1 Escape behavior: importance, scope, and variables

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1.1 Escape, fitness, and predator–prey encounters

Prey that do not escape when attacked by lethal predators die. Even prey that suffer nonlethal injuries inflicted by predators may incur substantial costs, such as reduced ability to reproduce, reduced social status, reduced ability to forage, and reduced ability to escape in later encounters with predators. Unsuccessful escape reduces fitness. A prey that is killed by a predator loses all fitness that might have been obtained in the future. More technically, residual reproductive value (expected remaining reproductive output over a lifetime) becomes zero when a prey is killed. Therefore predator–prey interactions have been a major force driving evolutionary changes to reduce the likelihood of predation. Numerous, often spectacular, antipredatory adaptations have evolved, including morphological defenses such as shells and other armature, weaponry, camouflage, and the ability to shed tails or other expendable body parts.

In addition to such adaptations, prey that rely on escape to avoid predation must be able to make appropriate escape decisions when confronted by predators. The degree of predation risk posed by a predator that is approaching or is immobile nearby determines expected loss of fitness if the prey does not flee, i.e., the cost of not fleeing. This cost of not fleeing varies with distance between predator and prey when escape begins, and in some cases with the length of time that the predator approaches or is immobile nearby. Besides avoiding being eaten, prey must do many things to maintain themselves and increase their fitness, such as foraging and defending foraging grounds, courting, mating, and aggressively interacting with sexual rivals. When fleeing interrupts an activity that increases fitness, it imposes a cost of fleeing. Therefore each time a prey encounters a predator, the prey has a current level of fitness. The greater its fitness, the more the prey has to lose if killed.

In everyday usage, escape seems to be a simple term, but misleadingly so. If we think of a prey and predator that meet, the prey may flee and/or enter refuge to escape. However, prey may employ other defenses that allow them to escape in a broad sense, including avoiding areas where predators occur, avoiding detection by predators, and a

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variety of chemical, mechanical, and aggressive defenses that come into play when a prey has been overtaken by a predator. These are all fascinating topics, but are not included in this book.

Predator–prey encounters are sometimes described in terms of sequential stages from a predator's perspective, beginning with detection by the predator, identification, approach, subjugation, and consumption (Endler 1986). Other descriptions of encounters take into account both the predator's and the prey's awareness and actions (Lima & Dill 1990). From the prey's perspective, the encounter begins when the prey detects the predator and ends when the predator moves away or when the prey has escaped or been killed. The defenses used by prey vary during the stages from predator's viewpoint. Camouflage and immobility, for example, are important for reducing the likelihood of being detected or identified, whereas autotomy and weapons are used during the subjugation stage, and defenses such as spines and biting of tails to roll into a ball too large to be swallowed are employed to prevent consumption.

Material in this book is limited to prey behaviors that occur during brief predator–prey encounters. Thus occupation of predator-free habitats to avoid predators is excluded. When it has detected a predator, a prey monitors the predator during the approach stage. Alternatively, monitoring may occur as the prey approaches the predator or when both are immobile. The prey may at some time begin to flee. If it flees, it may or may not be pursued by the predator. The prey may enter a refuge where it is safe from the predator. If it enters, the prey must decide how long to stay in the refuge before emerging. If the predator overtakes the prey, the prey may deploy one or more of several defenses in response to imminent or actual physical contact with the predator. The latter defenses are not discussed in this book. In this book the focus is on escape behavior and processes leading to escape decisions. The processes leading to escape decision begin when the prey detects and starts to monitor the predator and last throughout the monitoring phase. When the decision to flee and initiation of escape behavior have occurred, further evaluative processes must occur related to the prey's strategies to evade the predator during pursuit, refuge entry, and time spent hiding in refuge.

All times and defenses outside the above intervals are omitted, but have been discussed elsewhere. Three excellent recent books review knowledge of them. *Antipredator Defenses in Birds and Mammals* (Caro 2005) describes the broad range of these defenses for two taxa. In *Animal Camouflage: Mechanisms and Function*, Stevens and Merilaita (2011) describe evidence for several means of avoiding detection by predators. Importantly for our discussion, the probability of being detected is reduced by camouflage, which should influence the decision by prey to flee. Because risk of being detected is lower for camouflaged prey, they should permit closer approach before fleeing than more conspicuous prey. In *Avoiding Attack: the Evolutionary Ecology of Crypsis, Warning Signals and Mimicry*, Ruxton *et al.* (2004) discuss ways in which prey avoid being detected, avoid being attacked if detected, and some defenses that may be used when contact with the predator is unavoidable. Some of the defenses treated by Ruxton *et al.* (2004) affect the probability of being detected or of being attacked and are important for our topic because they affect predation risk, which in turn affects decisions to flee and hide.

1.2 Focus and goals of this book

This book fills the gap left by the three recent books between defenses used to avoid being attacked and defenses used when contact with the predator is unavoidable. Interest in escape behavior has grown steadily since publication of the first model that predicts how closely a prey will allow a predator to approach before fleeing based on costs to fitness of not fleeing and of fleeing (Ydenberg & Dill 1986).

Both theory and data have been accumulating a quickening pace. Several new models of escape, refuge use, and related behaviors that appeared during the 1990s and 2000s are discussed in some detail in a chapter on escape theory (Chapter 2). Numbers of publications recovered in a citation analysis search for a few of the major escape terms (approach distance, flight initiation distance, flush distance, hiding time, and latency to emerge) showed that numbers of publications and citations increased more than twenty-fold in a search spanning the years 1994 to 2013 (Figure 1.1).

The bulk of research by the editors has been about evolutionary and ecological aspects of escape decisions, and the development and testing of models predicting effects of various factors on escape variables. The core of the book that reflects our research interests is in Part II, which presents economic and other models of escape and refuge use, and empirical data that tests their predictions. However, a full understanding of escape behavior requires a broader approach. In addition to the focus on economic escape decisions, the book presents an integrative view of escape behavior, refuge use, and prey behavior during pursuit. This material follows the chapters on theory and factors affecting escape decision in a series of chapters about behaviors that occur before escape that may affect it, determinants of locomotor performance that is crucial to escape, physiological underpinnings of escape, maternal and genetic influences, personality traits, and use of information about escape behavior to inform wildlife management and conservation practices.

Our goals are to present the accumulated knowledge gained from these and earlier studies in an accessible form, interpret the findings using current theory, and to synthesize work to date. We sincerely hope that this book will stimulate new research. The interplay between theoretical and empirical studies of escape is a major success story in behavioral ecology because theory now permits many testable predictions that have been extensively verified. The story is still unfolding, and many aspects of our topic have not yet been addressed theoretically and many generalizations and exceptions remain to be discovered through empirical studies. Studying escape and refuge use in the field is fun and has provided us many memorable experiences. Laboratory experiments on these behaviors can also be exciting and satisfying to conduct. Developing new theoretical models of escape behavior often leads to very rewarding moments of insight. Join us in this research endeavor.

1.3 Escape theory and data

The interplay and trade-offs among factors that affect predation risk, cost of fleeing, and the prey's current fitness are the core features of theoretical models of escape and related

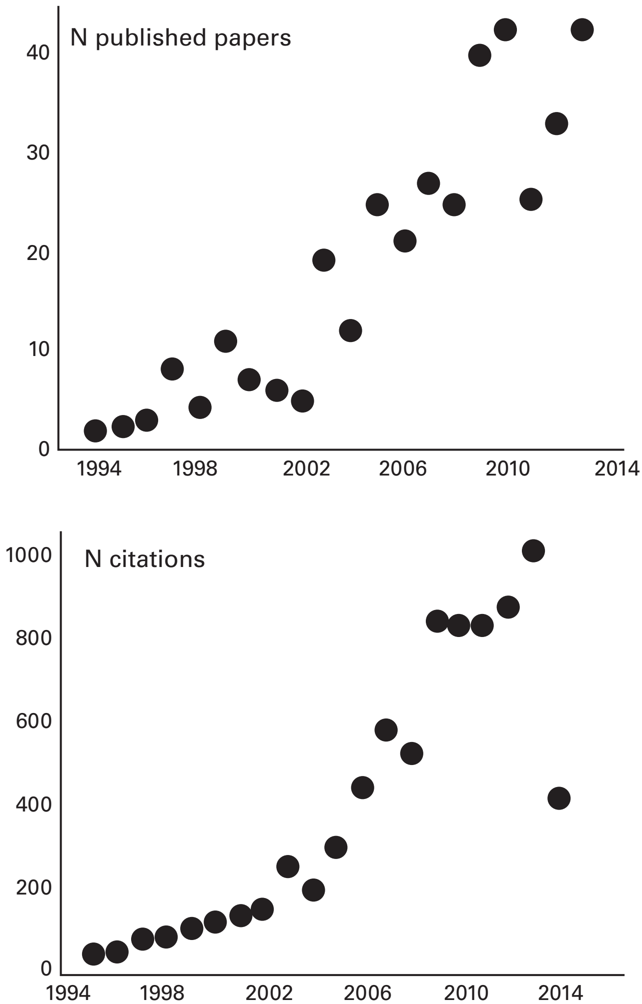

Figure 1.1 Citation analysis shows increasing numbers of articles and citations on escape behavior since the early 1990s. An ISI Web of Science search conducted on July 21, 2014 searching the terms following terms: “flight initiation distance” or “flush distance” or “hiding time” or approach distance” or “latency to emerge”. Citations for 2014 appear to be fewer because the analysis was done mid-year.

behaviors. These models predict decisions by prey about whether to flee, how close to allow a predator to approach before fleeing, or how long to keep still before fleeing when an immobile predator is nearby, how far to flee, and how long to hide in a refuge. In Chapter 2, Cooper presents a number of graphical models, optimality models, and game theoretical models of escape behavior, hiding time in refuge, and related behaviors. Some of the models are highly successful at predicting important, yet limited, features of escape behavior, especially decisions about when to start fleeing. Other models are novel.

Predictions of cost–benefit models of escape and refuge use have been tested extensively and permit interpretation of the effects of numerous factors that affect predation risk, cost of fleeing or emerging, and the prey's fitness at the outset of the encounter on escape and emergence decisions. In addition, variables not predicted by current economic theory affect the trajectories adopted when fleeing begins and changes in trajectory and speed used to foil pursuit.

In Chapters 3 to 9 we summarize our empirically obtained knowledge about economically based escape. Major taxa differ in many ways that may affect escape capacities and decisions. In Chapters 3 to 7 we present our empirical knowledge of escape in major taxa: Theodore Stankowich and Eigil Reimers (mammals), Anders Pape Møller (birds), William E. Cooper, Jr. (reptiles), Philip W. Bateman and Patricia A. Fleming (fish and amphibians, and, in a separate chapter, invertebrates). These chapters emphasize decisions about how close to let the predator approach before fleeing, how long to remain close to an immobile predator before fleeing, how far to flee before stopping if not pursued, and whether to enter refuge. In addition to these variables, factors influencing the initial direction of fleeing are discussed for some prey. In Chapter 8 Paolo Domenici and Graeme D. Ruxton present information about initial directions of escape flight and about strategic changes in prey escape behavior during active pursuit by predators. In Chapter 9 Jose Martín and Pilar López detail decisions about time spent hiding in refuge. Slight overlap occurs among certain taxonomically oriented chapters and Chapters 8 and 9, and the cases of overlap are cross-referenced.

1.4 The rest: related behaviors, locomotor performance, physiology, genetic and maternal influences, personality difference, best practices for field studies, and conclusions

Whereas most of the material in the preceding chapters deals with ultimate causes, i.e., those having been molded by evolutionary processes, Chapters 10 to 15 discuss a mixture of factors affecting escape. In Chapter 10, Guy Beauchamp discusses behaviors including vigilance, alarm calling, predator inspection and monitoring, and pursuit-deterrent signaling. All of these behaviors can affect the ability of prey to make economic assessments of risk or the likelihood that a predator will attack. Therefore they can affect escape decisions. These behaviors have been naturally selected, and effects of all of them except perhaps vigilance on escape decisions have ultimate interpretations. Natural selection favors vigilant prey, but prey that are not vigilant may be forced to flee when the predator is closer than the optimal distance for initiation of escape.

Proximate causes of escape behavior are discussed in Chapters 11 to 15. In Chapter 11, Kathleen L. Foster, Clint E. Collins, Timothy E. Higham, and Theodore Garland, Jr. present determinants of locomotor performance. Variation in the physiological capacities of prey to flee may explain variability in escape decisions among individual prey, populations, and species. Running, swimming, or flying speeds, acceleration, climbing and jumping ability, and endurance all are variable and should be taken into account by prey in assessing risk of being captured. Locomotor capacities place physiological limits of escape speed and other aspects of escape locomotion, and in this sense may be considered to be proximate causes of such aspects of escape behavior. In addition, these limits presumably affect escape decisions as ultimate causes because the risk assessment process must evolve to take locomotor abilities into account. Chapter 12, by Luke P. Tyrrell and Esteban Fernández-Juricic, covers aspects of sensory ecology important for escape decisions.

In Chapter 13 Yoav Litvin, D. Caroline Blanchard, and Robert J. Blanchard discuss the physiological bases of escape response. Physiological factors in escape behavior include neuroendocrine mechanisms of escape, including sensory bases of fleeing, and energetic costs of fleeing. Less is known regarding maternal and genetic effects on escape behavior, but some laboratory studies have begun to examine the development of escape behavior and to separate effects of the maternal environment from genetic transmission of escape traits. These topics are discussed by Lesley T. Lancaster in Chapter 14. Animal personalities have received increasing attention in recent years. A frequent finding has been that some individuals are consistently shyer or bolder than others, i.e., flee sooner or later during approaches or emerge later or sooner from hiding, respectively. In some species shyness and boldness are correlated with a variety of other traits to form adaptive suites of behaviors. In Chapter 15, Pilar López and Jose Martín discuss the literature on these personality traits and avenues for future research.

In Chapter 16, Daniel T. Blumstein, Diogo S. M. Samia, Theodore Stankowich, and William E. Cooper, Jr. discuss best practice for conducting field studies of escape behavior, a topic that we hope will be useful given differences in methods reported in the literature among investigators and recent findings that require new methods. In the final chapter the editors summarize and synthesize what we have learned about the diverse escape topics.

1.5 A standardized terminology for escape and time spent hiding in refuge

1.5.1 Current ambiguity in escape terminology

Studies of escape behavior and refuge use have often been done by investigators interested in a particular prey taxon. In some cases traditions using different terms for identical variables have developed for different taxa. The distance between a prey and an approaching predator when the prey starts to flee has been called reaction distance in many studies of fish; flush distance or flight distance, in studies of birds and mammals; and approach distance or flight initiation distance in studies of various taxa. Different terms for the same variable may be used in different subfields of escape studies, particularly between wildlife biologists and behavioral ecologists. In some cases, a single term may have multiple meanings. For example, flight distance is used to mean both predator–prey distance when escape begins and how far the prey flees before stopping.

Use of these diverse, conflicting, or ambiguous terms for different t taxa and in different conceptual fields of biology has at least two detrimental effects. One is confusion. Readers may be misled if they do not carefully examine the definitions of variables in methods sections. Sometimes the variables are not defined clearly, requiring the reader to assess the meaning from the study's context. The other primary problem with current terminology is that it makes literature searches difficult. This has affected researchers who were unaware of some synonyms.

In this section we hope to ameliorate such terminological problems by recommending a set of terms for standardized usage. We follow this terminology throughout the book and recommend that the terms defined be used in future publications on escape behavior and refuge use. Additional terms specific to their topics will be presented in Chapter 10 for escape trajectories and pursuit. In Chapter 17 we discuss set-back distance, one of several terms used in conservation biology and wildlife management.

1.5.2 Terminology for distance variables and proportions

Standing distance is the distance between an immobile prey and a predator that is immobile nearby. This term originated in studies in which researchers simulating predators stand still at some distance from a prey.

Starting distance (SD) is the distance between prey and predator when the predator begins to approach. Synonym – start distance.

Detection distance is the predator–prey distance when the prey detects the predator. Detection may be cryptic if it occurs before alert (see alert distance). For experiments in which prey are aware of the predator when approach begins, detection distance may be considered to be greater than or equal to starting distance. However, such experiments are of no value for determining detection distance.

Pre-detection distance is starting distance minus detection distance. This the distance approached by the predator before it is detected by the prey.

Alert distance (AD) is the distance between a prey and an approaching predator when the prey responds overtly to the predator by change of posture or orientation to monitor the predator. Synonym – alerting distance.

Minimum bypass distance (MBD) is the predator–prey distance at the point on the predator's path closest to the prey. This is zero for direct approaches that lead to contact with the prey. It increases as the approach angle (see below) increases to a maximum of 90° and increases as starting distance increases. Minimum bypass distance is greater than zero for all indirect, i.e., tangential, approaches.

Proportion (or percent) that flee (or fled). This refers to the proportion of individuals. Synonym – responsiveness. Proportion that flee is preferred because responsiveness, despite having the advantage of brevity, is not specific to escape and has multiple possible interpretations.

Flight initiation distance (FID) is the distance between a prey and an approaching predator when the prey begins to flee. Synonyms – approach distance, escape distance, fleeing distance, flight distance, flush distance, minimum approach distance, and reaction distance. Flight initiation distance is preferred as the clearest term. Approach distance was used frequently in the literature on economic escape, but might be confused with the distance the predator travels during its approach. Flight distance was recommended by Taylor and Knight (2003), but it is ambiguous and has been used to mean both flight initiation distance and distance fled. Flush distance is too specific for general use, being restricted to prey taxa. Escape distance and fleeing distance might also be misinterpreted to mean distance fled. Reaction distance has been used in recent reviews of escape by fish, but is less informative than flight initiation distance and might apply to other phenomena.

Buffer distance is alert distance minus flight initiation distance (Fernández-Juricic et al. 2002). This term suggests that long alert distance provides greater distance (and time) for risk assessment prior to fleeing. This term is distinct from buffer zone, which is the space within which human activity is restricted to reduce disturbance to wildlife (Camp *et al.* 1997). Synonym – assessment distance would highlight the relationship with assessment time, but we prefer buffer distance because it is established.

Margin of safety (MOS) is the distance that would separate an approaching predator from its prey when the prey reaches refuge. A refuging prey must select a flight initiation distance that will permit it to reach refuge before the predator. The margin of safety is the predator's distance to refuge when the prey enters the refuge.

Distance fled (DF) is the distance between a fleeing prey's starting and ending points if the prey is not pursued by a predator. Synonyms – escape distance, flight distance. Distance moved is preferred by Taylor and Knight (2003), but is not specific to studies of escape. A literature search for distance moved revealed thousands of papers that included distance moved, but the vast majority were irrelevant for escape.

Nearest approach distance is the distance between an immobile predator and a prey that is approaching it when the prey stops approaching. This term applies to prey that typically flee away from predators. Some prey may approach predators to counterattack or distract them, such as crabs that bite, autotomize the biting leg, and then flee (Robinson 1970). Others may approach to mob predators (Owings 1977; Gehlbach and Leverett 1995). Approaching to deploy a defensive alternative to fleeing is excluded from our topic. Nearest approach distance as used here is inappropriate to describe such behaviors. For prey that approach approaching predators to escape, nearest approach distance may also be an appropriate, accurate term.

Proportion (or percent) of individuals that enter refuge. This refers to the proportion of the individuals observed.

Proportion (or percent) of individuals that emerge before a trial is terminated after a predetermined time in refuge. Self evident.

1.5.3 Terminology for temporal variables

Detection latency is the time between the beginning of the predator's approach and its detection by the prey.

Escape latency is the time between onset of a sudden startling stimulus and the prey's first detectable reaction. In fish this occurs on a scale of milliseconds.

Latency to flee has different meaning in different contexts. When a predator approaches an immobile prey, latency to flee is the elapsed time between starting time and the time when the prey begins to flee. When an immobile prey has detected an immobile predator nearby, latency to flee is the time between detection of the predator and initiation of escape behavior. In experiments in which a predator approaches and stops near a prey that has detected it, this is the time when the prey flees minus the time when the predator stops.

Assessment time is the time spent monitoring the approaching predator before fleeing. For prey that exhibit alerting responses, assessment time is defined operationally as the time between alerting and initiation of fleeing. However, a prey may have detected a predator and have been monitoring its approach prior to adopting an alert posture. In many experiments using prey that do not show alerting, the prey may detect the predator before approach begins. Even if prey do not become aware until after the approach begins, assessment time is problematic for prey species that do not show overt alerting behaviors.

Margin of safety (temporal margin of safety) is the expected time between arrival at a refuge by a fleeing prey and arrival by the predator. Maintaining a margin of safety requires prey to assess arrival times based on relative velocities of predator and prey.

Hiding time (HT) is the elapsed time between entry into a refuge and emergence from the refuge. In typical experiments, trials are terminated if a prey does not emerge within a fixed maximum time. Therefore estimates of mean hiding time often underestimate the true mean hiding time and longer mean hiding times may be found using longer cut-off times. Synonyms – emergence time, latency to emerge, submergence time. Hiding time is preferred because it is used relatively widely and does not present numerous false positives during literature search, which is a problem that plagues searches for the synonyms that have alternate meanings unrelated to escape behavior.

1.5.4 Terminology for directional variables

Ideally, escape paths would be measured by vectors giving speed and direction throughout the encounter and would be related to similar information for the predator. This is not generally done and such vectors are more difficult to measure than the two-dimensional directions usually presented. We often measure only initial directions with no indication of escape speed. To indicate directions in Euclidian space when no information about speed is available, unit vectors could be used. In most studies of escape by non-volant terrestrial prey and even by some prey that escape in three dimensions, only two-dimensional angles have been measured. However, take-off angle, the vertical angle above horizontal, is an important aspect of the initial escape response by birds, grasshoppers, and presumably other insects. For prey escaping in air or water, the dive (swooping) angle or ascent angle of the predator is very likely to affect the degree to which the prey flees upward or downward. Prey that jump also may vary their vertical take-off angles. Climbing and descent angles of terrestrial and arboreal prey on slopes, logs, and trees may affect both escape speed and the speed and ability of predators to follow, both of which may affect predation risk, and, therefore, escape decisions. Other prey might vary the angle of rapid burrowing in sand or loose dirt. The terms listed below are the two-dimensional angles used in escape studies.

Approach angle has three distinct meanings. One is the difference in degrees between two predators simultaneously approaching a single prey. The other use of this term occurs in studies of effects of directness of approach by a predator on escape decisions. In the latter case approach angle is the angle from the apex point where the predator begins to approach between a line of direct approach and the actual linear approach path. In the third case, approach angle refers to the angle between the line of attack by the predator and the body orientation of the prey. We prefer the following two terms in this case.

Attack angle is the angle between the predator's line of approach and the body orientation of the prey. It has range of 0 to 180°. The attack angle is 0° when the prey is directly facing the predator and 180° when the prey is oriented directly away from the predator.

Stimulation (or stimulus) angle is equivalent to attack angle, but is used in situations in which the stimulus does not approach the prey, such as when a sudden sound is presented experimentally.

Direct approach is movement by the predator on a straight line toward the prey; the approach angle is 0°.

Tangential approach is movement by the predator along a straight path that does not lead to contact with the prey, but bypasses it. For tangential approaches, a minimum bypass distance (see above) is associated with each combination of starting points and approach angles. Synonym – indirect approach. Tangential approach is preferred because it emphasizes that the tangent line from the prey intersects the predator's path at the its closest point to the prey. Indirect approach may be used for contrast with direct approach, but the tangential nature of approach should be made clear.

Escape trajectory (ET) is the path taken by a fleeing prey. In typical studies, the initial escape trajectory is linear at a fixed angle in relation to the direction of the predator's position. Escape trajectory is often defined as this initial angle of fleeing. However, the prey's path may change during pursuit, as in classical mathematical models and cases in which prey make evasive maneuvers such as gradual or rapid turns, or even if no pursuit occurs. An escape trajectory of 180° is directly away from the predator; an escape trajectory of 0° is directly toward the predator. In some studies escape trajectories are considered to span 0 to 360°. In that case a distinction between sides may be made in one of two ways. In one, the right side of a circle corresponds to 0 to 180° and the left side to 180 to 360°. In the other, when a prey turning to flee ends with the threat on the opposite side of the prey's body than before the turn, escape trajectory falls in the range 0 to 180°; when turning to flee ends with the threat of opposite side opposite side of the prey's body than before the turn, the trajectory lies in 180 to 360°. Thus there are three commonly used measures of escape trajectory, two measured on a normal 360° scale and one on an axial (180°) scale. It is important to distinguish between these two interpretations of the escape direction and between circular (360°) and axial (180°) scales, which require use of different circular statistics. For detailed descriptions of the three types of ET, see Chapter 8. Synonyms – flight angle, escape angle. We prefer escape trajectory because this term has long been used in mathematical models of pursuit and in studies of escape by fish. Escape angle and flight angle may vary during pursuit, differing among the prey's positions along the path, the angular changes through space defining a trajectory. Because most studies have measured only the initial direction taken by the prey, the escape angle and escape trajectory defined as a direction for brevity are identical.

Escape angle is the angle of the prey's initial escape with respect to the predator's approach path. It is typically measured on an axial scale of 0 to 180° as discussed for escape trajectory. As noted, these angles may change during escape, in which case the path, or trajectory is altered. Synonyms – escape trajectory, flight angle. Escape angle is preferred over flight angle because flight angle may also refer to aerial flight in contexts other than escape.

Turn angle is the angle between the prey's body axis before the attack and its path during the initial phase of fleeing. It usually spans 0 to 180°, but can be larger if, for example, the prey turns in circles.

Directionality is the proportion of prey that rotate or bend their bodies in a direction directed away from the predator or predatory stimulus during the initial phase.

1.6 Electronic supplementary material

For several chapters space did permit full coverage of certain topics or data that may be useful to researchers. These files are available online at www.cambridge.org/9781107 02060548 (additional resources appear under the "Resources" tab). In the printed chapters and on the website, the electronic supplementary files are identified by chapter and number. For example, ESM 5.2 is the second electronic file for Chapter 5.

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