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INVESTIGATING THE OPTIMAL REARING STRATEGY FOR *AMBYSTOMA* SALAMANDERS USING A HEMATOLOGICAL STRESS INDEX

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***Abstract.*—Captive-rearing for conservation endeavors is often used as a management tool in response to amphibian declines. The goal of such projects should be to produce organisms that are as functionally equivalent to their wild counterparts as possible. Caudates (salamanders) in the genus *Ambystoma* represent a challenge for rearing because of their aggressive nature, and several recent projects have found higher than normal stress levels in captive-reared salamanders. In this study I compared various captive-rearing scenarios designed to minimize stress levels in Spotted Salamanders (*A. maculatum*). I reared larvae in five treatments, three that varied in starting density (six, 12, and 30 larvae per 1000 L tank), one with high food, and one with added environmental complexity to the tanks (sticks and refugia). After metamorphosis, I weighed the salamanders and collected blood samples to determine the relative abundance of two white blood cell types (neutrophils and lymphocytes) to calculate neutrophil-lymphocyte (N-L) ratios, which covary with stress hormone levels. Increasing density led to lower salamander body mass and decreased survival. Adding food, however, was not effective at increasing survival or body mass, or at lowering the average hematological stress index (N-L ratio). Likewise, adding complexity to the tanks did not affect these variables. Moreover, it was difficult to capture the metamorphosed salamanders from the tanks with the refugia and sticks. The treatment that led to the largest salamanders overall and the only one where N-L ratios were similar to those from the wild was the treatment with the lowest starting density (six larvae per 1000 L tank). Furthermore, N-L ratios across all treatments were a direct function of body size; larger salamanders exhibited lower stress.**

Key Words.—Ambystoma; captive-rearing; conservation; Spotted Salamander; stress

INTRODUCTION

A large component of amphibian conservation will involve captive-rearing of sensitive or declining species for release back into the wild or for maintaining captive colonies. Indeed, this practice is already implemented in response to species declines in many locations (e.g., Griffiths and Pavajeau 2008; Essner and Suffian 2010; Gagliardo et al. 2010). While the success of such programs varies (Griffiths and Pavajeau 2008), for many species on the brink of extinction, this is the only viable management tool left. For projects involving the reintroduction of post-metamorphic individuals, a goal is presumably to rear healthy, functional representatives of the species of interest to ensure maximum lifetime fitness. For some amphibian species, such as anurans, this is not exceedingly difficult, because robust, post-metamorphic individuals can be reared readily (Bloxam and Tonge 1995). However, rearing caudates, such as those in the genus *Ambystoma*, can be problematic because of their tendency to cannibalize conspecifics and their generally high levels of intraspecific aggression (Semlitsch and Reichling 1989; Walls and Blaustein 1995; Wildy et al. 2001; Brodman 2004). For these species, protocols for rearing must be developed that accommodate these behaviors.

Consistent with the high levels of aggression in ambystomatids, several recent studies have found higher than normal stress levels in captive-reared conspecifics. Late-stage, mesocosm-reared Jefferson Salamanders (*A. jeffersonianum*) larvae were found to have moderately elevated resting corticosterone (stress hormone) levels compared to wild larvae (Chambers 2009). In another example, Davis and Maerz (2009) reported that even at low densities (12 larvae per 600 L of water), Spotted Salamanders (*A. maculatum*) metamorphosed with higher than normal stress levels for this genus. Furthermore, stress levels of larval Marbled Salamanders (*A. opacum*) were found to be significantly higher than their wild counterparts of equivalent size, while similar examinations of captive-reared and wild frogs (*Lithobates sphenocephalus*) found no statistical difference (Davis and Maerz 2011). In both these aforementioned studies, stress levels were inferred based on counts of two white blood cell types from blood smears (neutrophils and lymphocytes) that covary with circulating stress hormone concentrations in all vertebrates (reviewed in Davis et al. 2008). Specifically, when stress hormones increase, numbers of circulating neutrophils increase, while numbers of lymphocytes decrease in the bloodstream. In other words, the ratio of neutrophils to lymphocyte (or N-L ratio) increases when individuals become stressed, and this can be a three- or four-fold increase (Davis and Maerz 2010; Davis and Maerz 2011) over typical N-L ratios (i.e., ratios of wild individuals). For wild ambystomatid salamanders, N-L

ratios have been found to be 0.22 in *A. opacum* (Davis and Maerz 2011) and 0.17 in *A. talpoideum* (Davis and Maerz 2008).

Clearly, ambystomatid salamanders represent a challenge in terms of captive-rearing, and their susceptibility to stress in captivity is problematic if the goal is to produce animals that are functionally equivalent to their wild counterparts. Rearing strategies that result in exceptionally stressed post-metamorphic individuals would therefore be undesirable. In fact, the optimal rearing strategy should be one that results in post-metamorphic individuals with resting stress levels that are on par with individuals in the wild. Several factors may influence stress levels during the larval stage. Starting density is well known to affect survival and growth in amphibians, with low densities leading to high survival and large body sizes (e.g., Wilbur 1976; Petranka 1989; Loman 2004). Low density then may lead to reduced stress. There is also evidence that food supplementation can promote survival and growth in amphibians (Werner and Glennemeier 1999; Wildy et al. 2001), and reduces cannibalism in Ambysomatid larvae (Wildy et al. 2001). Finally, adding structural complexity and refugia to the rearing environment may also lead to low stress levels as it may reduce aggressive interactions and competition among individuals (Walls 1995; Brodman 1996; Purrenhage and Boone 2009).

Herein I describe the results of an experiment designed to identify rearing conditions for *A. maculatum* that result in the least amount of stress (i.e., lowest N-L ratios), as well as the highest survival and largest body size. These conditions included low and 'ultra-low' densities, food supplementation, and the addition of structural complexity and refugia to the rearing containers.

MATERIALS AND METHODS

Animal collection.—On 2 February 2010, I collected 15 *A. maculatum* egg masses from three local ponds (five per pond). I brought the egg masses to a nearby field laboratory and placed them in 15 40-L aquaria (one egg mass per aquarium) filled with dechlorinated tap water. Most egg masses began hatching on 23 February. On 16 March, I removed the larvae from the aquaria, placed them all in a 100-L container of dechlorinated tap water, and haphazardly selected individuals from this container to add to mesocosms as described below.

Experimental setup.—I reared the salamanders in 1000 L UV-resistant polyethylene aquaculture tanks (mesocosms), which I filled to the top with dechlorinated tap water and covered the bottom with a layer of leaf litter. Three treatments included a 'low' density (six larvae per tank [0.006 larvae/L]), a 'medium' density (12 larvae per tank [0.012 larvae/L]) and a 'high' density (30 larvae [0.03 larvae/L]) environment. Prior work has shown that a starting density as low as 0.02 larvae/L (the lowest density in that experiment) results in post-metamorphic *A. maculatum* with resting N-L ratios that are twice as high as that of wild individuals (Davis and Maerz 2009). Because the ultimate goal of this study was to identify rearing conditions that minimize stress, the 'low' density in the current experiment was three times smaller than in the prior experiment, and the 'high' density used here is equivalent to the 'low' density used before (Davis and Maerz 2009).

There were two additional treatments; a food supplementation treatment (12 larvae per mesocosm but with triple the food), and a treatment where the tanks were filled to the top with tree limbs and where three cement cinder blocks were submerged in each tank, all to create a 'complex environment' with multiple refugia. This treatment had 12 larvae per tank. I replicated all mesocosm treatments three times (15 tanks total). Across all treatments, the total number of larvae at the start of the experiment was 216.

After I added larvae to each treatment, I added zooplankton from nearby ponds to each tank on a weekly basis. For this, I filled 1 L plastic bottles with concentrated zooplankton from a zooplankton net, and each tank received one bottle of zooplankton per week. Tanks in the high-food treatment received three bottles per week. I did not disturb the larvae and tanks thereafter (i.e., no larvae were netted) except when I added food. I visually inspected the tanks daily beginning in mid-April for metamorphosed individuals.

Salamander processing.—I dip-netted all newly-metamorphosed salamanders from the mesocosms, placed them individually in 1-L plastic containers, and brought them to the laboratory (10 min away). It is important to note that the hematological stress index used in this study is not as time-sensitive as direct measurement of stress hormone levels, in which samples must be obtained within minutes of capture (Romero and Reed 2005). In amphibians, the typical time course of the blood cell response to capture is on the order of hours to days (Bennett and Newell 1965; Bennett and Harbottle 1968). I then euthanized all salamanders immediately via overdose of MS-222, weighed them with an electronic balance, and obtained a blood sample via decapitation. With this method, blood from the heart region was dripped onto a clean microscope slide to make a blood smear (Davis et al. 2010; Davis and Maerz 2010). The time from collection to sampling for all salamanders was less than two hours.

Counting white blood cells.—I examined the dried, giemsa-stained blood smears under 1000X (oil) with a standard light microscope, and within each field of view, I counted all white blood cells. I identified cells as

neutrophils, lymphocytes, eosinophils, basophils and monocytes, following Hadji-Azimi et al. (1987), although in the present study I was concerned only with the numbers of neutrophils and lymphocytes. I counted at least 100 white cells per smear, and I calculated the percentage of cells that were neutrophils and lymphocytes. From this, I obtained the ratio of the two cell types (neutrophil-lymphocyte ratio) for each salamander.

Final data.—The last salamander metamorphosed on 6 June. At this point, I compiled the number of metamorphosed individuals per tank to calculate survival (based on starting densities). In addition, I calculated the average salamander body mass for each tank, as well as the average larval duration (time from hatching to completion of metamorphosis) per tank. Finally, I calculated the mean N-L ratio per tank to index salamander stress levels (Davis et al. 2008). I log-transformed (+1) these ratios prior to analyses to approximate normal distributions.

Data analyses.—The variables of interest in this study were percentage survival, body mass, larval development time, and the log-transformed N-L ratios at the level of the tank (mesocosm). Thus, for each tank I calculated the average body mass, development time, and N-L ratio for analyses. I examined these data across treatments using a one-way analysis-of-variance (ANOVA) and with Tukey's post-hoc tests to elucidate differences among treatments where appropriate (α = 0.05). I used Statistica 6.1 software (Statsoft Inc., Tulsa, Oklahoma, USA) to analyze data.

RESULTS

Survival, body size, and larval duration.—Across all treatments, I collected and examined 118 post-metamorphic salamanders from the initial 216 larvae, for an overall survival rate of 54%. In the statistical analyses of tank-level survival rates, there was significant variation among treatments ($F_{4,10}$ = 9.08, P = 0.002). Average survival of all three low density tanks (six larvae per 1000 L) was 94.4% (Table 1). The lowest mean survival was in the high density (30 larvae per 1000 L) tanks (33.3%).

Mean body mass varied considerably among treatments (Table 1), and this variation was significant ($F_{4,10}$ = 19.36, P < 0.001). The largest salamanders came from the low density treatment, with a grand mean of 1.84 g, followed by the complex environment salamanders (mean = 1.69 g). The smallest salamanders were from the high density treatment (mean = 0.90 g). The time from hatching to completion of metamorphosis did not vary across treatments ($F_{4,10}$ = 1.31, P = 0.3315). Thus, there was no difference in development time in the mesocosm treatments (averaging between 79-85 days; Table 1).

N-L ratios.—There was significant variation in N-L ratios among treatments ($F_{4,10}$ = 3.93, P = 0.036), although the only treatments that were significantly different (based on post-hoc tests) were the high density and low density (Table 1). The mean N-L ratio of salamanders from the low density tanks was 0.44, whereas the mean from the high density tanks was 2.24. Interestingly, the rank order of stress levels among mesocosm treatments was nearly the inverse of the rank order of mean body mass. In fact, when the tank-means of body mass were compared to mean N-L ratios, a highly-significant (negative) relationship was found (Pearson Correlation, r = -0.687, P < 0.001; Fig. 1). Thus, stress level of mesocosm-reared salamanders seem to be tightly linked with body size after metamorphosis; the larger the salamander, the lower its stress, and vice-versa. In contrast, there was no relationship between mean development time and mean N-L ratio among tanks (r = 0.234, P = 0.401), nor between average percentage survival and average N-L ratio (r = −0.347, P = 0.205).

TABLE 1. Summary of parameters measured across rearing treatments in this study of *Ambystoma maculatum*. In all cases, the tank (mesocosm) was the unit of replication. Standard deviations are indicated in parentheses next to means. Homogeneous subsets (based on Tukey's post-hoc tests) are indicated with letters. Treatments are arranged by average % survival.

Treatment*	N (replicates)	N (sals)†	% Survival	Mass (g)	Larval Duration (d)	N-L Ratio
High density (30)	3	31	33.3 (8.8)[a]	0.90 (0.20)[a]	85.4 (7.3)	2.24 (2.66)[a]
Complex environment (12)	3	18	50.0 (8.3)[ab]	1.69 (0.22)[bc]	80.8 (3.1)	0.65 (1.03)[ab]
Medium density (12)	3	23	66.7 (22.0)[abc]	1.58 (0.25) [bc]	84.0 (5.4)	1.48 (2.27)[ab]
High food (12)	3	31	88.9 (19.2)[bc]	1.36 (0.29)[c]	79.3 (4.9)	1.32 (1.98)[ab]
Low density (6)	3	15	94.4 (9.2)[c]	1.84 (0.25)[b]	81.0 (4.9)	0.44 (0.56)[b]
All Groups (216 initial larvae)		118	54.0	1.47 (0.38)	81.3 (2.1)	1.11 (0.83)

* Starting density per tank indicated in parentheses
† Number of surviving salamanders

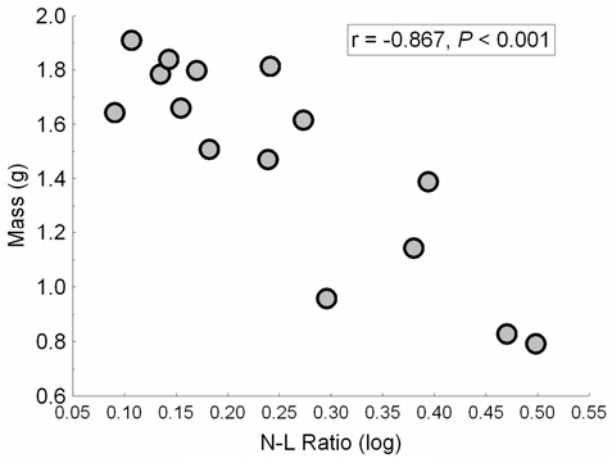

FIGURE 1. Relationship between body mass and neutrophil-lymphocyte ratios (an index of stress) in all post-metamorphic, mesocosm-reared *Ambystoma maculatum* salamanders. Each point represents a mesocosm mean.

DISCUSSION

This study provided a number of new insights into the suitability of various rearing strategies for *Ambystoma* salamanders, which should be of benefit to herpetologists, researchers, and conservationists. For example, results concerning the three densities (six, 12, and 30) within mesocosms were not altogether surprising; with increasing starting density, fewer individuals survived. Furthermore, surviving individuals in the high-density treatment were smaller and had greater stress indices than those in the low-density treatment. This is consistent with prior investigations into the effects of rearing density on stress levels, using both hematological stress indices (Davis and Maerz 2009) and direct measurement of stress hormone levels (Glennemeier and Denver 2002; but see Belden et al. 2007). This supports the idea that increasing density leads to increased aggression among *Ambystoma* salamanders (Semlitsch and Reichling 1989; Brodman 2004).

Adding additional food to mesocosms was not effective at increasing the quality of post-metamorphic salamanders. Survival was not significantly greater in this treatment compared to the medium density treatments, and post-metamorphic salamanders in the high-food tanks did not have larger body sizes than those from tanks with comparable densities. Moreover, their average N-L ratio (1.32) was approximately six times higher than that found in wild ambystomatid salamanders; prior work showed the average N-L ratio of wild *A. opacum* was 0.22 (Davis and Maerz 2011) and 0.17 for wild *A. talpoideum* (Davis and Maerz 2008). In fact, the average N-L ratio of this treatment was similar to the average ratio of salamanders that had been intentionally stressed (1.22) in a prior study (Davis and Maerz 2011). Thus, the N-L ratios of salamanders from this treatment were unacceptably high.

Adding sticks and refugia to the tanks (complex environment treatment) also was not effective at improving quality of post-metamorphic salamanders. Average survival in this treatment was not statistically different than in the tanks with similar densities, nor were body mass and N-L ratios different (Table 1). Moreover it was surprisingly difficult to dip net metamorphosed salamanders in these tanks because of the abundance of sticks and refugia. In fact, it was nearly impossible to sweep through these tanks with a dip net to capture the salamanders, and it was not always easy to see the metamorphosed salamanders during the daily inspections unless they were floating on the surface (often they would retreat to the refugia when I approached). Future rearing projects may want to consider modifying rearing containers with devices to either allow metamorphosing salamanders to freely crawl out into a moist holding chamber or that will trap them passively, which would eliminate the need to catch the metamorphs actively.

The largest salamanders were produced in the mesocosms with low starting densities of six larvae per 1000 L of water, or 166 L per larva (or 0.006 larvae/L). Overall survival in these tanks was over 90% and these individuals had low N-L ratios (Table 1). In fact, the average N-L ratio of salamanders in this treatment (0.44) was the closest of all treatments in this study to the typical ratios of wild ambystomatid salamanders (Davis and Maerz 2008, Davis and Maerz 2011). Of the various rearing conditions considered here, this treatment then appears to be the most effective for producing healthy, low-stress salamanders. Unfortunately, from a logistic standpoint, this means that for conservation-related projects, where producing large numbers of post-metamorphic individuals (for ultimate release into the wild) is a key goal, it may be difficult to produce large numbers of such salamanders without massive numbers of mesocosms. For example, to produce 100 of these large, low-stress salamanders, one would need approximately 20 1000-L cattle tanks (assuming five salamanders are produced per tank on average at this starting density of six). In fact, for the conservation practitioner, and even the herpetologist conducting routine rearing experiments, results from this study suggest that they face a dilemma when designing rearing projects, either produce large numbers of salamanders and face reductions in individual quality, or limit the number of individuals reared to produce the most robust salamanders possible. Given the very large body of literature showing how body size at metamorphosis is a key determinant of lifetime fitness in amphibians (e.g., Beck and Congdon 1999; Chelgren et al. 2006; Scott et

al. 2007), and the equally-large number of studies showing how high stress is detrimental to animals in the long run (e.g., Romero and Wikelski 2001; Blas et al. 2007; Cabezas et al. 2007), I would argue for producing fewer large, low-stress salamanders for conservation purposes. Such individuals would have the greatest chance of long-term survival and would most resemble their wild counterparts.

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