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Externally Attached Radio-Transmitters Have Limited Effects on the Antipredator Behavior and Vagility of *Rana pipiens* and *Rana sylvatica*

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ABSTRACT.—Anurans display a variety of antipredator behaviors from flight and crypsis to defensive postures. External attachment of a radio-transmitter is a commonly used technique that could potentially interfere with the antipredator behavior of anurans. We investigated the effect of an externally attached radio-transmitter on the antipredator behavior and vagility of adult Northern Leopard Frogs (*Rana pipiens*) and adult Wood Frogs (*Rana sylvatica*). We simulated attacks by birds and snakes and used fluorescent powder to follow the path of individuals through natural habitats. Both species displayed a different frequency of behaviors in response to each predator, but the presence of a transmitter did not affect the frequency of antipredator behaviors. When carrying a transmitter, *R. pipiens* exhibited a different escape angle during attacks by simulated aerial predators and exhibited a change in the mean turn angle over 4-h movement paths. *Rana sylvatica*'s escape behavior and vagility were unaffected by a transmitter during simulated attacks, although frogs with a transmitter did take more jumps per 4-h movement paths and followed straighter paths than did frogs without a transmitter. The body mass of the individual did not affect any of our behavior or movement metrics. Although most of our metrics did not change markedly in response to the presence of a transmitter, the subtle changes in vagility and escape behavior are analogous to the negative effects of externally attached transmitters seen in birds and mammals. These results suggest that transmitters may have consequences for the energetics, survival, and reproduction of anurans.

Anurans display a variety of antipredator behaviors from flight and crypsis to defensive postures (Marshisin and Anderson, 1978; Williams et al., 2000). Along with morphological and physiological adaptations, such as coloration, cryptic appendages, and skin secretions, these behaviors function to deter or elude predators by making the animal look too large to ingest or difficult to find, catch, or handle (Schall and Pianka, 1980; Duellman and Trueb, 1986).

Because anurans rely on morphology, behavior, and vagility to avoid predation, it is possible that constraints on any of these mechanisms could lead to increased predation. This phenomenon has been seen in other animals such as snow geese (*Chen caerulescens*), which became more susceptible to hunting by humans after attachment of a backpack radio-transmitter (Withey et al., 2001). The attachment of radio-transmitters could make an animal slower, more visible, or unable to assume certain postures (Kenward, 2001). For example, diving ducks (*Aythya* spp.) increased preening, stretching, and fluffing of feathers in response to the attachment of a backpack radio-transmitter (Withey et al., 2001).

External attachment of a radio-transmitter is a commonly used technique for studying

behavior in a variety of anurans that has been used for over four decades (Tester 1963; van Nuland and Claus, 1981; Hodgkison and Hero, 2001; Watson et al., 2003). External attachment of transmitters has two advantages over implanted transmitters: no surgery is required and detection range can be greatly increased (Richards et al., 1994). Increased detection range is advantageous with the small transmitter size necessary to study relatively small bodied, yet highly mobile, anurans that use refugia below the water or ground surface (e.g., Eggert, 2002). Possible disadvantages of using an externally attached radio-transmitter include increased stress to the animal, altered behavior, decreased vagility, harm to the animal's skin, and increased susceptibility to predation (Richards et al., 1994; Goldberg et al., 2002; Weick et al., 2005), although these effects have not been experimentally addressed for anurans. These effects are thought to be minimized if the transmitter's mass is <10% of the animal's body mass (White and Garrott, 1990; Richards et al., 1994). However, effects have been found in birds and mammals with a transmitter as light as 3% of the body mass (Kenward, 2001), and external attachment of a transmitter with a harness had effects in most studies on birds (Withey et al., 2001).

We investigated the effect of an externally attached radio-transmitter on antipredator behavior and vagility of adult Northern Leopard

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Frogs (*Rana pipiens*) and adult Wood Frogs (*Rana sylvatica*) in two experiments. First, we simulated attacks on frogs with and without a transmitter by models of ground (garter snakes, *Thamnophis* spp.) and aerial (raptors) predators. Second, we marked frogs with fluorescent powder and followed the movement paths of frogs with and without a transmitter through the terrestrial environment.

MATERIALS AND METHODS

Study animals.—We collected wild frogs from the University of Maine Demeritt and Penobscot Experimental Forests 1–13 days prior to the predation and vagility experiments described below. We captured frogs by hand, dip net, and in pitfall traps. We used telemetry to follow frogs with transmitters in the vagility experiment for 1–40 days prior to tracking with fluorescent powder. When in captivity, we housed all frogs individually in 2.3-liter plastic storage bins or in small groups (<5 frogs) in 38-liter glass aquaria. Each container had approximately 5 mm of standing water, holes in the top, and a wet paper towel for cover. We fed all frogs crickets ad libitum prior to the start of the trials and at the end of the trials. After each experiment was completed, we collected all frogs and released them at dusk at the original capture location.

Predation experiment.—We conducted all trials in a 48-m² fenced experimental arena in the northeast corner of a 0.5-ha forest clearing near the University of Maine campus. Surrounding forest canopy trees were gray birch (*Betula populifolia*), white pine (*Pinus strobus*), balsam fir (*Abies balsamea*), and American beech (*Fagus grandifolia*). Ground cover in the arena included grasses, bracken fern (*Pteridium aquilinum*), shrubs (*Spiraea* spp.), saplings of *A. balsamea* and *P. strobus*, haircap moss (*Polytrichum commune*), woody debris, and coniferous and deciduous leaf litter. The experimental arena was similar in vegetation to areas where we collected both species. We chose this area to standardize the cover available to each species because cover availability is an important variable in the risk perception of frogs (Hayes, 1990; Martin et al., 2005).

We randomly assigned each frog to a transmitter or no transmitter category prior to each trial. We attached a transmitter (Holohil BD-2, 0.9-g, 14-cm external whip antennae, 40-day battery life) with elastic thread beaded with glass beads snug enough to prevent slippage over the rear legs when extended but not so snug as to constrict the skin (Muths, 2003; Weick et al., 2005). The 24 (11 males, 13 females) *R. sylvatica* used in the experiment were 47 ± 1 mm

(mean \pm SE; range 40–56) snout–vent length (SVL) and weighed 10.1 ± 0.6 g (range 6.1–17.0). The 18 (eight males, 10 females) *R. pipiens* used in the experiment were 65 ± 2 mm (range 50–84) SVL and weighed 27.3 ± 3.1 g (range 9.5–54.2). Transmitters plus harness weighed 0.96–0.98 g and were on average 9.6% (range 5.7–15.8%) of the body mass for *R. sylvatica* and 3.5% (range 1.8–10.0%) for *R. pipiens*.

We used model predators to simulate attacks (Hayes, 1989; Brodie et al., 1998; Gomes et al., 2002; Meehan and Nisbet, 2002). These models work well because anurans rely primarily on visual cues to elicit antipredator behavior (Gregory, 1979; Heinen, 1994; Martin et al., 2005; Wirsing et al., 2005). *Rana pipiens* and *R. sylvatica* responded similarly to the movement of all models we tried in preliminary trials (e.g., a dipnet, brown plastic bucket, and model bird moved toward the frog through the air; and aluminum pole, bamboo pole, and model snake moved along the ground toward the frog). For our model of an aerial predator, we attached a three-dimensional, black model of a flying bird to a monofilament fishing line (5.4 kg [12 flb] test) that was anchored to the ground 0.4 m from the trial location and to a metal fencepost 2.6 m above the ground and 10 m from the trial location. We used a 1.2 m long by 1.5 cm diameter bamboo pole as our model of a ground predator.

We first simulated an attack by an aerial predator and then, if the frog did not move from its original location, we simulated an attack with a ground predator. We placed an individual frog at the trial location under a 2-liter plastic bucket, and then we allowed it to acclimate for 1 min. We removed the bucket and waited 2–5 sec before we released the bird model from the high end of the fencepost such that it slid down the line toward the frog. We coded the frog's behavior during the attack following Marshisin and Anderson's (1978) classification of 14 antipredator behaviors and used video recordings of each attack (taken with a Canon NTCA ZR 60 digital video camera mounted on a tripod outside the experimental arena) to proof our coding and distinguish between behaviors. We also recorded the distance and direction the frog moved immediately after the attack.

If the frog did not exhibit flight behavior during the initial aerial attack, we simulated an attack by a ground predator 5–10 sec later. We crouched on the edge of the experimental arena (hidden by black silt fencing), held the bamboo pole 1–5 cm above the ground, and slowly moved the pole toward the frog until the frog fled or the pole touched the frog. As for the aerial attack, we coded the frog's behavior

during the attack and recorded the distance and direction the frog moved after the ground attack.

We repeated trials over the span of four days (24–27 July 2006) from 0800–1800 h until we evaluated 10 trials for each frog and at least 150 trials for each species and predator type. We conducted four or fewer trials per day with each frog and allowed a resting time of ≥ 2 h between trials, so as not to physically stress the frogs and allow for trials to function as independent replicates. We chose timing and weather conditions to mimic when predation was likely to occur. The weather during trials was partly sunny to overcast with temperatures in the experimental arena of 23.7–33.8°C, relative humidity of 54–81%, and wind < 16 km/h. We terminated trials on 26 July when wind speed increased to > 24 km/h and a thunderstorm began. Both *R. pipiens* and *R. sylvatica* are primarily nocturnal but are frequently active during daylight hours during summer in Maine (Hinshaw, 1999; Knox, 1999; Redmer and Trauth, 2005; Rorabaugh, 2005). The aerial predators (raptors) and ground predators (snakes) we were mimicking are primarily diurnal and forage visually (Goodwin, 1976; Drummond, 1985; Sullivan and Dinsmore, 1992; Marzluff and Angell, 2005).

The data were primarily nonnormal based on histograms, skewness, and kurtosis of each variable; thus, we transformed each variable to achieve normality and homogeneity of variance for all comparisons between transmitted and non-transmitted frogs. We used repeated measures analysis of variance (rmANOVA; PROC MIXED; Wallace and Green, 2002) to compare the total distance a frog traveled, number of jumps a frog took to travel that distance, and the angle a frog moved in response to attacks with and without a transmitter. We used multiple linear regression (PROC GLM) to investigate the relationship between frog mass and mean coded behavioral response (following Marshisin and Anderson's [1978] classification), mean distance traveled, mean angle of the jumps, and the mean number of jumps per escape. We also investigated the frequency distribution of the coded behavioral response (following Marshisin and Anderson's [1978] classification) between species, predator types, and frogs with or without a transmitter using a chi-square or Fisher's exact test. We analyzed only the behaviors the frog exhibited in response to the approach and first contact with the ground predator. We performed all tests using SAS (SAS Institute, Cary, NC). We accepted significance at $P < 0.05$ for the multiple linear regression and used Bonferonni

adjusted P -values for each set of univariate comparisons ($P < 0.017$ for rmANOVA and $P < 0.013$ for chi-square and Fisher's exact tests). We also performed comparisons between transmitted and nontransmitted frogs using non-parametric tests. We report only parametric results because the results were qualitatively identical.

Vagility experiment.—To compare vagility and movement patterns of frogs with and without radio-transmitters, we tracked the movement paths of 26 (17 males, nine females) *R. sylvatica* and 33 (16 males, 17 females) *R. pipiens* with fluorescent powder (DayGlo Color Corporation, Cleveland, OH). Fluorescent powders are an effective, noninvasive way to track the movements of small, ground-dwelling animals, and these powders do not affect the movement patterns or physiology of amphibians (Graeter, 2005; Rittenhouse et al., 2006). We tracked 18 and 15 *R. pipiens* and 16 and 10 *R. sylvatica* without and with transmitters, respectively. *Rana pipiens* were tracked in June 2006, and *R. sylvatica* were tracked in June 2005. The 26 *R. sylvatica* were 48 ± 1 mm (range 43–58) SVL (mean \pm SE) and 11.1 ± 0.3 g (range 9.1–16.7). The 33 *R. pipiens* were 77 ± 1 mm (range 66–87) SVL and 40.7 ± 1.8 g (range 24.6–66.0). Transmitters plus harness were on average 8.7% (range 6.4–10.5%) of the body weight for *R. sylvatica* and 2.4% (range 1.5–3.6%) for *R. pipiens*.

Frogs were captured in clearcut, partially harvested, or unharvested forest, and individuals were released at dusk at a central location in each area at least 75 m from the nearest edge. We applied powder to each individual prior to release by dipping the ventral three-quarters of the body into powder avoiding the frog's head. Approximately 4 h after we released the frogs, we tracked the paths with a handheld ultraviolet light (Versalume, Raytech, Middletown, CT) and marked the path with nylon thread or pin flags. We followed the paths until no more powder could be seen or we found the frog. The following day, we used a meter stick and compass to record the distance and turn angle of each jump, which we defined as the distance between each turn of $\geq 10^\circ$, for the entire path. We used ArcGIS 9 (Environmental Systems Research Institute, Redlands, CA) to plot paths and calculate total path lengths for each species and VFractal (Nams, 1996) to calculate fractal dimension (a measure of how many turns the path contains) with the dividers method (see Mandelbrot, 1967) for each path.

The data were primarily nonnormal based on histograms, skewness, and kurtosis of each variable; thus, we transformed each variable to

achieve normality and homogeneity of variance for all comparisons between transmitted and nontransmitted frogs. To investigate the effect of the radio-transmitter on long-distance vagility and behavior, we used multivariate analysis of variance (MANOVA statement in PROC GLM) to compare total path length, number of jumps, mean turn angle, and fractal dimension of frogs with and without a transmitter. We used multiple linear regression (PROC GLM) to investigate the relationship between frog mass and total distance traveled, angle of the jumps, the number of jumps per path, and fractal dimension. We accepted significance at $P < 0.05$ for all tests.

RESULTS

Predation experiment.—We observed 420 simulated attacks by aerial predators and 322 simulated attacks by ground predators. During these attacks, we observed eight of the 14 behaviors described by Marshisin and Anderson (1979): remain motionless, crouch, chin tuck, body inflation, flight, hide, walk, and vocalize. The two species differed from one another in their frequency of antipredator behaviors in response to both predator types (Fig. 1; aerial, $\chi^2_6 = 89.1$, Fisher's exact $P < 0.001$; ground, $\chi^2_7 = 100.1$, Fisher's exact $P < 0.001$), and each species differed in their frequency of behaviors in response to aerial and ground attacks (*R. pipiens*, $\chi^2_7 = 197.9$, $P < 0.001$; *R. sylvatica*, $\chi^2_5 = 96.4$, Fisher's exact $P < 0.001$). These differences were primarily caused by *R. pipiens* remaining motionless in response to both attack types and the broader range of behaviors used by *R. pipiens* in reaction to ground attacks. *Rana sylvatica* never vocalized or inflated its body in response to either predator.

The antipredator behavior and vagility of *R. pipiens* and *R. sylvatica* were not greatly affected by the presence of a transmitter in response to simulated attacks. *Rana pipiens* with a transmitter exhibited a change in the escape angle of 1.5 rad (a sharper angle and in the opposite direction) in response to aerial predator attacks (Table 1A) and a marginally significant decrease in total escape distance (47 vs. 39 cm) in response to ground predator attacks (Table 1B). *Rana sylvatica* with a transmitter did not exhibit a change in the total distance moved, the number of jumps, or the angle of escape in response to attacks by aerial or ground predators. The presence of a transmitter did not change the frequency of antipredator behaviors for either *R. pipiens* (aerial, $\chi^2_5 = 7.9$, Fisher's exact $P = 0.140$; ground, $\chi^2_7 = 9.7$, Fisher's exact $P = 0.200$) or *R. sylvatica* (aerial,

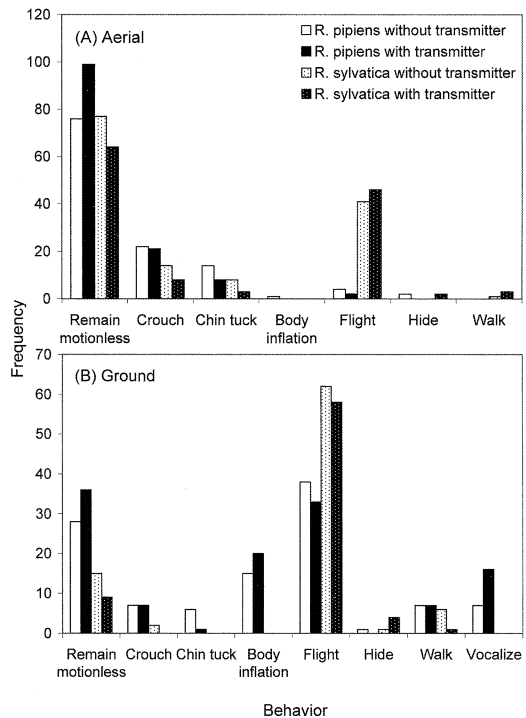


FIG. 1. Behaviors exhibited by *Rana pipiens* (solid bars) and *Rana sylvatica* (stippled bars) with (dark bars) and without (light bars) a radio-transmitter in response to simulated aerial (A) and ground (B) attacks.

ground, $\chi^2_5 = 7.6$, Fisher's exact $P = 0.192$; ground, $\chi^2_4 = 7.8$, Fisher's exact $P = 0.097$). For both species, the escape angle, escape distance, number of jumps, or coded behavioral response were not affected by the mass of the frog with a transmitter in response to either predator (*R. pipiens*, aerial: inadequate sample size ($N = 2$), ground: $F_{6,11} = 0.56$, $P = 0.810$; *R. sylvatica*, aerial: $F_{9,11} = 0.42$, $P = 0.898$, ground: $F_{7,15} = 2.72$, $P = 0.049$).

Vagility experiment.—*Rana pipiens* with and without a radio-transmitter did not differ overall in movement path characteristics (Wilk's $\lambda_{4,28} = 1.34$; $P = 0.278$), but frogs with a transmitter did exhibit a change in mean turn angle of 0.2 rad (Table 2). In contrast, *R. sylvatica* with and without a transmitter differed overall in movement path characteristics (Wilk's $\lambda_{4,21} = 8.99$; $P < 0.001$): individuals with a transmitter exhibited an increase of 14 steps per path and followed a straighter path than did frogs without a transmitter. For both species, the mean turn angle, distance traveled, number of jumps, or fractal dimension were not affected by the mass of the frog with a transmitter (*R.*

TABLE 1. Characteristics of escapes (mean \pm 1 SE) by *Rana pipiens* and *Rana sylvatica* with and without a radio-transmitter in response to a simulated attack by an aerial (A) or ground (B) predator.

	<i>R. pipiens</i>			<i>R. sylvatica</i>		
	With transmitter	Without transmitter	$F_{1,4}$	With transmitter	Without transmitter	$F_{1,67}$
(A)						
Number of attacks (escapes)	95 (2)	85 (4)		114 (46)	126 (46)	
Total distance (cm)	68 \pm 16	128 \pm 44	1.09	56 \pm 4	61 \pm 5	1.03
Number of jumps	1.0 \pm 0.0	1.3 \pm 0.3	0.44	1.0 \pm 0.0	1.0 \pm 0.0	0.50
Escape angle (rad)	0.69 \pm 0.28	-0.99 \pm 0.22	21.24	-0.21 \pm 0.16	-0.18 \pm 0.21	0.06
(B)						
Number of attacks	93	81		68	80	
Total distance (cm)	39 \pm 3	47 \pm 3	4.34	48 \pm 3	52 \pm 3	0.63
Number of jumps	1.0 \pm 0.0	1.0 \pm 0.0	0.16	1.1 \pm 0.0	1.0 \pm 0.0	1.13
Escape angle (rad)	-0.53 \pm 0.17	-0.82 \pm 0.18	0.91	-0.56 \pm 0.19	-0.74 \pm 0.18	0.32

TABLE 2. Characteristics of movement paths (mean \pm 1 SE) by *Rana pipiens* and *Rana sylvatica* with and without radio-transmitters over a 4-h period.

	<i>R. pipiens</i>			<i>R. sylvatica</i>		
	With transmitter	Without transmitter	$F_{1,31}$	With transmitter	Without transmitter	$F_{1,24}$
(A)						
Number of paths	15	18		10	16	
Path length (m)	13.14 \pm 1.80	15.20 \pm 3.40	0.06	9.67 \pm 2.82	9.91 \pm 3.08	0.05
Number of jumps	10 \pm 1	10 \pm 2	0.22	25 \pm 6	11 \pm 3	7.06
Turn angle (rad)	0.39 \pm 0.06	0.59 \pm 0.06	5.21	0.60 \pm 0.07	0.45 \pm 0.11	0.64
Fractal dimension	1.18 \pm 0.06	1.11 \pm 0.02	1.85	1.08 \pm 0.01	1.21 \pm 0.05	5.11
(B)						
Number of paths	15	18		10	16	
Path length (m)	13.14 \pm 1.80	15.20 \pm 3.40	0.06	9.67 \pm 2.82	9.91 \pm 3.08	0.05
Number of jumps	10 \pm 1	10 \pm 2	0.22	25 \pm 6	11 \pm 3	7.06
Turn angle (rad)	0.39 \pm 0.06	0.59 \pm 0.06	5.21	0.60 \pm 0.07	0.45 \pm 0.11	0.64
Fractal dimension	1.18 \pm 0.06	1.11 \pm 0.02	1.85	1.08 \pm 0.01	1.21 \pm 0.05	5.11

pipiens, $F_{4,10} = 0.71$; $P = 0.605$; *R. sylvatica*, $F_{4,5} = 0.14$; $P = 0.959$).

DISCUSSION

Transmitter effects.—These experiments revealed some subtle, short-term, effects of an externally attached radio-transmitter on the escape behavior and vagility of two amphibian species. During both experiments, each species responded differently to the presence of a transmitter. *Rana pipiens* exhibited a different angle of escape (Table 1A) and a marginally significant decrease in total escape distance (Table 1B) in the predation experiment and a change in turn angle in the vagility experiment (Table 2). *Rana sylvatica* exhibited an increase in the number of jumps per path and followed a straighter path in the vagility experiment (Table 2), and the frog's body mass was a marginally significant predictor of the antipredator behaviors and escape metrics in the predation experiment. Although most of our metrics did not change in response to the presence of a transmitter, these subtle changes are not surprising given that externally attached transmitters have negative effects on other taxa (Kenward, 2001). Multiple factors of a species' biology; including morphology, energetic constraints, and habitat use; will affect the sensitivity of a species to the external attachment of a transmitter. For example, waterfowl and upland game birds were very sensitive to a transmitter attached as a backpack, but raptors were affected only during times of limited resources (Withey et al., 2001).

A possible explanation for the differences in behavioral response between the two ranids could be the different ratio of body size to transmitter size. The mass and bulk of the transmitter, including battery placement and length of the transmitter antenna, could affect the frog's behavior. Bulk can increase drag in swimming animals, including *R. sylvatica* in the breeding pond (Kenward, 2001; Muths 2003), and whip antennae have caused decreased mobility and mortality in birds (e.g., Dunstan, 1977). Transmitter size has important implications for flying animals, which have high energetic demands (Gessamen and Nagy, 1988; Withey et al., 2001). The energetic demands of jumping through a complex environment and the added mass or bulk from a transmitter could have similar consequences for using and storing energy in anurans. Energetic constraints can have negative implications for survival and reproduction and lead to reduced fitness. These questions have been addressed in some larger animals (White and Garrott, 1990; Withey et al., 2001) but not in small animals. However, we did

not find a significant relationship with body mass for our movement metrics. Although we did not find a strong effect of body size on our movement metrics within each species, the larger and heavier *R. pipiens* was similarly affected by the presence of a radio-transmitter when compared to *R. sylvatica*. The size range of frogs we used overlapped between the two species, but on average *R. sylvatica* were approximately two-thirds the length and one-third the mass of *R. pipiens*. Body size is an important variable in the risk perception of frogs (Martin et al., 2005) and warrants future consideration.

Differences in sensitivity to the presence of a radio-transmitter between the species could result from differences in other antipredator mechanisms (Hayes, 1990). Although both *R. pipiens* and *R. sylvatica* routinely use the terrestrial environment (Hinshaw, 1999; Knox, 1999; Redmer and Trauth, 2005; Rorabaugh, 2005), they differ in their palatability to predators, skin secretions, jumping ability, habitat preferences, cryptic coloration, body size (Formanowicz and Brodie, 1979; Heinen and Hammond, 1997; Choi et al., 1999), and antipredator behaviors (this study). *Rana pipiens* exhibited a broader range of behaviors than did *R. sylvatica* in response to simulated aerial and ground attacks and used behaviors that may be constrained by the presence of a transmitter such as inflation of the body. We speculate that the diverse range of antipredator behaviors exhibited by *R. pipiens* may make it more sensitive to the presence of a transmitter than expected based on its body size.

Although we found some limited effects of a radio-transmitter on the vagility and escape behavior of *R. pipiens* and *R. sylvatica*, the frequency of antipredator behaviors was not profoundly affected by the presence of a radio-transmitter. *Rana pipiens* exhibited changes in both experiments, and *R. sylvatica* changed its behavior only in the longer vagility experiment, despite the short duration (<1 min for predator attacks and 4 h for movement paths) of both experiments. These differences between the species may indicate there is a different sensitivity of each species to a transmitter. The behavioral response of each may be susceptible to change at different temporal scales and have different energetic consequences for each species. Escape is only one strategy for avoiding predation, and a diverse suite of antipredator behaviors is essential to avoiding predators that form search images (Schall and Pianka, 1980).

Behavioral differences between species in response to different predators.—We observed some differences in behavior between the two species of

frog, and each species used different strategies in their response to simulated aerial and ground attacks (Fig. 1). These differences in behavioral response between predators could be considered a product of our experimental design. By attacking first with the aerial predator and then with the ground predator, the timing of the simulated attacks could have biased the frogs' antipredator response to ground predators. However, the order of repeated stimuli did not cause a bias toward active antipredator behaviors (e.g., fleeing) in *Scinax hiemalis* (Gomes et al., 2002), and we could not find an example where an amphibian was more likely to respond to repeated stimuli with flight, unless the animal was touched with excessive force (e.g., Williams et al., 2000). In addition, a passive antipredator response (e.g., remaining motionless, crouching, and chin tucking) was more likely if the amphibian was not touched (Ducey and Brodie, 1983; Dowdey and Brodie, 1989; Gomes et al., 2002). Both *R. sylvatica* and *R. pipiens* relied primarily on remaining motionless in response to aerial attacks in our predation experiment. Remaining motionless is a common antipredator behavior (Marshisin and Anderson, 1978; Heinen and Hammond, 1997; Williams et al., 2000), which complements cryptic coloration and decreases the risk of predation by predators that hunt visually (Heinen, 1994; Martin et al., 2005).

Both species relied more on flight behavior in response to ground attacks than in response to aerial attacks (Fig. 1). Such rapid movements followed by immobility can take the prey out of the predator's search window, and this behavior has been seen in newly metamorphosed *R. pipiens* (Heinen and Hammond, 1997). *Rana pipiens* exhibited a broader range of behaviors in response to ground attacks than aerial attacks including inflation of the body and vocalization. These behaviors can startle the predator, accentuate skin glands, and make the frog look too big to ingest (Duellman and Trueb, 1986; Williams et al., 2000). Although *R. sylvatica* relied on flight from both predators more than *R. pipiens*, it used flight most frequently in response to ground attacks. *Rana sylvatica* has less elaborate dorsal patterning, which may make this species rely more on flight behavior than *R. pipiens*. *Rana sylvatica* may also be able to find cover from predators more readily than *R. pipiens* because it is smaller.

We conclude that the presence of an externally attached radio-transmitter had some limited effects on the vagility and escape behavior of *R. pipiens* and *R. sylvatica*. We also conclude that these two species differ in their response to an attack from the air versus an attack from the ground. Behavior and vagility

are two important antipredator mechanisms, and the subtle effects that we observed could lead to increased predation and affect energetic balance.

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LITERATURE CITED

- BRODIE, E. D., JR., C. R. WILLIAMS, AND M. J. TYLER. 1998. Evolution of aposomatic behavior and coloration in the Australian frog genus *Uperoleia*. *Journal of Herpetology* 32:136–139.
- CHOI, I. H., S. H. LEE, AND R. E. RICKLEFS. 1999. Effectiveness and ecological implications of anuran defenses against snake predators. *Korean Journal of Biological Sciences* 3:247–252.
- DOWDEY, T. G., AND E. D. BRODIE JR. 1989. Antipredator strategies of salamanders: individual and geographic variations in responses of *Eurycea bislineata* to snakes. *Animal Behaviour* 38:707–711.
- DRUMMOND, H. 1985. The role of vision in the predatory behaviour of natricine snakes. *Animal Behaviour* 33:206–215.
- DUCEY, P. K., AND E. D. BRODIE JR. 1983. Salamanders respond selectively to contacts with snakes: survival advantage of alternative strategies. *Copeia* 1983:1036–1041.
- DUELLMAN, W. E., AND L. TRUEB. 1986. *Biology of Amphibians*. McGraw Hill, New York.
- DUNSTAN, T. C. 1977. Types and uses of radio packages for North American Falconiform and Strigiform birds. In F. M. Long (ed.), *Proceedings, First International Conference on Wildlife Biotelemetry*, pp. 30–39. University of Wyoming, Laramie.
- EGGERT, C. 2002. Use of fluorescent pigments and implantable transmitters to track a fossorial toad (*Pelobates fuscus*). *Herpetological Journal* 12:69–74.
- FORMANOWICZ, D. R., JR., AND E. D. BRODIE JR. 1979. Palatability and antipredator behavior of selected *Rana* to the shrew *Blarina*. *American Midland Naturalist* 101:456–458.
- GESSAMAN, J. A., AND K. A. NAGY. 1988. Transmitter loads affect the flight speed and metabolism of homing pigeons. *Condor* 90:662–668.
- GOLDBERG, C. S., M. J. GOODE, C. R. SCHWALBE, AND J. L. JARCHOW. 2002. External and implanted methods of radio transmitter attachment to a terrestrial anuran

- (*Eleuthrodactylus augusti*). *Herpetological Review* 33:191–194.
- GOMES, F. R., C. R. BEVIER, AND C. A. NAVAS. 2002. Environmental and physiological factors influence antipredator behavior in *Scinax hiemalis*. *Copeia* 2002:994–1005.
- GOODWIN, D. 1986. *Crows of the World*. University of Washington Press, Seattle.
- GRAETER, G. J. 2005. Habitat Selection and Movement Patterns of Amphibians in Altered Forest Habitats. Unpubl. master's thesis, University of Georgia, Athens.
- GREGORY, P. T. 1979. Predatory avoidance behavior of the Red-Legged Frog (*Rana aurora*). *Herpetologica* 35:175–184.
- HAYES, F. E. 1989. Antipredator behavior of recently metamorphosed toads (*Bufo a. americanus*) during encounters with Garter Snakes (*Thamnophis s. sirtalis*). *Copeia* 1989:1011–1015.
- . 1990. Comparative escape behavior of adult Green Frogs *Rana clamitans* and northern Leopard Frogs *Rana pipiens*. *Bulletin of the Maryland Herpetological Society* 26:81–99.
- HEINEN, J. T. 1994. Antipredator behavior of newly metamorphosed American Toads (*Bufo a. americanus*), and mechanisms of hunting by Eastern Garter Snakes (*Thamnophis s. sirtalis*). *Herpetologica* 50:137–145.
- HEINEN, J. T., AND G. HAMMOND. 1997. Antipredator behaviors of newly metamorphosed Green Frogs (*Rana clamitans*) and Leopard Frogs (*R. pipiens*) in encounters with Eastern Garter Snakes (*Thamnophis s. sirtalis*). *American Midland Naturalist* 137:136–144.
- HINSHAW, S. 1999. Northern Leopard Frog *Rana pipiens*. In M. L. Hunter Jr., A. J. K. Calhoun, and M. McCollough (eds.), *Maine Amphibians and Reptiles*, pp. 101–106. University of Maine Press, Orono.
- HODGKISON, S., AND J. M. HERO. 2001. Daily behavior and microhabitat use of the Waterfall Frog, *Litoria nannotis* in Tully gorge, Eastern Australia. *Journal of Herpetology* 35:116–120.
- KENWARD, R. 2001. *A Manual for Wildlife Radio Tagging*. Academic Press, London.
- KNOX, C. 1999. Wood Frog *Rana sylvatica*. In M. L. Hunter Jr., A. J. K. Calhoun, and M. McCollough (eds.), *Maine Amphibians and Reptiles*, pp. 111–118. University of Maine Press, Orono.
- MANDELBROT, B. 1967. How long is the coast of Britain? Statistical self-similarity and fractional dimension. *Science* 156:636–638.
- MARSHISIN, A., AND J. D. ANDERSON. 1978. Strategies employed by frogs and toads (Amphibia, Anura) to avoid predation by snakes (Reptilia, Serpentes). *Journal of Herpetology* 12:151–155.
- MARTIN, J., J. J. LUQUE-LARENA, AND P. LOPEZ. 2005. Factors affecting escape behavior of Iberian Green Frogs (*Rana perezi*). *Canadian Journal of Zoology* 83:1189–1194.
- MARZLUFF, J. M., AND T. ANGELL. 2005. *In the Company of Crows and Ravens*. Yale University Press, New Haven, CT.
- MEEHAN, T. D., AND I. C. T. NISBET. 2002. Nest attentiveness in common terns threatened by a model predator. *Waterbirds* 25:278–284.
- MUTHS, E. 2003. A radio transmitter belt for small ranid frogs. *Herpetological Review* 34:345–348.
- NAMS, V. O. 1996. The VFractal: a new estimator for fractal dimension of animal movement paths. *Landscape Ecology* 11:289–297.
- REDMER, M., AND S. E. TRAUTH. 2005. *Rana sylvatica*, Wood Frog. In M. J. Lannoo (ed.), *Declining Amphibians: A United States' Response to the Global Problem*, pp. 590–593. University of California Press, Berkeley.
- RICHARDS, S. J., U. SINSCH, AND R. A. ALFORD. 1994. Supplemental approaches to studying amphibian biodiversity: radio tracking. In W. R. Heyer, M. A. Donnelly, R. W. McDiarmid, L. C. Hayek, and M. S. Foster (eds.), *Measuring and Monitoring Biological Diversity: Standard Methods for Amphibians*, pp. 155–158. Smithsonian Institution Press, Washington, DC.
- RITTENHOUSE, T. A. G., T. T. ALTNETHER, AND R. D. SEMLITSCH. 2006. Fluorescent powder pigments as a harmless tracking method for Ambystomids and Ranids. *Herpetological Review* 37:188–191.
- RORABAUGH, J. C. 2005. *Rana pipiens*, Northern Leopard Frog. In M. J. Lannoo (ed.), *Declining Amphibians: A United States' Response to the Global Problem*, pp. 570–577. University of California Press, Berkeley.
- SCHALL, J. J., AND E. R. PIANKA. 1980. Evolution of escape behavior and diversity. *American Naturalist* 115:551–566.
- SULLIVAN, B. D., AND J. J. DINSMORE. 1992. Home range and foraging habitat of American crows, *Corvus brachyrhynchos*, in a waterfowl breeding area in Manitoba. *Canadian Field Naturalist* 106:181–184.
- TESTER, J. R. 1963. Radiotracking of Ducks, Deer, and Toads. Museum of Natural History, Technical Report Number 6, University of Minnesota, Minneapolis.
- VAN NULAND, G. J., AND P. F. H. CLAUS. 1981. The development of a radiotracking system for anuran species. *Amphibia-Reptilia* 2:107–116.
- WALLACE, D., AND S. B. GREEN. 2002. Analysis of repeated measures designs with linear mixed models. In D. S. Moskowitz and S. L. Hershberger (eds.), *Modeling Intraindividual Variability with Repeated Measures Data: Methods and Applications*, pp. 103–134. Lawrence Erlbaum Associates, Mahwah, NJ.
- WATSON, J. W., K. R. McALLISTER, AND D. J. PIERCE. 2003. Home ranges, movements, and habitat selection of Oregon Spotted Frogs (*Rana pretiosa*). *Journal of Herpetology* 37:292–300.
- WEICK, S. E., M. G. KNUTSON, B. C. KNIGHTS, AND B. C. PEMBER. 2005. A comparison of internal and external radio transmitters with Northern Leopard Frogs (*Rana pipiens*). *Herpetological Review* 36:415–421.
- WHITE, G. C., AND R. A. GARROTT. 1990. *Analysis of Wildlife Radio-tracking Data*. Academic Press, London.
- WILLIAMS, C. R., E. D. BRODIE JR., M. J. TYLER, AND S. J. WALKER. 2000. Antipredator mechanisms of Australian frogs. *Journal of Herpetology* 34:431–443.

- WIRSING, A. J., J. D. ROTH, AND D. L. MURRAY. 2005. Can prey use dietary cues to distinguish predators: a test involving three terrestrial amphibians. *Herpetologica* 61:104–110.
- WITHEY, J. C., T. D. BLOXTON, AND J. M. MARZLUFF. 2001. Effects of tagging and location error in wildlife radiotelemetry studies. *In* J. J. Millspaugh and J. M. Marzluff (eds.), *Radiotracking and Animal Populations*, pp. 43–75. Academic Press, San Diego, CA.

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