Title: How moths escape bats: predicting outcomes of predator-prey interactions

Aaron J. Corcoran[1*], and William E. Conner[1]

[1]Wake Forest University, Department of Biology, Winston-Salem, NC

[*]Correspondence: Aaron J. Corcoran

Wake Forest University

Department of Biology

P.O. Box 7325

Winston-Salem, NC, 27106

(office) 336-758-4348

(cell) 336-251-2638

(fax) 336-758-6008

aaron.j.corcoran@gmail.com

Summary Statement: We use 3-D reconstructions of bat-insect interactions to provide one of the first direct tests of mathematical predation models. Our results shed light on the co-evolution of predator and prey pursuit and escape strategies.

Abstract

What determines whether fleeing prey escape from attacking predators? To answer this question, biologists have developed mathematical models that incorporate attack geometries, pursuit and escape trajectories, and kinematics of predator and prey. These models have rarely been tested using data from actual predator-prey encounters. To address this problem we recorded multi-camera infrared videography of bat-insect interactions in a large outdoor enclosure. We documented 235 attacks by four *Myotis volans* bats on a variety of moths. Bat and moth flight trajectories from 50 high-quality attacks were reconstructed in 3-D. Despite having higher maximum velocity, deceleration, and overall turning ability, bats only captured evasive prey in 69 of 184 attacks (37.5%); bats captured nearly all moths not evading attack (50 of 51; 98%). Logistic regression indicated that prey radial acceleration and escape angle were the most important predictors of escape success (44 of 50 attacks correctly classified; 88%). We found partial support for the turning gambit mathematical model; however it underestimated the escape threshold by 25% of prey velocity and did not account for prey escape angle. Whereas most prey escaping strikes flee away from predators, moths typically escaped chasing bats by turning with high radial acceleration toward "safety zones" that flank the predator. This strategy may be widespread in prey engaged in chases. Based on these findings we developed a novel geometrical model of predation. We discuss implications of this model for the co-evolution of predator and prey kinematics and pursuit and escape strategies.

Introduction

Predator-prey interactions are ubiquitous in nature. Their life-and-death consequences are obvious and immediate for prey. The consequences of losing encounters is less severe for predators, but they too are often under selective pressure (Dawkins and Krebs, 1979). Predator and prey adaptations are frequently countered by the other party over evolutionary time leading to an "evolutionary arms race" where physiology and behavior are refined and diversified (Dawkins and Krebs, 1979; Brodie and Brodie, 1999; Abrams, 2000). Therefore it is important to study predator and prey together to understand either entity.

Predation is a complex interaction involving the sensory abilities, morphologies, decision making and behavior of both predator and prey (Endler, 1991). The majority of research on these interactions has focused on prey, at least in part because of the ease of eliciting robust defensive responses (Lima and Dill, 1990; Mitchell and Lima, 2002). Prey defenses are highly variable and include camouflage, aposematic signaling, armor, aggressive displays, evasion, and even interference with predator sensing (Edmunds, 1974; Ruxton *et al.* 2004; Conner and Corcoran 2012).

In many cases, predation events hinge upon chases that range along a continuum from the short strikes of sit-and-wait predators to extended hunts of pursuit predators (O'Brien et al. 1990; Perry, 1999). Chase dynamics depend upon when predator and prey detect one other (Endler, 1991), their relative kinematic abilities (Webb, 1976; Domenici and Blake, 1997), and the pursuit and evasion trajectories that are employed (Olberg et al. 2000; Ghose et al. 2006; Wei et al. 2009; Domenici et al. 2011a). These factors can be accounted for in mathematical models that attempt to provide a framework for determining the conditions that allow prey to escape.

Domenici developed a model (Fig. 1A) of the initial evasive response of prey to a striking predator (Domenici, 2002; Domenici, 2011a). The model assumes that the predator has a particular width of its capture device and the predator is committed to a linear interception trajectory. The prey will escape if it can move outside the projection of the capture device into the "safety zone" before being intercepted. This model predicts that prey should use an escape angle (angle between the escape vector and the predator pursuit vector) that takes them away from the approaching predator to increase the time until contact. The escape angle should depend

on the relative speed of the predator and prey, with relatively fast prey escaping directly away from the threat (escape angle of 180°) and slower prey escaping perpendicular to the threat (escape angle of 90°). Available data generally support the predictions of Domenici's model, as most prey escape at angles that take them away from approaching predators (Domenici *et al.* 2011a; Domenici *et al.* 2011b). Large escape angles have also been shown to increase survival in Guppies escaping attacks of Pike Cichlid fish (Walker et al. 2005). Other factors are also important in determining optimal escape behavior, including biomechanical constraints, the presence of a refuge, and the need to add random variation to escape trajectories to avoid being predictable to predators (Domenici *et al.* 2011a).

Whereas Domenici's model addresses the initial evasive response of prey to a striking predator, a separate question is how prey escape predators in the midst of a chase. Howland (Howland, 1974) developed a mathematical model to address this situation (Fig. 1B). This model assumes that a predator is pursuing the prey from behind, and the prey is fleeing directly away from the predator. The prey initiates an evasive turn of constant speed and constant turn radius. The model assumes the predator reacts immediately with a turn of its own, with a turn radius limited by the predator's locomotor abilities. Flanking the predator, beyond the range of the predator's maximal turn, is the "safety zone" (Fig. 1B). The prey survives the encounter if it crosses the path of the predator's minimum turn radius into the safety zone before being intercepted by the predator. Howland showed mathematically that this occurs when:

$$V_{prey} / V_{pred} > (R_{prey} / R_{pred})^{1/2},$$

(1)

Where V_{prey} and V_{pred} are the prey and predator velocities and R_{prey} and R_{pred} are the prey and predator minimum turn radii, respectively. Eqn. 1 can easily be rearranged as:

$$V_{prey}^2 / R_{prey} > V_{pred}^2 / R_{prey},$$

(2)

Eqn. 2 simply states that the prey will escape if it has a greater radial acceleration than the predator. Therefore, the turning gambit predicts that radial acceleration is the key parameter affecting the outcome of predator-prey interactions. In contrast, Domenici's model highlights the importance of speed (or linear acceleration) and escape angle. Despite its influential presence in the literature for more than 40 years, to our knowledge the turning gambit has not been tested empirically.

We set out to determine the proximate factors influencing the outcome of predator-prey chases using a well-established model system, bats and their insect prey. Bats and insects have been engaged in a global evolutionary arms race for at least 60 million years (Miller and Surlykke, 2001; Conner and Corcoran, 2012). More than 800 bat species hunt insects using sophisticated echolocation in complete darkness (Griffin, 1958). Insects have repeatedly evolved hearing organs that allow the prey to detect bat echolocation calls and initiate defenses (Fullard, 1998; Yager, 1999; Yack, 2004). Insect evasive maneuvers are highly complex, ranging from dives to loops, spirals, and erratic flight (Roeder, 1962; Miller and Sulykke, 2001). Evasive maneuvers increase the probability of moths surviving attack (Acharya and Fenton, 1999; Triblehorn et al. 2008; Corcoran and Conner, 2012). However, it remains unclear what proximate factors determine whether insects escape attack.

We attempted to address the following questions: 1) how do bats and insects compare in their kinematic flight abilities in predator-prey interactions? 2) Do existing mathematical models predict the outcome of attacks? And 3) what determines whether or not insects survive bat attacks? To answer these questions we recorded multi-camera video of attacks between long-legged Myotis bats (*Myotis volans* Allen) and a variety of wild-caught moths in a large outdoor flight cage. We predicted that Howland's model would best explain bat-insect interactions because moth escape maneuvers are typically elicited during a chase as noted by Howland himself (Howland, 1974). Our results led to the development of a novel geometrical model, which we use to discuss pursuit and escape strategies in the co-evolutionary arms races of predators and prey.

Materials and Methods

<u>Animal Care</u>

All research on vertebrate animals was approved by the Wake Forest University Animal Care and Use Committee (IACUC protocol A12-048). Bats were captured in mist nets placed in riparian areas at the Southwestern Research Station, Portal Arizona. After capture, individual bats were allowed to adjust to captivity for two nights prior to experimentation. Each of these two nights bats were allowed to fly and forage on free-flying, wild-caught insects in the animal observatory (see description below) for 1-2 h. Bats successfully captured prey beginning on their first night of captivity. When not foraging, bats were held in custom wooden cages (0.3 m by 0.3 m by 0.5 m) with *ad libitum* access to water. Bats were housed together in groups of 3-4 individuals to provide social interaction and enrichment.

Moths used as prey for training and experimentation were collected from local riparian areas using 15-watt ultraviolet light live-traps (Leptraps LLC, Georgetown, KY, USA). The traps funneled insects into a cylindrical mesh holding cylinder 30 cm in diameter and 1 m tall. Moths were collected from the live trap and released in the animal observatory within 4 h of capture. For training and experimentation we used a diversity of moth prey that reflected what was caught in the light traps with the following exceptions. We excluded prey smaller than 1 cm in body length or longer than 4 cm and prey known to produce anti-bat ultrasound. Based on surveys conducted at the same location as our moth traps, approximately 80-90% of moths used in the experiment had bat-detecting tympanic receptors (A. J. Corcoran, *unpublished data*). These included moths in the superfamilies Noctuoidea, Geometroidea, and Pyraloidea. Moths of the superfamily Bombycoidea were largely excluded because of their large size. The remaining 10-20% of moths that were used are not known to have ears and belonged to families Lasiocampidae, Ethmiidae, and Tortricidae, among others. Therefore we assume most, but not all moths used in the study had the ability to hear bats and initiate evasive responses. The rationale for using such a diverse array of prey was to determine broadly the features of escape maneuvers (both random and directly in response to the predator) that allow insects to survive attacks by bats.

Experimental setup

Experiments were conducted in the animal observatory at the Southwestern Research Station (Fig. 2). The observatory was an outdoor enclosure 6 m by 4 m wide and 2.2-3m tall. The walls and roof of the observatory were made of 1-mm diameter hardware cloth with 1 cm spacing. Two miniature ultraviolet light emitting diodes (5 mm diameter, 20 mA) were each suspended 1 m from the ceiling near the center of the room and 1.5 m from each other. The low-intensity lights attracted moths to the active space of the observatory, thereby increasing the likelihood of attacks.

Attacks were recorded on infrared video using three frame-synchronized Scout scA640-120gc cameras (Basler, Inc., Ahrensburg, Germany) operating at 100 frames-per-second and 658 by 492 image resolution. Video was acquired on a desktop computer running maxTraq 2.0 software (Innovision Systems Inc., Columbiaville, USA). Illumination was provided by two Raymax 200 Platinum infrared lights (Raytec, Ashington, UK). Bat echolocation was recorded using four Avisoft CM16/CMPA ultrasound microphones and an UltraSoundGate 416H recording unit (Avisoft Bioacoustics; Brandenburg, Germany). A TTL pulse provided time-synchronized sound and video recordings.

Experimental protocol

Each night of the experiment, adult *M. volans* (*n* = 4 individuals; 3 females, 1 male) were released into the observatory alone and allowed to fly and hunt wild-caught moths for 1-2 h ("foraging periods"). Experiments were stopped when bats showed signs of satiation, including reduced interest in hunting and landing on the observatory walls. Bats typically flew in circuits around the observatory for most of their foraging periods, periodically breaking from their regular paths to pursue prey. Bats occasionally landed on the walls or ceiling of the observatory for 1-5 min to eat or rest.

During foraging periods wild-caught moths were periodically released from their holding chambers to ensure nearly continuous availability of prey. Efforts were made to allow moths to take flight on their own to ensure they were physiologically prepared for flight and predator evasion. Between one and four moths were in flight at any time. Moths flew throughout the volume of the observatory, only occasionally flying close to the ultraviolet LEDs. Because it was

not possible to track all moths that were in flight, we were unable to identify the species of individual moths attacked by bats. The diversity of moth species used in the experiment ensured a wide array of evasive maneuvers were present.

The experimenter observed attacks using a low-intensity, deep-red light. The heterodyne output of the ultrasound microphone was monitored via headphones to help the observer detect predation events. An attack was defined as a bat breaking from its flight path toward an insect while noticeably increasing its calling rate. Audio and video were recorded continuously in a 5-s buffer in the computer's memory. After any predation event (successful or unsuccessful), the observer triggered a TTL pulse that signaled acquisition of the previous 5 s of audio and video. Surviving prey were captured and removed from the observatory to prevent pseudo-replication.

Video analysis

Each 5-s video clip was visually inspected to determine 1) whether the attack resulted in capture or escape; and 2) presence or absence of prey evasive behavior. Because this study focused on predator and prey maneuvering, an attack was considered successful ("capture") if the bat made contact with the prey, regardless of whether the bat consumed the prey.

Presence or absence of evasive maneuvering was first determined qualitatively through visual inspection of attack videos. Evasive maneuvers consisted of one or more sharp accelerations or turns that caused a deviation of the moth's flight path during the approach of the bat (Fig. 3). Non-evasive flight was indicated by low acceleration and relatively slow or wide turns (Fig. 4). A quantitative analysis of a subset of the attacks was conducted to confirm the qualitative assessments. The close timing of prey maneuvers to the presence of an attacking bat suggests most maneuvers were triggered by the attacking bat. However, we cannot rule out the possibility that some maneuvers were random movements.

Efforts were made to categorize prey evasive maneuvers into discreet categories (e.g., dives, spirals, turn-aways, etc…). However, these efforts failed, as evasive maneuvers appeared to span a continuum between categories. Therefore no distinction was made between different types of evasive maneuver. Out of 235 attacks that were recorded, we randomly selected 25 captures and 25 escapes that occurred within view of all three cameras for 3-D reconstruction and kinematic analysis.

Three-dimensional reconstruction

Cameras were calibrated for three-dimensional (3-D) reconstruction of bat and moth flight trajectories using the "wand calibration" method described by Theriault *et al* (Theriault *et al.* 2014). All digitization was done in Matlab using the software package DLTdv5, and calibration was completed using the package easyWand5 (Hedrick 2008; Theriault *et al.* 2014). The center of mass was used as the digitization point for all animals.

Each night of the experiment a wand with two spherical calibration points spaced 0.75 m apart was moved through the calibration space of the observatory for 60 s and recorded on all cameras at 30 frames-per-second, yielding 1800 calibration frames. This was well above the minimum of 30 frames suggested by Theriault *et al* (Theriault et al. 2014). The digitized bats and moths were also added as "background points" to ensure the calibration covered the entire recording volume. The option for fourth order radial distortion coefficients was selected to account for distortion caused by camera lenses. We checked for outliers using the method described by Theriault et al., and removed <1% of digitized points. Our calibrations had reprojection errors of <1 pixel and "wand scores" (mean standard deviation of reconstructed wand lengths) of 0.5-0.7%, values that indicate high-quality calibrations (Theriault *et al.* 2014). Three-dimensional positions of bats and moths were smoothed using a 5th-order smoothing spline with error tolerances that were based on our estimates of position error.

Kinematic measurements

The smoothed 3-D bat and moth flight trajectories were used to extract five kinematic parameters for each time point: velocity, (linear) acceleration, radial acceleration, turn rate, and turn radius. The methods described by Combes *et al*. (Combes *et al* 2012) were used to calculate these parameters. From each attack sequence we extracted the maximum values of velocity, acceleration, radial acceleration and turn rate, and also the minimum values of acceleration (i.e., maximum deceleration), and turn radius for both the bat and the moth. The time point of maximum radial acceleration for both the bat and moth were used to indicate the maximum turn of each attack.

In addition to kinematic variables, three variables were measured relating to prey escape maneuvers: turn distance, start angle and escape angle. Turn distance is the distance between bat

and moth at the time of peak moth radial acceleration. Start angle is the angle between the moth-bat vector and the moth flight vector 200 ms before maximum moth radial acceleration (estimated time for turn initiation; See Fig. 3 for an example escape maneuver). Escape angle is the angle between the moth-bat vector at the beginning of the moth's turn and a vector representing the direction of the moth's escape (this escape vector is indicated by the arrows for moths in Fig. 3 and Fig. 4). The escape vector was calculated from the moth's positions at (1) the time of maximum radial acceleration and (2) the time point when the angle between the bat flight vector and the bat-moth vector was > 90°, which was used to represent the end of the attack. This definition of the end of the attack was chosen because it would require the bat to make a 90-180° turn to continue pursuit. We would consider this a separate attack on the prey.

Statistical analysis

Matlab R2012a (Natick, USA) was used for conducting statistical procedures. We tested the distributions of kinematic parameters for normality using Shapiro-Wilk tests and by examining histogram plots. A square-root transformation was applied to linear acceleration and radial acceleration values to achieve normality. We compared mean kinematic values between bats, evasive prey and non-evasive prey using one-way analysis of variance. Pairwise comparisons of mean values were made using Tukey tests. Alpha was set to 0.05.

Logistic regression was used to determine what minimum set of the nine variables measured from each attack best predicted the outcome of bat-moth interactions (Tabacknick and Fidell, 2012). Attacks by the four individual bats were combined for analysis. Odds ratios scaled by the standard deviation of each variable were used as indicators of effect size (Walker et al., 2005). Odds ratios indicate the increased likelihood of escape caused by a change of one standard deviation of a parameter. We calculated Pearson correlation coefficients for pairwise combinations of all nine variables and examined pairwise scatter plots. Based on these data and models of prey escape behavior we selected particular combinations of variables to calculate classification accuracy and odds ratios using logistic regression. We repeated the analysis with "dummy variables" encoding individual bat identities. Adjusted *P*-values were employed to account for the false discovery rate of multiple comparisons (Benjamini and Hochberg, 1995).

Results

We documented 235 attacks by four adult *M. volans* on unidentified moths (A1 n = 87; A2, n = 25; A3, n = 31; A4, n = 92). Evasive maneuvers were present in 184 attacks (78%), which was approximately equal to or slightly below the estimated percentage of eared moths used in the experiments. It should be noted that some of these maneuvers may have resulted from random motions of prey. Evasive prey were captured in 69 of 184 encounters (37.5%), whereas non-evasive prey were captured in 50 of 51 encounters (98%). This difference was highly significant (Chi-squared test, X^2 = 55.4, P < 0.0001), indicating that evasive maneuvers decreased capture success. Capture success of evasive prey (range 22-52%) was significantly different between individual bats (Chi-squared, X^2 = 10.0, P = 0.02). Capture success of non-evasive prey (range 93-100%) did not differ between individuals (Chi-squared, X^2 = 2.105, P = 0.55).

Bats outperform moths in most flight parameters

We compared six aspects of flight performance between bats, evasive moths and non-evasive moths (Fig. 5). Not surprisingly, evasive prey outperformed non-evasive prey in nearly all flight metrics, with the one exception being that deceleration was not significantly different (See Fig. 5 for statistics). More importantly, bats outperformed evasive moths in maximum velocity, deceleration, and radial acceleration, but also had larger minimum turning radius. No difference was observed in linear acceleration or turn rate (Fig. 5).

We next examined the relationships between turn velocity, turn radius and radial acceleration for bats and moths. The peak bat and moth turn was extracted from each attack, as indicated by maximum radial acceleration. A single turn from each attack was used for this analysis to avoid pseudoreplication. Because not all animals may have been turning maximally in each attack, we excluded the turns having radial acceleration below the 35th percentile. If radial acceleration is independent of flight speed, turn velocity should equal a constant multiplied by the square root of the turn radius. This relationship provided a good fit for bats (R^2 = 0.71; Fig. 6A), and accordingly, radial acceleration was independent of turn velocity (R^2 = 0.01; Fig. 6B). Turn radius was also a good predictor of the square of turn velocity in moths (R^2 = 0.57; Fig. 6A), but unlike in bats, radial acceleration increased significantly with turn velocity, albeit with a relatively weak correlation (R^2 = 0.31; Fig. 6B). A small cluster of low-velocity (< 1.5 m·s^{-1})

data points may be responsible for the observed effect. Further research is required to confirm whether radial acceleration is independent of flight speed in moths.

The turning gambit under-estimates prey escape ability

The turning gambit predicts that prey should escape when relative prey velocity (prey velocity divided by predator velocity) is greater than the square root of relative prey turn radius (prey turn radius divided by predator turn radius). This relationship is illustrated in Fig. 7A. Prey velocity and turn radius were taken from the time point of maximum prey radial acceleration for each attack. Predator velocity was also taken from that time point. However, because bats may not have been turning maximally, predator turn radius was derived from the bat's velocity and the regression equation in Fig. 6A.

If the turning gambit predictions were held, all the escapes (blue triangles) would fall in the white area of Fig. 7A, and all the captures (red circles) would fall below in the shaded area. This relationship was not upheld. Most attacks, regardless of outcome, fall in the predicted capture area. The ability of the model to predict capture success was not statistically different from chance (see Fig. 7A for statistics).

However, there was some separation between the escape and capture data points. By lowering the threshold along the relative prey velocity axis by 25% (the dashed line in Fig. 7A), the model correctly predicts outcomes in 40 of 50 attacks (80%), which is statistically greater than chance (Chi-squared test; $X^2 = 18.0$; $P < 0.0001$). The same classification accuracy can be achieved using the original threshold proposed by Howland (Howland, 1974), but using prey escape velocity averaged over the entire escape, instead of during the peak of the turn (Fig. 7B). These results provide support for Howland's model, but indicate that at least some assumptions of the model were violated.

Radial acceleration and escape angle predict outcomes of bat-moth interactions

We used logistic regression to test the ability of six prey kinematic variables and three escape trajectory variables to predict the outcome of interactions (Table 1). Dummy variables were also included to account for individual differences in capture success, but were not significant in any of the models (P > 0.10). As an effect size, we used the odds ratio scaled by each parameter's

standard deviation, $[\exp(\text{ß})]^{sd}$, where ß is the regression coefficient. The odds ratio indicates the change in likelihood of escape given an increase of one standard deviation of a particular variable. When considered alone, six of nine variables were significant, with odds ratios of 2.5-14.0 (Table 1). Radial acceleration had the largest effect size, a result that supports a primary prediction of the turning gambit.

Because of the theoretical and empirical support for prey radial acceleration affecting outcomes of predator-prey attacks, we conducted additional logistic regressions that combined radial acceleration with each of the other variables. With the effect of radial acceleration accounted for, only a single variable—escape angle—remained significant ($P = 0.01$; $P\text{-}Adj = 0.05$). The other variables that were individually significant—escape velocity, linear acceleration, deceleration, and turn rate—were all highly correlated with radial acceleration ($R^2 = 0.66\text{-}0.79$) and were not significant in the logistic regression model when paired with radial acceleration ($P > 0.21$; $P\text{-}adj > 0.53$). Therefore our final model for predicting bat-moth interactions includes radial acceleration and escape angle (Fig. 7C). This model correctly classified the outcomes of 44 out of 50 attacks (88%).

Discussion

Differences in kinematic performance alone do not allow moths to escape bats

We first tested the hypothesis that moths escaped bats by having superior kinematic abilities. Moths could potentially have kinematic advantages either because of their small size (Domenici, 2001), or because of specializations in flight muscle or wing morphology (Marden, 1987; Wootton, 1992). However, bats outperformed moths in most flight abilities, including measures of velocity, acceleration, and overall turning ability (radial acceleration; Fig. 5). Given these advantages, it is somewhat surprising that bats failed to capture evasive prey in a majority of attacks (37.5% capture success). In contrast, dragonflies, who also have superior locomotor abilities compared to their prey, capture fruit flies with 83-95% success rates (Combes et al. 2012). A primary difference in the two systems is that bats give away their presence via their echolocation, whereas dragonflies use a more stealthy approach (Combes et al. 2012).

The one kinematic advantage held by moths was their ability to make tight turns at low speed (Figs. 5, 6). However, minimum turn radius was a poor predictor of whether moths survived attacks (Table 1). Kinematic measurements alone do not appear to explain how insect prey escape bats.

Partial support for the turning gambit

The turning gambit has been an influential mathematical model of predator-prey interactions (Howland, 1974). It is frequently cited as evidence for why turning ability is important for predators and prey (Gazzola *et al.* 2012; Wilson *et al.* 2013; Wilson et al. 2015), and has been used to predict what prey species should be able to escape from predators (Hedenstrom and Rosen 2001). However, to our knowledge the model has remained untested for more than 40 years.

The turning gambit, as originally proposed (Howland, 1974), failed to predict the outcome of bat-insect interactions (Fig. 7A). However, a modified capture-escape threshold that gives prey an advantage in relative speed of 25% was a good predictor of predation outcomes, as was a model that used average prey escape speed instead of peak turn speed (Fig. 7B). These findings

provide empirical support for the turning gambit, but indicate that prey behavior was not accurately captured by the original model.

Howland modeled prey escape trajectories as turns with constant turn radius and constant velocity (Howland, 1974). We frequently observed moths making sharp turns at low velocity and then accelerating while maintaining a nearly straight flight path. For example, the moth in Fig. 3 makes a sharp turn at approximately -400 ms, followed by an acceleration with a low turn rate from -400 ms to -200 ms. The strategy of making a tight turn at low speed, then accelerating toward safety appears to allows prey to increase their overall escape speed by approximately 25%. In many cases this could mean the difference between life and death.

The turning gambit correctly predicted that radial acceleration should be the most important kinematic variable allowing for prey escape. However, the model did not predict the second important predictor of prey escape—escape angle. Surviving prey often escaped toward or perpendicular to the approaching predator (mean escape angle 83.3°; Table 1; Fig. 7C), whereas captured prey tended to escape away from the predator (mean escape angle 125.5°; Table 1; Fig. 7C). A difference of 40° (1 st dev) in escape angle corresponded with an odds ratio of 3.17, or 317% increased likelihood of escape. These findings support the hypothesis that a useful strategy for prey evading predators during a chase is to "undercut" the predator to move to a position that makes it difficult for the predator to continue pursuit. In this situation a bat may entirely lose track of the prey because of its relatively narrow sonar field of view (Jakobsen and Surlykke 2010; Jakobsen et al. 2013).

Empirical data supports a revised geometrical predation model

Based on the results of this study, we developed a novel geometrical predation model (Fig. 8A) that incorporates components from Howland's turning gambit (Fig. 1B) and Domenici's escape model (Fig. 1A). In this new model it is assumed the prey initiates an escape maneuver some distance (D_{turn}) from the predator, and initially the predator is headed directly toward the prey along the x-axis. The safety zone depends on the half-width of the predator capture device (W_{pred}), the predator minimum turn radius (R_{pred}), and the predator reaction distance (D_{react}), which equals predator reaction time (t_{react}) multiplied by predator speed (V_{pred}). To simplify modeling efforts, we model the prey escape trajectory as a linear path at a particular escape angle

(α). In many cases real prey escape trajectories would have an initial turning component that is not addressed by our model, but has been modeled previously (Howland, 1974).

We model the position of the edge of the predator's capture device [X_{pred}, Y_{pred}], which is indicated by the edge of the shaded safety zone in Fig. 8A. Over the time interval [0, t_{react}], this position is given by:

$$X_{pred} = V_{pred} \cdot t, \tag{3}$$

$$Y_{pred} = W_{pred}, \tag{4}$$

After time t_{react} it is assumed the predator makes a turn with minimum turn radius (R_{pred}). During the turn the position of the edge of the predator's capture device is given by:

$$X_{pred} = V_{pred} \cdot t_{react} + R_{pred} \cdot \sin[V_{pred}(t - t_{react})/R_{pred}], \tag{5}$$

$$Y_{pred} = W_{pred} + R_{pred} - R_{pred} \cdot \cos[V_{pred}(t - t_{react})/R_{pred}], \tag{6}$$

The prey position [X_{prey}, Y_{prey}] at time t is given by:

$$X_{prey} = D_{turn} - \sin(\alpha) \cdot V_{prey} \cdot t, \tag{7}$$

$$Y_{prey} = \cos(\alpha) \cdot V_{prey} \cdot t, \tag{8}$$

Following eq. 10 from Howland (Howland, 1974), the prey successfully escapes if when $X_{pred} = X_{prey}$:

$$Y_{prey} > Y_{pred}, \tag{9}$$

Otherwise, the encounter results in capture.

We used this model to conduct simulations of bat-moth encounters assuming the following values: 100 ms bat reaction time (Ghose and Moss. 2006), 0.1 m capture device width; and 0.365 m minimum turn radius (Fig. 5). We determined what combinations of escape angle, turn distance, and relative prey speed should allow moths to escape bats. Prey would also need to make an initial turn with sufficiently high radial acceleration to prevent continued pursuit.

The escape parameter space is illustrated as shaded areas for escape angles covering 20-140° (Fig. 8B). The simulations indicate that moderately small escape angles (40-80°) provide prey with the greatest range of turn distances and escape velocities to successfully avoid capture. For example, moths using an escape angle of 60° should survive attacks if they initiate escape when the predator is at a distance of approximately 1-2.5 turn radii, and achieve mean velocity of 30-50% of predator velocity. In contrast, prey employing a 140° escape angle, could survive with slightly lower speeds (ca. 40-60% of predator velocity) but only if turns were precisely initiated when the predator was at a distance of 0.5-1 turn radii. Because our model does not incorporate prey reaction time, prey would need to detect the predator and send the motor command for escape when the predator is at a slightly further distance.

The empirical results from this study largely support predictions from the proposed predation model. Most prey that were eventually captured took trajectories away from the approaching bat and failed to reach the safety zone (Fig. 9A). In contrast, escaping prey usually flew partially toward the approaching bat into the safety zone where they could not easily be followed (Fig. 9B). Prey using escape angles of 40-100° escaped 15 of 21 attacks (71%), compared to only 7 of 26 prey (27%) escaping using escape angles >100° (Fig. 7C). Escaping prey began maneuvers when bats were at a distance of 0.47 ± 0.25 m, or 1.3 ± 0.75 bat turning radii. These values are near the center of the escape thresholds predicted in Fig. 8B. These findings provide support for the proposed geometrical model of predator-prey interactions.

Moths escape bats using a different strategy compared to most other prey that have been studied

Most studies of prey escape behavior have been conducted in captivity where predatory strikes are simulated on prey that are otherwise unaware of the presence of a predator (Domenici et al. 2011a; Domenici et al. 2011b). Under these conditions prey routinely make an initial body rotation to increase the escape angle, and therefore the distance between predator and prey. Exceptions to this rule have been explained as means of increasing unpredictability, tradeoffs between speed of escape and ability to obtain an optimal escape trajectory, or errors in sensorimotor processing (Domenici et al. 2009; Domenici and Batty, 1997; Domenici et al. 2011a). Increasing escape angle in response to a striking predator appears to be an adaptive response, as larger escape angles are correlated with higher survival in both larval and adult fish (Fuiman, 1993; Walker et al., 2005).

In contrast to these studies, moths survived attacks by decreasing the escape angle from a start angle of 155.5° to a final escape angle of 83.3° (Table 1). Smaller escape angles (typically 40-100°) were also correlated with increased survival (Table 1; Fig. 7C), as predicted by our model (Fig. 8). We suggest that this difference in escape strategy results from prey escaping predators in a different context—moths are escaping bats during a chase, whereas most other prey who have been studied were escaping sudden predatory strikes (Domenici et al. 2011a).

Strikes and chases require different escape responses

What determines whether an attack results in a chase or an attempted escape from a strike? We suggest that our model (Fig. 8) helps discriminate the two scenarios by emphasizing the safety zones available to prey. We define an escape from a strike as a situation where the prey begins escape within the reaction distance of the predator, meaning that the predator is unable to adjust its pursuit trajectory in response to the prey maneuver. In a chase, prey initiate escape at a further distance, with sufficient time for the predator to adjust course. Prey that detect a predator within the reaction distance (for example a sit-and-wait or stealthy predator), are by definition restricted to escaping a strike. In contrast, prey that detect a predator beyond the reaction distance (such as a pursuit predator or a sit-and-wait predator attacking from a further distance) may initially flee away and a chase ensues. Alternatively, prey detecting predators beyond the predator's reaction distance could wait for the appropriate time to attempt to immediately undercut the predator's approach. This may be a strategy employed by rodents escaping owls, where escape angles of 45-90° are most effective (Shifferman and Eilam, 2004).

We propose that many prey pursued by predators in chases use an undercutting strategy similar to that employed by moths escaping bats. Potential model systems include the prey of terrestrial pursuit predators such as cheetah (Wilson et al. 2015) or aerial prey of raptorial birds (Hedenstrom and Rosen, 2001) or dragonflies (Combes et al. 2012).

Escape rule 1: maximize radial acceleration

The single best predictor of whether moths escaped bats was their maximum radial acceleration (Table 1). Moths did not need to exceed the radial acceleration of their predators to escape, as predicted by the turning gambit (Howland, 1974), but they did need to make a sufficiently fast and tight turn to avoid being followed. Bats, as well as dragonflies and goshawks, use a constant

absolute target direction strategy (also referred to as motion camouflage) for intercepting evasive prey (Olberg et al. 2000; Ghose et al. 2006; Kane et al. 2015). It appears with this predator pursuit strategy, a key component of successful prey evasion is making a rapid and tight turn that will be difficult for the predator to follow. In fact, when sufficiently high radial acceleration was generated (>20 m·s^{-2}), prey survived all attacks regardless of other parameters of the escape such as escape angle (Fig. 7C).

In moths, a small but significant increase in radial acceleration was observed with increased turn velocity. It was not possible to determine how much of this variation came from differences between or within species, but an exciting future direction is examining how species-specific escape strategies relate to differences in flight morphology and turning ability. Moths and other insects often make dives when pursued by bats (Roeder, 1962; Triblehorn et al. 2008; Corcoran and Conner, 2012). A key component of this strategy may be using gravity to increase radial acceleration. Bats do not appear to be able to increase radial acceleration by changing flight speed (Fig. 6). However slowing down late in an attack, a strategy seen in dragonflies (Combes et al. 2012) would decrease the size of the safety zone by reducing the predator's minimum turn radius and reaction distance.

Escape rule 2: turn toward the threat

For an escape maneuver to be successful, it should take the prey into the safety zone flanking the predator (Fig. 8A). When escape is initiated beyond the predator's reaction distance, this is best achieved with moderately small escape angles of 40-100°. Within the predator's reaction distance our model is effectively the same as Domenici's model and prey should escape at least partially away from the approaching predator (90-180° escape angle), with the exact angle depending on relative prey velocity [Fig. 1A (Domenici, 2002)].

Predators may learn to anticipate stereotyped defensive maneuvers (Catania, 2009). Both empirical evidence and our model indicate that a variety of escape angles may be used to avoid capture (Figs. 7, 8). There appears to be no single optimal escape trajectory. Instead, prey may benefit from having a diversity of escape behaviors, either between or within individuals of a species, or between species hunted by a particular predator (Domenici et al. 2011a).

Escape rule 3: flee at an intermediate distance

Our model indicates that prey should initiate escape when the predator is at a distance of approximately 0.5-3 predator turning radii, depending on the escape angle (Fig. 8B). Predators will easily intercept prey escaping either too early or too late. Predators could take advantage of prey by causing them to initiate escape either too early or too late. Some predators are known to actively provoke prey defenses, including painted redstarts that make wing movements to flush insects into a chase (Jablonski, 1999), and tentacled snakes that make body movements to elicit fish fast starts (Catania 2009). We predict that escape-inducing strategies are used by many more predators. Bats could potentially provoke early defensive responses of prey using specialized acoustic signals.

Alternatively, if predators avoid being detected until they have closed within 0.5-1 turning radii, most escape maneuvers would be ineffective. This appears to be a strategy employed by barbastelle bats (*Barbastella barbastellus*), which echolocate at low intensity and eat numerous eared moths (Goerlitz et al. 2010). Behavioral observations of hunting barbastelles are required to determine whether prey evade too late, or not at all. A rapid transition in bat echolocation behavior from search to buzz prevented mantids (*Parasphendale agrionina*) from initiating defensive responses (Triblehorn et al. 2008), so it may also be possible for bats that echolocate at high intensity to manipulate prey behavior.

Conclusions and future directions

We have attempted to provide an empirically-tested theoretical framework for rules underlying pursuit and evasion of predator-prey interactions. Our results provide partial support for the turning gambit proposed by Howland (Howland, 1974); however, details of evasion trajectories required some modification. Prey with inferior locomotory abilities can escape predators if they make appropriately timed evasive maneuvers with particular escape trajectories and high radial acceleration. For prey escaping bats, this response is facilitated by the reliable ability to hear the predator approaching and to determine when attack is imminent (Ratcliffe et al. 2010; Corcoran et al. 2013).

Our approach was to study a single predator species hunting a diversity of insect prey exhibiting evasive behaviors. Anti-bat evasive behavior has long eluded attempts at quantitative

categorization (Roeder, 1962). Considering the diversity of escape behavior, we were surprised to find a simple set of parameters that could explain whether prey survived attack in most cases. Studies are required to test whether these findings hold in other systems, including different aerial, aquatic and terrestrial predators and prey involved in chases. Because of the extraordinary global diversity of bats and insects, different species of predator and prey likely employ specialized pursuit and escape strategies. It is our contention that these strategies are built upon a basic set of rules, which we have attempted to outline here.

Competing interests

No competing interests declared

Author contributions

AJC contributed to study design, data collection and analysis, and writing the manuscript. WEC contributed to study design, project oversight, and writing the manuscript.

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Table

Table 1 Flight Parameters for discriminating capture and escape.

Parameter	Capture Mean (s.d.)	Escape Mean(s.d.)	ß	*P*	*P-Adj*	**Odds Ratio**
Esc velocity (m s⁻¹)	**1.41 (0.62)**	**2.16 (0.55)**	**-1.993**	**0.0006**	**0.0032**	**5.39**
Lin. accel. (m s⁻²)	**3.89 (3.9)**	**8.76 (3.3)**	**-0.405**	**0.0005**	**0.0032**	**7.03**
Lin. decel (m s⁻²)	**-8.4 (7.5)**	**-11.9 (9.1)**	**0.236**	**0.0063**	**0.019**	**3.70**
Turn radius (m)	0.34 (0.37)	0.15 (0.09)	5.25	0.0338	0.068	1.33
Turn rate (° s⁻¹)	**599 (638)**	**1362 (467)**	**-0.0035**	**0.0009**	**0.0036**	**9.16**
Radial accel. (m s⁻²)	**6.0 (5.7)**	**18.8 (10.6)**	**-0.299**	**0.0002**	**0.0027**	**14.0**
Start angle (°)	152.0 (20.9)	155.5 (26.4)	**-0.0047**	0.826	0.881	1.29
Escape angle (°)	**125.5 (35.4)**	**83.3 (44.6)**	**-0.026**	**0.007**	**0.0186**	**3.17**
Turn dist. (m)	0.63 (0.38)	0.42 (0.26)	2.35	0.033	0.068	1.93

Regression coefficients (ß), significane (*P*) and odds ratios are from univariate logistic regression analyses. The odds ratio indicates the change in the likelihood of escape caused by a difference of one standard deviation. Note that for ease of comparison, odds ratios were converted to values >1, but for linear deceleration, turn radius, and escape angle, lower values correlated with greater escape success. Parameters include escape velocity, linear acceleration, linear deceleration, turn radius, turn rate, radial acceleration, start angle, escape angle, and turn distance. An adjusted significance value (*P*-adj) was used to control for the false discovery rate of multiple comparisons (Benjamini and Hochberg 1995). *n = 50*.
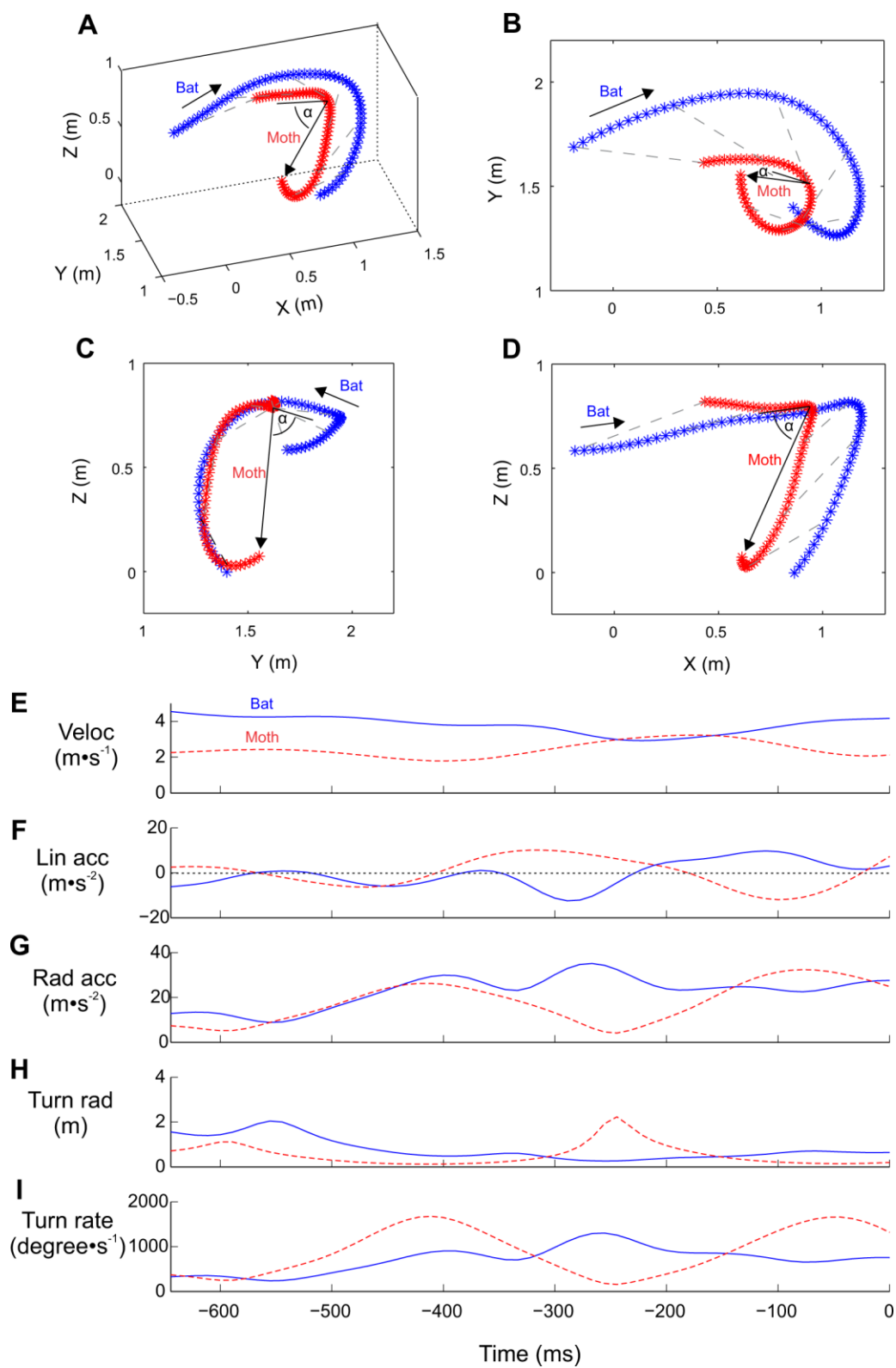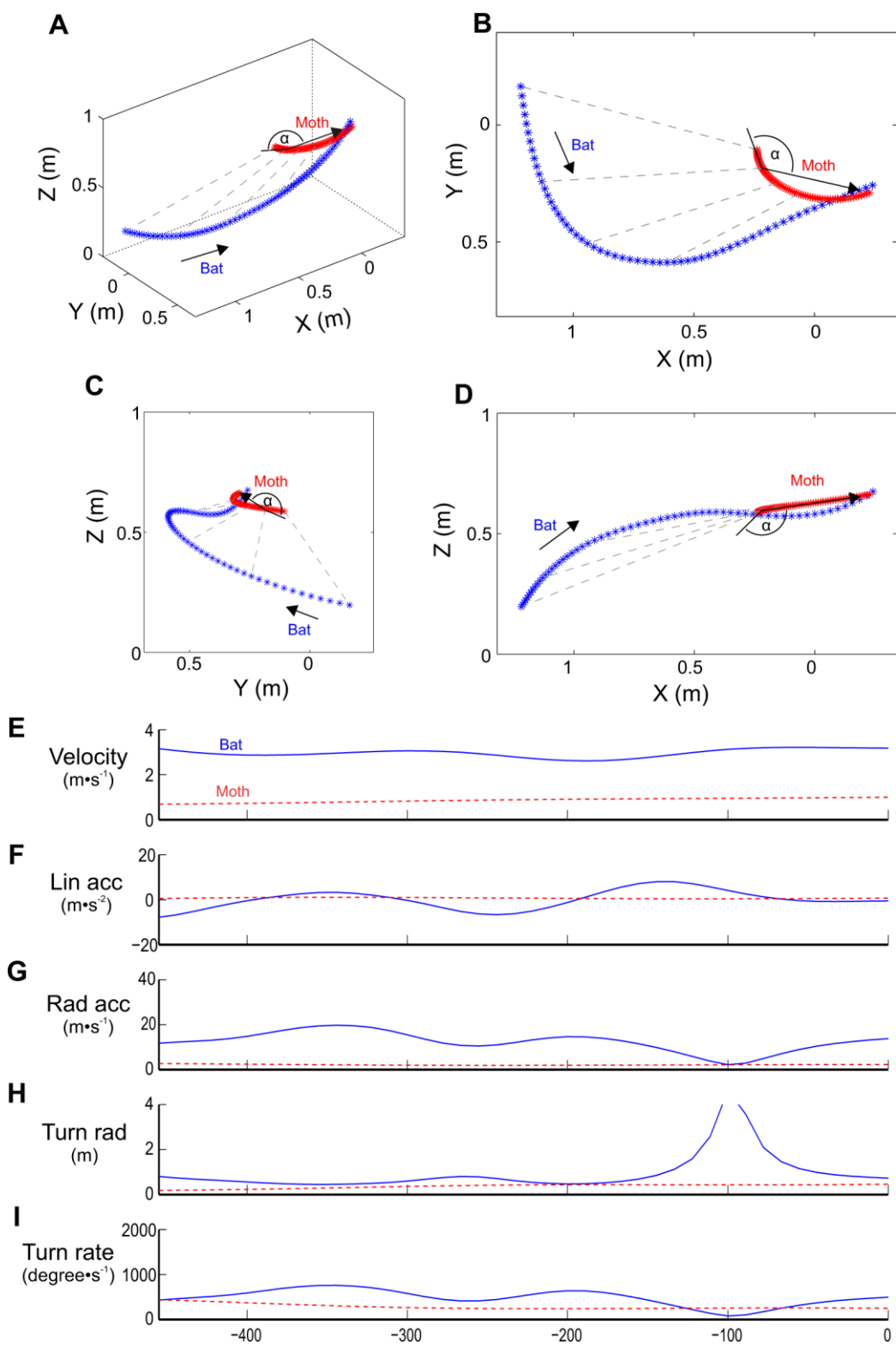
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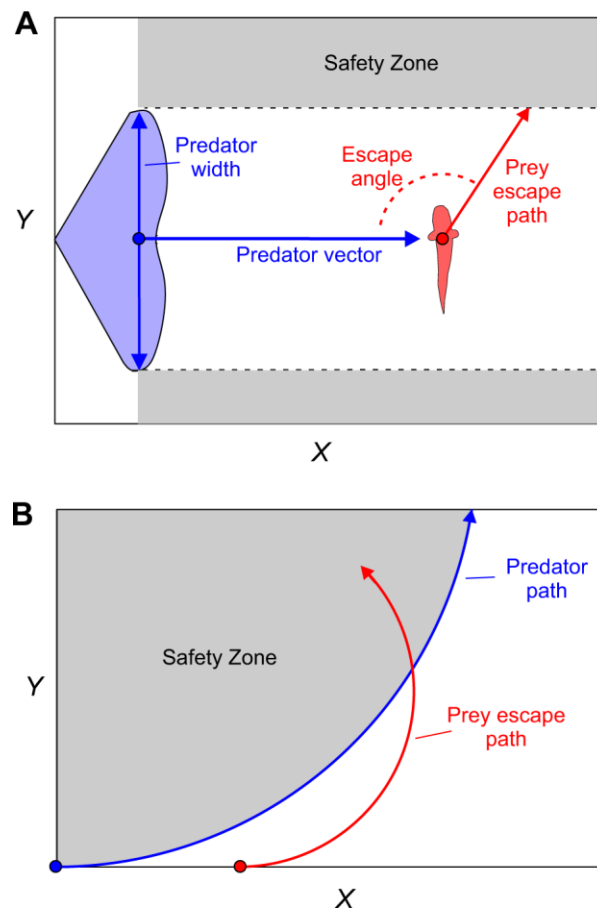
Figure 1. Geometrical models of predator-prey interactions. (A) Model of an escape from a predatory strike (Domenici, 2002). Here the predator is committed to an interception trajectory centered on the prey. The prey will escape if it can cross out of the path of the predator before being captured. This model predicts that prey should use a large escape angle of 90-180°, depending on its speed relative to the predator. (B) Turning gambit model of escape during a chase (Howland, 1974). Predator and prey trajectories are modeled as turns of constant radius and velocity, both initiated at the same time (blue and red curves, respectively). The prey escapes if it crosses the predator's path—which is limited by the predator's minimum turn radius—into the safety zone before the predator can intercept the prey. This model predicts that prey should turn towards the flank of the predator with maximum velocity and minimum turn radius. Modified figures have been re-printed with permission from the publishers.
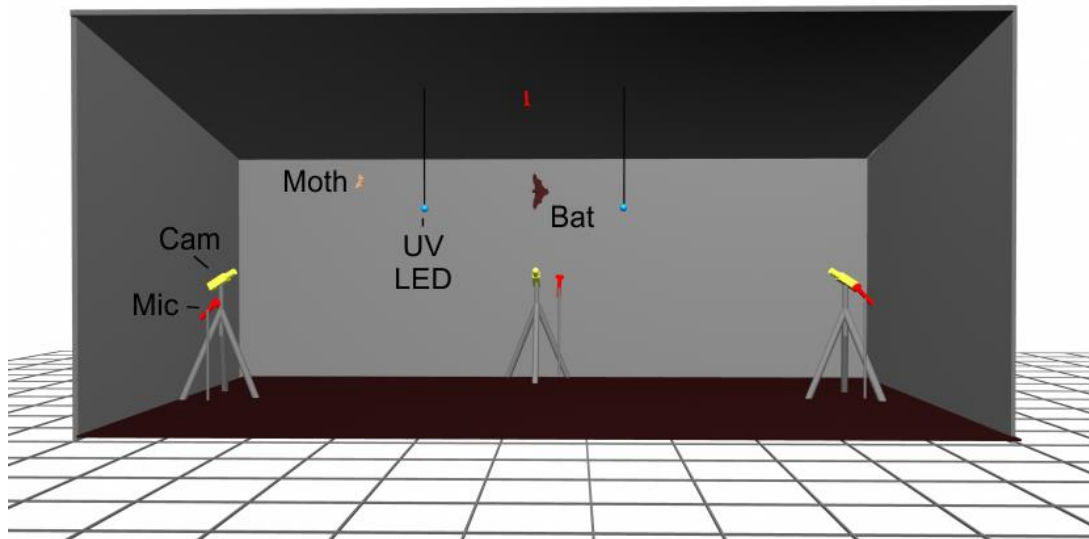
Figure 2. Experimental setup. Bat-moth interactions were observed in an observatory 6 m by 4 m wide and 2.2-3 m tall. Walls of the observatory were made of thin metal grating spaced at 1 cm intervals. Interactions were captured on three infrared cameras ("Cam") and four ultrasonic microphones ("Mic"). Two miniature ultraviolet light-emitting diodes ("UV LED") were suspended from the ceiling to attract moths to the middle of the enclosure, however moths and bats flew throughout the available space.

Figure 3. Example evasion escape sequence including 3-D plots of flight trajectories (A-D) and kinematics (E-I). Shown are (A) 3-D, (B) top, and (C, D) profile perspectives of a single attack. Smoothed bat and moth positions are plotted at 90 Hz. Dashed grey lines connect bat-moth positions at 100 ms intervals. Arrows indicate the general direction of bat flight and the escape vector of the moths (See text for more details). The prey escape angle (α) is also shown, which is formed by the intersection of the prey escape vector and the predator flight vector at the beginning of the escape maneuver, which here has been translated to end at the beginning of the prey escape vector. Kinematics include (E) velocity, (F) linear acceleration, (G) radial acceleration, (H) turn radius, and (I) turn rate. Note the turns made by the moth (-420 ms) and bat (-275 ms) as indicated by minima in turn radius and maxima in radial acceleration and turn rate.

Figure 4. Example sequence of bat capturing a non-evading moth including 3-D plots of flight trajectories (A-D) and kinematics (E-I). Shown are (A) 3-D, (B) top, and (C, D) profile perspectives of a single attack. Smoothed bat and moth positions are plotted at 90 Hz. Dashed grey lines connect bat-moth positions at 100 ms intervals. Arrows indicate the general direction of bat flight and the escape vector of the moths (See text for more details). The prey escape angle (α) is also shown. Kinematics include (E) velocity, (F) linear acceleration, (G) radial acceleration, (H) turn radius, and (I) turn rate. Note the large escape angle and low values of moth kinematic parameters compared to the escape in Fig. 3.
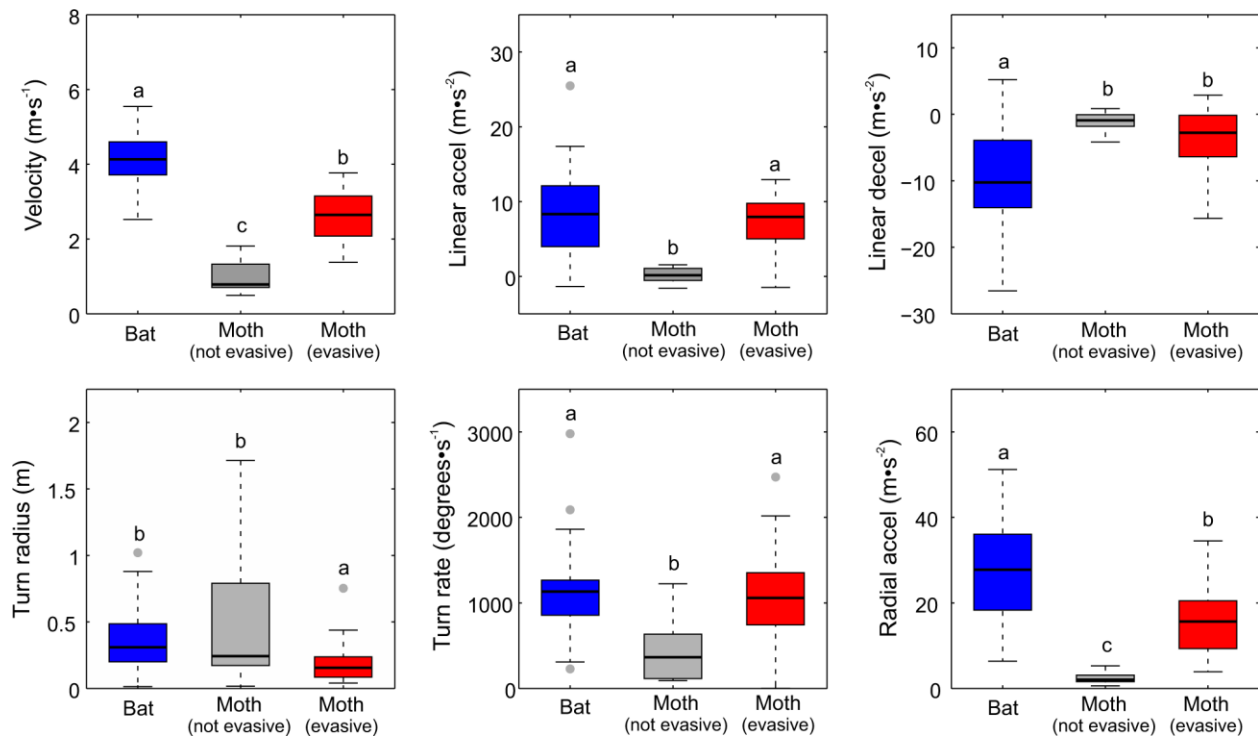
Figure 5. Box plots of peak bat and moth kinematic performance in predator-prey interactions. Kinematics include velocity, linear acceleration and deceleration, turn radius, turn rate, and radial acceleration. Box plot values indicate 10th, 25th, 50th, 75th, and 90th percentiles. Mean values were compared using one-way analysis of variance with pairwise comparisons being made with Tukey tests. Data were combined from attacks made by four individual *Myotis volans* bats. Sample sizes in number of attacks: bats ($n = 50$); non-evasive moths ($n = 9$); evasive moths ($n = 41$).
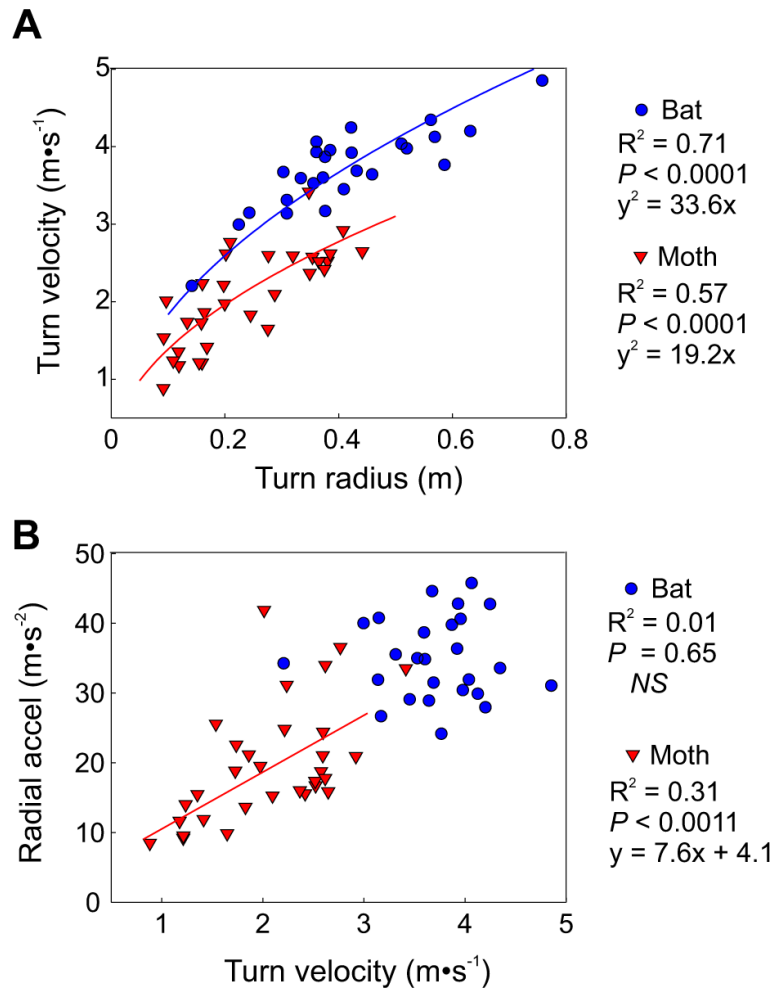
Figure 6. Kinematics of bat and moth turns in predator-prey interactions. (A) If radial acceleration is independent of turn velocity, then the square of turn velocity will be proportional to turn radius, as is shown here for both bats and moths. (B) Radial acceleration is plotted against turn velocity for both bats and moths. The two parameters are independent in bats, but a weak correlation is observed in moths. This difference appears to result from a cluster of points with turn velocity < 1.5 m s^{-1}. Therefore, it appears radial acceleration is independent of velocity and turn radius in bats, but this relationship is less clear in moths. *NS*, not statistically significant. Data were combined from four individual *Myotis volans* bats. Moth data were taken from a variety of unidentified moths making evasive maneuvers. *n* = 32.
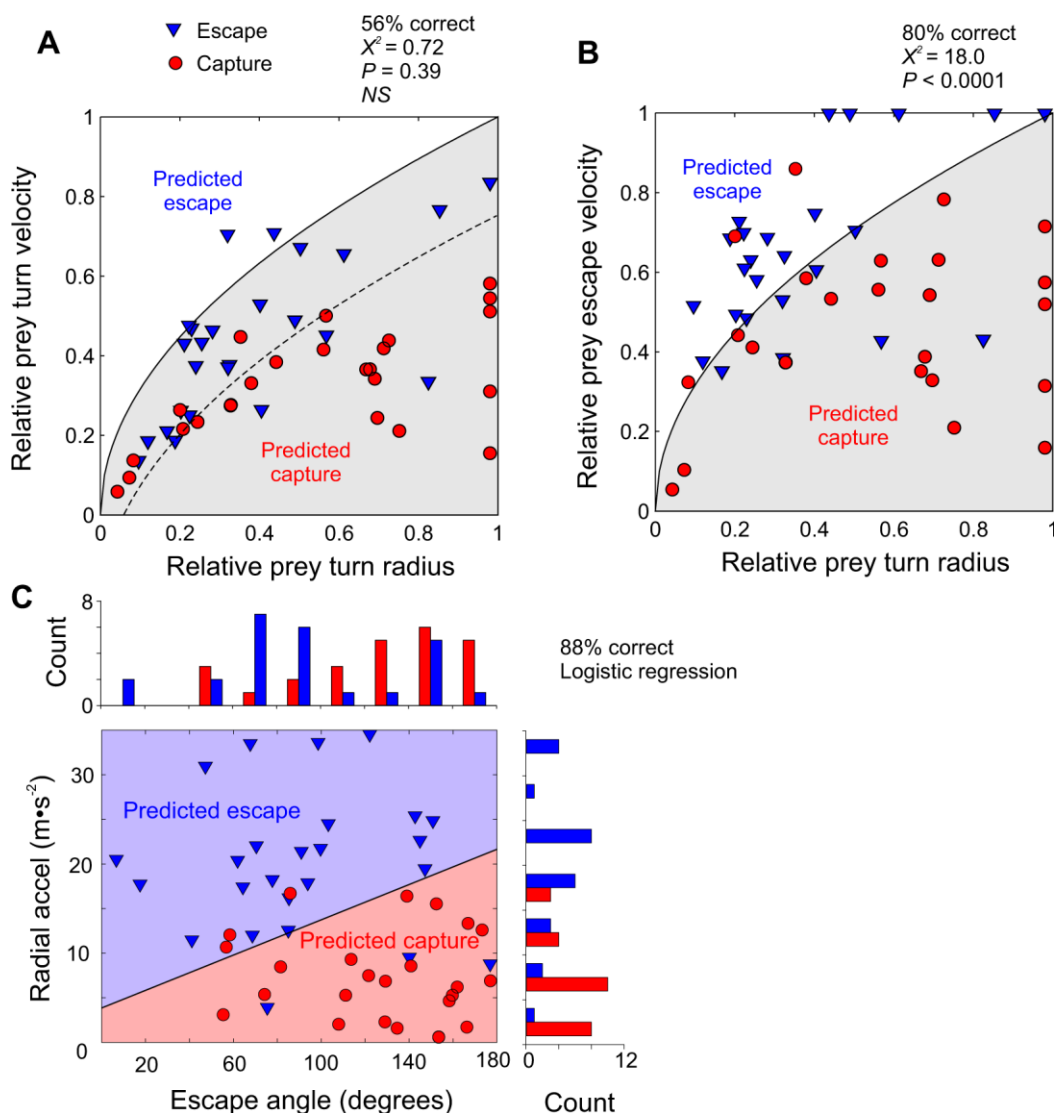
Figure 7. Predicting outcomes of bat-insect interactions. Two approaches were taken to predict predator-prey outcomes: first, (A, B) predictions of the turning gambit were tested. Second, (C) logistic regression was used to find what combination of variables best predicted outcomes. The turning gambit predicts that prey escape when relative prey velocity (prey velocity divided by predator velocity) exceeds the square root of relative prey turn radius (prey turn radius divided by predator turn radius). This relationship is depicted here with predicted captures occurring in the shaded region of the plots and predicted escapes occurring in the white areas. (A) Simultaneous prey turn radius and velocity are shown, as originally conceived by Howland (Howland, 1974). The original threshold (solid curved line) does poorly at discriminating captures and escapes (statistics provided in the figure). However, a modified threshold that is lowered by 25% of prey velocity (dashed curved line) successfully classifies

82% of attacks. (B) Here the turning gambit is tested using mean prey velocity during the escape instead of peak prey velocity during the turn. (C) Logistic regression indicates that moths best escape bats by combining high radial acceleration turns with moderately small escape angles of 40-100°. Histograms of are shown for escape angle and radial accelerations of prey that escaped (blue bars) and prey that were captured (red bars). Data were combined from four individual *Myotis volans* bats on a variety of moth species. $n = 50$ attacks.
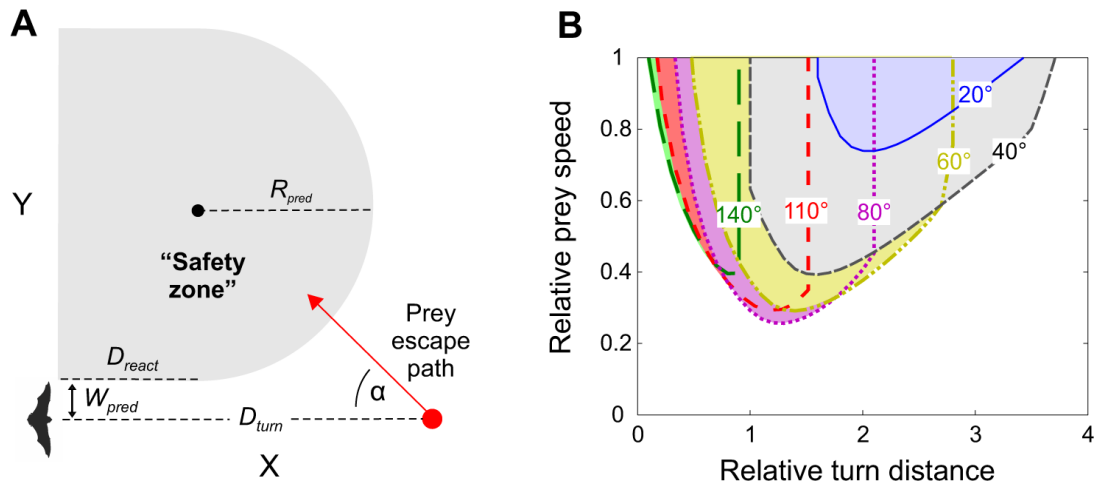
Figure 8. A geometrical model of predator-prey interactions. (A) Geometry of the model. Prey can escape predators by fleeing into the "safety zone" that flanks either side of an approaching predator. Capture occurs if the predator intercepts the prey before the prey reaches the safety zone. The dimensions of the safety zone are determined by the reaction distance (D_{react}), the half-width of the predator's capture device (W_{pred}), and the minimum predator turn radius (R_{pred}). A simplified prey escape path is modeled as vector starting at a particular distance from the predator (D_{turn}) and at a particular escape angle (α) relative to the direction of movement of the approaching predator. It should be noted that in many cases, prey would need to make an initial turn that is not incorporated in the current model, but has been modeled previously (Howland, 1974). (B) Predicted capture-escape thresholds are shown for escape angles ranging 20-140°. Partially overlapping shaded areas indicate parameter space where prey are predicted to survive attacks. Relative turn distance is the absolute turn distance divided by predator turn radius and relative prey speed is prey speed divided by predator speed. Note that moderately small escape angles (approximately 40-80°) have the largest parameter space allowing prey escape. Higher escape angles (110-140°) require more precise timing and should be initiated when the predator is at shorter distances. Calculations are based on a minimum bat turn radius of 0.365 m, a reaction distance of 0.96 predator turn radii and a capture device width of 0.27 predator turn radii (see text for more details).
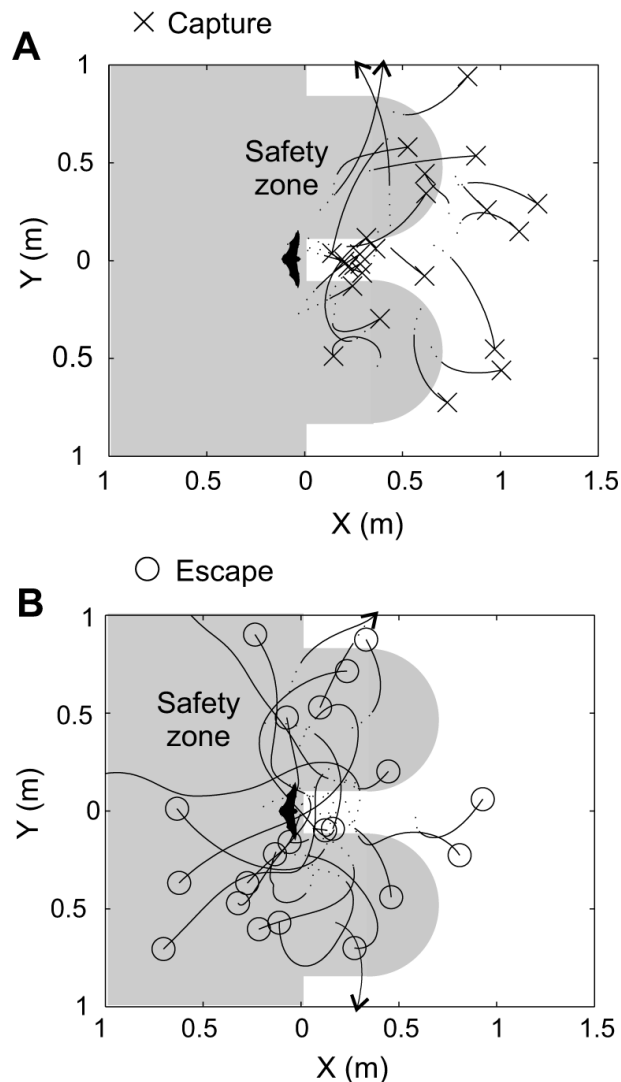
Figure 9. Escape trajectories are plotted with respect to modeled safety zones for (A) captured and (B) surviving moths. (A) Prey that were captured typically fly away from the modeled safety zone. (B) Prey that escaped attack typically flew into the modeled safety zone. See Fig. 8 and the text for descriptions of how the safety zone was modeled. Prey flight paths are shown from the time point of maximum radial acceleration to the end of the attack, which was either capture or the time when angle between the bat flight vector and bat-moth vector was >90°. Three-dimensional prey flight paths were translated and rotated along the X-Y axis so that at the time of maximum prey radial acceleration the bat is at the origin with a flight vector oriented along the positive X-axis. Prey flight paths were then rotated along the Y-Z axis (Z axis not shown) to show the maximum distance of prey travel.