Resource Availability and Costs of Reproduction in the Salamander
Plethodon cinereus

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We examined trade-offs between current reproduction and future reproductive potential in a terrestrial salamander (*Plethodon cinereus*) in outdoor enclosures. We raised females that differed in brooding status under manipulations of food level and tail condition in two years (1993 and 1994), and measured the effects of our treatments on current reproductive success (egg survival) and indicators of future reproductive potential (female growth and production of ova). Current reproductive success depended strongly on clutch size but not resource availability. Brood abandonment was higher among females with small clutches. Both brooding status and tail condition affected future reproductive potential. Brooding females gained less mass and produced fewer new ova than nonbrooders. Tail loss resulted in increased tail regeneration but decreased production of new ova. These strong main effects were consistent between years, despite differences in experimental protocol and limited sample sizes. Food levels affected female growth only in interaction with brooding status, and these effects differed between years. Gain in mass was affected by this interaction more strongly in 1993 than in 1994, and tail regeneration was only affected in 1994. Understanding costs of reproduction in natural populations will require understanding how the condition of both the organism and its environment influence energy allocation to current reproduction and different components of future reproductive potential.

E VIDENCE that costs of reproduction exist has accumulated for a variety of taxa (reviewed in Reznick, 1985; Roff, 1992; Stearns, 1992), but what determines how and when such costs are expressed phenotypically? This may have important consequences for understanding how individuals' investment in reproduction affects their interactions with the environment and other organisms. We examined the nature and magnitude of reproductive costs for a terrestrial salamander by comparing the growth and production of new ova for females that differed in their current reproductive status (i.e., successful brooders vs nonbrooders). Further, we manipulated food levels and female tail condition to better understand how reproductive costs are manifested under different circumstances. Thus, we address physiological costs resulting from allocation of limited energy between different functions (Calow, 1979).

The Red-Backed Salamander (*Plethodon cinereus*) is well suited for the study of reproductive costs. The lifespan of these small (∼1 g) salamanders is unknown, but females do not reach maturity until the end of their second or third summer (Sayler, 1966; Nagel, 1977; J. Secki and H. Wilbur, unpubl.). After reaching maturity, females reproduce annually or biennially (reviewed in Petranka, 1998), and they make a substantial investment in each reproductive season in terms of clutch size and brooding behavior.

At our study site, *P. cinereus* lays a clutch of about seven (range: 2–13) relatively large eggs in late May or early June and remains coiled around the eggs until they hatch in August (pers. obs.). While brooding, females generally do not leave their eggs to forage but rather rely upon their fat reserves and whatever small arthropods they encounter at their oviposition site (Bachmann, 1964; Ng and Wilbur, 1995). In addition, females may incur metabolic costs while protecting their broods from desiccation, intruders, and predators (Highton and Savage, 1961; Bachmann, 1984).

We manipulated resource availability by altering food levels in the environment and the tail condition of the female salamanders. The tail comprises 20–35% of the total mass of these adult females (pers. obs.) and is an important site of energy storage (Fitzpatrick, 1976; Fraser, 1980). By removing salamanders' tails, we were able to reduce the internal energy reserves available to females. Comparing the effects of the two resource manipulations permits inferences about how reproductive costs may be influenced by different kinds of changes in resource availability.

We addressed three main questions about the costs of reproduction. First, are there trade-offs between current reproductive effort and future reproductive potential? If reproduction and parental care are costly, females that attend their

broods should show grow less and produce fewer new ova than females that desert their broods or do not reproduce in a given season. Second, if such trade-offs exist, how do they affect different aspects of the phenotype? We measured the females' change in mass, tail regeneration, and production of new ova to gain insight into how reproductive costs affected indirect and direct measures of future reproductive potential. Finally, under what conditions are trade-offs between current and future reproduction evident? In particular, can resource limitation influence behavioral decisions about brood desertion and magnify differences in growth and production of new ova among females differing in reproductive status?

MATERIALS AND METHODS

In 1993 and 1994, we raised female *P. cinereus* in field enclosures under a $2 \times 2 \times 2$ factorial design, crossing two tail condition treatments (control or tailless), two food levels (low or high), and two brooding status treatments. In 1993, we used 28 brooding females with their clutches in the experiment. At the end of this experiment, we defined brooding status by categorizing females as either "successful" or "unsuccessful." Successful brooders had at least one surviving egg or hatchling at the end of the experiment, whereas unsuccessful brooders had no surviving offspring. We chose this criterion for defining success because females (even those with small clutches) remain coiled around their egg(s) (pers. obs.) and have limited opportunities for foraging compared to females that have lost, eaten, or abandoned their eggs (Bachmann, 1964; Ng and Wilbur, 1995). In 1994, we were unable to find enough brooding females to repeat the original experimental design. Instead, we used 12 brooding females with clutches and 12 nonbrooding females to compare the effects of tail condition and food treatments on females that differed in their reproductive investment for that season. The nonbrooders were drawn from the pool of adult-sized females that did not reproduce that year; they did not differ significantly from brooders in initial mass ($t_{22} = 1.75$, $P = 0.094$) or initial snout–vent length ($t_{22} = 1.59$, $P = 0.126$). We transilluminated each female with a fiber-optic light to confirm that they had neither mature ova nor the enlarged, convoluted oviducts of reproductively active females that had laid eggs that season.

We collected salamanders from beneath rocks and logs near Mountain Lake Biological Station in Giles County, Virginia. Females and their clutches were transported to the laboratory where they were housed individually in petri dishes with moistened filter paper. We assessed both female and clutch condition at the beginning of each experiment. For each female, we measured mass to the nearest 0.01 g and snout–vent length (SVL) and tail length to the nearest 0.01 mm. In 1993, the average mass and SVL ($\pm$ SE) of females at the start of the experiment was 1.08 ± 0.03 g and 44.44 ± 0.50 mm, respectively. In 1994, females averaged 0.99 ± 0.03 g and 42.41 ± 0.45 mm. For each clutch, we counted the number of eggs and measured clutch mass and egg diameter. In 1993, clutches averaged 7.29 ± 0.46 eggs and 0.80 ± 0.07 g at the start of the experiment. In 1994, clutches averaged 7.00 ± 0.78 eggs and 0.66 ± 0.07 g.

The two tail condition treatments were the same for both years of the study. For the tailless treatment, we grasped females' tails with forceps 5 mm posterior to the end of the vent and applied light pressure. *Plethodon cinereus* autotomize their tails by a sharp muscular contraction that cleaves the vertebra proximal to the forceps in response to this stimulus (Wake and Dresner, 1967). We removed 5 mm from the tip of control animals' tails. After performing the tail treatment, we re-measured each female's mass, snout–vent length and tail length. The amount of biomass removed from females was 0.27 ± 0.01 g (mean $\pm$ SE) in the tailless treatment and 0.03 ± 0.01 g in the control treatment. We observed females for at least two days after administering the tail treatments. All of the brooding females used in our experiments remained coiled around or positioned near their eggs during this period and, therefore, were considered to be brooding normally when they were introduced into the experimental units.

Salamanders in high food treatments were given four times the ration offered to females in low food treatments, but we manipulated different food resources in the two years of the study. In 1993, we provided salamanders with 40 week-old crickets (low food treatment) or 160-week-old crickets (high food treatment) once per week. These levels were chosen because they yielded some growth differences in a previous experiment with brooding *P. cinereus* (Ng and Wilbur, 1995). However, we changed our treatment in the following year after responses to food were relatively small. In 1994, we manipulated food level by adding either 2 cm of leaf litter (low food treatment) or 8 cm of leaf litter (high food treatment) atop the mulch in the experimental enclosures, reasoning that salamanders were probably getting their food sup-

ply from small invertebrates that were introduced with the leaf litter (see Petranka, 1998).

The 1993 experiment was conducted in seven wooden boxes ($1.18 \times 1.18 \times 0.15$ m) placed in a forested area that exposed the salamanders to natural conditions of light, temperature, and moisture. Each box was divided equally into four compartments, and each female salamander was randomly assigned to a treatment and to a compartment within one of the boxes. An aluminum screen lid covered the top of each box and ensured that salamanders and crickets could not move between compartments. At the beginning of the experiment, we placed a 7 cm layer of soil, a 7 cm layer of shredded hardwood mulch, and a 7 cm layer of leaf litter into each compartment. Next, we placed each female and her clutch under a rock on the mulch layer beneath the leaves. We then secured the screen lids onto each box. Once each week, we introduced either 40 or 160 crickets through a port on the side of each compartment.

The 1994 experiment was conducted in 24 plastic tubs ($0.61 \times 0.38 \times 0.22$ m) placed in a similar natural setting. We drilled two small holes 2 cm from the bottom of opposite ends of each tub for drainage and covered these with mesh wire. The tubs were filled with a 2 cm layer of gravel, a 6 cm layer of soil, and a 6 cm layer of hardwood mulch. Atop the mulch, we added a layer of either 2 cm or 8 cm of leaf litter from a well-mixed collection of leaves gathered from the forest floor. We placed each nonbrooding female or female with her clutch under a small rock on the mulch layer beneath the leaves. A screen lid was caulked onto each tub, and then tubs were left undisturbed for the duration of the experiment.

The experiment ran from 15 July to 14 August in 1993 and from 22 July to 13 August in 1994. At the end of each experiment, we removed the screen lids and carefully searched through all of the material in each unit to recapture the females and collect any eggs and hatchlings that were present. All salamanders were transported to the laboratory where we measured mass and tail length and counted the surviving offspring. We also transilluminated each female with a fiber-optic light to count the number of ova being yolked for the next year.

Statistical analyses.—Because of the differences in experimental methods, data from the two years were analyzed separately. In 1993, two control females in low food enclosures were not recovered at the end of the experiment, leaving a total sample size of 26. In 1994, two females in the high food treatment were not recovered at the end of the experiment (one tailless brooder and one control nonbrooder), and one tailless brooding female in the low food treatment abandoned her clutch and was eliminated from the analysis, leaving a total sample size of 21.

We compared the initial masses, snout–vent lengths, clutch sizes, and clutch masses for successful and unsuccessful brooders in 1993 using a multivariate analysis of variance (MANOVA). When the MANOVA revealed significant differences, we conducted univariate tests and Fisher's LSD mean comparison tests. We then used Fisher's exact test to examine the main effects of food and tail treatments on the likelihood of a female being a successful brooder in 1993. Among successful brooders in both 1993 and 1994, we conducted a two-way analysis of variance (ANOVA) to assess the impact of the tail and food treatments on the proportion of eggs surviving in our experiments. We used Lilliefors and Bartlett's tests to examine normality and homoscedasticity of errors, respectively, and found no serious violations. To investigate a potential trade-off between egg size (measured as egg diameter) and egg number, we also calculated the Pearson product moment correlation coefficient between these two variables for all the clutches that we collected each year.

We conducted a MANOVA for each year's data to test the main effects and two-way interactions of brooding status, food level, and tail treatment on female growth (change in mass and tail length from the time the tail treatments were administered to the end of the experiment) and reproductive investment for the next season (the number of new ova seen yolking among the follicles of the female at the end of the experiment). The three-way interaction between factors was not included in the analysis because two of the treatment groups being compared (1993 control and tailless nonbrooders with high food) would have contained only one individual based on < 100% recapture of females at the end of the experiment. In 1994, we included initial mass as a covariate in the MANOVA after an ANOVA revealed that females assigned to different tail treatments differed significantly in initial mass in spite of our randomization procedure ($F_{1,15} = 8.93$, $P = 0.009$). In 1993, mean initial mass did not differ significantly between treatment groups ($F_{1,24} = 2.96$, $P = 0.098$). When a MANOVA revealed significant multivariate effects, we conducted univariate tests and Fisher's LSD mean comparison tests. Bartlett's tests indicated that the data on production of ova did violate the assumption of homoscedasticity, but we were unable to correct this by transforming the data. However, because

TABLE 1.   RESULTS FROM THE MANOVAS AND SUBSEQUENT UNIVARIATE TESTS EXAMINING THE EFFECTS OF BROODING STATUS, FOOD LEVEL, AND TAIL TREATMENT ON FEMALE SALAMANDER GROWTH AND PRODUCTION OF NEW OVA.

1993	Multivariate test			Univariate test P-values		
Effect	Wilks' Lambda	$F_{3,17}$	P	Change in mass	Change in tail	Number of ova
Status	0.308	12.75	<0.001	<0.001	0.063	0.002
Food	0.892	0.69	0.571	0.289	0.252	0.416
Tail	0.435	7.37	0.002	0.082	0.003	0.019
Status*Food	0.625	3.41	0.042	0.005	0.714	0.829
Status*Tail	0.928	0.44	0.726	0.554	0.631	0.349
Tail*Food	0.773	1.66	0.212	0.121	0.476	0.728
1994	Multivariate test			Univariate test P-values		
Effect	Wilks' Lambda	$F_{3,11}$	P	Change in mass	Change in tail	Number of ova
Status	0.169	18.05	<0.001	<0.001	0.306	0.013
Food	0.660	1.89	0.190	0.116	0.436	0.563
Tail	0.196	15.06	<0.001	0.888	<0.001	0.037
Status*Food	0.310	8.15	0.004	0.060	0.017	0.144
Status*Tail	0.460	4.31	0.031	0.008	0.011	0.822
Tail*Food	0.878	0.51	0.683	0.704	0.632	0.221

the MANOVA generally is robust against departures from this assumption, this variable was still included in the analysis.

RESULTS

Current reproductive success.—In 1993, eight of the 26 females recaptured at the end of the experiment were unsuccessful brooders (i.e., there were no eggs or hatchlings recovered from their experimental units). Initial size of the clutch, but not the size of the female, was related to brooding success (Wilks' $F_{4,21} = 3.45$, $P = 0.026$). Successful and unsuccessful brooders had similar initial snout-vent lengths and masses (univariate $F_{1,24} = 1.13$, $P = 0.299$), but females that were unsuccessful had fewer eggs at the start of the experiment than successful females (mean ± SE: 5.13 ± 0.64 eggs vs 8.00 ± 0.42 eggs, respectively; univariate $F_{1,24} = 14.29$, $P = 0.001$). The initial total clutch masses of unsuccessful females also tended to be smaller than initial clutch masses of successful females, but this difference was marginally nonsignificant (mean ± SE: 0.58 ± 0.09 g vs 0.86 ± 0.08 g, respectively; univariate $F_{1,24} = 3.92$, $P = 0.059$).

Brooding success was not strongly related to our experimental treatments. There was a trend toward increased success in high food treatments (12/14 = 86% of females successful) compared to low food treatments (6/12 = 50% successful). However, sample sizes were small

and this difference was marginally nonsignificant (Fisher's exact test, $P = 0.090$). The probabilities of brooding success for females in the control and tailless treatments were virtually identical (67% vs 71%; Fisher's exact test, $P > 0.99$).

For successful brooders, offspring survival was 58.7 ± 6.2% in 1993 and 67.6 ± 7.7% in 1994 (mean ± SE). We did not find dead eggs or hatchlings in these enclosures at the end of the experiment, so the sources of mortality in these clutches are unknown. In both years, ANOVAs revealed that offspring survival was unaffected by food level, tail treatment, or the interaction between these factors (in 1993, all $F_{1,14} \leq 1.81$ and all $P \geq 0.199$; in 1994, all $F_{1,5} \leq 1.19$ and all $P \geq 0.325$). We did not find a significant correlation between egg number and diameter among the clutches we collected in either 1993 ($r = 0.132$, $P = 0.502$) or 1994 ($r = -0.319$, $P = 0.339$).

Future reproductive potential.—In each year, a MANOVA revealed strong multivariate effects of brooding status and tail treatment on indicators of female salamanders' future reproductive potential (gain in mass, tail regrowth, and production of ova). At the multivariate level, the interaction between food level and brooding status affected female growth in both years, but the interaction between tail treatment and brooding status affected growth only in 1994 (Table 1).
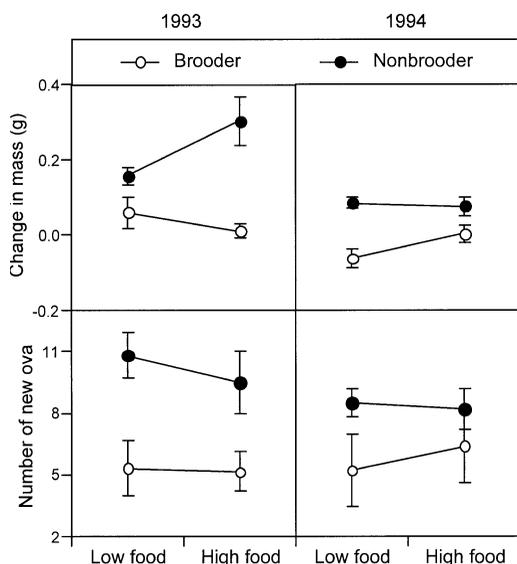
Fig. 1. Mean ± SE change in mass (top panels) and production of new ova (bottom panels) by food treatment for females differing in brooding status in 1993 (left panels) and 1994 (right panels). In both years, successfully brooding females grew less and yolked fewer new ova than nonbrooders. Food level and brooding status interacted to affect change in mass.

Fig. 2. Mean ± SE tail regeneration (top panels) and production of new ova (bottom panels) by tail treatment for females differing in brooding status in 1993 (left panels) and 1994 (right panels). In both years, control females regenerated less tail length but yolked more new ova than tailless females.

Brooding status affected changes in mass and allocation to future reproduction similarly in 1993 and 1994 (Fig. 1, Table 1). Univariate analyses indicated that females that successfully brooded gained less mass and yolked fewer new ova than did females that were either non-brooding or unsuccessful brooders.

The interaction between brooding status and food level had different effects on females in the two years of the study (Fig. 1, Table 1). In 1993, unsuccessful brooders gained more mass than successful brooders, but mean comparison tests indicated that the difference in growth was strong in the high food treatment ($P < 0.0001$) and marginally nonsignificant in the low food treatment ($P = 0.075$). Only the unsuccessful brooders gained more mass in the high food treatment than in the low food treatment ($P = 0.020$). In 1994, the interaction between brooding status and food level had a marginally nonsignificant effect on change in mass (univariate test: $P = 0.060$). In this case, mean comparison tests revealed that nonbrooding females always grew more than brooding females ($P \leq 0.020$), and only the brooders grew more with high food than with low food ($P = 0.023$). Univariate analyses also indicated that tail regeneration was significantly affected by this interaction only in 1994: brooding females under low food condi-

tions regenerated more tail length than either nonbrooders under low food or brooding females under high food (mean comparisons: $P \leq 0.027$).

Tail treatment affected allocation to future reproduction and tail regeneration similarly in both years (Fig. 2, Table 1). Univariate tests revealed that tailless females yolked significantly fewer new eggs but regenerated more tail tip than control females. This result was not simply a consequence of the fact that tailless females were missing more tail length and thus had more scope for regrowth. In 1993, tailless females regenerated an average of 4.29 ± 0.39 mm (± SE) of tail, whereas in 1994 tailless females regenerated an average of 3.76 ± 0.46 mm of tail. Both of these values are less than the 5 mm of tail tip that was removed from each control female.

The interaction between tail treatment and brooding status significantly affected mass change and tail regeneration only in 1994 (Fig. 2, Table 1). Mean comparison tests indicated that among tailless females, successful brooders regenerated more tail length than nonbrooders (mean ± SE: 4.72 ± 0.52 mm vs 3.12 ± 0.57 mm, $P = 0.016$) but tended to gain less mass than nonbrooders (0.02 ± 0.02 g vs 0.07 ± 0.01 g, $P = 0.065$). Among control females, tail regeneration was similarly low for brooders and nonbrooders ($P = 0.239$), but brooders gained

much less mass than nonbrooders (-0.06 ± 0.02 g vs 0.10 ± 0.03 g, $P < 0.0001$).

DISCUSSION

Current reproductive success.—Among organisms with parental care, individuals can modify their reproductive investment for a given season even after offspring are produced. In 1993, 31% of our brooding females had no surviving eggs or hatchlings by the end of the experiment. Three observations suggest that these females abandoned their clutches. First, at the end of the experiment, only 25% (2/8) of unsuccessful females were found under the rock where they had initially been placed with their clutch of eggs, whereas 94% (17/18) of successful females were still found in this location. Second, all eggs were healthy when they were placed into the experiment, and we found no evidence that any predators capable of consuming eggs or hatchlings had invaded the experimental enclosures. Third, abandoned *P. cinereus* eggs have a much lower likelihood of survival than eggs that are attended by females, even in controlled laboratory conditions (Highton, 1960; Highton and Savage, 1961).

Brood desertion may be advantageous for an iteroparous organism when the costs associated with attendance are great enough to outweigh the fitness value of the current clutch (Tait, 1980; Clutton-Brock, 1991; Roff, 1992). For *P. cinereus*, brood desertion would allow females to avoid investing the time and energy required for attending their eggs (Bachmann, 1964; Ng and Wilbur, 1995) and defer further reproductive effort until conditions may be more favorable. Brood desertion was relatively infrequent in our study, suggesting that current reproductive investment in this species is guarded, even at a cost to future reproductive potential, unless conditions are severe.

Two factors appeared to affect female behavioral decisions about brood desertion. First, females that abandoned their clutches in 1993 had significantly fewer eggs at the start of the experiment than females that remained with their eggs. The level of offspring mortality observed in clutches of successful brooders (mean ± SE: 3.39 ± 0.53 eggs lost) was not enough to explain the disappearance of the entire broods of the unsuccessful females (5.13 ± 0.64 eggs lost). Larger clutches have higher fitness values and, therefore, should be less likely to be abandoned than smaller clutches (Roff, 1992). Indeed, examples from birds and fish also illustrate that small broods are more likely to be abandoned or cannibalized than large broods (Mrowka, 1987; Armstrong and Robertson, 1988; Bustnes and Erikstad, 1991). Second, low resource levels may induce females to reduce their allocation of energy to current reproduction. In our study, females in low food treatments tended to be more likely to abandon their eggs than females in high food treatments. In other taxa, if brooding becomes more energetically expensive because of changes in food availability or parental condition, parents may decrease investment in their current clutch rather than jeopardize their own growth and survival (Townshend and Wootton, 1985; Sæther et al., 1993; Mauck and Grubb, 1995).

Removing the tails of the female salamanders, however, had no impact on their likelihood of brood desertion. This suggests that caudal lipid reserves are not critical for a female's maintenance during brooding. In another plethodontid salamander with similar brooding behavior (*Desmognathus ochrophaeus*), Fitzpatrick (1976) found that only a small percentage of the total carcass lipids were used during periods of energetic stress including brooding and overwintering. He postulated that carcass lipids may be used primarily for rapid replenishment of ovarian fat bodies associated with vitellogenesis. If this is the case with *P. cinereus*, caudal lipid reserves should be more likely to affect future reproductive potential than current reproductive success; in fact, this is what we observed.

For females that did not abandon their broods, none of the experimental manipulations affected offspring survival. In natural settings where females may also have to defend their nests, female condition should have a greater impact on egg survival: a smaller or tailless female may be more likely to lose her eggs to predators or to lose her brooding territory to another individual (Mathis, 1990; Wise and Jaeger, 1998).

Future reproductive potential.—We measured the expectation of future reproduction through growth (increase in mass and tail length) and production of ova. We assume that growth affects future reproductive success in this species because there are positive correlations between female body size and number of mature ova in several populations (Nagel, 1977; Lotter, 1978; Fraser, 1980). Further, body size and tail condition provide advantages in acquiring and defending high-quality territories (Mathis, 1990; Gabor, 1995; Wise and Jaeger, 1998), which in turn provide enhanced foraging opportunities (Jaeger et al., 1981) and can improve access to mates (Mathis, 1991) or oviposition sites.

A more direct measure of future reproductive

potential is the number of yolking follicles at the end of the summer. Because oocyte maturation in *P. cinereus* is simultaneous rather than sequential (Fraser, 1980), the number of ova that we counted in a female in August represented the maximum number of eggs she could lay the following year (Crespi, 2001). We did not find a significant relationship between egg diameter and egg number for the clutches we collected in either year. Thus, females that produced fewer eggs did not produce larger eggs that might survive better or generate more vigorous hatchlings. Consequently, females that produce more offspring per season should have higher relative fitness than females with fewer offspring.

Brooding status strongly affected direct and indirect measures of future reproductive potential. Females that successfully brooded gained less mass than females that either abandoned their clutches (1993) or did not brood that season (1994). This response reflects a cost that females incur as a consequence of staying with their clutches (also see Ng and Wilbur, 1995), and it has been observed in a variety of taxa. In fishes (van den Berghe, 1992; Marconato et al., 1993; Balshine-Earn, 1995), reptiles (Schwarzkopf, 1993; Brown and Weatherhead, 1997), and invertebrates (Berglund and Rosenqvist, 1986), parents that incubate or guard their offspring often exhibit reduced growth compared to nonreproductive individuals or individuals that provide less parental care. In both years of our study, females that brooded successfully also yolked fewer new ova than unsuccessful brooders or nonbrooders. This represents a trade-off between current reproduction and a direct measure of future reproductive potential, and our study is one of relatively few that have documented this trade-off in animals through manipulative experiments (also see Nalepa, 1988; Smith and Wootton, 1994; Balshine-Earn, 1995).

Our food level manipulations also affected female condition, but only in interaction with brooding status. In 1993, only unsuccessful brooders gained more mass with increased food, whereas in 1994, only brooding females responded to higher food levels with increased growth. The contrast between our results in the two years of the study suggests that differences in the condition of brooding versus nonbrooding females depend on the types of resources available as well as their abundance. In 1994, food level did not affect tail regrowth in nonbrooders, but brooding females regenerated more tail length under low food than high food conditions and, in the low food treatment, re-

generated more tail length than nonbrooders. Although we cannot explain why low food was associated with enhanced tail regeneration in brooders, this result illustrates the value of examining multiple aspects of performance when investigating costs of reproduction. If we had examined only tail growth, we would have concluded that brooding females outperformed nonbrooders. However, because we also compared gain in mass and production of ova, we were able to discern a cost of reproduction for females in the low food treatment.

In neither year did we observe effects of the food treatments on our measure of direct allocation to future reproduction. Thus, even when female salamanders benefited from higher food levels in terms of increased growth, they did not yolk more ova for the next reproductive season. This result is contrary to observations in other organisms that increasing food availability can lead to increases in fecundity (Calow and Woollhead, 1977; Reznick and Yang, 1993; Smith and Wootton, 1995). The lack of response to food level in our study may be related to the fact that the food manipulations did not cover the entire brooding season, and much of the energetic commitment to reproduction may already have been made by the time our experiments began (Fraser, 1980). However, Fraser (1980) also reported that raising *P. cinereus* on different food rations for 180 days did not alter the number of ova females produced. This suggests that, even under good growth conditions, females may be limited by their ability to accumulate sufficient lipid reserves for enhanced production of ova. This interpretation is consistent with the observation of strong effects of the condition of the tail (a lipid reserve) on direct allocation to future reproduction.

In both of our experiments, tailless females invested more in regenerating lost tail length than control females but yolked fewer new ova by the end of the brooding season. Among control females, the low level of investment in tail regeneration was not surprising, since most of the functions of a tail are probably not severely compromised by losing the 5 mm tip (mean $\pm$ SE = $14.1 \pm 0.7\%$ of original tail length, $3.6 \pm 0.6\%$ of original mass) that we removed. Instead, available energy was directed toward gaining mass and developing ova. In contrast, females that had almost all of their tail length removed ($83.6 \pm 0.6\%$ of original tail length, $24.9 \pm 0.7\%$ of original mass) were unable to yolk as many new ova, which is likely because of the loss of lipid reserves needed for vitellogenesis (Fitzpatrick, 1976). A similar trade-off was observed in another plethodontid salamander

(*Batrachoseps attenuatus*), in which tailless individuals invested energy into tail regeneration but were less likely to achieve reproductive status than animals with full tails (Maiorana, 1977). These results, as well as examples with birds (Mauck and Grubb, 1995; Svensson and Nilsson, 1997), illustrate trade-offs between direct investment in reproductive effort and somatic maintenance functions.

Acknowledgments

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