

Orientation and directional escape by Blanchard's Cricket Frog, *Acris blanchardi* (Amphibia: Anura: Hylidae), in response to a human predator

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Abstract. I investigated the seemingly haphazard jumping pattern of Blanchard's Cricket Frog (*Acris blanchardi*) to determine if it was random or patterned. I approached frogs from the front (cranial), back (caudal), and side (lateral) simulating an attacking predator. On average, frogs jumped away at 135.73° (SE = 2.31°) from the direction of attack. I did not distinguish between right and left directions in this study. There were significant differences in the angle of escape among the three attack directions ($F_{2,87} = 17.64$, $P < 0.001$). There were no significant differences in escape angle between frogs that I approached from the front (mean = 130.4°, SE = 2.59°) or the side (mean = 126.3°, SE = 3.75°, Tukey interval: -0.261, 0.626). The angle of escape was not uniform and directional escape was around 120° across all tests. Frontal and side approaches led to escape angles near 120° but attacks from the rear resulted in two modes of escape, at about 180° and 120° from the angle of approach. These frogs have a possible blind spot in the rear of their field of vision that might explain this bimodal escape pattern in rear attacks. The tendency to jump away at an angle rather than straight away from the predator likely represents an evolutionary compromise between an attempt to maximize angular and linear displacement from the attacking predator. This optimal strategy may demonstrate a fitness and survival advantage.

Keywords. *Acris blanchardi*, Blanchard's Cricket Frog, predator-prey, evolutionarily stable strategies.

INTRODUCTION

Anuran jumping patterns are important to investigate in order to understand the evolutionary forces that led to, and have maintained this behavior's prevalence in anurans. Previous studies on anuran jumping have focused on the jump length (Stokely and Berberian, 1953; Gans and Rosenberg, 1966; Rand and Rand, 1966; Zug, 1978), the jump angle above the substrate (Gans and Rosenberg, 1966), the endurance of the behavior (Rand,

1966) especially under environmental stress (Beuchat et al., 1984), and the physiological effects of jumping (Miller et al., 1993; Lutz and Rome, 1994). Understanding the nature of this behavior is also important from a conservation perspective in that any environmental stressor (e.g. contaminants that retard reaction time) could reduce the effectiveness of escape behavior, hence demonstrating key linkages between evolutionary biology, natural history and conservation (Bury, 2006; McCallum and McCallum, 2006).

The objective of this study was to investigate how the direction of predator approach can influence the direction of escape in *Acris blanchardi* (Harper, 1947). *Acris blanchardi* is a small, semelparous (McCallum et al., 2011), non-arboreal tree frog known for its confusing taxonomy (McCallum, 2003; McCallum and Trauth, 2006; Gamble et al., 2008). Like many amphibians (McCallum, 1999a; Trauth et al., 2000; Wheeler et al., 2002; McCallum, 2007) *A. blanchardi* is a conservation concern in many parts of its range (Reeder et al., 2005; Lehtinen and Skinner, 2006). It has a low stress threshold which can stimulate declines (McCallum and Trauth, 2007), a wide range of limb and other abnormalities are becoming more common in otherwise healthy populations (McCallum and Trauth, 2003), and it is at a probable risk due to climate change (McCallum, 2010). Its erratic style of escape, jumping long bounds (Zug, 1978) in a seemingly random, zigzag pattern away from the on-looker (Conant, 1986) escaping to refuges where it remains motionless (McCallum, 1999b) is of interest. This behavior is a possible reason for its success along many streams, ponds, and lakes in North America because the combined behavior in a group of frogs is very confusing to an onlooker who attempts to catch them (Tynning, 1990).

I hypothesized that Blanchard's Cricket Frogs escape in a patterned response. If this is true, I expected frogs to display a common angle of escape regardless of the angle of approach. If the escape angles were uniformly distributed, then the frogs escape behavior is random

MATERIALS AND METHODS

All frogs originated from White Oak Park Lake (Normal, McLean Co., Illinois, U.S.A.). I introduced each of 90 *A. blanchardi* (estimated SVL = 2.0-2.7 cm) into a circular arena with a diameter of 60 cm and a vertical wall height of 10 cm. Recent studies suggest that a height of 20 cm might be better (Royan et al., 2010), but the implementation of my study predates these later published investigations so we were not privy to these later studies. Each frog was tested once without replacement. Because the size of a frog may influence aspects of its jumping (Rand and Rand, 1966; Tejedo et al., 2000), I balanced the distribution of body sizes among the treatment groups. I hung an incandescent lamp above the arena to counteract the possibility of a sun-compass in this species (Ferguson, 1967). I marked the floor of the arena in light pencil at 0°, 30°, 45°, 60°, 90°, 120°, 135°, 150°, and 180° on both sides of the median. For the purposes of data recording, analysis and graphical presentation, I measured all jump angles between 0-180° regardless if the prey jumped to the left or the right of the predator (e.g. I recorded a jump angle of 270° as 90°). I conducted tests during the day (~13:00-15:00 hr) when this diurnal species is normally actively foraging (McCallum, unpubl. data).

Upon introduction into the arena, I covered each frog an inverted 1 L opaque plastic drinking cup that had a 1 cm hole in the bottom to observe the specimen. After the subject settled down (ca. 2-3 min), or became alert if it was death feigning (McCallum, 1999a), I positioned myself at the appropriate angle (either head on [n = 35], from behind [n = 26], or laterally [n = 29]) as an

attacking predator. So, although the arena was in a fixed position, the position of the frog under the cup was random. By coincidence, this led to an effect similar to rotating the arena to avoid possible magnetic compass effects (Royan, et al., 2010). At this time I lifted the cup and reached for the frog with my right hand to simulate an approaching predator (the releaser) to induce the escape response. I recorded the direction of each leap as degrees from the angle of attack.

I calculated descriptive statistics with Oriana 2.0 (Kovach Computing Services, Anglesey, Wales), and I used a one-way ANOVA to compare the three approach angles using Minitab 13.30 (Minitab, Inc., State College, Pennsylvania, USA). I used Oriana 2.0 to calculate Rayleigh's Uniformity Test to test the null hypothesis that the data from each direction of approach were uniformly distributed, and the V-test to test uniform escape angles against the mean escape angle for each direction of attack. I hand calculated Chi Square to compare the number of frogs that turned before jumping at each angle of attack. I used $\alpha = 0.05$ to assign significance for all inferential statistics.

RESULTS

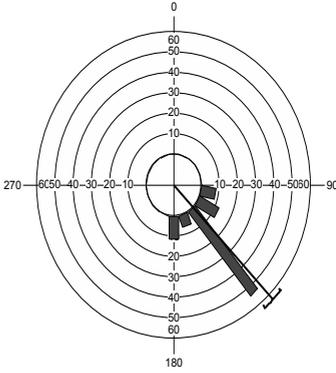
On average, frogs jumped away at 135.73° (SE = 2.31°) from the direction of attack (Fig. 1a). There were significant differences in the angle of escape among the three attack directions ($F_{2,87} = 17.64$, $P < 0.001$). There were no significant difference in escape angle between frogs that I approached from the front (Fig. 1b, mean = 130.4° , SE = 2.59°) or the side (Fig. 1c, mean = 126.3° , SE = 3.75° , Tukey interval: -0.261, 0.626); whereas, the rear approach resulted in different angles compared to attacks from the front (Tukey interval: 0.470, 1.38) and side (Tukey interval: 0.633, 1.58). The angle of escape was not uniform when approached from the rear ($Z = 22.83$, $P \ll 0.001$), front ($Z = 32.58$, $P < 0.001$), or the side ($Z = 25.61$, $P < 0.001$). When approached from the rear (Fig. 1d), frogs escaped at a more obtuse angle (mean = 153.9° , SE = 4.05° ; $V_{153.9^\circ} = 0.937$, $P < 0.001$) than either from the front (mean = 130.4° , SE = 2.59 ; $V_{130.4^\circ} = 0.965$, $P < 0.001$) or side (mean = 126.3° , SE = 3.75 ; $V_{126.3^\circ} = 0.940$, $P < 0.001$). However, rear attacks led to a bimodal escape pattern in which most frogs jumped away at either $\sim 130^\circ$ (50% [13/26]) or $\sim 180^\circ$ (34.6% [9/26]) and the balance jumping somewhere in between these two modes.

The angle of approach influenced if a frog repositioned itself prior to jumping ($\chi^2 = 3.69$, $df = 2$, $P < 0.001$). Frogs turned more frequently before jumping ($\chi^2 = 14.86$, $df = 1$, $P = 0.0001$) when approached from the front (97%, $n = 34$) than from the side (21%, $n = 29$). They also turned more frequently ($\chi^2 = 5.32$, $df = 1$, $P = 0.021$) when approached from the side (21%, $n = 29$) than when approached from the rear (0%, $n = 26$).

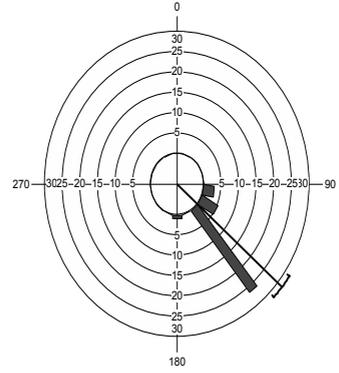
DISCUSSION

There is a strong tendency for *A. blanchardi* to make its initial jump from a pursuer at approximately 135° from the angle of attack, especially when approached from the front or the side. This may be advantageous when pursued by a predator such as a snake. If a frog jumps away at 90° from an on-coming predator, it would maximize displacement from the direction of attack on its first leap (Fig. 2a). This may maximize the likelihood that a lunging predator would lose track of the frog during pursuit and its lunge would carry the

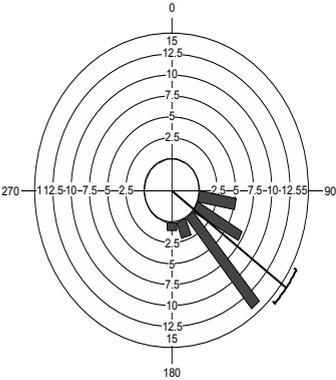
A.



B.



C.



D.

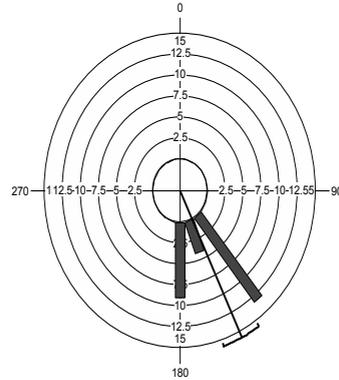


Fig. 1. The average angle of escape by Blanchard's Cricket Frogs (*Acris blanchardi*) when approached by a predator from (A) all three directions combined, (B) the front, (C) the side, (D) behind. The bars indicate the number of frogs jumping at the designated angle from the predator's approach. In all cases, the predator is approaching from 0°. No distinction is made between jumps to the left or right.

on-comer away from the prospective prey. If the frog jumped at 180° from the angle of attack (Fig. 2b), it would sacrifice displacement and remain in the general line of sight of the lunging predator. Furthermore, the lunge would carry the aggressor toward the frog, thus sacrificing maximum distance from the predator. If a frog jumps at 120-150° from the lunging predator, it optimizes displacement and distance from the predator, especially after a second jump using the same patterned response. The second jump on any of these attack directions is important to explain why frogs should not jump 180° from the angle of approach. A first jump at either 90° or 135° followed by any angular jump will make it very likely that the predator loses the predator among vegetation and other frogs.

In fact, these frogs metamorphose in explosive numbers where the populations are strong (pers. obs.). Metamorph abundances reaching 45 frogs/m² are common in some areas of the Ozarks (unpubl. data, 2000-2003) and I recall similarly abundant juveniles in some populations in central and southwestern Illinois from 1980-1999. Where large numbers of closely aggregated frogs occur, two leaps may be sufficient to confuse a potential

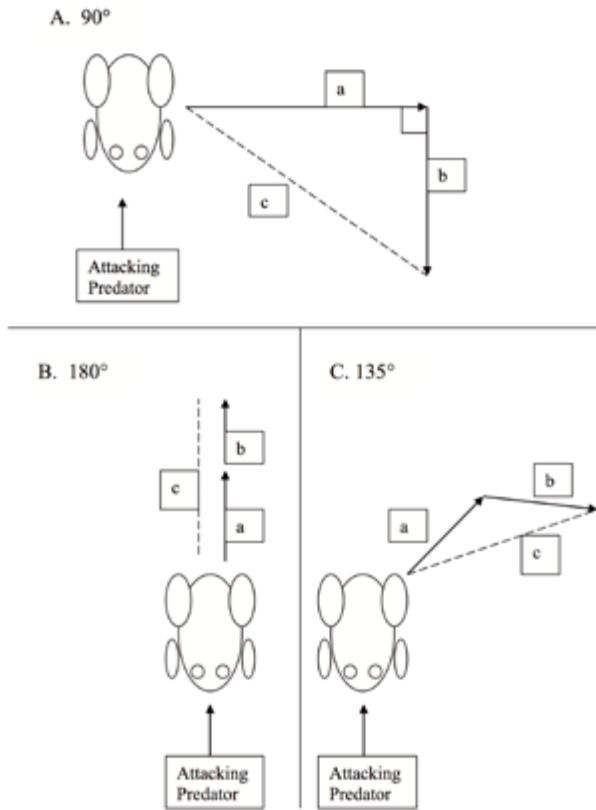


Fig. 2. Potential adaptive significance for Blanchard's Cricket Frog's (*Acris blanchardi*) that escape at 90° versus 180° or 135°. A = 1st jump, B = 2nd jump, C = compromise between distance and displacement.



Fig. 3. A Blanchard's Cricket Frog (*Acris blanchardi*) viewed from above. Notice that the eyes are tilted slightly forward to potentially provide better binocular vision while leaving a potential blind spot behind.

predator, especially as neighboring frogs get disturbed during the encounter. In fact, my personal experience is that if a group of *A. blanchardi* starts jumping it creates sufficient confusion for the collector that catching an individual frog by hand is near impossible if you did not successful on the first try. Even where not abundant, a second jump could be sufficient for an individual to find an abode in which to hide from an aggressor. In fact, *A. blanchardi* often occurs along the banks of creeks, although they sometimes venture far from such habitats (Gray, 1983; pers. observ.). After a few jumps, especially if they reach an aquatic habitat, the frog will either lie quietly on the substrate (McCallum, 1999b) where it often blends in with the mud (Gray, 1984), or it floats motionless, suspended in vegetation (McCallum, 1999b) where its color stripe provides a cryptic disguise (Gray, 1984; pers. observ.). These behavioral observations seem to support the adaptive significance of patterned jumping in this frog.

When approached from behind, Blanchard's Cricket Frog jumps at a much more obtuse angle than at either other angle of attack. This may stem from its ocular anatomy as revealed by the tendency to turn prior to jumping when approached at angles other than behind. When I approached subjects from behind the frogs never turned and jumped at 130-180° from the angle of attack. About one third of the escaping frogs jumped at 180° from my approach. The eyes of cricket frogs appear to be positioned to improve binocular vision (Fig. 3). This may create a blind spot behind the frog (Fig. 3). If a predator approaches a cricket frog from behind, it may get much closer before the frog detects the pursuer. This is supported by the fact that none of the frogs in this study turned prior to jumping, and that frogs approached from the front and the side frequently turned. Predators approaching from the front or side are clearly in the frog's field of view. This allows a frog to detect an aggressor earlier, turn in preparation for jumping at an optimum escape angle and in an anatomical conformation that likely provides maximum thrust from both rear legs. Predators approaching from behind may not be detected so readily, providing less time to prepare for escape, thus leading to less ideal escape angles relative to the aggressor and reduced thrust. Because frogs attacked from behind did not turn and had less ideal escape angles, combined with their ocular anatomy suggests these frogs have a blind spot that causes the altered jumping pattern associated with a rear attack. Further, it is a less ideal escape angle if as is the case in other species (Royan et al. 2010) jump distance is negatively correlated with angle of escape. By turning, the frog can jump further in its initial leap, a clear advantage in escaping an approaching predator.

Other frogs vary in their angular escape from predators (Royan et al., 2010). *Manophryne trinitatis* does not demonstrate angular escape preference when approached from the front. However, when approached from the right or left they jump at 90-135° and when attacked from the back they jumped at 135-180° away from the predatory stimulus. *Hypsi-boas geographicus* demonstrates confusing patterns of stimuli response that are difficult to interpret (Royan et al., 2010). At some ages this species jumps in patterns similar to that of *M. trinitatis* and *A. blanchardi*; whereas, other ages do not exhibit preferred escape trajectories. *Trachycephalus venulosus* also demonstrates preferred escape trajectories (Royan et al., 2010). When it is attacked from the front it does not escape in a preferred direction. However, when an attacker approaches from behind, the frog jumps directly forward and away from the attacker. When approached from the right or left, this species also jumps at an optimizing angle from the predator's approach. It appears that the response patterns dem-

onstrated by *A. blanchardi* may be more widely distributed among anurans and represent a tactic that may have evolved independently in many other anuran lines.

An early source of error to this study was this species apparent attraction to the sound of running water. During the initial experiment, the frogs generally jumped toward the aquarium present in the room, regardless of the direction they faced or from which the attacker approached. Upon turning off the aquarium bubbler, they ceased responding to it. These data were discarded and not used in this study, but this observation suggests that patterned jumping is subject to additional outside influences not addressed in our study and that these frogs may phonotactically respond to moving water.

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