Habitat ephemerality affects the evolution of contrasting growth strategies and cannibalism in anuran larvae

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Abstract

Ephemeral streams are challenging environments for tadpoles; thus adaptive features that increase the survival of these larvae should be favored by natural selection. In this study, we compared the adaptive growth strategies of *Bombina orientalis* (the oriental fire-bellied toad) tadpoles from ephemeral streams with those of such tadpoles from non-ephemeral streams. Using a common garden experiment, we tested the interactive effects of location (ephemeral vs. non-ephemeral), food availability, and growing density on larval period, weight at metamorphosis, and cannibalism. We found that tadpoles from ephemeral streams underwent a shorter larval period compared with those from non-ephemeral streams but that this difference was contingent on food availability and density. The observed faster growth is likely to be an adaptive response because tadpoles in ephemeral streams experience more biotic/abiotic stressors, such as desiccation risk and limited resources, compared with those in non-ephemeral streams, with their earlier metamorphosis potentially resulting in survival benefits. As a trade-off for their faster growth, tadpoles from ephemeral streams had a lower body weight at metamorphosis compared with those from non-ephemeral streams, but only when food was sufficient. We also found lower cannibalism rates among tadpoles from ephemeral streams, which can be attributed to the indirect fitness costs of cannibalizing their kin. Our study is the first to demonstrate how ephemeral habitats have affected the evolutionary change in cannibalistic behaviors in anurans and provides additional evidence that natural selection has mediated the evolution of growth strategies of tadpoles in ephemeral streams.

Introduction

Anurans in ephemeral habitats have been central to the environmental adaptations of animals (Newman 1989; Spieler and Linsenmair 1997; Dayton and Fitzgerald 2001). Ephemeral streams/ponds are highly heterogeneous in various biotic and abiotic stressors, including water holding potentials, predation/competition, and food availability, thus an appropriate choice of where to stay heavily influence the survivorship of both themselves and their progeny (Blaustein 1999; Stubbington et al. 2017). Studies of ephemeral habitats have largely focused on parental care because females' choice of oviposition sites directly determines the fitness of their progeny (Rieger et al. 2004; Pintar and Resetarits Jr 2017). Accumulating evidence has consistently demonstrated the adaptive behavior of female anurans: species in ephemeral habitats generally avoid sites that have a high risk of desiccation, predation, and competition (Rudolf and Rödel 2005; Buxton and Sperry 2017; Pintar and Resetarits 2017), although exceptional peculiar adaptations, such as feeding their eggs to tadpoles, have also been reported (Poelman and Dicke 2007).

Considerable research has been devoted to identifying adaptive parental strategies under ephemeral conditions, whereas less attention has been given to the adaptive responses of tadpoles. Tadpoles are known for their developmental plasticity: generally, they develop faster if they are exposed to greater risks (e.g. predation and desiccation) and slower when resources are limited (Newman 1989; Nicieza 2000; Richter-Boix et al. 2011). For example, studies using both interspecific and intraspecific comparisons have demonstrated that frogs under higher risk of desiccation develop faster (Richter-Boix et al. 2006;

Richter-Boix et al. 2011; Pujol-Buxó et al. 2016). However, most studies have examined the plastic response of tadpoles under different conditions or conducted interspecific comparisons where disentangling the roles of shared ancestry and environmental adaptations is difficult (Tejedo and Reques 1994; Van Buskirk 2002; Székely et al. 2017; Lent and Babbitt 2020). To date, direct evidence of whether and how directional selection has shaped the genetic basis of anuran growth strategies in ephemeral habitats and the interactive effects of multiple factors is scarce.

Here, we studied the oriental fire-bellied toad (*Bombina orientalis*) to examine the patterns of evolution in shaping tadpole developmental strategies in ephemeral streams. *B. orientalis* is a semi-aquatic frog species distributed mainly across Eastern Asia. We primarily focused on comparing populations between ephemeral (Jeju Island) and non-ephemeral (mainland South Korea, hereinafter referred to as "mainland") streams. Importantly, unlike on the mainland, the surface of Jeju Island is covered by basalt layers formed by volcanic activities that drain water quickly into the underground. This geological feature has shaped most Jeju Island streams ephemeral, whereas the mainland's habitats consist of continuously flowing non-ephemeral streams (Fig. 1). *B. orientalis* colonized Jeju Island during the Cenozoic Era via a single dispersal event from the mainland (estimated mean population age, 4.32 Ma), and no gene flow has occurred since then (Fong et al. 2016). After this separation, the mainland and Jeju Island populations have diverged phenotypically (Kang et al. 2017).

The fundamental difference in habitat structure between the mainland and Jeju Island and the fact that gene flow has not been observed after the separation of populations provide an ideal testing ground for exploring how natural selection shapes the adaptive growth strategies of tadpoles in response to different environmental pressures. Because tadpoles in Jeju Island streams are isolated in small pools, with the surface area of most pools ranging from 0.01 to 36 m^2, during development at least until it rains (Baek et al. unpublished), they confront several additional environmental stressors compared with tadpoles in mainland streams. First, they are exposed to a greater risk of desiccation such that even several days without rain can be fatal to those in pools with low water holding potential. Second, resources are limited because movements among pools are impossible during the larval stage. Third, flooding occurs under heavy rain, which could potentially wash away all eggs and tadpoles downstream —where predatory risks are likely to increase owing to the presence of fish.

Several predictions can be made regarding tadpole growth strategies based on the additional stressors imposed on ephemeral habitats. First, tadpoles in ephemeral streams would develop faster than those in non-ephemeral streams until they become froglets, when they are liberated from the environmental stressors associated with isolated pools (Enriquez-Urzelai et al. 2013; Dittrich et al. 2016). Second, as a trade-off for their faster growth, froglets in ephemeral streams would reach a smaller size at metamorphosis (Edge et al. 2013). Third, because populations exposed to highly variable and unpredictable environments are expected to show high phenotypic plasticity (Van Buskirk 2002), tadpoles in ephemeral streams would show higher developmental plasticity.

In addition, we predict that the two populations would differ in their cannibalistic behaviors. There are two alternative hypotheses about the degree of their cannibalism. First, because pools in ephemeral streams are isolated from one another, thus a closed system for organic matters, there is limited food available for tadpoles. Under this food-limited environment, natural selection may favor cannibalistic behaviors that increase individual survival and enhance development (Crump 1990; Wildy et al. 1998). In this circumstance, tadpoles in ephemeral streams may be more cannibalistic than those in non-ephemeral streams (Semlitsch and Reichling 1989; Gould et al. 2020). Alternatively, because *B. orientalis* females avoid laying their eggs in pools already occupied by conspecifics (Baek et al. unpublished), tadpoles in the same pool are likely to be their kin; therefore, as cannibalizing their kin decreases tadpoles' indirect fitness (Pfennig et al. 1993; Pfennig 1997), natural selection may favor tadpoles in ephemeral streams that cannibalize less.

We tested the abovementioned predictions by comparing the growth of tadpoles from ephemeral streams with that of tadpoles from non-ephemeral streams using a common garden experiment. Moreover, to examine whether multiple factors interactively affect tadpole growth and cannibalistic behaviors, we manipulated two factors that are expected to differ between ephemeral and non-ephemeral habitats, namely, food availability and density (Newman 1987; Álvarez and Nicieza 2002; Lent and Babbitt 2020).

Methods

Experimental treatment and procedure

To examine whether differences in habitat structure between ephemeral and non-ephemeral streams populations have affected the evolution of their growth strategies, we conducted a common garden experiment using the progenies of frogs from the mainland and Jeju Island under water temperature control (22°C). First, we collected adult frogs from streams in the mainland (34.7°−35.1°N, 126.5°−126.7°E) and Jeju Island (33.45°N, 126.56°E) and brought them to the laboratory. We placed three to five individual frogs from both sexes together in a semi-aquatic terrarium (40 · 23 · 23 cm) filled with dechlorinated water, rocks, and aquatic plants to facilitate mating. We provided calcium and vitamin D−powered juvenile crickets and mealworms *ad libitum*. We maintained seven mating chambers for each location until we collected enough eggs to fill all experimental cages (as described below). In total, 67 Jeju Island frogs and 48 mainland frogs (approximate sex ratio, 1:1) contributed to egg laying. We controlled the room temperature using an air conditioner (22°C) and provided natural light through transparent windows.

Egg clutches were found every 1−4 days in all chambers. On the day that new egg clutches were found in at least three mating chambers, we collected the eggs and relocated them to experimental cages (25 · 16 · 17 cm) filled with 3.5 L of dechlorinated water where the eggs were allowed to develop until they became froglets. To provide genetic variability within and among experimental cages, we filled each cage with eggs from at least three mating chambers and never filled the same treatment on the same day. The order of egg filling was random among experimental treatments. Egg collection was completed within a

2-week period (from 1st to 13th July 2020). We released all adult frogs back to the collection sites after then.

We manipulated three treatments in a full factorial design: (1) the density of tadpoles (low vs. high), (2) the amount of food provided each day (scarce vs. abundant), and (3) the location where parental frogs were collected (ephemeral vs. non-ephemeral streams). For density treatment, we kept either 5 (low-density) or 30 (high-density) individuals in each cage. For food treatment, we provided either 0.01 (scarce) or 0.1 g (abundant) of fish food (TetraBits Complete; Tetra, Germany) every day. We proportionally reduced the amount of food provided to cages in which some tadpoles had died or became froglets. We replaced half of the water every 2–3 days and removed any remaining food daily. We replicated each treatment twice and tested 280 tadpoles in total.

We surveyed the survival of all tadpoles and whether any tadpoles became froglets (Gosner stage 46) (Gosner 1960) each day. When a tadpole reached Gosner stage 46, we calculated the number of days that had passed from oviposition (larval period), measured the weight of the froglet (weight at metamorphosis), and then brought it out of the cage. We did not measure snout–vent length because all froglets were tiny, making accurate measurements for inter-individual comparisons impossible. We considered tadpoles to have been cannibalized when either tadpoles were missing or we directly observed cannibalistic behaviors. We also noted the occurrence of non-cannibalistic deaths where tadpoles were found dead without any signs of attack. All froglets were released to the location where their parental frogs were collected at the end of the experiment.

Data analysis

We used R 4.0.2 (R Core Team 2018) for all analyses. To compare the proportion of cannibalized tadpoles among treatments, we fitted generalized linear models (GLMs) with a binomial error structure. We used a binary variable of whether each tadpole was cannibalized or not as a response variable and our treatments (food, density, and location) as predictors of up to two-way interactions. We also used GLMs to compare the occurrence of non-cannibalistic deaths among treatments. Comparisons of larval period and weight at metamorphosis among treatments revealed substantial heterogeneity of variance among them. Thus, we employed permutational analysis of variance implemented in 'permuco' package for the comparisons. For both analyses, we used food, density, location, and their two-way interactions as predictor variables. Larval period and weight at metamorphosis were used as response variables.

As the information-theoretic approach of model selection is not possible in permutational analysis (Burnham and Anderson 1998), we selected the best model by sequentially removing the non-significant terms ($P > 0.1$) from the full model until the P values of all remaining terms were less than 0.1. To assess the degree of phenotypic plasticity, we performed Levene's test for homogeneity of variance to compare the variances of larval period and weight at metamorphosis between the ephemeral and non-ephemeral stream populations.

Results

Comparison of non-cannibalistic deaths and cannibalism

Overall, 151 tadpoles (54% of the total) that survived until they became froglets were measured for larval period and weight. Of the tadpoles that had died, 40 (14%) did not show any signs of cannibalism and 89 (32%) were found to have been cannibalized. Low food availability primarily affected the occurrence of non-cannibalistic deaths (χ^2_1 = 5.86, P = 0.02). The number of individuals found dead under the scarce food and high-density condition comprised 65% of all non-cannibalistic deaths. No other predictor explained the occurrence of non-cannibalistic deaths (all P > 0.15).

Cannibalism occurred more frequently when food was scarce (χ^2_1 = 5.14, P = 0.02) and among mainland tadpoles (χ^2_1 = 16.56, P < 0.001). The density effect was marginally significant in that the rate of cannibalism was greater in the high-density groups (χ^2_1 = 3.45, P = 0.06). Although the interactions between all predictors were not significant (all P > 0.14), we further analyzed their interactive effects owing to the patterns that emerged in the graph (Fig. 2B). Individual analysis of the density groups revealed that food (χ^2_1 = 2.59, P = 0.1), location (χ^2_1 = 0, P = 1), and the interaction between these predictors (χ^2_1 = 0, P = 1) had no effect on the occurrence of cannibalism in the low-density groups but that tadpoles from ephemeral streams cannibalized significantly less than did those from non-ephemeral streams in the high-density groups (χ^2_1 = 18.51, P < 0.001). In the high-density group, we also found borderline evidence that cannibalism occurred more frequently when food was scarce (χ^2_1 = 3.42, P = 0.06) and determined that the interaction between location and food treatments had no effect (χ^2_1 = 1.29, P = 0.26).

Comparison of larval period and weight at metamorphosis
Analysis of the larval period showed that all three treatments interactively affected the larval period of tadpoles (see Table 1 for full statistics). Larval periods were shorter in the abundant food and low-density treatment (Fig. 3A). The interactive effect of density and food treatments was not significant. The effect of location depended on both density and food levels: tadpoles from ephemeral streams had shorter larval periods compared with those from non-ephemeral streams in all density and food treatments, with tadpoles from ephemeral streams becoming froglets 3–4.5 days (6–10%) faster on average compared with those from non-ephemeral streams in these treatments (Fig. 3A), except when they were under the scarce food and high-density condition, where tadpoles from ephemeral streams became froglets 12.6 days (17%) later on average compared with those from non-ephemeral streams. The larval periods under this harsh condition were substantially longer than those in other treatments (Fig. 3A).

Table 1

Summary of generalized linear models (GLMs) examining the effects of food, density, and location on larval period and weight at metamorphosis.

Response	Predictor	Coefficient	F (df = 1, 144)	P
Larval period	Food[a]	−9.94	45.23	<0.001
	Density[b]	−10.65	52.24	<0.001
	Location[c]	1.42	1.41	0.23
	Food · Density	7.50	25.89	<0.001
	Food · Location	−2.94	6.04	0.02
	Density · Location	−1.85	1.60	0.21
Weight at metamorphosis	Food[a]	0.08	161.45	<0.001
	Density[b]	0.06	95.74	<0.001
	Location[c]	−0.01	8.23	0.005
	Food · Density	0.02	15.00	<0.001
	Food · Location	−0.01	7.55	0.006
	Density · Location	0.006	0.86	0.35

[a]Scarce vs. abundant.

[b]Low vs. high.

[c]Jeju Island (ephemeral stream) vs. mainland South Korea (non-ephemeral stream).

The weights at metamorphosis were heavier under the abundant food and low-density condition (Fig. 3B; Table 1). We found no significant interaction effect between food and density treatments. Froglets from ephemeral streams were generally lighter than those from non-ephemeral streams, but the location effect varied among food and density conditions. We further compared weights at metamorphosis for each food group separately and found that froglets under a less dense condition were heavier when food was scarce ($F_{1,56}$ = 24.42, P < 0.001). Other effects (location and the interaction between location and density) were all non-significant, with P > 0.9. In contrast, we observed that froglets from ephemeral streams were lighter than those from non-ephemeral streams when food was abundant (F = 7.54, P = 0.005). This effect was principally driven by high-density (interaction between density and location, F = 6.73, P = 0.01), with froglets from ephemeral streams being only 1.5% lighter than those from non-ephemeral streams in the low-density group but 24% lighter than those in the high-density group (Fig. 3B). Similar to the

observation for scarce food conditions, froglets in less dense conditions were heavier when food was abundant ($F = 85.41$, $P < 0.001$).

Comparison of phenotypic plasticity

We found no evidence that developmental plasticity was higher in tadpoles from ephemeral streams than in those from non-ephemeral streams in terms of the larval period ($F_{1,149} = 2.08$, $P = 0.15$). However, the variance in weight at metamorphosis was lower in tadpoles from non-ephemeral streams than in those from ephemeral streams ($F_{1,149} = 6.14$, $P = 0.01$). This difference was largely due to the lower weights of tadpoles from ephemeral streams (Fig. 3B).

Discussion

Our results demonstrate three major differences between the mainland (non-ephemeral habitat) and Jeju Island (ephemeral habitat) tadpoles. First, the larval period was generally shorter for Jeju Island tadpoles, although this difference was conditional. Second, there was substantial variation in weight at metamorphosis among the treatments largely induced by the correlation between larval period and weight at metamorphosis. However, the difference between the Jeju Island and mainland populations was only apparent when food was abundant. Third, Jeju Island tadpoles cannibalized less than did mainland tadpoles. Although studies have predicted higher levels of developmental plasticity in highly variable environments, such as those in Jeju Island, our findings do not support this (Cook and Johnson 1968; Van Buskirk 2002).

Our results align well with the prediction that tadpoles in more variable and unpredictable environments would grow faster than those in more stable environments: tadpoles from Jeju Island grew faster than did those from the mainland in all comparisons except when both available resources were scarce and density was high, thereby intensifying the competition for food. Early metamorphosis is not always preferred because it often results in a smaller size at metamorphosis, which can affect post-metamorphic growth and survival (Altwegg and Reyer 2003; Edge et al. 2013). Therefore, early metamorphosis should evolve only when the benefits of developing early exceed the costs of having a smaller size. The survival advantage seems to be a key factor that has facilitated the observed earlier metamorphosis of Jeju Island tadpoles because early metamorphosis would benefit tadpoles living under higher environmental stressors more. The larval period was substantially extended under the food-limited and high-density condition for both tadpole populations (on average, a 37-day extension, which corresponds to an 83% increase in the larval period), suggesting that adaptive responses were hampered under this harsh condition. We also found a general trend that weight at metamorphosis is negatively correlated with the larval period within each treatment (Fig. S1). However, comparison of the two populations revealed that this negative correlation was somewhat alleviated in Jeju Island tadpoles: weights at metamorphosis were heavier in mainland tadpoles when there was enough food, whereas weights were similar when food was limited.

Collectively, the Jeju Island tadpoles grew faster than did the mainland tadpoles unless their growing environments were extremely challenging. When food was limited, which is a likely situation in Jeju Island pools, they developed faster with no apparent cost to their weight at metamorphosis. However, when food was abundant, they gained less weight compared with the mainland tadpoles. Thus, Jeju Island tadpoles' growth strategies may be tuned to adapt to situations where both resources are limited and growing environments are unpredictable. Because Jeju Island frogs have been separated from mainland frogs since their initial colonization (Fong et al. 2016), the genetic differences between them should account for the observed differences. Given the adaptive nature of growth strategies in tadpoles from ephemeral habitats, we consider natural selection as a key factor that has shaped the differences.

Our results are congruent with previous findings that cannibalism occurs more frequently under food-limited and high-density conditions (Wildy et al. 2001; Vaissi and Sharifi 2016). The difference between Jeju Island and mainland tadpoles was prominent only when the growing density was high, thus providing more opportunities for cannibalism. Our finding that Jeju Island tadpoles cannibalized less than did mainland tadpoles can be explained by indirect fitness costs (Pfennig 1997). In ephemeral habitats, such as Jeju Island, that consist of a large number of small pools, tadpoles living in the same pool are likely to be their kin, especially when the parental frogs are known to avoid conspecific cues, as was previously demonstrated in *B. orientalis* Jeju Island populations (Baek et al. unpublished). Thus, the fitness advantage of cannibalizing conspecifics should be lower in Jeju Island tadpoles because of the indirect fitness costs of cannibalizing their kin. Lower cannibalism rates in Jeju Island tadpoles support this kin selection view of cannibalism.

In conclusion, our study highlights that environmental differences have shaped the divergence in growth strategies between tadpoles from ephemeral streams and those from non-ephemeral streams. Differences in growth strategies generally follow predictions of adaptation to ephemeral conditions (Richter-Boix et al. 2006; Dittrich et al. 2016), but we found that this effect was contingent on growing density and food availability. We also found lower cannibalism rates among tadpoles from ephemeral streams, which may be accounted for by the indirect fitness costs involved (Pfennig 1997). By comparing two geographically isolated populations using a common garden experiment, we have confirmed that the observed differences have genetic basis. Environmental differences between mainland South Korea and Jeju Island provide a unique opportunity to explore how natural selection shapes phenotypic divergence in anurans through local adaptation. We also speculate that differences in tadpoles' developmental/physiological responses to other factors, such as temperature and hydroperiod, exist, but this hypothesis remains to be tested.

Declarations

Acknowledgments

Availability of data and material

The dataset used during the current study is available from the corresponding author on reasonable request.

Conflict of Interest

The authors declare that we have no conflict of interest.

Ethical approval

All animals were cared for following the guidelines for the treatment of animals in behavioral research and teaching. All protocols were approved by the institutional committee for animal care and use (approval no: MNU-IACUC-2020-001).

Consent to participate

Not applicable

Consent for publication

Not applicable

Code availability

Not applicable

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Figures

Figure 1

Images showing the differences in habitat between mainland (left; non-ephemeral) and Jeju Island (right; ephemeral) streams.
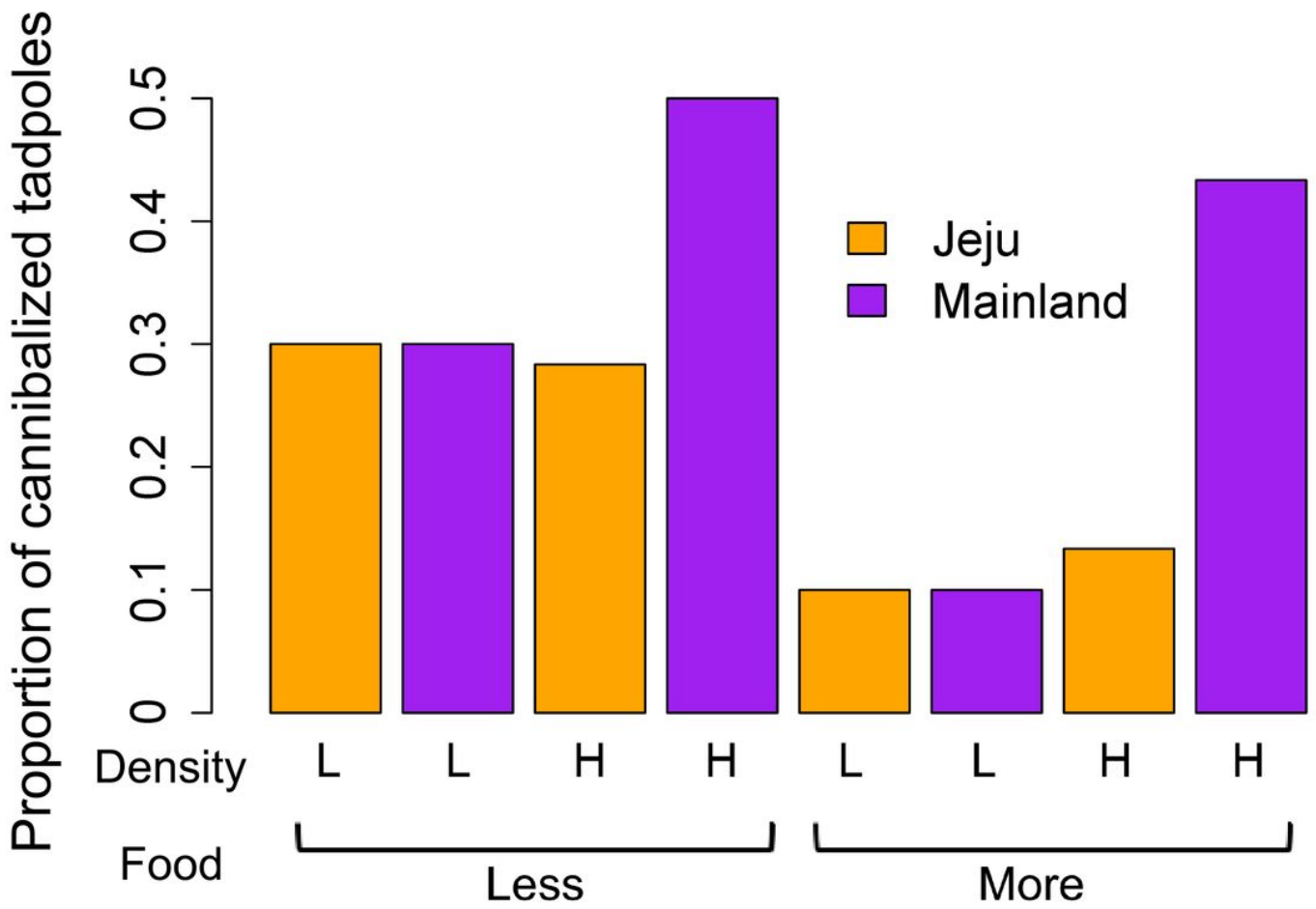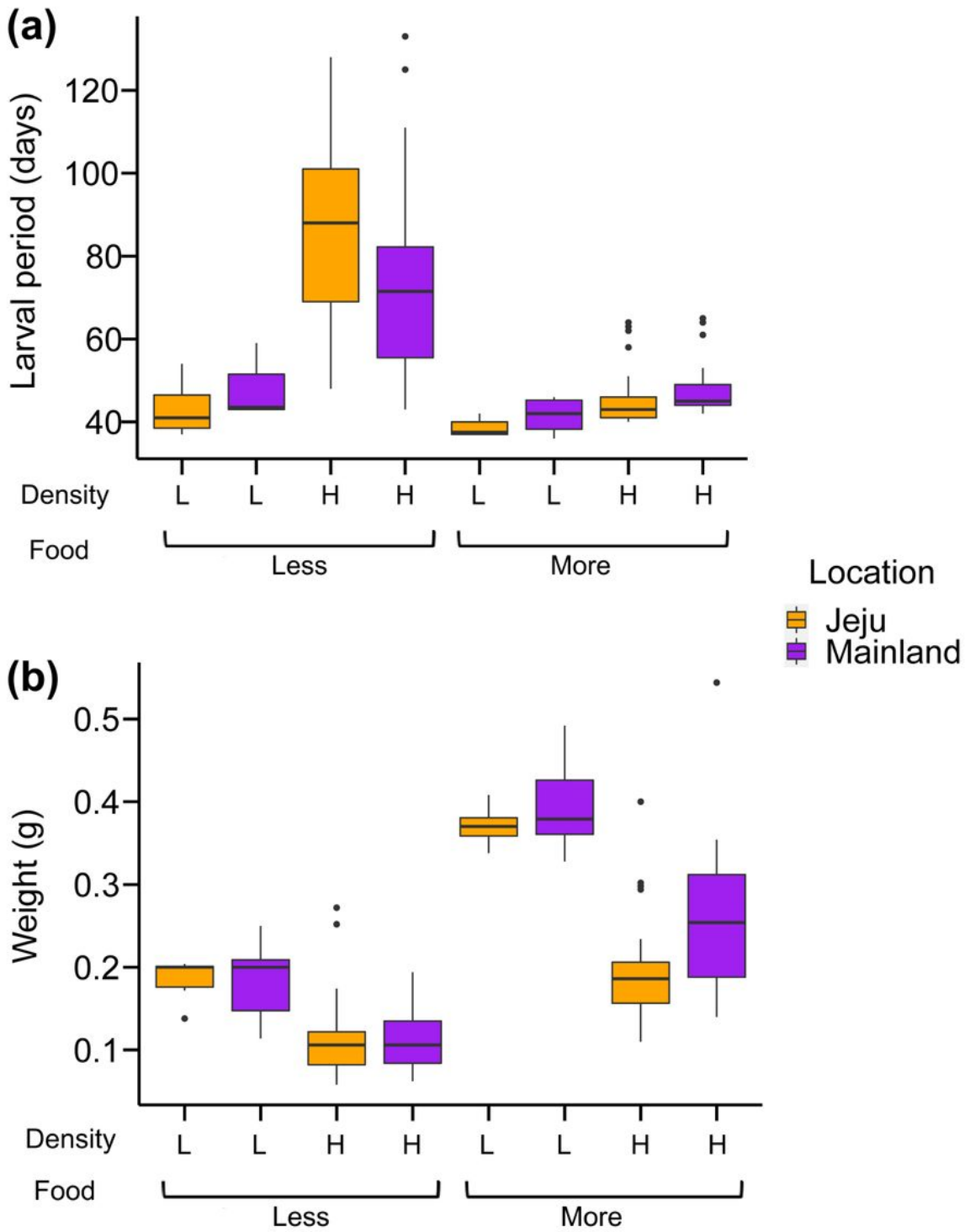
Figure 2

Comparison of the mean proportion of cannibalized tadpoles among treatments (density, food, and location). L, low; H, high.

Figure 3

Box–whisker plots showing the effects of density, food, and location on (a) larval period (days passed from oviposition to Gosner stage 46) and (b) weight at metamorphosis.

Supplementary Files

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- SupplementaryMaterials.pdf