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PATHOGEN REVERSES COMPETITION BETWEEN LARVAL AMPHIBIANS

JOSEPH M. KIESECKER^{1,3} AND ANDREW R. BLAUSTEIN²

¹*School of Forestry and Environmental Studies, 370 Prospect, Yale University,
New Haven, Connecticut 06511 USA*

²*Department of Zoology, Oregon State University, Corvallis, Oregon 97331 USA*

Abstract. Ecologists have often suggested that the presence of pathogens that differentially affect interacting species may affect the outcome of interactions, yet few experimental studies have documented pathogen-mediated interactions using a natural host–parasite system. We studied the effects of a pathogenic water mold, *Saprolegnia ferax*, on competitive interactions between the Cascades frog *Rana cascadae* and the Pacific treefrog *Hyla regilla*. Previous studies have shown that outbreaks of *Saprolegnia* infection in the Cascade mountains of Oregon, USA, result in high embryonic mortality for *Rana* but not for *Hyla*. Thus, we examined how infections of *Saprolegnia* during amphibian embryonic development could influence larval recruitment and competitive interactions between larval *Rana* and *Hyla*. We manipulated the presence of *Saprolegnia* and embryonic *Hyla* and *Rana* in replicated artificial ponds and determined mean survivorship to hatching per pool from daily observations during embryonic development. Pools were then followed throughout larval development, and we recorded mean mass of tadpoles at metamorphosis and time to metamorphosis per pool. The presence of *Saprolegnia* differentially affected larval recruitment of the two species; larval recruitment of *Rana* was reduced by 46.2% in the presence of *Saprolegnia*, whereas *Hyla* survival was not affected. However, larval *Rana* that survived *Saprolegnia* infection developed faster and were larger at metamorphosis compared to individuals not exposed to *Saprolegnia*. In the absence of *Saprolegnia*, *Rana* had strong negative effects on the growth, development, and survival of *Hyla*. However, in the presence of *Saprolegnia*, the outcome of competitive interactions between the two species was reversed. *Saprolegnia* may have positive indirect effects on both *Hyla* and *Rana* by regulating both intra- and interspecific competition. These results suggest that pathogens can have strong effects on species interactions and may ultimately influence community structure.

Key words: anuran larvae; competition; *Hyla*; interspecific competition; intraspecific competition; *Rana*; *Saprolegnia*; species interactions; pathogen mediated.

INTRODUCTION

Ecological studies at the community level have traditionally focused on the role of competition, predation, and disturbance (e.g., Wilbur 1972, Menge and Sutherland 1976, Connell 1983, Wellborn et al. 1996). Yet, numerous studies suggest that pathogens likely play important roles in determining species performance and influencing community structure (e.g., Park 1948, Price et al. 1986, 1988). Despite the prevalence of pathogens and the diseases they cause, few quantitative data are available on how they influence organisms in nature (see Sousa 1991, Marcogliese and

Cone 1997). Furthermore, few manipulative experimental studies have examined how pathogens affect species interactions and ultimately influence community dynamics (but see Washburn et al. 1991, Dobson and Crawley 1994, Kohler and Wiley 1997). Thus, a key step in the further development of community theory is to document the role of pathogens at the community level.

The strength and direction of pairwise species interactions often change in the presence of other species (Vandermeer 1969, Levine 1976, Yodzis 1988). Such indirect effects are predicted by theoretical treatments (Holt 1977, Abrams 1987, Yodzis 1988), and have been observed in several natural systems (e.g., Schoener 1993, Menge 1995). The presence of pathogens that affect species differentially could similarly result in

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³ E-mail: joseph.kiesecker@yale.edu

alterations of species interactions (Park 1948, Price et al. 1988, Grosholz 1992, Schall 1992). In this way, pathogens may act as keystone species (Power et al. 1996) by diminishing performance of dominant competitors, and in turn allowing for coexistence of competitively inferior species.

Ideally, ecologists should conduct controlled field experiments to examine pathogen-mediated interactions. However, it is typically difficult to identify, isolate, and control pathogens under field conditions. These difficulties probably underlie the general lack of empirical ecological studies that have explored the role of pathogens (but see Hudson 1986, Lehmann 1992, Fuller and Blaustein 1996).

Criteria needed to examine pathogen-mediated interactions should include: (1) a host-pathogen system where the effects of pathogens on hosts are readily observable, (2) host species that show interspecific variation in susceptibility to infection, and (3) a pathogen and host species that occur together in nature. Pathogenic water molds of the family Saprolegniaceae meet these criteria. *Saprolegnia*-infected embryos of fishes and amphibians become covered with a visible crown of white hyphal filaments and embryos usually do not hatch. Infection can spread through either direct contact from growing hyphae or by colonization by free-swimming zoospores (Wood and Willoughby 1986). *Saprolegnia* is cosmopolitan in distribution, occurring in most freshwater habitats (Wood and Willoughby 1986, Blaustein et al. 1994a, Kiesecker and Blaustein 1997), yet host species show strong interspecific variation in their susceptibility to infection (Richards and Pickering 1978, Wood and Willoughby 1986, Kiesecker and Blaustein 1995, 1997). The ease with which *Saprolegnia* infection can be identified and manipulated under experimental conditions (Kiesecker and Blaustein 1995) makes it a model system for examining the influence of a pathogen on species interactions.

In the Pacific Northwest of the United States massive amphibian embryo mortality is associated with the presence of *Saprolegnia ferax* (hereafter *Saprolegnia*) alone or in conjunction with exposure to ultraviolet-B radiation (Blaustein et al. 1994a, b, Kiesecker and Blaustein 1995, 1997). Although certain species (e.g., *Rana cascadae*, hereafter *Rana*) experience high mortality from these factors, other species (e.g., *Hyla regilla*, hereafter *Hyla*) appear unaffected (Kiesecker and Blaustein 1997).

In this study we explored the effect of *Saprolegnia* during amphibian embryonic development and its influence on competitive interactions between larval *Rana* and *Hyla*. Embryos of both species are deposited in open shallow water where they are exposed to infection with *Saprolegnia* (Kiesecker and Blaustein

1997). Larvae of both species feed on periphyton, phytoplankton, and detritus (Nussbaum et al. 1983). Both species have larval periods of similar duration, and frequently breed in the same ponds in the Oregon Cascade Range in spring (Nussbaum et al. 1983; J. Kiesecker, *personal observation*). The presence of pathogens like *Saprolegnia*, which are known to differentially influence larval recruitment of *Rana* and *Hyla*, may affect the outcome of larval interactions between these two species, and ultimately community structure.

METHODS AND MATERIALS

We manipulated the presence of *Saprolegnia* and densities of embryonic *Hyla* and *Rana* in replicated artificial ponds. These ponds were located in a field adjacent to a natural breeding site of *Rana* and *Hyla* in the Deschutes National Forest (24 km south of Sisters, Deschutes County, Oregon, USA). Experiments were conducted during the natural breeding season, from 20 June to 6 August 1996. We created pond communities in plastic pools that were 1.5 m in diameter and were filled to a depth of ~20 cm. Ponds contained ~150 L of water. To provide food for developing larvae, we added 55 g of leaf litter and macrophytes, and 15 g of Purina Trout Chow (Ralston Purina Company, St. Louis, Missouri) to each pool. This method provided conditions for growth that were at least as good as conditions in natural ponds. Mean masses of metamorphs in our experiment were at the high end of the range of masses from metamorphs collected from natural ponds.

We used a fully factorial design that crossed the presence of *Hyla* (alone or with *Rana*) and *Rana* (alone or with *Hyla*) at two natural densities: low (30 embryos per pool, 0.2 embryos/L) and high (60 embryos per pool, 0.4 embryos/L). These densities are comparable to natural densities of both species, which vary from 0.05 to 1.1 animals/L. We also crossed these treatments with *Saprolegnia* (present or absent), and the resulting twelve treatments were replicated four times for a total of 48 pools. We controlled for density of embryos between the single species and the combined species treatments to ensure that effects were due to interspecific effects and not increased density (Underwood 1986).

All embryos used in the experiment were collected within 12 h of fertilization and were matched for developmental stage (Gosner Stage 1–4, Gosner 1960). For *Rana* we added eggs from each of six different clutches into each pond. Because of small clutch sizes, in *Hyla*, we used eggs from more than six clutches and randomly assigned eggs from at least six clutches to each pond. Initially all embryos were rinsed in a dilute (2 μ L/L) solution of malachite green, to eliminate any

Saprolegnia that may have been present on the embryos (Kiesecker and Blaustein 1995).

Using standardized protocol (Laskin and Lechevalier 1978), *Saprolegnia* was cultured in the laboratory on 20-mL cornmeal agar in standard petri dishes. Boiled hemp seeds were added to cultures, which were allowed to incubate for ~240 h. In ponds where *Saprolegnia* was added, we introduced three hemp seeds laden with *Saprolegnia*. Control pools receiving no *Saprolegnia* received three, clean, boiled hemp seeds.

Ponds were left uncovered during the embryonic period of *Rana* and *Hyla*. After embryos had hatched, larval predators that had entered ponds were removed (a total of three Notonectids) and screen lids, designed to prevent predators from colonizing, were placed over the top of each pond.

During the embryonic period of *Hyla* and *Rana* we monitored ponds daily and recorded mean survivorship to hatching per pond. Continuing our daily monitoring, we removed individuals from the pools as they metamorphosed (front limb emergence; Gosner stage 42, Gosner 1960), and recorded mass (to the nearest milligram) at, and time (in days) to, metamorphosis. We terminated the experiment when all tadpoles had either metamorphosed or died.

Statistical analyses

We used multivariate analysis of variance (MANOVA) to test for the effects of independent factors, including density (high or low), *Saprolegnia* (present or absent), and association (alone or with competitor), on the dependent variables mean survivorship to hatching, and mean time, mass, and survivorship (from initial stocking) to metamorphosis (Tabachnick and Fidell 1989). After MANOVA, we used a Bonferroni-adjusted univariate analysis of variance (ANOVA) on each response variable to help assess which variables were responsible for significant main effects. Because individuals in ponds were not independent of one another, all variables were analyzed as pond means. We arcsine-transformed the data on survivorship before the analysis; and after transformation the data met the parametric assumptions. For all other dependent variables parametric assumptions were met without transformations.

RESULTS

Rana responses

Neither the presence of *Hyla* nor total density had a significant effect on *Rana* mass, development, or survival (Table 1, Figs. 1 and 2). There were, however, strong effects of *Saprolegnia* on the responses of *Rana* (Table 1, Figs. 1 and 2). Survival to hatching, survival to metamorphosis, and time to metamorphosis de-

TABLE 1. Results of MANOVA for overall effect of *Hyla*, *Saprolegnia*, and density on *Rana* survival, mass, and time to metamorphosis and ANOVAs for each response variable.

Variable	$F_{4,21}$	P
MANOVA		
Constant	2383.898	<0.0001
<i>Hyla</i>	0.150	0.961
<i>Saprolegnia</i>	172.974	<0.0001
Density	1.127	0.371
<i>Hyla</i> × <i>Saprolegnia</i>	0.251	0.906
<i>Hyla</i> × Density	0.431	0.784
<i>Saprolegnia</i> × Density	1.047	0.407
<i>Hyla</i> × <i>Saprolegnia</i> × Density	0.213	0.928
ANOVAs		
Survival to hatching		
<i>Saprolegnia</i>	775.189	<0.0001
Mass		
<i>Saprolegnia</i>	21.592	<0.001
Time		
<i>Saprolegnia</i>	4.982	0.035
Survival to metamorphosis		
<i>Saprolegnia</i>	268.502	<0.001

Notes: The significance level for univariate tests is 0.00625 (Bonferroni-adjusted for four response variables). Response variables are proportion surviving to hatching (survival to hatching), mass at metamorphosis (mass), time to metamorphosis (time), and proportion of initial surviving to metamorphosis (survival to metamorphosis). For simplicity we have only included ANOVA comparisons that are significant.

creased for *Rana* in the presence of *Saprolegnia* (Figs. 1 and 2). In contrast, mean mass at metamorphosis increased in the presence of *Saprolegnia* (Fig. 2).

Hyla responses

Hatching success of *Hyla* was relatively high in all treatments (Fig. 1) and there were no significant differences among treatments (Table 2). Density, *Rana*, and *Saprolegnia* all had significant effects on *Hyla* mass, development, and survival to metamorphosis (Table 2). However, the main effects of *Rana* and *Saprolegnia* were secondary to the interaction effect between the two factors (Table 2). In the absence of *Saprolegnia*, *Rana* reduced survival to, and mass at, metamorphosis and increased time to metamorphosis of *Hyla* (Table 2, Fig. 3). However, in the presence of *Saprolegnia*, the outcome of the interaction between *Rana* and *Hyla* was reversed (Table 2, Fig. 3). *Hyla* had higher survival, faster development, and were larger at metamorphosis when exposed to both *Saprolegnia* and *Rana* compared to *Rana* alone.

DISCUSSION

Our experiment indicates that pathogens can have strong effects on species interactions and thus may have strong influences on larval amphibian assemblages. Because *Saprolegnia* differentially affected larval recruitment of *Rana* and *Hyla*, the presence or absence of

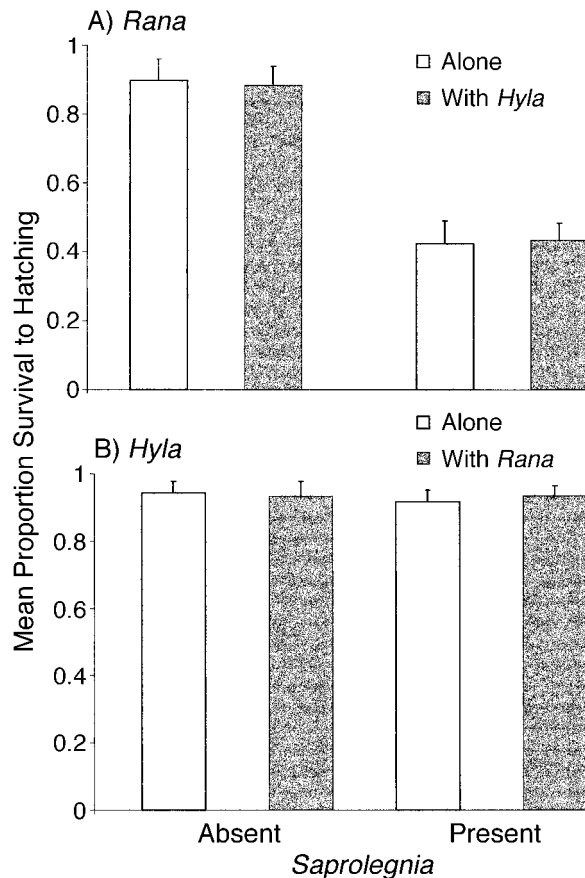


FIG. 1. Summary of the effects of *Saprolegnia* (absent or present) and *Rana* (alone or with *Hyla*), or *Hyla* (alone or with *Rana*) on the mean survivorship to hatching of (A) *Rana* and (B) *Hyla*. Error bars represent ± 1 SE; $N = 4$.

Saprolegnia affected the competitive relation between *Rana* and *Hyla*. In the absence of *Saprolegnia*, *Rana* had strong negative effects on the mass and survival of *Hyla*. However, increased mortality of *Rana*, resulting from *Saprolegnia* infection of embryos, led to a reversal of the outcome of interactions between *Rana* and *Hyla*. The overall effect of *Saprolegnia* on *Rana* is more difficult to predict. Although survival of *Rana* exposed to *Saprolegnia* was decreased, *Rana* larvae that survived infection were released from intraspecific competition and thereby developed faster and were larger at metamorphosis. Thus, *Saprolegnia* may have positive effects on both *Hyla* and *Rana*.

The potential effects that *Saprolegnia* may have on *Rana* and *Hyla* assemblages will likely be the direct result of changes in the survival patterns it can cause. Alteration of embryo and larval survivorship patterns may ultimately influence recruitment into the adult population of both of these species. In addition, *Saprolegnia* may also induce secondary effects as a result

of changes in developmental time and mass at metamorphosis, which can influence individual fitness and thus may ultimately affect populations and the communities of which they are components. Rates of growth and development are crucial features of the population ecology of amphibians that breed in temporary ponds because they must reach a certain minimum size to metamorphose before pond drying (Wilbur 1972, Skelly 1996). Extending the larval period can result in increased exposure to aquatic predators, and can affect the post-metamorphic stage by leaving juvenile amphibians inadequate time to store fat for winter survival (e.g., Morin 1983, Woodward 1983). Smaller size at metamorphosis can decrease both survival and reproductive success in the terrestrial environment (Wilbur 1972, Morin 1983, Woodward 1983).

There have been a large number of experiments that have evaluated the causes for distributional patterns and the composition of amphibian assemblages (e.g., Wilbur 1972, Morin 1983, Werner and Anholt 1996). This research has revealed important interrelationships

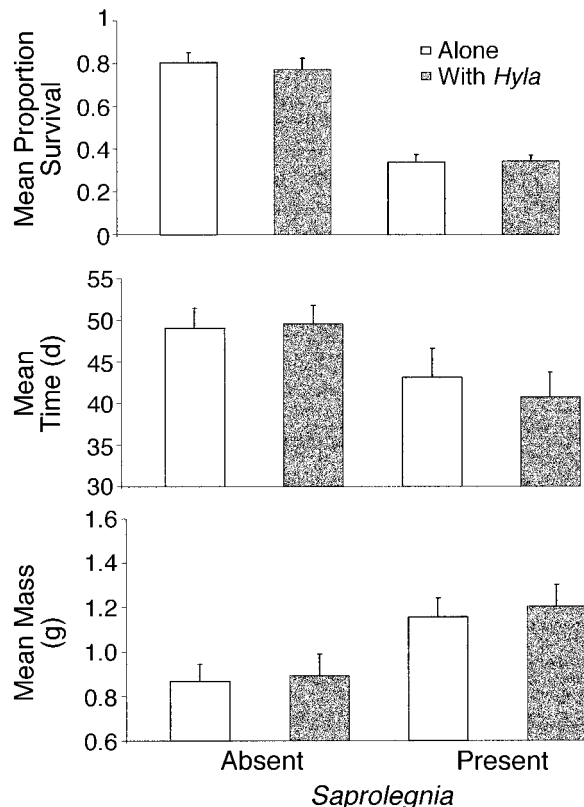


FIG. 2. Summary of the effects of *Saprolegnia* (absent or present) and *Hyla* on the mean survival (survival to metamorphosis), mean time (time to metamorphosis), and mean mass (mass at metamorphosis) of *Rana*. Bars represent the mean ± 1 SE; $N = 4$.

TABLE 2. Results of MANOVA for overall effects of *Rana*, *Saprolegnia*, and density on *Hyla* survival to hatching, survival to metamorphosis, mass, and time to metamorphosis and ANOVAs for each response variable.

Variable	$F_{4,21}$	P
MANOVA		
Constant	1329.63	<0.0001
<i>Rana</i>	9.928	0.0001
<i>Saprolegnia</i>	11.725	<0.0001
Density	4.084	<0.013
<i>Rana</i> $\times$ <i>Saprolegnia</i>	7.712	<0.001
<i>Rana</i> $\times$ Density	0.896	0.484
<i>Saprolegnia</i> $\times$ Density	1.033	0.413
<i>Rana</i> $\times$ <i>Saprolegnia</i> $\times$ Density	0.848	0.482
ANOVAs		
Mass		
<i>Saprolegnia</i>	9.767	0.005
<i>Rana</i> $\times$ <i>Saprolegnia</i>	14.608	0.001
Time		
<i>Rana</i> $\times$ <i>Saprolegnia</i>	2.273	0.001
Survival to metamorphosis		
<i>Rana</i>	22.896	<0.001
<i>Saprolegnia</i>	24.865	<0.001
<i>Rana</i> $\times$ <i>Saprolegnia</i>	27.440	<0.001

Notes: The significance level for univariate tests is 0.00625 (Bonferroni-adjusted for four response variables). Response variables are proportion surviving to hatching (survival to hatching), mass at metamorphosis (mass), time to metamorphosis (time), and proportion surviving to metamorphosis (survival to metamorphosis). For simplicity we have only included ANOVA comparisons that are significant.

between both abiotic and biotic factors. Specifically, these studies show how timing of pond drying, competition for food, and predation can all have important effects on tadpole performance and thus on larval amphibian assemblages (see reviews in Skelly 1996, Wellborn et al. 1996). Pathogens of amphibians can also directly affect performance and may play a role in mediating larval competitive interactions (e.g., Steinwascher 1979, Goater et al. 1993, Beebe 1995, Griffiths 1995, Petranks 1995). Unfortunately, there have been few systematic attempts to evaluate the importance of pathogens in influencing community-level patterns.

Numerous studies have documented that predators can alter the outcome of interspecific competition among their prey (e.g., Paine 1966, Wilbur 1972, Morin 1981, Werner and Anholt 1996). Pathogens such as *Saprolegnia* may also act as a keystone species (Power et al. 1996) by causing differential mortality that reduces the density of competitively superior species resulting in patterns similar to those observed for keystone predators. In our system, the density of the superior competitor, *Rana*, was reduced while the inferior competitor, *Hyla*, was not affected by the presence of *Saprolegnia*. Thus, both predators and pathogens may provide a competitive release for competitively inferior

species, by increasing mortality of competitively superior species.

Recent studies suggest that outbreaks of disease may also play an important role in population declines and reductions in range experienced by many amphibian species (Blaustein et al. 1994a, Laurance et al. 1996, Kiesecker and Blaustein 1997). However, the factors that influence outbreaks of disease and the consequence they may have for amphibian communities are poorly understood. The differences in susceptibility to infection with *Saprolegnia* experienced by *Rana* and *Hyla* may result from differences in their ability to cope with stressful ambient UV-B radiation. Both species lay their eggs in open shallow water where they are likely exposed to high levels of ambient UV-B radiation (Blaustein et al. 1994b, Kiesecker and Blaustein 1997). Field experiments demonstrated that *Rana* embryos have increased susceptibility to *Saprolegnia* infection when exposed to ambient UV-B radiation (Kiesecker and Blaustein 1995). In contrast, infection of *Hyla* embryos with *Saprolegnia* was not affected by UV-B exposure (Kiesecker and Blaustein 1995). Any factor that could

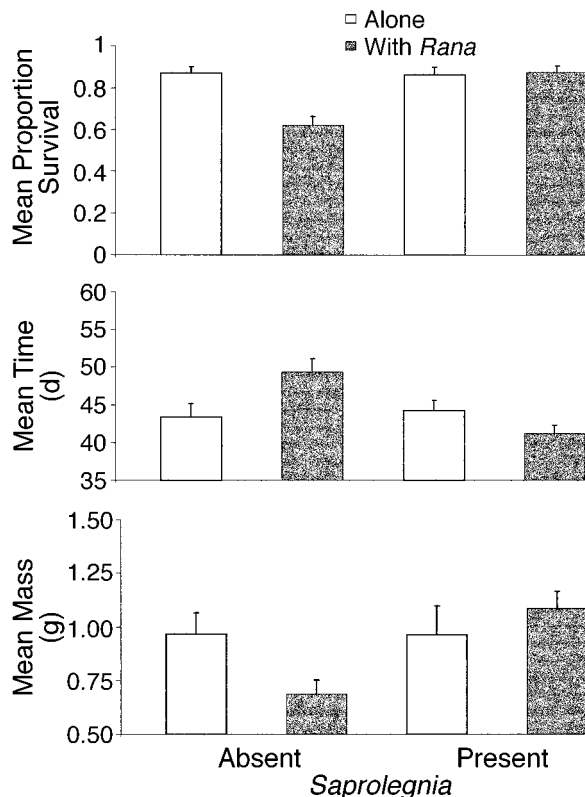


FIG. 3. Summary of the effects of *Saprolegnia* (absent or present) and *Rana* on the mean survival (survival to metamorphosis), mean time (time to metamorphosis), and mean mass (mass at metamorphosis) of *Hyla*. Bars represent the mean $\pm$ 1 SE; $N = 4$.

increase the exposure of embryos to UV-B radiation (e.g., ozone thinning, drought-induced changes in water depth) could result in outbreaks of *Saprolegnia* infection for *Rana*. Understanding the complex interaction between stress and disease will contribute to our understanding of how disease may ultimately influence community dynamics.

Our results suggest that any general predictive theory of community ecology must incorporate the importance of pathogens and their ability to alter the outcome of interactions. Only when we increase the number of experimental manipulations of pathogens under natural conditions will we understand their importance to communities.

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ERRATA

During final preparation of the article by J. H. Braatne and L. C. Bliss (1999) entitled “Comparative physiological ecology of lupines colonizing early successional habitats on Mount St. Helens,” *Ecology* **80**(3):891–907, editorial staff incorrectly substituted the term “evergreen” for “wintergreen” in various references to *Lupinus lepidus*. The errors occur in the first line of the abstract (p. 891); in the first paragraph of the Introduction (p. 891); in the legend to Plate 1 (p. 892); and in the first sentence of the Methods (p. 892). The Publications Office of the Ecological Society of America regrets this error, and we apologize to the authors and to our readers.

In the article by C. E. Cáceres (1998) entitled “Interspecific variation in the abundance, production, and emergence of *Daphnia* diapausing eggs,” *Ecology* **79**(5):1699–1710, a transcription error was made when converting the raw emergence data to number emerging per square meter. All reported values for daphniid emergence (e.g., Fig. 7, and “Direct estimate” in Table 2) should be multiplied by a factor of 7.7. This does not include the “indirect” estimates for emergence reported in Table 2. This error affects only the values for emergence rates; the conclusions of the paper are unaffected.

In the article by Christopher R. Tracy (1999) entitled “Differences in body size among chuckwalla (*Sauromalus obesus*) populations,” *Ecology* **80**(1):259–271, the first line of the first full paragraph on p. 260 should read as follows: “The association between small lizards with larger fat stores in areas with **low** plant diversity vs. large lizards with lesser fat stores in areas with **higher** plant diversity might represent a trade-off in resource allocation” (corrected wording appears here in bold type).
