Consumptive and nonconsumptive effects of cannibalism in fluctuating age-structured populations

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Abstract. Theory and empirical studies suggest that cannibalism in age-structured populations can regulate recruitment depending on the intensity of intraspecific competition between cannibals and victims and the nature of the cannibalism window, i.e., which size classes interact as cannibals and victims. Here we report on a series of experiments that quantify that window for age-structured populations of salamander larvae and paedomorphic adults. We determined body size limits on cannibalism in microcosms and then the consumptive and nonconsumptive (injuries, foraging and activity, diet, growth) effects on victims in mesocosms with seminatural levels of habitat complexity and alternative prey. We found that cannibalism by the largest size classes (paedomorphs and ≥age 3+ yr larvae) occurs mainly on young-of-the-year (YOY) victims. Surviving YOY and other small larvae had increased injuries, reduced activity levels, and reduced growth rates in the presence of cannibals. Data on YOY survival in an experiment in which we manipulated the density of paedomorphs combined with historical data on the number of cannibals in natural populations indicate that dominant cohorts of paedomorphs can cause observed recruitment failures. Dietary data indicate that ontogenetic shifts in diet should preclude strong intraspecific competition between YOY and cannibals in this species. Thus our results are consistent with previous empirical and theoretical work that suggests that recruitment regulation by cannibalism is most likely when YOY are vulnerable to cannibalism but have low dietary overlap with cannibals. Understanding the role of cannibalism in regulating recruitment in salamander populations is timely, given the widespread occurrences of amphibian decline. Previous studies have focused on extrinsic (including anthropogenic) factors that affect amphibian population dynamics, whereas the data presented here combined with long-term field observations suggest the potential for intrinsically driven population cycles.

Key words: age structure; Ambystoma tigrinum nebulosum; *cannibalism; consumptive and nonconsumptive effects; Mexican Cut Nature Preserve, Colorado, USA; population fluctuations; recruitment failure; tiger salamanders.*

Introduction

Cannibalism is widespread in nature (Fox 1975, Polis 1981, Elgar and Crespi 1992, Woodward and Hildrew 2002), especially in size-structured populations where it has consequences for community and food web dynamics (Woodward et al. 2005, Rudolf 2007a, b, 2008) and population regulation (e.g., Diekmann et al. 1986, Hastings and Constantino 1991, Claessen et al. 2004, Persson et al. 2004a, b). When cannibals and victims are in different year classes or life stages (e.g., adults and larvae), dominant cohorts of cannibals can regulate recruitment (Gaines and Roughgarden 1985, Hastings and Constantino 1987, McCauley and Murdoch 1987,

Van Buskirk 1992). Negative density dependence and recruitment regulation by cannibalism have been best studied in *Tribolium* beetles (Park et al. 1965, Mertz 1972, Benoît et al. 1998) and predatory fishes (Donovan et al. 1997, Juanes 2003, Post 2003, Andersson et al. 2007). In both cases, whether cannibalism stabilizes or destabilizes populations depends on an interplay between the positive effects on cannibal growth and fecundity and negative effects on victim survival and growth (Hastings and Constantino 1991, Claessen and de Roos 2003, Persson et al. 2004a). That interplay depends in part on the strength of competition between cannibals and victims (de Roos and Persson 2003) and in part on the size window of vulnerability; i.e., the size thresholds that determine which age classes interact as cannibals and victims (Claesson et al. 2004). Although knowing the bounds on this window is fundamental for predicting the population-level consequences of canni-

balism, they are often poorly documented (Claesson et al. 2004).

Most studies on cannibalism focus on consumptive effects on victims. However, the threat of cannibalism can have nonconsumptive effects (sensu Abrams 2007) on victim activity, foraging, and refuge use (Polis 1980, Sih 1982, Leonardsson 1991, Van Buskirk 1992, Persson and Eklöv 1995, Claus-Walker et al. 1997, Biro et al. 2003, Rudolf 2006). Cannibal-induced changes in behavior can reduce victim growth and survival and hence should also affect population dynamics (Peckarsky et al. 2008). For example, in dragonfly populations with three age classes, nonconsumptive effects of the oldest year class were stronger on the adjacent than on the smallest year class, thus explaining the two-year cycles of year class dominance observed in natural ponds (Van Buskirk 1992). Injuries that result from cannibals will also affect victim survival and growth and hence population dynamics (Harris 1989, Van Buskirk and Smith 1991). Although nonconsumptive effects of predators can be as or more important than consumptive effects (Lima and Dill 1990, Werner and Peacor 2003, Sih 2004, Peckarsky et al. 2008), there are relatively few studies that have experimentally quantified both of these effects of cannibalism in long-lived species with age-structured populations.

In this paper we report on consumptive and nonconsumptive effects of cannibalism in age-structured populations of tiger salamanders (*Ambystoma tigrinum nebulosum*). At low elevations, metamorphosis to the terrestrial adult stage occurs after one season of larval growth; thus, size structure and cannibalism occur within cohorts and are often facilitated by the polyphenic development of "typical larvae" vs. "cannibalistic morphs" (Collins 1981, Maret and Collins 1997, Whiteman et al. 2003, Denoël et al. 2006). In contrast, at high elevations, short growing seasons and cool temperatures retard larval development so that metamorphosis to the terrestrial adult stage is delayed until the third or fourth summer (= age 2+ yr and 3+ yr larvae) (Sprules 1974, Sexton and Bizer 1978). Slowly growing individuals that do not reach the minimum size for metamorphosis by the fourth year remain in ponds where they mature as long-lived (10–20 years) paedomorphic (larval morphology) adults (Whiteman 1994). High-elevation populations in the western United States contain 10+ year classes of salamanders that are the top predators in ponds and fishless lakes (Wissinger et al. 1999a, b, Whiteman and Wissinger 2005).

Annual mark–recapture censuses at our main study site document salamander population fluctuations that are not correlated with interannual variation in climate, nor coupled with the abundances of other species (predators, prey, parasites, pathogens) (Wissinger and Whiteman 1992, Whiteman and Wissinger 2005). Instead, these fluctuations are associated with interannual variation in the survival of young-of-the-year (YOY) larvae (Whiteman and Wissinger 2005). The purpose of the experiments reported here was to determine the potential role(s) of cannibalism in these recruitment failures. Specifically, our goals were to (1) establish whether paedomorphs and large larvae (age ≥3+ yr) actually cannibalize YOY and other small size classes of conspecifics under seminatural conditions of habitat complexity and alternative prey, (2) explore the size windows for the consumptive and nonconsumptive effects of cannibals on potential victims, and (3) quantify the relationship between cannibal densities and victim survival in order to make inferences about the number of paedomorphs required to eliminate recruitment. Understanding the factors that underlie population fluctuations in amphibians is of timely importance for understanding the causes of natural population fluctuations and distinguishing them from those associated with human-induced amphibian declines (Houlahan et al. 2000, Alford et al. 2001, Kiesecker et al. 2001, Collins and Storfer 2003, Skelly et al. 2003).

METHODS

Size constraints on the potential for cannibalism

The experiments were conducted in central Colorado, USA, at the Mexican Cut Nature Preserve (elevation 3400–3600 m), a remote wilderness site owned by The Nature Conservancy and managed for research by the Rocky Mountain Biological Laboratory (site description in Wissinger et al. [1999a]; photographs in Appendix A). To determine the range of victim body sizes that would be of interest to study in the mesocosms, we first conducted short-term (72 h) experiments in microcosms (0.25-m^2 bottom area plastic storage containers; 15-cm water depth; 2.5-cm detrital substrate depth). Microcosms were housed in a portable field laboratory located adjacent to the ponds. Small invertebrates were retained in the detritus as a prey base, but large predators such as beetles and odonate larvae were removed. For each size combination, two potential victims were introduced into each microcosm and allowed to acclimate for 24 h, after which the potential cannibal was introduced. Potential cannibals were held separately without prey for 24 h prior to introduction to standardize hunger levels. Neither potential cannibals nor victims were reused across trials. For each combination, we conducted five replicates with and five without the potential cannibal. In 2002, we combined paedomorphs with three year classes of larvae (ages 1+, 2+, and 3+ yr), and three size classes of YOY that corresponded to sizes typically found in July, August, and September, respectively. In 2003 we repeated the experiments with age ≥3+ yr larvae as potential cannibals on YOY, age 1+ yr, and age 2+ yr larvae. Size data for all combinations are given in Appendix B. Because of the nonnormal nature of the data, we used Mann-Whitney U tests to compare survival of victims with and without cannibals.

Consumptive and nonconsumptive effects of cannibalism under seminatural conditions

The results of the microcosm experiments allowed us to choose size classes for studying cannibalism under seminatural levels of habitat heterogeneity, escape space, and prey abundances. Field experiments were conducted in mesocosms (1.75-m^2 bottom area plastic cattle watering tanks) located adjacent to the ponds at our study site. Each of the 30 tanks contained 10 cm of detrital substrate from the ponds, two rocks (~400 cm^2), and two 400-cm^2 clumps of emergent vegetation (*Carex aquatilis*) to provide the types of refugia that larvae use in the littoral zone of the ponds. The tanks were initially set up in 2001 and by the start of the experiments in 2002 contained a variety of benthic and planktonic invertebrates that were added with the substrate (e.g., worms, midges, epibenthic crustaceans), had colonized as winged adults (beetles, corixid hemipterans), and/or hatched from oviposited eggs (e.g., chironomids midges, mosquitoes, odonates, caddisflies). Pre-experimental samples indicated that invertebrate biomass (total ash-free dry mass [AFDM]), especially that of zooplankton, was slightly lower than that in the source ponds (Wissinger et al. 1999*a*). Because we wanted cannibal and potential prey hunger levels to be comparable to those in natural populations, we supplemented the prey resource with zooplankton from the ponds (*Leptodiaptomus coloradensis, Hesperodiaptomus shoshone, Daphnia middendorfiana, Daphnia rosea-pulex* complex) prior to the start of each experiment (June 2002, 0.222 ± 0.017 g AFDM; July 2002, 0.210 ± 0.034 g AFDM; June 2003, 0.205 ± 0.029 g AFDM).

For each experiment, we added five potential victims followed by one potential cannibal that had been held without prey for 24 h. All experiments included no-cannibal controls, and the average size of victims and cannibals (given as snout–vent length [SVL]; mean ± SD) did not differ among treatments (all *P* >0.05). In 2002, we quantified the effects of paedomorphs (92 ± 5 mm SVL) on age 1+ yr (48 ± 3 mm SVL) and age 2+ yr (65 ± 5 mm SVL) larvae and, in a second experiment, on two sizes of YOY larvae that corresponded to those encountered in late summer ("small YOY" = 25 ± 5 mm SVL) and early autumn ("large YOY" = 37 ± 4 mm SVL). During each experiment, we conducted 15-min behavioral trials during which we recorded time spent foraging (see Wissinger et al. [1999*b*] for a description of foraging behaviors) and activity levels on one individual per tank. We quantified activity by placing a 6 × 6 grid (each square = 0.058 m^2) over the cattle tanks and recorded the number of grids traversed by a randomly chosen focal animal during the 15-min trials. Time spent foraging and activity levels were highly correlated; thus we present only the latter to avoid redundancy. During the two experiments in 2002, we conducted 28 trials (4 treatments × 7 replicates) on day 6 of the experiment. The rapid disappearance of potential victims precluded additional observations later in the experiments. In

2003, we conducted a third experiment with large larvae (age ≥3+ yr = 83 ± 2 mm SVL) as potential cannibals on two sizes of YOY (small = 27 ± 7 mm SVL and large = 37 ± 3 mm SVL) and on age 1+ yr larvae (49 ± 3 mm SVL) using the same protocols as in the experiments with paedomorphs. Behavioral observations of victim activity levels (6 treatments × 5 replicates = 30 trials) were conducted on day 6 as described above in 2002.

During each experiment, we removed cannibals after 14 d, pumped their stomachs (see Denoël et al. [2006] for a description of methods), and returned each to its source pond. Tanks were drained to ensure a complete count of survivors, which were screened for new injuries (vs. those present at the beginning of the experiment), weighed, and measured (snout–vent length). Because there was no mortality in the controls (i.e., treatment variances = 0), we compared mortality in the presence and absence of cannibals for each combination using Mann-Whitney *U* tests. Data for nonconsumptive effects met parametric assumptions and were analyzed first with a MANOVA for all responses in the survivors (injuries, activity rates, biomass of gut contents [AFDM], and final body mass), then with ANOVAs for each nonconsumptive response, and finally with Tukey's post hoc test to compare treatment means (Day and Quinn 1989, Scheiner 1993).

Paedomorph density and recruitment

In July 2003, we conducted a fourth mesocosm experiment to quantify the manner in which paedomorph density affected YOY survival. The experimental protocol was identical to the previous three except that we used 25 YOY per tank and varied the number of potential cannibals (0, 1, 2, 4, 6, or 8 paedomorphs). These paedomorph and YOY densities correspond to those observed historically in the natural population (Whiteman and Wissinger 2005). The size of victims (SVL = 26 ± 5 mm; *n* = 750) and cannibals (96 ± 7 mm; *n* = 95) was comparable to that used in "small YOY" treatments in the mesocosm experiments conducted during the previous two summers.

RESULTS

Microcosm experiments: size constraints on the potential for cannibalism

We observed cannibalism in the microcosms during attacks (victims in the gape of cannibals). The statistics for the survival data in the microcosm experiments are given in Appendix B. In summary, paedomorphs consumed all or nearly all YOY and a few age 1+ yr larvae in microcosms, but not age 2+ yr or 3+ yr larvae. Age 2+ yr larvae had injuries that suggested attempted cannibalism. These results led us to conduct mesocosm experiments with paedomorphs as potential cannibals and YOY, age 1+ yr, and 2+ yr larvae as potential victims (see *Consumptive and nonconsumptive effects...* below). Cannibalism by age 3+ yr larvae in the microcosms occurred mainly on the two smallest size

classes of YOY, and injuries were found for YOY and age 1+ yr survivors (Appendix B). Thus, for the mesocosm experiments, we combined age 3+ yr larvae with age 1+ yr and two size classes of YOY larvae.

Consumptive and nonconsumptive effects of cannibalism in field mesocosms

In field mesocosms, survival of YOY larvae was reduced in the presence of large conspecifics for four of the seven size combinations (Fig. 1). Paedomorphs did not consume any age 2+ yr larvae and only a few age 1+ yr larvae, but preyed heavily on both size classes of YOY (Fig. 1A). There was no cannibalism by age 3+ yr on age 1+ yr larvae, but there was cannibalism on both sizes of YOY (Fig. 1B). In addition to consumptive effects of cannibalism, we observed several nonconsumptive effects on survivors. Statistics for all three experiments and the graphical results for the first experiment (paedomorphs with age 1+ yr and 2+ yr larvae) are summarized in Appendix C. MANOVA indicated that cannibals had a significant overall impact on the four response variables that we measured during (foraging/activity) and at the end of each experiment (survivors with injuries, gut content biomass, final body mass). Subsequent protected ANOVAs and post hoc comparisons revealed that small larvae had more injuries (missing or damaged appendages or body scars) with cannibals than in the control treatments for all treatment combinations, including those in which successful cannibalism rarely or never occurred (i.e., paedomorphs and age 3+ yr larvae with age 1+ yr and 2+ yr larvae; Appendix C, Table 1). For all but the largest potential victims, we also detected significant reduced activity/foraging rates in the presence of cannibals and reduced gut contents at the end of the experiment. These nonconsumptive effects were most evident in small YOY larvae in which activity rates were ~60–80% lower with than without cannibals (Figs. 2 and 3; Table 1). In those treatments, small YOY hid under rocks or in vegetation or burrowed in the substrate. At the end of the experiment, the presence of cannibals resulted in ~60–90% reductions in the invertebrate biomass in the guts of small YOY larvae and ~30–40% reductions in body mass. Paedomorph cannibals also reduced activity rates and gut contents of large YOY and age 1+ yr larvae (Table 1). Across all experiments, there was a clear trend from multiple, strong nonconsumptive for the most disparate sizes to weak or no detectable effect for combinations that differed little in size (Table 1).

Ontogenetic shifts in diet

Stomach contents of potential cannibals and victims were conflated into the following four categories before weighing and ashing to obtain ash-free dry mass (AFDM): (1) large benthic invertebrates (damselflies, dragonflies, beetles, water bugs, and caddisflies), (2) small benthic invertebrates (diptera larvae, mites, and miscellaneous small invertebrates), (3) epibenthic and planktonic microcrustaceans, and (4) terrestrial and adult insects (emerging diptera, caddisflies, moths, and other terrestrial insects) and miscellaneous benthos (worms and clams). MANOVA indicated there was no shift in diet for either potential cannibals or victims across all prey categories (all $P > 0.05$). We therefore combined the data for each salamander size combination within each experiment to compare the diets of the potential victims and cannibals with one-way MANOVA and subsequent ANOVA. The diets of the paedomorphs and age 3+ yr larvae were dominated by large invertebrates, whereas the diets of YOY larvae were dominated (>95%) by microcrustaceans and chironomid larvae. The ontogenetic shift in diet was most striking when comparing early YOY larvae, whose diets were dominated by microcrustaceans (70–80% AFDM), to potential cannibals for which this prey category was a minor component of the diet (10–20%; see Appendix D). The diets of age 1+ yr and 2+ yr larvae were intermediate diets that included both small prey items (microcrustaceans and chironomids) and larger taxa. Small benthic prey (mainly chironomid fly larvae) were eaten by all salamander size classes.

Paedomorph density experiment

The results of the mesocosm experiments clearly established that small YOY larvae were vulnerable to both consumptive and nonconsumptive effects of cannibalism by paedomorphs. Thus, we wanted to describe the relationship between paedomorph abundance and survival of these small YOY larvae. In this experiment, we used a range of paedomorph densities that we had observed during fluctuations in the natural population (Whiteman and Wissinger 2005) and found that YOY survival declined exponentially with increasing paedomorph abundance (Fig. 4). The per capita consumption rate of cannibals was nearly constant across these densities, with an average of ~0.4 YOY·paedomorph^{-1}·d^{-1}.

DISCUSSION

Measuring ecologically relevant cannibalism size thresholds

Cannibalism in size-structured populations typically occurs only above a threshold of the proportional difference between the sizes of cannibals and victims. That difference is probably related to constraints on cannibal gape or the ability of victims to flee or escape during capture and handling (Christensen 1996, Mittlebach and Persson 1998, Juanes 2003). Comparative data suggest that species with age-structured populations typically have higher thresholds (e.g., 55% to >140% for piscivorous fishes; Popova 1967, Claesson et al. 2004, Persson et al. 2006) than those in which size structure occurs mainly within generations (e.g., 20–30% for dragonflies, Wissinger 1992; 40% for caddisflies, Greig and Wissinger 2010; <40% for terrestrial invertebrates, Polis 1981). Although cannibalism within
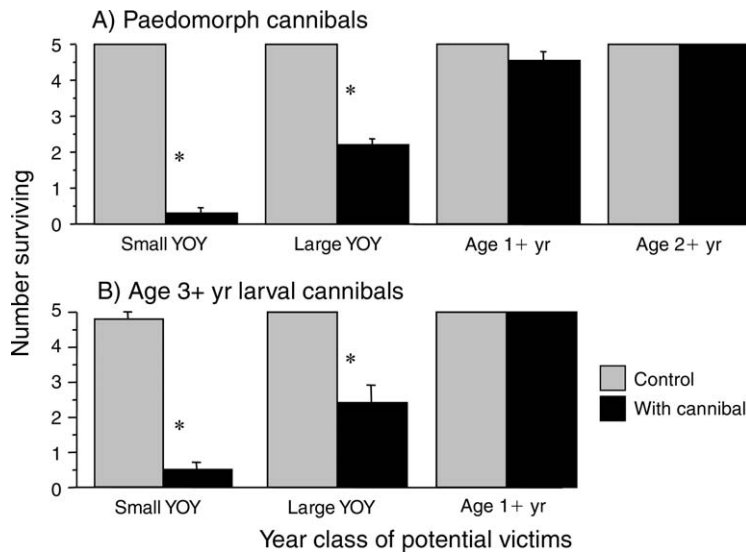
Fig. 1. Survival (mean + SE) of tiger salamander (*Ambystoma tigrinum nebulosum*) larvae with and without (A) paedomorph cannibals and (B) large (age 3+ yr) larval cannibals. See *Methods* for salamander sizes. "YOY" indicates young-of-the-year larvae. Asterisks indicate significant differences ($P < 0.05$) based on Mann-Whitney U tests. The experiments were conducted at the Mexican Cut Nature Preserve in central Colorado, USA.

cohorts of ambystomatid salamanders is commonplace and facilitated by the development of size structure, size thresholds have not been reported (e.g., Polis and Myers 1985, Petranka 1989, Van Buskirk and Smith 1991, Crump 1992, Maret and Collins 1997, Hoffman and Pfennig 1999, Ziemba and Collins 1999, Wildy et al. 2001). In our study, we found that cannibalism between different year classes of tiger salamanders only occurred between individuals that differed by >50% in body size (Fig. 5), a threshold that is nearly identical to that found in size-structured populations of stream salamanders (Rudolf 2006). Some size classes that were cannibalized in the microcosms (e.g., age 1+ yr larvae) were never or rarely cannibalized in the mesocosms (Fig. 5), suggesting that potential victims can avoid detection and/or escape

attacks in unconstrained habitats. Although detailed behavioral studies would be needed to quantify the relative importance of avoidance mechanisms, the nonconsumptive data suggest that both might play a role. Reduced activity levels (Figs. 3 and 4) appear to be most important for early YOY larvae, which, in the presence of cannibals, spend most of the time buried motionless in the substrate (see also Walls 1995), making it difficult to locate and observe them during the behavior trials. In contrast, late YOY and age 1+ yr larvae spent little time in the substrate and did not reduce activity in the presence of cannibals. However, there were increased injuries, suggesting that escape after attack plays a role in avoiding cannibals for these size classes. For age classes that were never cannibalized,

TABLE 1. Summary of nonconsumptive effects of the threat of tiger salamanders (*Ambystoma tigrinum nebulosum*) cannibalism in mesocosm experiments with the size combinations shown in Fig. 1.

Potential cannibal	Potential victim	Injuries (on survivors)	Activity	Gut contents	Growth in body mass
Paedomorphs	Small YOY	+83%***	−88%***	−93%***	−46%***
	Large YOY	+61%***	−45%***	−81%***	−8% NS
	Age 1+ yr	+63%***	−47%***	−28%**	−10% NS
	Age 2+ yr	+47%**	−12% NS	−12% NS	−7% NS
Age 3+ yr	Small YOY	+80%***	−61%***	−63%***	−32%***
	Large YOY	+77%**	−22% NS	−12% NS	−2% NS
	Age 1+ yr	+26%**	−6% NS	−19% NS	−6% NS

Notes: Values are calculated as the relative percentage change with vs. without a potential cannibal to standardize the strength of effects across experiments. Asterisks indicate level of significance (** $P < 0.01$; *** $P < 0.001$) based on Tukey's multiple comparisons tests on significant one-way ANOVA results from the original data (see Appendix C). Gut contents were measured as grams of ash-free dry mass. Activity was measured as number of grid moves per 15 minutes. Abbreviations are: NS, not significant; YOY, young-of-the-year larvae. The experiments were conducted at the Mexican Cut Nature Preserve in central Colorado, USA.
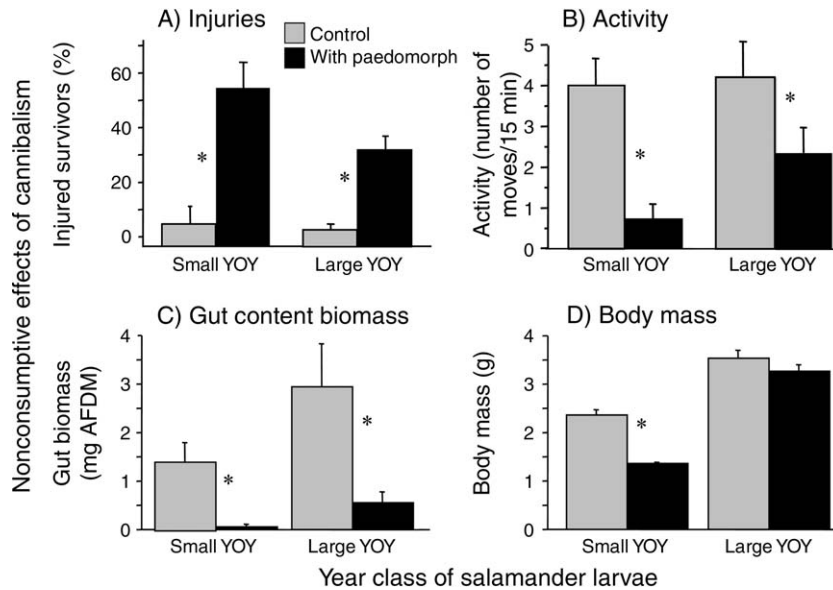
FIG. 2. Nonconsumptive effects (mean + SE) of the threat of cannibalism by paedomorphic adult tiger salamanders on two size classes of young-of-the-year (YOY) larvae (see Fig. 1). Asterisks indicate significant differences based on Tukey's post hoc tests after ANOVA (see Appendix C). "AFDM" indicates ash-free dry mass.

injuries provide evidence for asymmetric interference competition (Van Buskirk and Smith 1991, Post et al. 1999, Byström et al. 2003). The results of these microcosm and mesocosm experiments emphasize that inferences about the intensity of cannibalism in natural populations should be based on experiments conducted in spatially heterogeneous habitats with freely interact-

ing predators and prey (Persson and Eklöv 1995, Hammond et al. 2007).

When the intensity of cannibalism has been measured for size differences beyond the victim size threshold, two patterns have been observed (Claesson et al. 2004). In many fishes, there are both upper and lower size thresholds, the latter of which is related to low detection
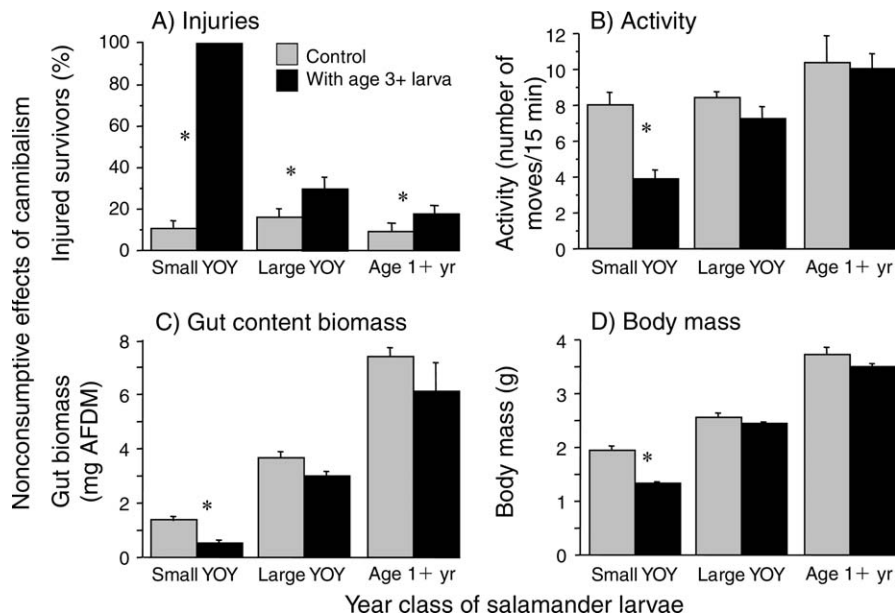

FIG. 3. Nonconsumptive effects (mean + SE) of the threat of cannibalism by age 3+ yr tiger salamander larvae on age 1+ yr larvae and two size classes of young-of-the-year (YOY) larvae (see Fig. 1). Asterisks indicate significant differences based on Tukey's post hoc tests after ANOVA (see Appendix C). "AFDM" indicates ash-free dry mass.
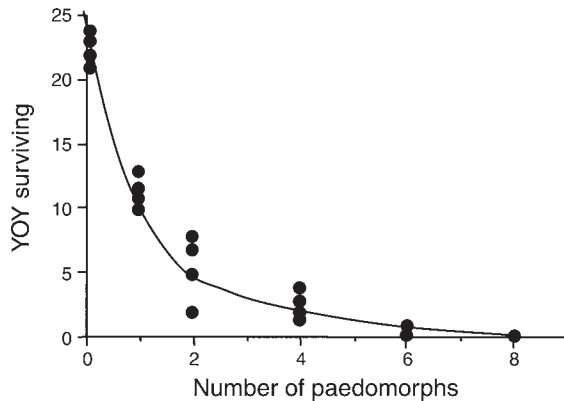
FIG. 4. Survival of young-of-the-year (YOY) tiger salamander larvae across a range of abundances of paedomorphs. Regression statistics for the transformed ($\ln[Y + 1]$) dependent variable are $Y = 1.254 - 0.173 \times X$; $R^2 = 0.92$; $P < 0.0001$.

rates of small conspecifics and/or low retention during handling and ingestion (Lundvall et al. 1999, Juanes 2003). That some cannibals prefer intermediate sizes of conspecifics is consistent with prey profitability models for trade-offs between search/handling time and energy rewards (Stephens and Krebs 1987). In such cases, new cohorts should be initially unaffected by cannibals and can attain sizes that overwhelm the resource base and cause starvation in older size classes, thus creating population dynamics largely driven by competition (Persson et al. 2000, 2004b). In contrast, for many invertebrates and some fishes, there is no lower threshold and cannibalism is most intense on the smallest size classes (Claesson et al. 2004). Our data are consistent with the second pattern; i.e., there is not a second lower victim size threshold in tiger salamanders and cannibalism increases asymptotically to a maximum for YOY victims (Fig. 5). The microcosm data suggest that this pattern is driven mainly by gape-size limitation and that there is a premium on YOY growth rate (see *Cannibalism and recruitment failures*). When YOY (or eggs) are the most vulnerable size class in cannibalistic species, dominant cohorts can regulate recruitment and drive cannibalism-induced population cycles (Hastings and Constantino 1987, Claessen et al. 2004).

Nonconsumptive effects of cannibals on victims

The nonconsumptive effects of cannibals on victims that we observed (increased injury and decreased activity, stomach contents, and growth) have been documented in other cannibalistic species (e.g., Van Buskirk 1992, Ziemba and Collins 1999, Biro et al. 2003, Rudolf 2006, 2008) and are a common feature of the interactions between coevolved predators and prey (Lima and Dill 1990, Werner and Peacor 2003, Sih 2004, Peckarsky et al. 2008). The strengths of these effects are highest on YOY salamanders and decrease as victim size increases so that injury is the only nonconsumptive consequence of cannibals on adjacent or next

to adjacent age classes (Table 1). This size variation in nonconsumptive effects on victim activity, foraging, and growth is consistent with previous empirical and theoretical studies for predators in general (Abrams and Rowe 1996). That we observed decreased rather than increased YOY activity in the presence of cannibals is perhaps surprising given the evidence for gape limitation. It is precisely in this situation that one might expect the opposite strategy; i.e., increased foraging in order to grow fast and escape the size window of cannibalism (Urban 2007). The growth–predation risk trade-off we observed could be related to the inability of YOY salamanders to grow fast enough during their first summer to escape the size threshold. Although large YOY are slightly less vulnerable than small YOY, consumptive and nonconsumptive effects decrease substantially when larvae reach the size typical for larvae in their second summer (age 1+ yr; Figs. 1–3).

Decreased YOY growth in the presence of cannibals could affect population dynamics by (1) offsetting compensatory growth responses in thinned cohorts (e.g., Persson et al. 2004a, Craig et al. 2006, de Roos et al. 2007, van Kooten et al. 2007), (2) reducing winter survival as a result of low body mass (Jørgensen 1992, Pope and Matthews 2002), (3) increasing body size variation, hence asymmetric competition within cohorts (Ziemba et al. 2000, Peacor et al. 2007), and (4) determining whether larvae mature into metamorphic or paedomorphic adults (Whiteman 1994). Injury could also affect population dynamics by diverting resources for growth to regeneration (Harris 1989) and increasing the incidence of skin disease (e.g., Walls and Jaeger 1987). Short-term nonconsumptive effects (growth and survival) of predators on prey are well studied, but the population-level consequences have rarely been demonstrated (Van Buskirk 1992, Peckarsky et al. 2008). A first step for studying the long-term consequences for salamander population dynamics will be to determine
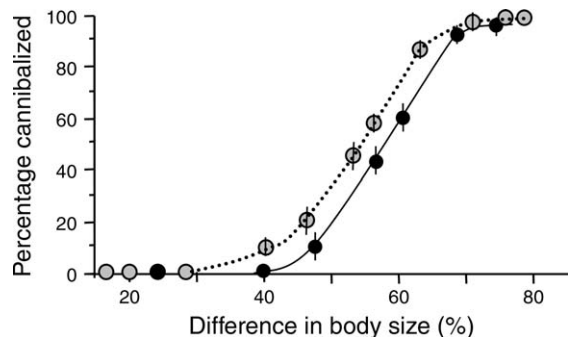

FIG. 5. Summary of the percentage (mean ± SE) of larval tiger salamanders cannibalized by large conspecifics in microcosms (gray circles and dotted line) and mesocosms (black circles and solid line) vs. the percentage difference in size calculated as [(cannibal SVL − victim SVL)/cannibal SVL] × 100. "SVL" indicates snout–vent length.
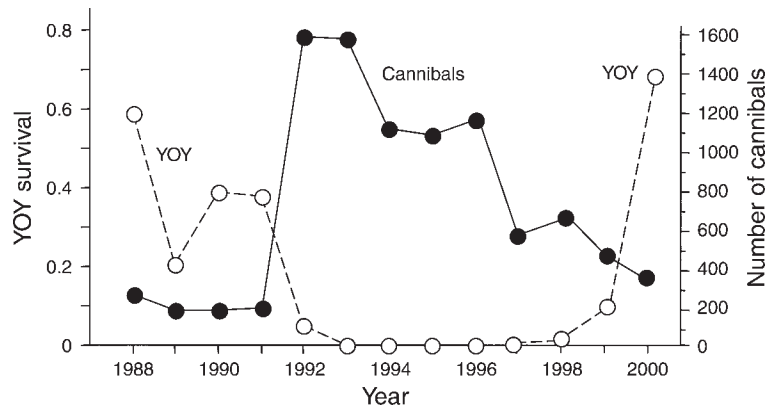
FIG. 6.   Relationship between the numbers of potential cannibals inferred from experimental data presented in this paper (i.e., large larvae [≥age 3+ yr] + paedomorphs) and young-of-the-year (YOY) tiger salamander survival in natural populations at the Mexican Cut Nature Preserve, central Colorado, USA. Field data on the number of cannibals and YOY are based on mark–recapture censuses from 1988 to 2000 of individually marked (hence known aged) salamanders (Wissinger and Whiteman 1992, Whiteman and Wissinger 2005).

how key indicators (body size, injuries, and disease) vary in late summer between YOY cohorts that develop in years with high vs. low densities of paedomorphs.

Cannibalism and recruitment failures

Long-term census data at our main study site provide evidence that fluctuations in salamander populations are related to recruitment failures (Wissinger and Whiteman 1992, Whiteman and Wissinger 2005). The fluctuations are characterized by three to four years of strong recruitment followed by six to seven years during which most or all YOY disappear annually before reaching age 1+ yr larvae (Whiteman and Wissinger 2005). The onset of cohort failures occurs when the first of the three to four strong cohorts from the recruitment period reach the size threshold for cannibalism that we experimentally identified in this paper (i.e., age 3+ yr larvae and paedomorphs). The relationship between the abundance of these cannibalistic size classes and YOY survival is striking (Fig. 6) and similar to the patterns observed in other "dominance–repression" cycles (e.g., Gaines and Roughgarden 1985, Hastings and Constantino 1987, McCauley and Murdoch 1987, Van Buskirk 1992). The results of the paedomorph density experiment (Fig. 4) indicate that the number of large salamanders that are able to cannibalize YOY in dominant cohorts is more than sufficient to eliminate recruitment. In that experiment, we observed a consumption rate of 0.4 YOY·paedomorph^{-1}·d^{-1} (see Fig. 4). The number of large larvae and paedomorphs (600–1400 cannibals; Fig. 6) in the population during the years of recruitment failures indicate that they have the potential to consume ~14 000–33 600 YOY annually (60 d × 0.4 d^{-1} × 600–1400 cannibals), assuming a time window of two months. In contrast, the maximum starting size of cohorts is likely to be only ~4800–8600 embryos (maximum fecundity per female × number of females breeding during those years; H. H. Whiteman, *unpub-*

lished data). The actual number of YOY larvae in a given year is likely to be much lower given that (1) we used maximum rather than mean fecundity values, (2) some embryos are eaten by invertebrate predators (Wissinger et al. 1999a), and (3) the window of YOY vulnerability is probably longer than two months. Thus, even if encounter rates in the ponds are lower than those observed in the mesocosms, cannibalism by the large number of paedomorphs observed in dominant cohorts should completely eliminate YOY. Theory suggests population cycles that are driven by recruitment regulation are most likely when YOY are the most vulnerable size class (see *Measuring ecologically relevant … above*) and when there is little overlap in diet between cannibals and YOY (Claesson et al. 2004, Persson et al. 2004b), as is suggested by the dietary data from our experiments (Appendix D). We cannot eliminate the possibility that dominant cohorts of paedomorphs also affect recruitment through resource depression (de Roos and Persson 2003, Claesson et al. 2004, Persson et al. 2004a). Although dietary data presented here (Appendix D) suggest that is unlikely, paedomorphs have extremely broad diets (Wissinger et al. 1999a), and it is conceivable that individuals in dominant cohorts switch to less preferred small-prey categories after reducing densities of large benthic taxa. Regardless of the potential interplay with intraspecific competition, our results strongly implicate cannibalism as one likely explanation for recruitment patterns in this species.

Understanding the mechanisms that underlie natural fluctuations in population size of amphibians, and thus distinguishing them from amphibian declines related to human activities, requires a combination of long-term data and experimentation (Pechmann and Wilbur 1994, Marsh 2001). Most long-term studies on natural fluctuations have focused on extrinsic factors such as rainfall (Pechmann et al. 1991), shifts in canopy cover

from terrestrial succession (Skelly et al. 1999), changes in preferred breeding habitats within metapopulations (Petranka et al. 2004), and episodic recruitment associated with climatically favorable and unfavorable years for breeding (reviewed by Marsh 2001). Our results provide evidence that at least for some amphibians, fluctuations can be generated intrinsically and that cannibalism can play an important role in the long-term dynamics of species with age-structured populations.

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APPENDIX A

Photographs of the study site and of paedomorphic adult and young-of-the-year tiger salamanders (*Ecological Archives* E091-039-A1).

APPENDIX B

Results of short-term microcosm experiments to determine the manner in which size affects the potential for inter-cohort cannibalism in tiger salamanders (*Ecological Archives* E091-039-A2).

APPENDIX C

Statistical analyses of four nonconsumptive responses to the threat of cannibalism by tiger salamanders in mesocosm experiments (*Ecological Archives* E091-039-A3).

APPENDIX D

Comparative dietary data of salamander cannibals and victims in mesocosms (*Ecological Archives* E091-039-A4).