
DIFFERENCE IN FLIGHT INITIATION DISTANCE BETWEEN RECENTLY METAMORPHOSED OREGON SPOTTED FROGS (*RANA PRETIOSA*) AND AMERICAN BULLFROGS (*LITHOBATES CATESBEIANUS*)

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Abstract.—Observations that recently metamorphosed Oregon Spotted Frogs (*Rana pretiosa*) appear to allow close approach before fleeing led us to contrast their flight initiation distances with those of introduced American Bullfrogs (*Lithobates catesbeianus*) in order to determine whether this anti-predator variable had the potential to make *R. pretiosa* vulnerable to predation. Using a rangefinder radio-linked to a high-resolution global positioning system unit, we quantified flight initiation distance for recently metamorphosed juveniles of both species using a controlled approach at Conboy Lake National Wildlife Refuge, Washington State, USA. Recently metamorphosed *R. pretiosa* typically allowed extremely close approach (median flight initiation distance, \bar{x} = 0.07 m, range: 0–6.5 m) with over 30% of frogs approached allowing themselves to be touched prior to fleeing. In contrast, recently metamorphosed *L. catesbeianus* typically did not allow close approach, always fleeing at distances \geq 1.7 m (flight initiation distance, \bar{x} = 6.1 m, range: 1.7–13.9 m). The close approach tactic of *R. pretiosa* would be consistent with a crypsis-based anti-predator strategy; whereas, *L. catesbeianus* uses a flight-oriented method of avoiding predation. Permitting close approach may place recently metamorphosed *R. pretiosa* within the typical predatory strike range of *L. catesbeianus*, which may explain the disappearance of *R. pretiosa* in areas invaded by *L. catesbeianus*. *Rana pretiosa* at Conboy Lake represents a unique instance of long-term co-occurrence with *L. catesbeianus*, raising questions about the basis of this co-occurrence.

Key Words.—American Bullfrog; comparative behavior; flight initiation distance; *Lithobates catesbeianus*; Oregon Spotted Frog; predator-prey; *Rana pretiosa*

INTRODUCTION

Anti-predator behavior is basic for survival (Harvey and Greenwood 1978; Lass and Spaak 2003; Stankowich and Blumstein 2005). One important aspect of anti-predator behavior is how close an organism will allow a predator to approach prior to taking evasive action, a distance termed the flight initiation distance (Ydenberg and Dill 1986; Cooper and Frederick 2007; Cooper 2009). Flight initiation distances or their equivalent have been examined in mammals (Altmann 1958; Dill and Houtman 1989; Bonenfant and Kramer 1996; Recarte et al. 1998), birds (Burger and Gochfeld 1991; Bednekoff 1996; Blumstein 2003), lizards (Rand 1964; Heatwole 1968; Cooper 1997b, 2003a, 2009), snakes (Mori and Burghardt 2001; Brown and Shine 2004), fishes (Dill 1990; Domenici 2002; Kiyoko et al. 2009), and invertebrates (Ydenberg and Dill 1986; Cooper 2006; Chan et al. 2010), but until recently, have remained relatively unstudied in amphibians (Martin et al. 2005; Cooper 2011; McCallum 2011).

Our interest in flight initiation distances arose from the field observation that Oregon Spotted Frogs (*Rana pretiosa*) appeared to allow closer approach than American Bullfrogs (*Lithobates catesbeianus*). If close approach (short flight initiation distance) represents an anti-predator tactic (as discussed by Ydenberg and Dill 1986; Broom and Ruxton 2005; Cooper and Frederick 2007), it may signify a vulnerability for *R. pretiosa*, which is an endangered species in Washington State (McAllister and Leonard 1997), particularly in the face of the opportunistic introduced *L. catesbeianus*. For this reason, we conducted a study comparing flight initiation distance between these species to determine the extent to which their anti-predator tactics differ. We conducted the study at Conboy Lake National Wildlife Refuge, the only location where *R. pretiosa* has successfully co-existed long-term (over 60 years) with *L. catesbeianus*, in an effort to provide insight into the reason for their unique co-occurrence. We chose to use recently metamorphosed frogs for this comparison because we felt that behavioral

inexperience resulting from entry into a new life stage and influenced by a different predator set (e.g., larval vs. frog predators) might best reveal where fundamental differences exist in the flight initiation distance of both species.

MATERIALS AND METHODS

Study area.—Our study area was located on Conboy Lake National Wildlife Refuge (NWR) in Klickitat County, Washington State, USA (Fig. 1). This refuge includes roughly two-thirds of the large (4,046 ha) wetland complex in the Glenwood Valley, which is located 20 km southeast of Mount Adams at slightly over 550 m above mean sea level. Construction of conveyance channels in the period 1911–1914 (Ladiges 1978) greatly altered drainage patterns across this wetland. These channels now provide permanent aquatic habitat in this system, habitat

that is a basic life history requirement for both of the highly aquatic frog species in this study.

We performed this study in one ≥ 200 m reach in two of these conveyance channels, Cold Springs Ditch and Outlet Creek (Fig. 1). Vegetation in both reaches was a mosaic of floating mats and selected emergents. The Cold Springs Ditch reach had floating and emergent vegetation patches and was narrower (3–4 m wide) than the Outlet Creek reach (4–5 m wide), which had mostly floating vegetation.

Reconnaissance surveys.—We performed reconnaissance surveys to obtain size distributions of the two target frog species to allow rapid identification of the recently metamorphosed cohort for both species based on size and to determine precisely where to locate our study reaches for flight initiation distance trials. These surveys were conducted between

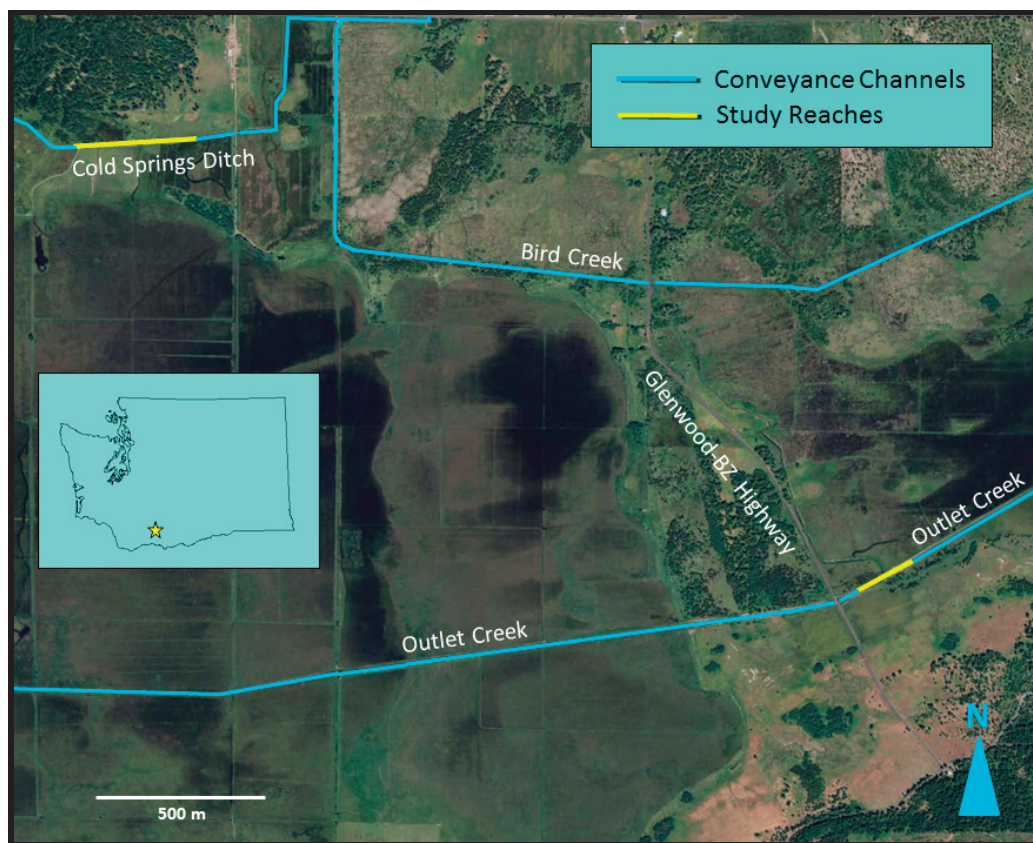


FIGURE 1. Aerial photograph of the portion of Conboy Lake National Wildlife Refuge showing the Cold Springs Ditch and Outlet Creek conveyance channels and study reaches used in the flight initiation distance trials. The inset shows the location of Conboy Lake National Wildlife Refuge within Washington State, USA.

0900 and 1700 during the day and between 2030 and 0130 at night over the two days immediately prior to our quantification of flight initiation distance. We used headlamps with a 60–200 lumen illumination range to conduct nighttime surveys.

Quantification of flight initiation distance.—

We quantified flight initiation distance by performing controlled approaches to individual recently metamorphosed frogs of both species between 1000 and 1755 on 2 and 3 September 2012. We modified the two-investigator approach that Martin et al. (2005) used on *Rana perezi* by using binoculars to assist locating frogs and recording distances with a rangefinder. During approaches, investigators moved in parallel, one in mid-channel, the other on the channel bank. We always moved in a direction back- or over-lit by the sun to ensure favorable illumination to detect frogs and to improve opportunities for approached frogs to clearly see the mid-channel investigator. Reconnaissance surveys had established that recently metamorphosed frogs of both target species were almost invariably in water, so the mid-channel investigator took on the pseudo-predator role to maintain greater uniformity in quantifying approaches. In each of the two study reaches used, we began at an arbitrary point in the channel and consistently moved slowly in the same direction until we finished that reach. Working in a uni-directional pattern and surveying each reach once ensured independence among approach observations. We stopped periodically at short-distance intervals (1–2 m) to completely scan the channel with binoculars up to 20 m in advance of our position, and initiated a controlled approach when one investigator located a frog of the target species. Upon locating a frog of the appropriate age cohort, we stopped and recorded the species. The on-bank investigator recorded data using a pull-down menu-enhanced personal digital assistant that was imbedded in a Trimble GeoExplorer 6000XT™ global positioning system (GPS) unit (Trimble Navigation Limited, Sunnyvale, California, USA). To maintain adequate precision, we recorded all locations in the GPS unit after logging at least 30 points for

each location. After initial data were recorded, the on-bank investigator remained stationary while the in-channel investigator conducted the approach. Led by an extended arm and open palm hand similar to the method used by McCallum (2011), the in-channel investigator approached the target frog at a velocity of 0.5–0.75 m/s on a direct line-of-sight vector. We verified the identification of the species during approach, and approach continued until the frog fled. As soon as fleeing occurred, the in-channel investigator stopped and obtained the flight initiation distance of the frog with a Trimble Laser Ace™ 1000 digital range finder that was Bluetooth-linked to the GPS unit and recorded all flight initiation distances ≥ 0.5 m with decimeter accuracy. If the flight initiation distance was < 0.5 m, we measured it with a steel tape to the nearest centimeter. Frogs that did not flee (allowed the investigator to touch them) were assigned a flight initiation distance of 0 m. If the frog did not flee, it was repeatedly touched until it fled.

We were able to confidently visually assess the size of both species as representing recently metamorphosed animals during the trials based on having captured > 200 individuals of both species measured over all body sizes (snout-to-vent length [SVL]) during mid-July-early September efforts in 2011–2012. Recently metamorphosed *R. pretiosa* averaged $39.3 \pm [SD] 2.1$ mm SVL (range: 36.0–46.0 mm SVL, $n = 29$) and one year after metamorphosis averaged 63.2 ± 1.8 mm SVL (range: 60.7–65.2 mm SVL, $n = 5$). Similarly, recently metamorphosed *L. catesbeianus* averaged 60.2 ± 4.8 mm SVL (range: 53.0–70.0 mm SVL, $n = 50$) and one year after metamorphosis averaged 93.2 ± 9.5 mm SVL (range: 77.5–107.5 mm SVL, $n = 20$). Hence, the > 10 mm gap (measured as SVL) that existed between recently metamorphosed animals and the next year class after metamorphosis facilitated recognizing the cohort that had just metamorphosed.

Measurement of potential co-factors.—We measured three factors that previous investigators had shown might influence flight initiation distance. Those co-factors were temperature at the location of the animal (Rand

1964; Rocha and Bergallo 1990; Smith 1997; Cooper 2003a), the orientation of the frog to the approaching investigator (Cooper 1997a; McCallum 2011) and the concealment level of approached animals (Heatwole 1968; Cooper 2003b; Martin et al. 2006). We recorded water temperature at the location from which a frog had fled within 30 s of the escape response with a digital Taylor thermometer (Taylor Precision Products, Oak Brook, Illinois, USA) to the nearest 0.1 °C. We estimated the frog's orientation on an axis relative to the in-channel investigator in 45-degree increments on a 0–4 scale. A frog estimated to be within 22.5° of facing directly away from that investigator scored 0, whereas a frog within 22.5° of facing directly towards the investigator scored 4 and frogs facing to the right or left scored 1–3 depending on whether they had an orientation closer to or further from facing the investigator. Lastly, we estimated degree of cover around approached frogs categorically on a 0–3 scale. A

zero score meant no emergent vegetation was present immediately around a frog, a score of 1 indicated that roughly one-third of the frog was cover-obstructed to the approaching investigator's visual field, a score of 2 indicated that about two-thirds of the frog was cover-obstructed, and a score of 3 indicated that nearly all the frog was cover-obstructed.

Analyses.—Because the distribution of flight initiation distances for recently metamorphosed *R. pretiosa* was strongly negatively skewed (Fig. 2), we compared the distributions of recently metamorphosed individuals between the two species with a Kolmogorov-Smirnov Goodness of Fit test and compared the medians of those distributions with a Mann-Whitney U test (Zar 2010). To ensure uniformity of conditions between the two species, we also compared cover, orientation, and water temperature for approached frogs between the two species using Mann-Whitney U tests. Finally, to determine

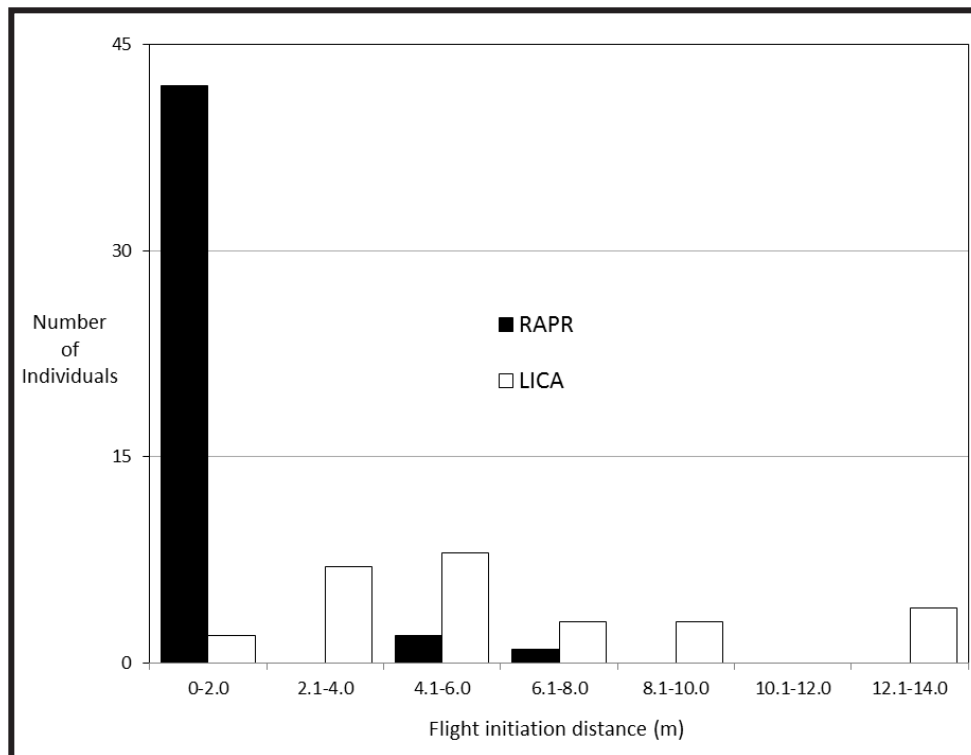


FIGURE 2. Distributions of flight initiation distances for recently metamorphosed individuals of *Rana pretiosa* (RAPR) and *Lithobates catesbeianus* (LICA) at Conboy Lake National Wildlife Refuge on 2–3 September 2012.

whether any relationship existed between flight initiation distance and each of the co-factors measured for approached frogs (cover, orientation, and water temperature), we conducted Spearman Rank correlations (ρ) for each species. For comparative purposes, we report means and standard errors in addition to medians and ranges for both the flight initiation distances and each co-factor. We describe effect size for flight initiation distance between the species with Hedges g ; whereas, effect size for co-factors on flight initiation distance was described with the aforementioned Spearman Rank correlations. All statistical analyses were performed using JMP version 9. For all analyses, we set $\alpha = 0.05$; all tests were two-tailed.

RESULTS

Comparison of flight initiation distances.—We quantified flight initiation distance for 45 recently metamorphosed *R. pretiosa* and 27 recently metamorphosed *L. catesbeianus*. The distributions of flight initiation distance differed

significantly between the species (Table 1; Fig. 2). Median flight initiation distance for *R. pretiosa* was less than 1/60th that for *L. catesbeianus* (Mann-Whitney U : $P < 0.0001$; Table 1). Fourteen of the *R. pretiosa* did not flee until after they were touched, and 87% ($n = 39$) of *R. pretiosa* allowed approach to within or equal to 0.25 m (Fig. 3). In contrast, none of the 27 *L. catesbeianus* allowed closer approach than 1.7 m. We found no significant differences among each of the cover, orientation, and temperature co-factors between the two species (Table 1).

Co-factors versus flight initiation distances.—We found no clear relationship between flight initiation distance and either temperature or orientation for recently metamorphosed individuals for either *R. pretiosa* (orientation: $P = 0.1061$; temperature: $P = 0.7784$) or *L. catesbeianus* (orientation: $P = 0.1371$; temperature: $P = 0.7094$; Table 1). However, we found a significant inverse relationship between flight initiation distance and extent of cover for *R. pretiosa* ($P < 0.0001$),

TABLE 1. Variation in flight initiation distance and co-factors in *Rana pretiosa* (RAPR) and *Lithobates catesbeianus* (LICA). For comparative purposes, we provide means and their standard errors (SE) in addition to the medians and ranges. Effect size for flight initiation distance between the species is described with a Hedges g , whereas that between flight initiation distance and each co-factor for each species used a Spearman Rank correlation (ρ). The statistic contrasting distributions in flight initiation distance between species is a Kolmogorov-Smirnov χ^2 , whereas those contrasting medians between the species and each co-factor are Mann-Whitney U values. Cover and orientation were measured categorically (see text for details).

Variable	Species	Mean \pm SE	Median	Range	Effect size	Analysis	
						Statistic	P
Flight Initiation Distance (m)	RAPR	0.45 \pm 0.19	0.07	0.0–6.5	$g = -2.2346$	$\chi^2 = 58.8$	< 0.0001
	LICA	6.07 \pm 0.72	5.44	1.7–13.9			
Co-factors:							
Temperature ($^{\circ}\text{C}$)	RAPR	21.1 \pm 0.7	21.8	14.0–27.4	$\rho = 0.044$	$U = 764.5$	0.0674
	LICA	22.7 \pm 0.4	22.7	18.2–25.8	$\rho = -0.075$		
Cover	RAPR	1.4 \pm 0.2	2.0	0–3	$\rho = -0.657$	$U = 719.0$	0.1989
	LICA	1.1 \pm 0.2	1.0	0–3	$\rho = -0.105$		
Orientation	RAPR	1.9 \pm 0.2	2.0	0–4	$\rho = -0.244$	$U = 643.0$	0.6867
	LICA	2.0 \pm 0.3	3.0	0–4	$\rho = -0.296$		

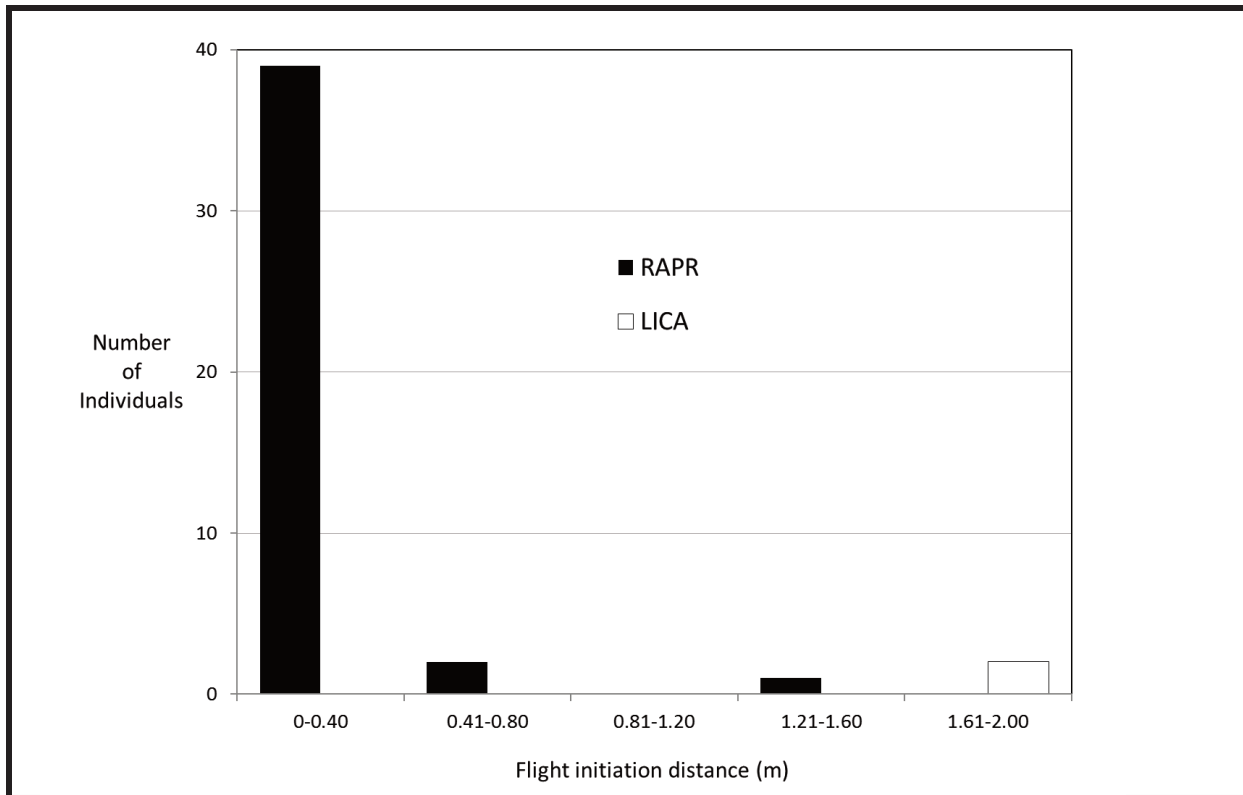


FIGURE 3. Distributions of flight initiation distance for recently metamorphosed individuals of *Rana pretiosa* (RAPR) and *Lithobates catesbeianus* (LICA) at Conboy Lake National Wildlife Refuge on 2–3 September 2012 for those individuals that fled at distances ≤ 2 m.

but not for *L. catesbeianus* ($P = 0.5930$).

DISCUSSION

Our hypothesis that *R. pretiosa* allow closer approach than *L. catesbeianus*, at least for recently metamorphosed individuals, was confirmed. The fact that flight initiation distance for *R. pretiosa* was typically so short that recently metamorphosed frogs frequently allowed themselves to be touched or almost touched by the investigator seemed counter-intuitive for predation avoidance. However, the highly cryptic litter-dwelling frogs in the genus *Craugastor* exhibit behavior that is clearly more extreme; $> 90\%$ of individuals approached by a human observer did not flee until touched (Cooper et al. 2008). Further, where degree of crypsis has been quantified, more cryptic taxa or individuals generally have shorter flight initiation distances (Heatwole 1968; Cooper and Sherbrooke 2010; Camp et al. 2012). Hence, the

longer flight initiation distances of *L. catesbeianus* appear to reflect a fundamentally different way to avoid capture.

The inverse relationship between cover and flight initiation distance in *R. pretiosa*, but not in *L. catesbeianus* supports the idea that *R. pretiosa* also uses a crypsis-based immobility tactic that differs fundamentally from the flight-based escape behavior we observed in *L. catesbeianus*. Such a tactic depends on crypsis until the risk of detection is high (Stankowich and Blumstein 2005; Cooper and Sherbrooke 2010), and since a greater level of cover is known to reduce the risk of detection (Cooper et al. 2008; Camp et al. 2012), flight initiation distances would indeed be expected to decrease with greater cover. Although we did not quantify the degree of crypsis that could help assess any difference between the two species, the color and pattern of recently metamorphosed *R. pretiosa* appeared to match to their background better than recently metamorphosed *L. catesbeianus*.

The differences we found in flight initiation behavior between recent metamorphs of the two species raise important questions about the basis of the differences, which may inform the unique long-term co-occurrence of the two species at Conboy Lake NWR. First, the flight initiation distances of recently metamorphosed *R. pretiosa* are very short, and this may put them at a disadvantage in the face of potential predation by *L. catesbeianus*. Vulnerability of recently metamorphosed *R. pretiosa* may be high if the predatory striking range of large *L. catesbeianus* encompasses the flight initiation distance of *R. pretiosa*. Secondly, although large (older) *L. catesbeianus* are known major predators (Werner et al. 1995; Pearl et al. 2004), details of how they take their prey remain unquantified. Third, our focus on recent metamorphs raises the question of whether older post-metamorphic life stages display similar differences in flight initiation behavior or whether shifts in those differences occur with size and experience.

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