments of the same density received the same amount of food.

We positioned all 16 tanks on the same bench centered in the middle of a windowless room, under a 14 L:10 D photoperiod. We randomly assigned tank positions and made no markings to indicate kinship (pure kin or mixed) composition. Thus, measurements were blind with respect to kinship. Tanks were cleaned and filled with dechlorinated tap water every three to five d with all tanks being cleaned on the same day.

When tadpoles metamorphosed (forelimb emergence, stage 42, Gosner 1960), we measured four variables: body length (snout-to-tail base), mass, number of days to metamorphosis, and the proportion of tadpoles metamorphosed per tank. Tanks were checked daily for metamorphs. We used metal dial calipers to measure body length to the nearest 0.1 mm and measured mass, after blotting each individual dry, to the nearest 0.001 g on an electronic scale. We measured metamorphs up to 100 d after hatching (total number of metamorphs measured = 1037), at which time we terminated the experiment. One hundred d is a long larval period for *R. cascadae* (Nussbaum et al. 1983), with many natural sites drying up within this period (O'Hara 1981).

We tested for density and kinship effects by using multivariate analysis of variance (MANOVA). To meet parametric assumptions of normality, measurements of body length, mass, and days to metamorphosis were \log_e transformed, whereas the proportion of metamorphs produced per tank was arcsine transformed (Zar 1984). Because individuals in tank cohorts may not be independent of one another, these measures were analyzed as tank means. We performed univariate analysis of variance (ANOVA) on each response variable within each main effect to assess which variables were responsible for significant main effects.

RESULTS

Kinship and density both affected the growth and development of tadpoles (MANOVA, table 1). Density levels significantly influenced larval period, body length and mass at metamorphosis, and the proportion of metamorphs (ANOVAs, table 1). Tadpoles took longer to develop, were shorter and weighed less, and proportionally fewer metamorphs were produced in the high-density treatments (fig. 1). No significant differences appeared between kin and mixed groups with respect to body length, larval period, or the proportion of tadpoles metamorphosed per tank (ANOVAs, table 1). However, the individual mass of tadpoles raised in kin groups was smaller than for tadpoles raised in mixed groups (fig. 1).

Travis (1980) found significant differences in larval growth rates between different sibships of *Hyla gratiosa*. To assess whether differences in mass among sibships might alone have caused the differences between kin and mixed groups, we performed a post hoc variance ratio test on mass. This test revealed that the range in vari-

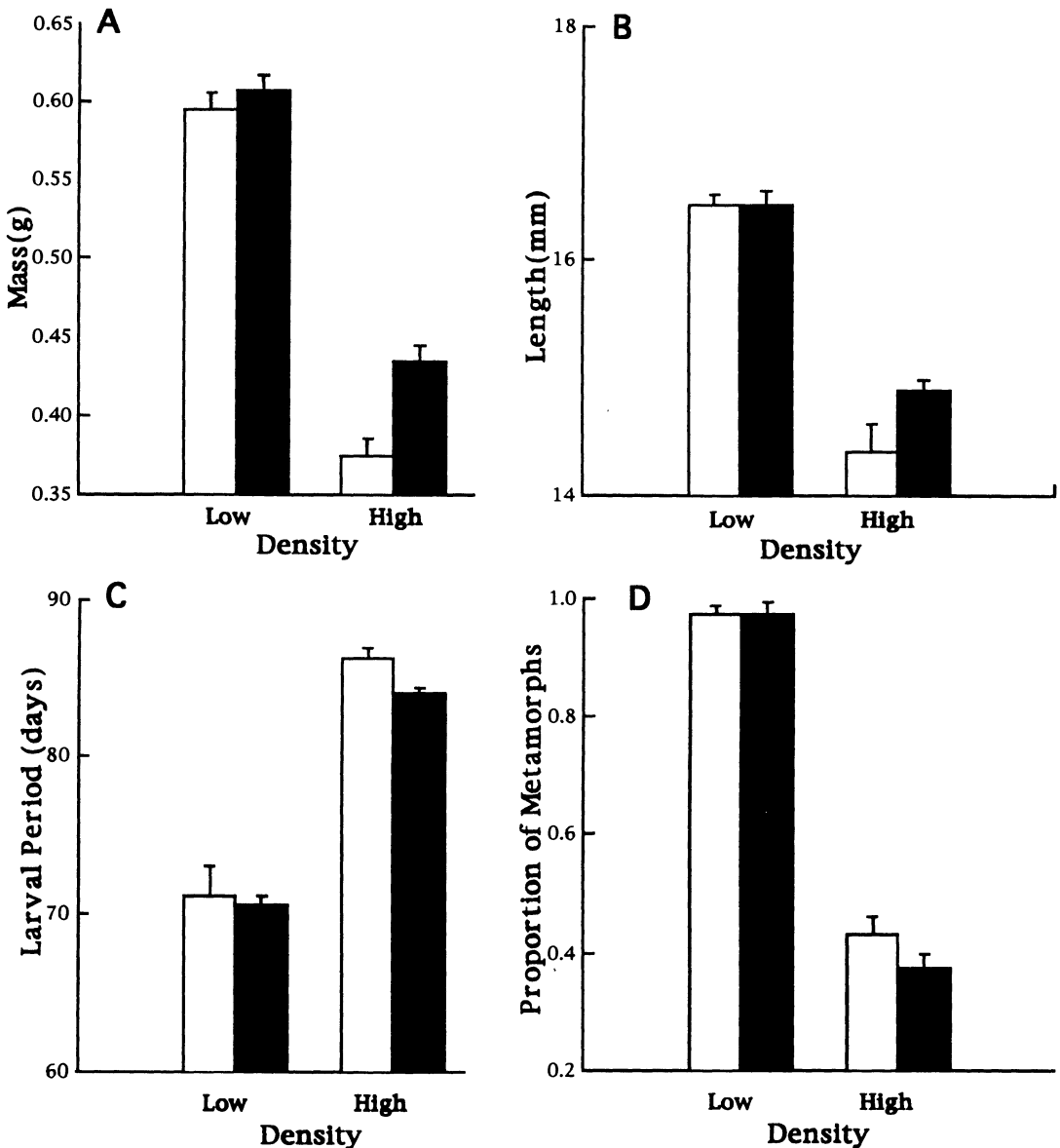


FIG. 1. Mean (\pm SE) mass (A), body length (B), larval period (C), and proportion of metamorphs produced per tank (D) for kin groups (open bars) and mixed groups (solid bars) at both low and high density.

ance among kin groups did not differ significantly from the range in variance among mixed groups ($F = 1.78$; $\alpha = 0.05$, two-tailed; $df = 7, 7$; $P \gg 0.5$; Zar 1984). Additionally, the standard deviation of metamorph mass was greater within the sibling groups than among the sibling groups in both the low- and high-density treatments (table 2). Thus, it is unlikely that the kinship effect on mass is the result of differences in mass among sibling groups. Although mortality may alter

densities enough to affect the mass at metamorphosis, mortality was low in all our tanks (less than 5%), and there was no apparent relationship between mortality and the experimental treatments.

Although the MANOVA revealed no significant interaction between density and kinship, there was a trend toward an interaction in all four response variables (fig. 1). In particular, the difference in mass between kin and mixed tanks

TABLE 2. Means, standard deviations, and ranges for number of days to metamorphosis (days), body length (length), mass at metamorphosis, and the proportion of metamorphs produced per tank (mets) for each tank within each treatment group. Treatment groups are low-density kin groups (LDKG), low-density mixed groups (LDMG), high-density kin groups (HDKG), and high-density mixed groups (HDMG).

| Treatment | <i>n</i> | Days | Length | Mass | Mets |
|-----------|----------|-----------------------|--------------------------|---------------------------|------|
| LDKG | 47 | 69.77 ± 11.29 (50–97) | 16.63 ± 1.51 (14.0–19.7) | 0.601 ± 0.204 (0.34–1.16) | 0.98 |
| | 47 | 70.40 ± 12.09 (52–94) | 16.24 ± 1.27 (13.6–19.2) | 0.563 ± 0.153 (0.33–1.03) | 0.98 |
| | 45 | 76.51 ± 7.93 (65–94) | 16.56 ± 1.22 (13.5–19.5) | 0.607 ± 0.130 (0.35–0.93) | 0.94 |
| | 48 | 67.52 ± 12.39 (45–95) | 16.44 ± 1.57 (12.9–19.6) | 0.606 ± 0.193 (0.33–1.11) | 1.00 |
| LDMG | 48 | 68.79 ± 13.09 (48–94) | 16.39 ± 1.69 (13.1–19.7) | 0.618 ± 0.225 (0.30–1.38) | 1.00 |
| | 48 | 70.91 ± 12.55 (49–97) | 16.64 ± 1.43 (13.9–19.6) | 0.612 ± 0.168 (0.39–1.12) | 1.00 |
| | 44 | 71.18 ± 11.79 (50–95) | 16.69 ± 1.48 (13.4–19.7) | 0.620 ± 0.189 (0.32–1.08) | 0.92 |
| | 47 | 71.21 ± 11.36 (52–91) | 16.16 ± 1.39 (13.2–19.1) | 0.578 ± 0.163 (0.32–1.01) | 0.98 |
| HDKG | 80 | 87.83 ± 7.92 (71–99) | 14.88 ± 1.05 (11.8–17.0) | 0.399 ± 0.068 (0.22–0.54) | 0.40 |
| | 78 | 86.19 ± 9.42 (66–99) | 13.85 ± 0.98 (12.0–16.8) | 0.348 ± 0.076 (0.21–0.61) | 0.39 |
| | 101 | 84.47 ± 10.42 (50–99) | 14.60 ± 0.96 (12.6–17.4) | 0.382 ± 0.090 (0.24–0.67) | 0.50 |
| | 88 | 86.17 ± 9.09 (60–99) | 14.13 ± 1.14 (11.6–17.3) | 0.371 ± 0.092 (0.21–0.63) | 0.44 |
| HDMG | 88 | 84.60 ± 10.38 (54–99) | 14.90 ± 1.03 (12.9–18.2) | 0.428 ± 0.113 (0.11–0.90) | 0.44 |
| | 76 | 84.40 ± 9.70 (52–99) | 14.78 ± 1.39 (12.0–18.6) | 0.422 ± 0.131 (0.23–0.82) | 0.38 |
| | 66 | 82.77 ± 10.85 (52–99) | 14.73 ± 1.29 (11.5–17.7) | 0.424 ± 0.123 (0.23–0.80) | 0.33 |
| | 70 | 84.01 ± 10.16 (54–99) | 15.14 ± 1.36 (12.1–17.9) | 0.464 ± 0.139 (0.20–0.79) | 0.35 |

was much greater in the high-density treatments than in the low-density treatments.

DISCUSSION

Our results revealed density-dependent effects on metamorphic characters of *Rana cascadae* that are consistent with previous studies of other anuran species (e.g., Brockelman 1969; Wilbur 1977, 1980; Steinwascher 1978; Dash and Hota 1980; Semlitsch and Caldwell 1982; Smith 1990). Additionally, our results revealed a negative kinship effect on mass at metamorphosis. Consequently, the effects of intraspecific competition on mass were greater in kin groups than in mixed groups of *R. cascadae*, and these effects may be greater at high density.

Several other studies report negative effects of kinship on growth and development. For example, Shvarts and Pyastolova (1970) found that solitary *R. arvalis* tadpoles reared in water conditioned by siblings grew slower than tadpoles reared in water conditioned by nonsiblings. Waldman (1986) observed the same effect in some families of *Bufo americanus* but not in others. The negative kinship effect in our study is particularly intriguing given that *R. cascadae* tadpoles can discriminate between kin and nonkin (i.e., kin recognition) and, therefore, could potentially avoid competitive interference with kin. Moreover, *R. cascadae* kin recognition is relatively sensitive: individuals prefer to associate

with siblings over nonsiblings and even half siblings over nonsiblings (Blaustein and O'Hara 1982), and kin recognition persists after metamorphosis (Blaustein et al. 1984). Why do *R. cascadae* tadpoles form aggregations composed primarily of kin in the field (O'Hara and Blaustein 1985), given that the negative effects of intraspecific competition appear greater within kin groups?

Smith (1990) suggested that either type of kinship effect (positive or negative) could be favored by kin selection depending on how body size and larval period affect fitness. For example, rapid growth and development through metamorphosis may lower the risk of predation (e.g., Calef 1973; Heyer et al. 1975; Werner 1986) and reduce the risk of desiccation where the aquatic habitat is ephemeral (e.g., Heyer et al. 1975; O'Hara 1981). However, costs are associated with early metamorphosis. Early metamorphosis may not allow full exploitation of the aquatic habitat, resulting in lower mass at metamorphosis and potential reductions in subsequent reproductive output (e.g., Berven and Gill 1983; Smith 1987; Semlitsch et al. 1988). Presumably, smaller mass at metamorphosis in kin groups of *R. cascadae* may be offset by enhanced performance in other metamorphic traits, such as increased per capita probability of metamorphosis or acceleration of the larval period. However, none of the other variables measured in our study showed an in-

creased response for kin groups except for a slight, but nonsignificant, increase in the proportion of metamorphs produced in the high-density treatment (fig. 1).

It is possible that the results observed in our study are context dependent (i.e., depend on the testing conditions). For example, Smith (1990) found that growth rate and the proportion of tadpoles that attain metamorphosis are greater in sibling groups of *Pseudacris triseriata* than in mixed groups but only at high density and with a particular size of container. Our results also indicate that kinship effects may be greater at high density. Although MANOVA did not reveal a statistically significant interaction between kinship and density, this could be a result of the conservative nature of MANOVA analysis (a bias toward avoiding type I errors) and the relatively small sample sizes. In any case, the data indicate a trend toward an interaction in all response variables, particularly in the case of mass.

The kinship effect also may be specific to the particular sibling groups involved and their relative ratios in the mixed groups. Classic studies on genotypic viabilities (e.g., Dobzhansky and Spassky 1944; Levene et al. 1954; Lewontin 1955; Bhalla and Sokal 1964; Bell 1991) indicate that genotypic interactions are often nonlinear and difficult to predict. For example, the relative survival of different strains of *Drosophila* depends on their rearing densities, the particular combination of genotypes, and their relative ratios in mixed groups (Dobzhansky and Spassky 1944; Levene et al. 1954; Lewontin 1955). These complex interactions may result in certain combinations of genotypes (i.e., mixed groups) outperforming isolated genotypes via more efficient or harmonious resource use (Lewontin 1955). However, working with genotypically distinct populations of *Chlamydomonas*, Bell (1991) found no evidence of genotypic interactions, yet mixed cultures had higher productivity than did pure cultures. Rather than complementary resource use, replacement of one genotype by another resulted in a performance that was higher for mixed cultures than for the average pure culture.

In our experiment, as with previous studies (Travis 1980; Jasienski 1988; Smith 1990), each sibship was equally represented in each mixed tank. This design reduced the chance that differences in growth and development between sibships (Travis 1980; Smith 1990) might alone have caused differences between kin and mixed

groups. However, with this design, every mixed tank had the same genetic structure. The kinship effect observed in our study could indicate more intense competition in kin groups or, conversely, complementary resource use in mixed groups (e.g., different tadpoles may feed in different regions of the tank or may feed by coprophagy versus eating rabbit chow). Alternatively, certain sibships may outperform (in terms of growth rate) other sibships, resulting in a "replacement" response (i.e., competition is asymmetrical with respect to sibships). Replacement could be exacerbated if the initial condition (e.g., size) of individuals were biased toward a particular sibling group. This latter possibility was minimized in our study, given that all sibling groups were collected simultaneously, and all treatment replicates were maintained under identical laboratory conditions. However, other factors, such as maternal investment in egg size, may produce clutch-biased competitive advantages (Kaplan 1989).

Nevertheless, because individual tadpoles in our study were not identifiable by sibship in the mixed tanks, it is difficult to distinguish between complementary resource use and "replacement." Ideally, experiments using tadpoles that are individually or genetically marked would allow examination of sibships in all treatments and allow examination of facilitation or replacement processes. Regardless, the kinship effect observed in our study may be relevant only to the particular sibships involved, their relative ratios, and the particular densities used in our study.

ACKNOWLEDGMENTS

We thank R. Alford, P. S. Dawson, B. Menge, and D. Parichy for reviewing an early draft of the manuscript. We thank S. C. Walls for laboratory help and critical review of the manuscript. For technical assistance, we thank R. Ryan, J. Brickley, and B. MulCahey. This research was supported by Oregon State University Zoology Research Funds to D.G.H. and National Science Foundation grants BNS 9020957 and BNS 9107171 to A.R.B.

LITERATURE CITED

- Bell, G. 1991. The ecology and genetics of fitness in *Chlamydomonas*. IV. The properties of mixtures of genotypes of the same species. *Evolution* 45: 1036-1046.
- Berven, K. A., and D. E. Gill. 1983. Interpreting geographic variation in life history traits. *American Zoologist* 23:85-97.

- Bhalla, S. C., and R. R. Sokal. 1964. Competition among genotypes in the housefly at varying densities and proportions (the *green* strain). *Evolution* 18:312-330.
- Blaustein, A. R. 1988. Ecological correlates and potential functions of kin recognition and kin association in anuran larvae. *Behavior Genetics* 18:449-464.
- Blaustein, A. R., and R. K. O'Hara. 1982. Kin recognition in *Rana cascadae* tadpoles: maternal and paternal effects. *Animal Behaviour* 30:1151-1157.
- . 1987. Aggregation behavior in *Rana cascadae* tadpoles: association preferences among wild aggregations and responses to non-kin. *Animal Behaviour* 35:1549-1555.
- Blaustein, A. R., and B. Waldman. 1992. Kin recognition in anuran amphibians. *Animal Behaviour* 44:207-221.
- Blaustein, A. R., R. K. O'Hara, and D. H. Olson. 1984. Kin preference is present after metamorphosis in *Rana cascadae* frogs. *Animal Behaviour* 32:445-450.
- Brockelman, W. Y. 1969. An analysis of density effects and predation in *Bufo americanus* tadpoles. *Ecology* 50:632-644.
- Calef, G. W. 1973. Natural mortality of tadpoles in a population of *Rana aurora*. *Ecology* 54:741-758.
- Dash, M. C., and A. K. Hota. 1980. Density effects on survival, growth rate, and metamorphosis of *Rana tigrina* tadpoles. *Ecology* 61:1025-1028.
- Dobzhansky, T., and B. Spassky. 1944. Genetics of natural populations XI. Manifestation of genetic variants in *D. pseudoobscura* in different environments. *Genetics* 29:270-290.
- Gosner, K. 1960. A simplified table for staging anuran embryos and larvae with notes on identification. *Herpetologica* 16:183-190.
- Hamilton, W. D. 1964. The genetical evolution of social behaviour. I. *Journal of Theoretical Biology* 7:1-16.
- Heyer, W. R., R. W. McDiarmid, and D. L. Weigmann. 1975. Tadpoles, predation, and pond habitats in the tropics. *Biotropica* 7:100-111.
- Jasienski, M. 1988. Kinship ecology of competition: size hierarchies in kin and nonkin laboratory cohorts of tadpoles. *Oecologia (Berlin)* 77:407-413.
- Kaplan, R. H. 1989. Ovum size plasticity and maternal effects on the early development of the frog, *Bombina orientalis* Boulenger, in a field population in Korea. *Functional Ecology* 3:597-604.
- Levene, H., O. Pavlovsky, and T. Dobzhansky. 1954. Interaction of the adaptive values in polymorphic experimental populations of *D. pseudoobscura*. *Evolution* 8:335-349.
- Lewontin, R. C. 1955. The effects of population density and composition on viability in *Drosophila melanogaster*. *Evolution* 9:27-41.
- Nussbaum, R. A., E. D. Brodie, and R. M. Storm. 1983. Amphibians and reptiles of the Pacific northwest. University Press of Idaho, Moscow, Idaho.
- O'Hara, R. K. 1981. Habitat selection behavior in three species of anuran larvae: environmental cues, ontogeny, and adaptive significance. Ph.D. diss. Oregon State University, Corvallis.
- O'Hara, R. K., and A. R. Blaustein. 1981. An investigation of sibling recognition in *Rana cascadae* tadpoles. *Animal Behaviour* 29:1121-1126.
- . 1985. *Rana cascadae* tadpoles aggregate with siblings: an experimental field study. *Oecologia* 67:44-51.
- Semlitsch, R. D., and J. P. Caldwell. 1982. Effects of density on growth, metamorphosis, and survivorship in tadpoles of *Scaphiopus holbrooki*. *Ecology* 63:905-911.
- Semlitsch, R. D., D.E. Scott, and J. H. K. Pechmann. 1988. Time and size at metamorphosis related to adult fitness in *Ambystoma talpoideum*. *Ecology* 69:184-192.
- Shvarts, S. S., and O. A. Pyastolova. 1970. Regulators of growth and development of amphibian larvae. I. Specificity of effects. *Soviet Journal of Ecology* 1:58-62.
- Smith, D. C. 1987. Adult recruitment in chorus frogs: effects of size and date at metamorphosis. *Ecology* 68:344-350.
- . 1990. Population structure and competition among kin in the chorus frog (*Pseudacris triseriata*). *Evolution* 44:1529-1541.
- Steinwascher, K. 1978. Interference and exploitation competition among tadpoles of *Rana ultricularia*. *Ecology* 59:1039-1046.
- Travis, J. 1980. Phenotypic variation and the outcome of interspecific competition in hyliid tadpoles. *Evolution* 34:40-50.
- Waldman, B. 1986. Chemical ecology of kin recognition in anuran amphibians. Pp. 225-242 in D. Duvall, ed. *Chemical signals in vertebrates* 4. Plenum Press, New York.
- . 1991. Kin recognition in amphibians. Pp. 162-219 in P. G. Hepper, ed. *Kin recognition*. Cambridge University Press, Cambridge.
- Werner, E. E. 1986. Amphibian metamorphosis: growth rate, predation risk, and the optimal size at transformation. *American Naturalist* 128(3):319-341.
- Wilbur, H. M. 1977. Density-dependent aspects of growth and metamorphosis in *Bufo americanus*. *Ecology* 58:196-200.
- . 1980. Complex life cycles. *Annual Review of Ecology and Systematics* 11:67-93.
- Zar, J. H. 1984. *Biostatistical analysis*. Prentice-Hall, Englewood Cliffs, N.J.

Corresponding Editor: B. Grosberg