

REVIEW

Animal escapology I: theoretical issues and emerging trends in escape trajectories

Paolo Domenici^{1,*}, Jonathan M. Blagburn² and Jonathan P. Bacon³

¹CNR-IAMC Localita Sa Mardini, 09072 Torregrande (Or), Italy, ²Institute of Neurobiology, University of Puerto Rico, San Juan 00901, Puerto Rico and ³School of Life Sciences, University of Sussex, Falmer, Brighton BN1 9QG, UK

*Author for correspondence (paolo.domenici@cnr.it)

Accepted 30 January 2011

Summary

Escape responses are used by many animal species as their main defence against predator attacks. Escape success is determined by a number of variables; important are the directionality (the percentage of responses directed away from the threat) and the escape trajectories (ETs) measured relative to the threat. Although logic would suggest that animals should always turn away from a predator, work on various species shows that these away responses occur only approximately 50–90% of the time. A small proportion of towards responses may introduce some unpredictability and may be an adaptive feature of the escape system. Similar issues apply to ETs. Theoretically, an optimal ET can be modelled on the geometry of predator–prey encounters. However, unpredictability (and hence high variability) in trajectories may be necessary for preventing predators from learning a simple escape pattern. This review discusses the emerging trends in escape trajectories, as well as the modulating key factors, such as the surroundings and body design. The main ET patterns identified are: (1) high ET variability within a limited angular sector (mainly 90–180 deg away from the threat; this variability is in some cases based on multiple peaks of ETs), (2) ETs that allow sensory tracking of the threat and (3) ETs towards a shelter. These characteristic features are observed across various taxa and, therefore, their expression may be mainly related to taxon-independent animal design features and to the environmental context in which prey live – for example whether the immediate surroundings of the prey provide potential refuges.

Key words: escape response, escape trajectory, locomotion, predator–prey interaction.

Introduction

Escape responses are used by many taxa as their main defence against predator attacks (Bullock, 1984). These escape responses are the result of complex sensorimotor control, in which the stimulation caused by an approaching predator generates a motor command that moves the animal in a direction that, supposedly, maximizes its chances of survival. For this reason, escape responses have long attracted the attention of neurophysiologists, behavioral biologists and ecologists (Bullock, 1984; Camhi, 1983; Godin, 1997; Ydenberg and Dill, 1986). Typically, escape responses consist of high accelerations, often accompanied by a change in direction, aimed at displacing the prey away from the threat. In addition, escape responses are characterized by extremely fast reaction times, with escape latencies as short as 5–10 ms (Eaton, 1984). In many invertebrates and lower vertebrates, short response times are mediated by rapidly conducting giant neurons that mediate the escape manoeuvres (Bullock, 1984).

Success in avoiding predation when under attack can result from various components of the escape response, such as timing, reaction distance, locomotor performance, and the direction of escape [escape trajectory (ET)] (Domenici, 2010; Ilany and Eilam, 2008; Walker et al., 2005). Although theoretically it could be argued that escape performance should be maximized – for example with minimal latencies, maximum locomotor performance and maximum reaction distance – some previous work has shown that this is often not the case (Domenici, 2010; Godin, 1997; Ydenberg and Dill, 1986). A number of studies have focused on testing the hypothesis that prey do not escape at the greatest distance at which a threat is perceived, but at a distance that is determined by the

relative cost and benefit of escaping; the cost is higher when the prey has more to lose by escaping [i.e. the economic hypothesis (Ydenberg and Dill, 1986)]. For example, prey engaged in feeding activities tend to show a shorter reaction distance than prey that are not foraging because the former may lose a feeding opportunity (e.g. Cooper, 2000; Krause and Godin, 1996). Similarly, prey that are near refuges may also show shorter reaction distances because they are at lower risk of predation than prey further away from refuges or in open spaces (e.g. Bonenfant and Kramer, 1996; Cooper, 1997; Dill and Houtman, 1989).

Given all the theoretical and experimental work investigating the issue of when to escape in relation to the predator's approach, it is surprising that a unifying theory on where (in which direction) to flee has not been fully formulated. Previous geometrical models (Arnott et al., 1999; Domenici, 2002; Weihs and Webb, 1984) show that, theoretically, optimal ETs might be predicted on the basis of the relative speeds of predator and prey. However, these predictions do not accommodate one of the main properties postulated for ETs, their unpredictability (Comer, 2009; Godin, 1997; Humphries and Driver, 1970), which seems fundamental for preventing predators from learning a repeated pattern of prey response. Although high variability in ETs is expected for maximum unpredictability, escaping towards the threat is arguably not a good choice. Hence, completely random trajectories are not expected.

This paper reviews theoretical issues and emerging trends in animal ETs. First, we address the issue of directionality, i.e. whether prey escape by rotating their body away from or towards the threat. A theoretical framework for predicting escape trajectories is then presented, followed by a discussion of the emerging trends of escape

trajectories in various animal taxa that is based on a survey of ET data from the literature in the accompanying paper (Domenici et al., 2011). We also consider taxon-specific physiology and ecology, the implications for the sensory and locomotor systems, the issue of context dependency and conclude with the significance of escape trajectories in terms of survival. Although a number of potential defence strategies that do not result in an escape (e.g. freezing) can be used by prey (Eilam, 2005; Godin, 1997), these are beyond the scope of the present review.

Here, the term ET refers mainly to the direction of initial prey response relative to the direction of the predator attack (or of an artificial threatening stimulus), because trajectories are commonly measured at the end of the main rotation observed during the escape response, often corresponding to a specific kinematic stage of the animal's locomotion. Beyond this point, prey may move in a zigzag path (Edut and Eilam, 2004), especially if predators follow up their attack with a chase. The term ET is used throughout to refer to escape trajectories in general, unless the particular way an ET has been measured needs to be noted. In these cases, the metrics ET^0 , ET' and ET'' , briefly defined below, are used (Domenici et al., 2011). ET^0 spans 360deg based on whether, at the end of the escape, the threat remains on the side of the original stimulation (0–180deg) or not (180–360deg); ET' spans 360deg, with the sectors 0–180deg and 180–360deg corresponding to escapes directed to the right and left of the line directly away from the threat, respectively; ET'' spans only 180deg from the threat, regardless of the side stimulated. In all three cases, 0 and 180deg correspond to escapes oriented towards and directly away from the threat, respectively. This review mainly discusses ETs in the horizontal plane, as this is the main plane of motion for many terrestrial and some aquatic species. However, vertical components of ETs will also be discussed in birds and some aquatic animals, such as crayfish.

Directionality

The meaning of directionality

We define directionality as the proportion of responses in which the body rotation is initiated in a direction away from the stimulus (i.e. away responses/total responses) rather than towards it. The most common definition (which will be used here unless indicated) for away and towards responses is based on the direction of the initial rotation [or body bend in flexible animals such as fish (Blaxter and Batty, 1987)] of an escape response relative to the stimulation (Comer and Dowd, 1987; Domenici and Blake, 1993). Away and towards responses are escapes with a rotation directed away from and towards the stimulus, respectively. A towards response does not necessarily imply that the final escape trajectory will be towards the stimulus, because an animal initially oriented at 170deg that makes a 20deg rotation towards the stimulus will end up having an escape trajectory of 150deg from the stimulus itself (Domenici et al., 2011). We note that, in contrast to the general convention adopted in this paper, some authors have based their definition of away and towards responses on the final trajectory (e.g. Martin and Lopez, 1996).

The dichotomy of away *versus* towards responses has a specific physiological correlate in a number of taxa, particularly in invertebrates and lower vertebrates, which provide most of the directionality data in the literature. In many species, escaping with a rotation directed away from the stimulus is triggered by the sensory system ipsilateral to the stimulation. In fish, mechanical or visual stimulation directed to one side of the fish usually results in the excitation of the ipsilateral Mauthner neuron, one of the pair of

reticulospinal neurons controlling fish escape responses (Eaton et al., 2001). In turn, the excited Mauthner cell activates the contralateral musculature, typically bending the fish into a C-shape directed away from the stimulus (Eaton et al., 2001; Weiss et al., 2009). Interestingly, after firing, the Mauthner neuron is subjected to a prolonged inhibition during which the contralateral Mauthner cell is released from inhibition, ready for an alternative escape (Hatta and Korn, 1999). This mechanism allows consecutive escape responses in rapid succession (with intervals as short as 35ms) on opposite sides of the fish (Hatta and Korn, 1999), which might increase the unpredictability of the response.

Unpredictable or protean¹ escape behaviour has often been postulated as a means of preventing countermeasures by predators (Comer, 2009; Edut and Eilam, 2004; Godin, 1997; Humphries and Driver, 1970). Complete unpredictability of escape direction would result in an equal proportion of responses away and towards the threat, but work on a number of species from different taxa (Table 1) shows that away responses tend to be more common than towards responses. Intuitively, away responses seem advantageous because they allow prey to increase their distance from the threat, but they typically only comprise 50–90% of the total escapes (Table 1). The explanations for the presence of a (albeit limited) proportion of towards responses may be ultimate, e.g. explained as a behavioural survival strategy, or proximate, e.g. related to animal design or factors affecting the sensory (directional) performance. These explanations need not be mutually exclusive.

Although away responses may be advantageous because the prey moves further away from the attack, a small context-dependent proportion of towards responses may introduce a significant element of protean unpredictability, enough to prevent predator learning. In addition, we show below that a number of other factors can affect directionality. The resulting variability provides some insights into the mechanisms driving directionality.

Factors affecting directionality

The variability in escape directions can be influenced by sensory performance constraints. Towards responses in fish generally have shorter escape latencies than away responses, suggesting a possible trade-off between short latency (and therefore short neural processing time) and directional accuracy (Domenici and Batty, 1997; Turesson et al., 2009). In addition, the initial orientation of the prey's body axis relative to the approaching threat modulates directionality, i.e. stimulation directed perpendicularly to the prey results in a high proportion of away responses whereas stimulation directed to the anterior or posterior 30deg angular sector results in proportions of away and towards responses that do not differ statistically (Domenici and Blake, 1993). A proximate explanation for this result is that the directional sensitivity of fish is poor for stimuli that are almost in line with the fish's axis (Domenici and Blake, 1993). In this situation, from an ecological perspective it may make little difference in survival if the prey makes an away or a towards response, and similar proportions of towards and away responses may increase unpredictability (Domenici, 2010).

In fish, directionality can be biased in certain species in which lateralized individuals are found (e.g. Cantalupo et al., 1995; Heuts, 1999). Heuts has observed that zebrafish (*Brachydanio rerio*) and

¹Proteus, the mythological Greek God, could predict the future. To avoid capture and the misappropriation of his clairvoyant skills, he could assume many different body forms. 'Protean' escape behaviour refers to its unpredictable characteristics (Comer, 2009).

Table 1. Proportion of away responses

Species	Directionality (away/total; %)	N	Type of stimulus	Reference
Copepod <i>Acartia hudsonia</i>	55–83 (range)	28–96 (range)	Two species of Scyphomedusae	Suchman, 2000
Cockroach <i>Periplaneta americana</i>	86	161	Wind	Camhi and Tom, 1978
	81	253	Wind	Comer and Dowd, 1987
	94, 97	86, 431	Wind	Domenici et al., 2008
Cricket <i>Gryllus bimaculatus</i>	87	46	Wind	Tauber and Camhi, 1995
Cave cricket <i>Troglophilus neglectus</i>	84	95	Wind	Schrader, 2000
Cricket <i>Gryllus sigillatus</i>	82	68	Wind	Kanou et al., 2006
Cricket <i>Gryllus bimaculatus</i>	94	93	Wind	Kanou et al., 1999
Locust <i>Locusta migratoria</i>	95	60	Visual	Santer et al., 2005
Shrimp <i>Crangon crangon</i>	81 ^a	76	Fish predator	Arnott et al., 1999
Soldier crab <i>Mictyris longicarpus</i>	71	31	Visual	Nalbach, 1990
Frog <i>Rana pipiens</i>	77	564	Visual	King and Comer, 1996
Lizard <i>Psammotromus algirus</i>	67.5 ^a	40	Predator model	Martin and Lopez, 1996
Angelfish <i>Pterophyllum eimekei</i>	77	62	Mechanical	Domenici and Blake, 1993
Goldfish <i>Carassius auratus</i>	87	48	Mechanical	Eaton et al., 1981
	47	36	Mechanical	Heuts, 1999
Herring <i>Clupea harengus</i> larvae	74	74	Tactile	Yin and Blaxter, 1987
	74	42	Acoustic	Blaxter and Batty, 1985
	92	183	Visual	Batty, 1989
Herring (school) <i>Clupea harengus</i>	88	253	Sound	Domenici and Batty, 1994
Herring (solitary) <i>Clupea harengus</i>	64	117	Sound	Domenici and Batty, 1997
<i>Xenopus laevis</i> embryos	64 (head)	163	Tactile	Boothby and Roberts, 1995
	78 (trunk)	240		
	83 (tail)	35		

Away responses are responses with an initial rotation directed away from the stimulus unless otherwise indicated. Only indicative examples are reported.

^aAway and towards responses were defined on the basis of escape trajectories in the semicircle away from or towards the stimulus, respectively.

goldfish (*Carassius auratus*) tend to turn right irrespective of which side of the body they were stimulated, leading to a similar overall number of towards and away responses when left and right stimuli are used (Heuts, 1999). Undisturbed fish showed more frequent fast turns to the right and slow turns to the left, suggesting that the right bias in fast turns and escape responses may be explained by anatomical muscle size asymmetries (Heuts, 1999). Hence a further potential (proximate) explanation for towards responses in certain species may be the occurrence of lateralized individuals within the population, for which the detrimental effects of turning towards a threat on one particular side of the body might be compensated by higher muscle performance and escape acceleration (Heuts, 1999). More recent studies on escape responses triggered by non-directional stimuli in fish (roach *Rutilus rutilus*) show directional bias related to morphological asymmetries (Izvekov and Nepomnyashchikh, 2008; Krylov et al., 2008). Escape directionality bias has also been noted in frog (*Hyla regilla*) jumps in response to a simulated predator, which are biased leftwards, possibly because of anatomical differences in limb length at the population level (Dill, 1977). Both *Bufo viridis* and *B. marinus* responded with more sideways jumps to left stimulation and with more frontal jumps to right stimulation (Lippolis et al., 2002). In another study, directional biases found in adult and larval anurans to presumed predators were suggested to be related to laterality in the telencephalon of adults and the Mauthner neurons of tadpoles, respectively (Malashichev and Wassersug, 2004). Lizards (*Podarcis muralis*) also show directional right bias in response to a predator approaching from behind (Bonati et al., 2010). Invertebrates can also respond asymmetrically; atyid shrimp (*Neocaridina denticulata*) show bias in escape directionality, possibly resulting from asymmetries in abdominal morphology (Takeuchi et al., 2008).

The mode of stimulation can affect directionality. Herring (*Clupea harengus*) larvae responded with the highest proportion of away responses to visual stimuli compared with tactile and sound stimuli (Batty, 1989; Blaxter and Batty, 1985; Yin and Blaxter, 1987). Escape directionality increases with ontogenetic stages in this species, possibly because of the development of sensory organs (Blaxter and Batty, 1985).

Any movement the prey is already making at the time of predator stimulation can affect its escape response. For example, fish that are gliding respond with more away responses than when actively swimming (Blaxter and Batty, 1987). Similarly, the escape responses of larval anurans (*Xenopus laevis*) to touch stimuli are gated by rhythmic postsynaptic inhibition. It turns out that *X. laevis* tadpoles respond to stimulation only to the side opposite to the one that is already contracting during routine swimming; this ensures that the resulting escape response is directed away from the stimulation (Sillar and Roberts, 1988). In contrast, fish escape responses can be triggered during any phase of cyclic swimming (Jayne and Lauder, 1993), and the swimming phase does not affect directionality (Domenici and Batty, 1994). Providing a possible neural substrate for these observations, it was subsequently found that Mauthner neuron firing overrides the cyclic swimming motor output and thereby produces the appropriate output for escape, regardless of the swimming phase (Svoboda and Fetcho, 1996).

Acute changes in environmental factors, such as temperature and hypoxia, can also influence escape direction. Rapid cooling was shown to increase the proportion of responses towards the stimulus in fish (Preuss and Faber, 2003), similar to that observed in hypoxic conditions (Domenici et al., 2007). These acute environmental changes probably affected the sensorimotor system directly, supporting the notion that directionality can be constrained by sensory performance. Unsurprisingly, direct manipulation of

sensory structures can also affect directionality. For example, removal or covering of the wind-sensitive cerci situated at the rear end of the cockroach (*Periplaneta americana*) increased the proportion of towards responses, thus reducing directionality of the escape response (Camhi and Tom, 1978; Comer and Dowd, 1987; Vardi and Camhi, 1982). This reduction in directionality could result from an imbalance, in the two sides of the central nervous system, of the activation of the giant interneurons (GIs), which control the escape response. In support of this idea, hemisection of the abdominal nerve cord, where the GIs are located, caused a dramatic decrease in directionality because most escape responses to stimuli on the hemisectioned side were oriented towards the stimulation (Comer and Dowd, 1987). More subtle manipulations that alter the molecular identity of some of the cercal sensory neurons and hence the pattern of their connections to GIs, also alters the directionality of juvenile cockroach escape responses (Booth et al., 2009).

Directionality can also be affected by the surroundings, such as the presence of refuges and obstacles in the immediate environment (Domenici, 2010; Eaton and Emberley, 1991). In addition to avoiding barriers when performing an escape response, anurans avoid the direction in which a barrier had been previously positioned (Ingle and Hoff, 1990). The presence of conspecifics can also affect the direction of escape. For example, solitary herring escape with a higher proportion of towards responses than herring in a school (Domenici and Batty, 1997). Perhaps solitary herring respond with more towards responses as an alternative strategy to increase unpredictability whereas schooling individuals can take advantage of the confusion effect on the predator (Domenici, 2010; Domenici and Batty, 1997). At the proximate level, however, high directionality in schooling fish might be explained by their longer latencies and possibly higher sensory threshold, increasing the signal to noise ratio and therefore left/right discrimination (Domenici and Batty, 1997).

The context dependency of escape response directionality indicates the flexibility in what are often simply regarded as hard-wired behaviours. Indeed, startle behaviours can be conditioned; goldfish conditioned to a light stimulus associated with a food reward subsequently react with startle-like towards responses in the direction of the light source alone (Moulton and Dixon, 1967). Clearly, there is need for further work on the mechanisms underlying the flexibility of the escape system in terms of its directional response, and on the functional significance of directionality.

Can towards responses be considered mistakes?

Previous work has described towards responses as 'incorrect', 'wrong' or 'apparent tactical errors' compared with away responses (e.g. Eaton and Emberley, 1991; King and Comer, 1996; Tauber and Camhi, 1995). This seemingly reasonable idea can be assessed by considering how an away or towards response actually results in the final escape trajectory, which is a major determinant of escape success (Walker et al., 2005). In other words, can towards responses produce trajectories similar to those of away responses?

The away and towards responses of solitary fish actually result in different ET⁰s (Domenici and Batty, 1997; Domenici and Blake, 1993). In contrast, schooling fish (Domenici and Batty, 1994) and startled cockroaches (Domenici et al., 2009) react with towards responses that can result in ET⁰s similar to those of away responses. In cockroaches, the absolute turn angle (measured relative to the body axis) of towards responses shows a relatively narrow range, with almost all the responses less than 30deg, whereas away

responses occupy a much larger range, up to approximately 150 deg (Domenici et al., 2009). The <30deg turn observed in towards responses approximately corresponds to the angular distance between the modes of preferred escape trajectories. Cockroaches may be minimizing their turn when making a towards response, allowing them to reach one of the preferred ET⁰s in the shortest time, and thereby producing effective anti-predator behaviour (Domenici et al., 2009). Soldier crabs (*Myctiris longicarpus*) and frogs (*Rana pipiens*) seem to exhibit a similar strategy (Domenici et al., 2011). Towards responses may therefore not necessarily represent mistakes (i.e. a misjudged assessment of threat direction); rather, they may represent: (1) specific time-minimization strategies (e.g. cockroaches) (Domenici et al., 2009) or (2) a means of generating unpredictability [e.g. in solitary herring (Domenici and Batty, 1997)]. In contrast, the increase of towards responses as a result of acute exposure to environmental factors such as hypoxia and temperature shock is better interpreted as a malfunction of the nervous system, possibly leading to a sub-optimal proportion of away responses.

In the context of this general variability in escape directionality, it is important to consider the accuracy of fast directional movements in other behavioural contexts. When roles are reversed and fish (Wohl and Schuster, 2007) are observed as predators, their fast attacking movements have kinematics similar to their escapes, but show remarkable high directional accuracy. In frogs, however, high directional accuracy in attacks implies lower rotational speed compared with escape responses (King and Comer, 1996). Although in some cases accuracy may imply a cost in terms of speed of execution, organisms appear to be capable of performing fast reactions with high directional accuracy. This reinforces the idea that towards responses may be, at least in some cases, an adaptive feature of the escape system rather than the result of simple mistakes made under extreme time constraints.

Escape trajectories: theoretical issues

Geometric models of escape trajectories

Simple geometric models have been developed to predict optimal ETs based on the relative speed of the predator and the prey (Arnott et al., 1999; Domenici, 2002; Weihs and Webb, 1984). For simplicity, these models assume constant speeds of predator and prey. Because they make similar predictions about optimal ETs, only one (Domenici, 2002) will be described in detail here. Fig. 1 shows the main variables for the geometric model. In this model, ETs are considered to span only 0–180 deg and are defined as the angle between the threat and the escape direction of the animal, with 0 deg indicating motion towards the threat, 180 deg motion away from the threat and 90 deg motion perpendicular to the line of attack of the threat (i.e. ET⁰) (Domenici et al., 2011). Escaping with an ET⁰ (β in Fig. 1A) of 180 deg corresponds to maximizing the distance from a static stimulus, or from a threat approaching at a speed lower than that of the prey. However, it is possible that predators pursue their attack by moving along the strike trajectory at a speed higher than that of the prey. In this case, a prey escaping with an ET⁰ of 180 deg would eventually be captured. For predator speeds higher than the prey's, this simple geometric model provides the solution for the escape angle needed in order to reach a safe position before being caught by the predator. The model presented here is based on the geometry of killer whales (*Orcinus orca*) stunning herring by means of tail-slaps (Domenici et al., 2000a; Domenici et al., 2000b), but it can be readily applied to most other predator–prey interactions.

For prey to successfully escape a tail-slap, they need to reach the projection of the edge of the flukes (i.e. point E in Fig. 1A) before the predator (i.e. its flukes) does. This corresponds to:

$$T_{\text{pred}} > T_{\text{prey}}, \quad (1)$$

where T_{pred} and T_{prey} are the times the predator and the prey take to reach point E from the instant the prey responds, respectively. Substituting distance and speed into Eqn 1, we obtain:

$$\frac{D_{\text{pred}} + d_{\text{pred}}}{U_{\text{pred}}} > \frac{D_{\text{prey}} + d_{\text{prey}}}{U_{\text{prey}}}, \quad (2)$$

where D_{pred} is the distance between the flukes and the prey at the onset of the response (i.e. the reaction distance); d_{pred} is the projection of the prey's escaping path, along the path of the projection of the edges of the fluke; U_{pred} is the flukes' mean speed; D_{prey} is half the flukes' width; d_{prey} is the distance between the prey at the onset of the response and point E, minus D_{prey} ; and U_{prey} is the prey speed. The terms d_{pred} and d_{prey} can be eliminated from Eqn 2 by solving for them with a known morphological variable such as D_{prey} . Thus, Eqn 2 becomes:

$$\frac{D_{\text{pred}} + D_{\text{prey}} \tan \alpha}{U_{\text{pred}}} > \frac{D_{\text{prey}}}{\cos \alpha U_{\text{prey}}}. \quad (3)$$

The prey can maximize its probability of survival by reaching point E earlier than the predator (i.e. the flukes). This corresponds to maximizing the difference between T_{pred} and T_{prey} . The difference between T_{pred} and T_{prey} (t_d) is given by:

$$t_d = \frac{D_{\text{pred}} + D_{\text{prey}} \tan \alpha}{U_{\text{pred}}} - \frac{D_{\text{prey}}}{U_{\text{prey}} \cos \alpha}. \quad (4)$$

The escape angle α that maximizes this difference can be found by deriving for α :

$$\delta t_d / \delta \alpha = 0. \quad (5)$$

A few steps (Domenici, 2002) yield:

$$\sin \alpha = U_{\text{prey}} / U_{\text{pred}}, \quad (6)$$

from which:

$$\alpha = \arcsin (U_{\text{prey}} / U_{\text{pred}}). \quad (7)$$

Therefore, for prey speeds lower than predator speeds, prey should escape at an angle α between 0 and 90deg, which, when calculated relative to a threat direction centred at 0deg, corresponds to ET's (β in Fig. 1A) between 90 and 180deg, as a function of the ratio between U_{pred} and U_{prey} (Fig. 1B). In the extreme case in which U_{pred} is similar to U_{prey} , α tends to 90deg (i.e. β tends to 180deg). However, when $U_{\text{pred}} \gg U_{\text{prey}}$, α tends to 0deg (i.e. β tends to 90deg). This result is in accordance with those of Arnott et al. (Arnott et al., 1999) and Weihs and Webb (Weihs and Webb, 1984) for moving coordinates, although they used a different theoretical approach. For $U_{\text{prey}} > U_{\text{pred}}$, the best solution is $\alpha=90$ deg ($\beta=180$ deg) (Weihs and Webb, 1984), because escaping directly away from a predator that is slower than the prey allows the prey to maximize its distance from the predator.

All these models generate solutions suggesting that β should be within the 90–180deg sector depending on the relative speed of predator and prey. Arnott et al. predict that the actual size of the angular sector that yields a 100% probability of escape is a function of the prey size, speed and reaction distance (Fig. 1C) (Arnott et al., 1999). Indeed, 90–180deg is the main range of ETs used by prey (when measured as ET⁰ or ETⁿ) (Domenici et al.,

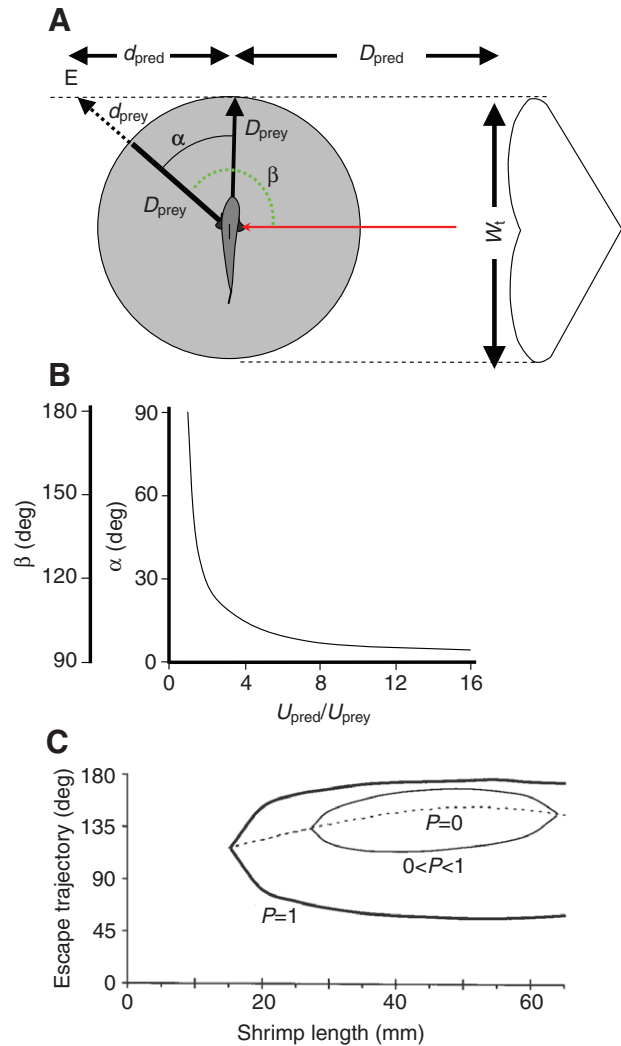


Fig. 1. (A) The geometry of escape trajectories. The shaded area has a radius D_{prey} , which is the minimum distance the prey needs to cover in order to exit the capture zone, and is the projection of W_f , the width of the predator's capture device. The prey will be safe if it reaches the escape point E before the predator, by travelling at an angle α from the line perpendicular to the predator's attack (i.e. β from the line of attack). The prey reacts to the predator at a distance D_{pred} . In order to reach E before the predator, the prey needs to cover distance $D_{\text{prey}} + d_{\text{prey}}$ in a shorter time than the time the predator takes to cover $D_{\text{pred}} + d_{\text{pred}}$ [based on fig. 7 from Domenici (Domenici, 2002), reproduced with permission from Taylor & Francis Ltd]. (B) The angles α and β as a function of the ratio of predator speed to prey speed ($U_{\text{pred}}/U_{\text{prey}}$) [based on fig. 8 from Domenici (Domenici, 2002), reproduced with permission from Taylor & Francis Ltd]. (C) Escape trajectories as a function of prey length, using a predator speed of 1.2 m s^{-1} and a reaction distance of 2 cm. The dotted line indicates the optimal ETⁿ, and the boundaries separate areas with different probability of capture P [fig. 10a reproduced with permission from Arnott et al. (Arnott et al., 1999)].

2011). Other factors may also affect the optimal ETs, such as keeping the threat within an angular zone that can be tracked by the prey's sensory system. The model presented here is admittedly simplistic because it is only based on speed. Inclusion of other performance variables such as response latencies and breaking/acceleration abilities of predators and prey could lead to alternative theoretical solutions, such as waiting until the last instant before escaping with angles < 90 deg, which is observed in some prey species (Fuiman, 1993).

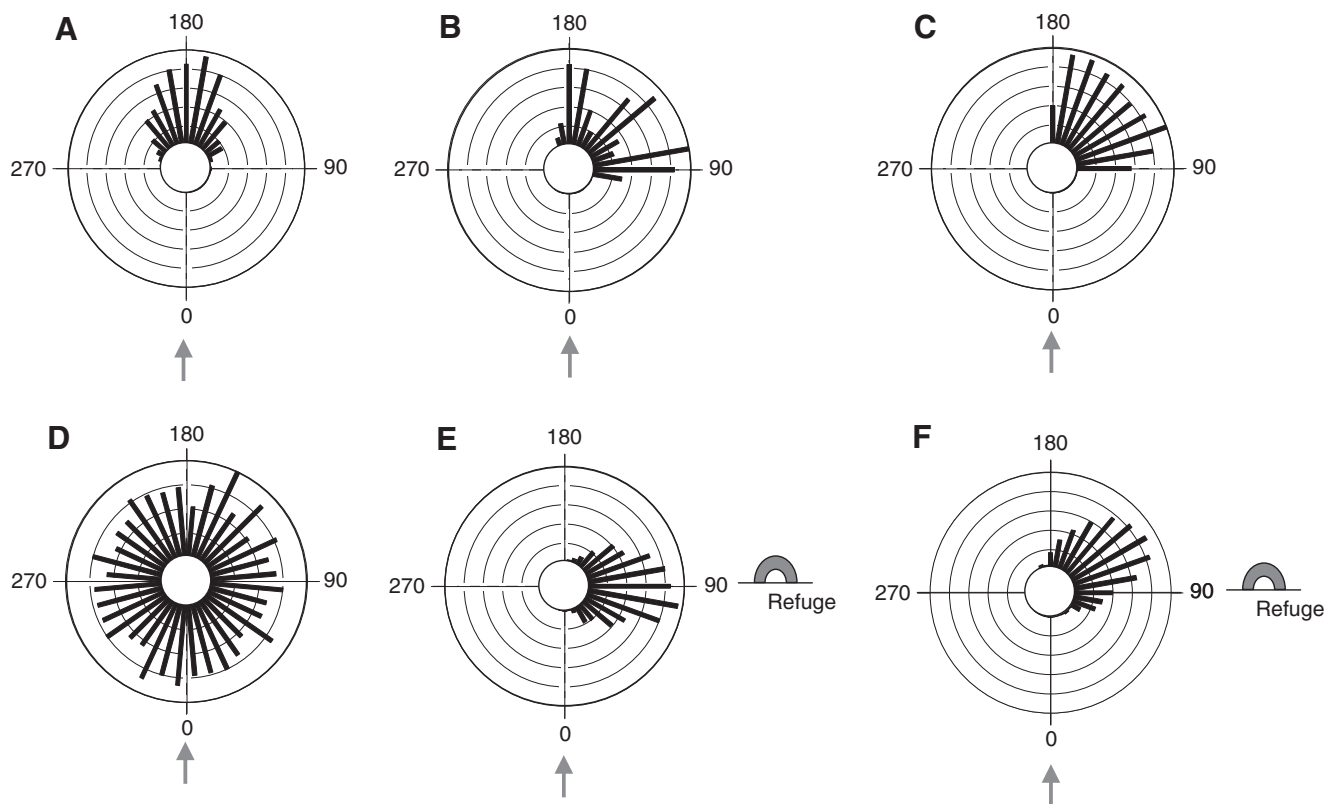


Fig. 2. The various hypothetical ET distributions relative to a threat (grey arrows at 0 deg). (A) A circular normal distribution (generated with the random number generator at http://www.wessa.net/rwasp_rngnorm.wasp#output, using 180 deg as mean, 30 deg as s.d., $N=1000$). Each concentric circle represents a frequency of 30. (B) A distribution with manually generated preferred ETs. Each concentric circle represents a frequency of 6. (C) A random, 90–180 deg range-limited distribution (generated with www.random.org/integers/, number from 90 to 180, $N=1000$). Each concentric circle represents a frequency of 25. (D) A random distribution (generated with www.random.org/integers/, number from 1 to 360, $N=1000$). Each concentric circle represents a frequency of 10. (E) A circular normal distribution as in E, but directed towards a refuge, independent of threat direction. Each concentric circle represents a frequency of 30. (F) A circular normal distribution as in E, with the mode being a compromise between escaping towards a refuge and escaping directly away from the threatening stimulus. Each concentric circle represents a frequency of 30.

Optimal or unpredictable ETs? Theoretical issues and emerging trends

Although there might be a single optimal trajectory for any given predator–prey encounter, as derived from the model described above, other factors might play a role, such as the learning abilities of predators and the presence of refuges. ETs could fall into a number of theoretical distributions. These are shown in Fig. 2 and described below, along with a synthesis of relevant supporting behavioural data [reviewed in detail in Domenici et al. (Domenici et al., 2011)].

Case A: optimal trajectory (Fig. 2A)

Previous models show that there exists an optimal trajectory of escape for any given ratio of predator and prey speed (Domenici, 2002; Weihs and Webb, 1984) (Fig. 1B). Hence adopting such a strategy would allow prey to maximize their distance from the threat. The inclusion of other variables (e.g. morphology of the predator's feeding apparatus, sensory system constraints, etc.) into the model may increase its complexity. For example, an optimal trajectory could be modeled based on the compromise of both achieving the maximum distance from the predator, while keeping it within the field of view (Hall et al., 1986). Nevertheless, such models would still yield a single optimal solution. It seems likely that for single events with a naive predator, there will always be an optimal ET that maximizes the chances of survival (Fig. 3A).

However, repeating the same ET as a response to every attack may allow predators to predict the response by learning, or through a process of natural selection. This is illustrated in Fig. 3B, in which the length of the escape vector represents the probability of escape, which decreases with time as the predator's learning is reinforced.

A single trajectory is apparent in a number of taxa, such as some species of schooling fish, certain species of insects such as *Triatoma* bugs, and some species of crab (Domenici et al., 2011). In most of these cases, prey are not maximizing distance from the threat, but rather keeping (tracking) the predator within the limits of their sensory field. In some planktonic prey, the observed ET may correspond to the direction at which prey maximize distance from the suction flow created by the predator. More work could test whether ETs in these animals are also modulated by the relative speeds of predator and prey, as predicted by geometric models (Arnott et al., 1999; Domenici, 2002; Weihs and Webb, 1984).

Cases B and C: preferred trajectories (Fig. 2B) and random ETs within a limited angular sector (Fig. 2C)

These two possibilities are discussed together because both these alternatives result from highly variable ETs and are not easily distinguished experimentally. As an alternative to the optimal trajectory strategy, animals may adopt a number of preferred ETs that are not as good as the optimal ET in terms of the probability of successful escape when considering a single isolated event such

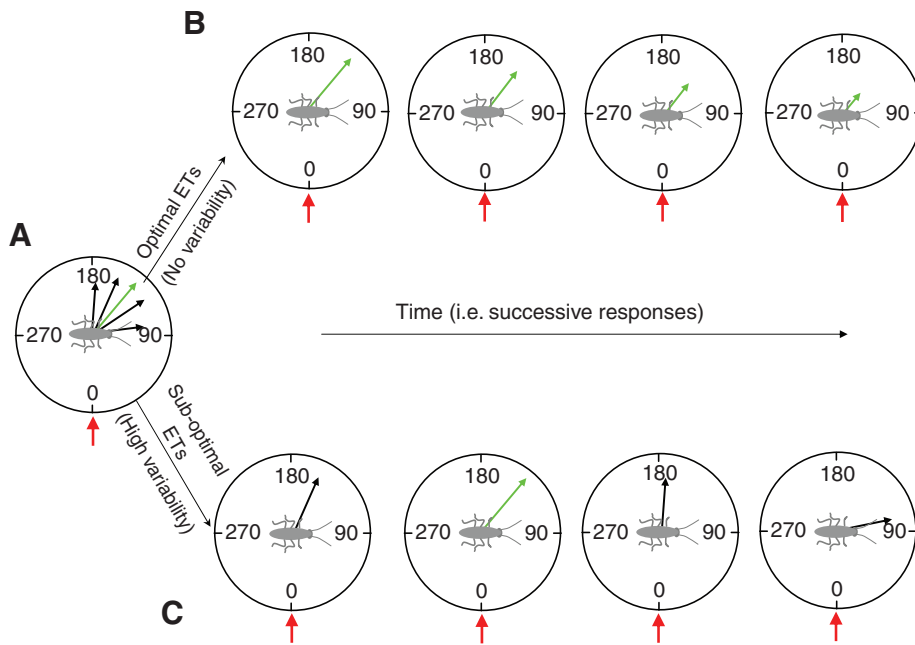


Fig. 3. Schematic showing the potential effect of successive attacks (predator positioned at 0 deg, red arrows) and ETs on escape probability (represented by the length of the escape vector). (A) An ET with maximum escape probability (green) with other ETs (black) with lower probabilities of escape as a function of their angular distance from the optimal ET. (B) The ET with the highest escape probability is used in all four successive responses. Escape probability decreases as a result of predators learning to anticipate which ET will be used in successive responses. (C) Different ETs (both optimal and suboptimal) are taken in four successive responses; therefore, escape probability does not decrease with successive responses because predators cannot learn which ET will be taken.

as the encounter with a naive predator (i.e. the length of the escape probability vector is lower than that of the optimal ET; Fig. 3C). However, the occurrence of multiple trajectories would prevent learning by the predators, thus avoiding the decrease in escape probability observed for the optimal (i.e. single) trajectory strategy (Fig. 3B). The result could, in principle, yield a higher overall probability of escape (i.e. the mean of the lengths of all the vectors in Fig. 3C may be higher than that of Fig. 3B, in which consecutive encounters are considered). In principle, random ETs within a limited angular sector (Fig. 2C) would yield similar results in terms of escape probability as the preferred ET strategy (Fig. 2B), perhaps associated with even higher unpredictability. Whether random ETs within a limited angular range or preferred ETs are used may depend on the flexibility of neural circuitry controlling escape directions in a given species.

Indeed, most species do not exhibit a unimodal normal distribution of ETs, but rather show highly variable ETs within a limited angular sector (Domenici et al., 2011). To determine whether this variability can be ascribed to multiple peaks or to random noise, large data sets, such as those gathered by Domenici et al. (Domenici et al., 2008), must be analysed statistically. Regardless of the type of distribution, the main sector occupied by ET^0 s spans 90–180 deg (Domenici et al., 2011). Animals tend to keep the threat on the side of the initial stimulation, rather than overturning (i.e. they rarely show ET^0 s in the semicircle 180–360 deg) (Domenici et al., 2011). Variability of ET^0 s within this sector may therefore provide sufficient unpredictability while minimizing the time needed to complete the body rotation. The sector 90–180 deg is preferred whether ETs are measured as ET^0 or ET'' , the two most common types of ET measurements considered here. This preferred sector would correspond to either 90–180 deg or 180–270 deg if measured as ET' . In all cases (ET^0 , ET' and ET''), a trajectory of 90 deg represents escaping in a direction perpendicular to the line of attack of the predator whereas 180 deg represents escaping directly away from the predator [a more detailed explanation of the differences between ET^0 , ET' and ET'' is given in Domenici et al. (Domenici et al., 2011)]. Various species from a number of taxa show two main trajectories, one at 180 deg (corresponding to maximizing distance from the threat) and

one at a smaller angle, at approximately 90–130 deg. In birds, these two alternative strategies depend on the approach speed of the predator, with high speed and low speed eliciting ET' s at 90 and 180 deg, respectively, in line with the general prediction that ET' s decrease with predator speed (Fig. 1B). In fish, these two escape modes are thought to correspond to maximizing distance and keeping the threat within an angular field in which the prey can track the predator. In other animal groups, such as frogs, deer and some plankton species, no potential explanation is yet available to explain these peaks, other than that of increasing unpredictability. In soldier crabs, the two ET^0 modes (at 150 and 210 deg) are symmetric with respect to 180 deg, and therefore they may both correspond to keeping the stimulus within the limits of the visual field (Domenici and Blake, 1993). In some species (e.g. some larval fish, lizards, small mammals attacked by birds), alternative ETs include both escapes directed away and towards the threat, possibly as a strategy to undercut the predator (Domenici et al., 2011). Multiple (>2) ETs appear to occur mainly in insects. A full demonstration of this pattern was provided for the cockroach (Domenici et al., 2008). Testing whether high variability in some of the other species can be ascribed to multiple peaks or random noise awaits further work using large sample sizes. Although ultimately there may be no difference in survival value whether variability (i.e. unpredictability) is generated *via* multiple peaks or random noise within the 90–180 deg sector, this issue is crucial for understanding how variability is generated at the neural level.

Case D: random trajectories spanning 360 deg relative to the threat (Fig. 2D)

This is the option that would make ETs the least predictable, in line with the need for maximizing protean unpredictability (Godin, 1997; Humphries and Driver, 1970). However, this strategy would include ETs that are directed towards the predator, which could result in an almost zero probability of escape. The crucial issue is whether this potential cost is outweighed by the increased unpredictability compared with other options [e.g. a limited range of random (Fig. 2C) or preferred ETs (Fig. 2B)], which do generate some unpredictability without the foolhardy alternative of moving directly towards the threat.

Although rare, some of the species investigated so far do show a relatively fixed direction of escape with respect to their own body orientation (e.g. collembolans and *Culex pipiens* pupae) resulting in random ETs relative to the stimulus (Brackenbury, 1999). In these cases, ETs may be relatively unpredictable, unless predators can predict ETs by judging the body orientation of the prey at the onset of the response.

Case E: ETs towards a refuge (Fig. 2E)

If present, refuges may represent the direction towards which prey escape regardless of the approach direction of the predator, because entering a refuge would negate any further attempt of the predator to catch the prey.

Refuges appear to have an important effect, particularly in many vertebrate species such as lizards and small mammals that live in habitats in which shelter and cover may be readily available (Domenici et al., 2011). In some of these species, field observations have shown that the effect of refuges decreases with refuge distance [e.g. in lizards (Zani et al., 2009)].

Case F: intermediate strategy (Fig. 2F)

It is possible that some of the above strategies may be used simultaneously, e.g. resulting in ETs directed midway between maximizing distance from the predator and reaching the refuge in the shortest time.

Work on some species shows that ETs may indeed be a compromise between escape from the threat and reaching cover, as has been shown for the blue crab (Woodbury, 1986). More work using different positions and/or distances of threats and refuges should be carried out on more species in order to test the relative importance of refuge and threat on ETs.

It is clear that animals show a variety of escape strategies with respect to their ET distribution. The most common features are: (1) high ET variability (in some cases due to ET peaks), (2) ETs that allow the threat to be continually tracked as the prey makes its escape and (3) ETs towards a refuge. Whether animals choose unpredictable (Cases B, C and D; Fig. 2) or potentially predictable (Cases A, E and F; Fig. 2) escape strategies may be related to the type of interaction and the habitat in which they live. Clearly, in Cases A and E, the potential advantage of protean unpredictability seems to be overridden by the need to track the predator or reach a refuge, respectively. Perhaps predator tracking may be more important in relatively slow and distant interactions in which the prey can accommodate the changing movement of the predator. Similarly, reaching a safe refuge seems more beneficial than generating unpredictability when the refuge is nearby. These same strategies are observed across various taxa, and therefore their expression may be largely related to the taxon-independent design features and the environmental context in which the prey lives, for example whether it provides potential refuges.

Design constraints

Constraints on turning angle

Some species are constrained in their turning ability and this may affect their distribution of ETs. For example, collembolans, *Culex pipiens* pupae and certain decapod crustaceans have only one potential direction (or axis) of turning relative to their body orientation (Domenici et al., 2011). Other species, although more flexible in their response, may not show turning angles (TAs) in specific angular regions, as is the case for the shrimp *Crangon crangon*, possibly because of anatomical constraints (Arnott et al., 1999). Potential limitations in TA could be due to body rigidity as

well as constraints related to the propulsive mechanism (e.g. a spring, legs, fins). These limitations in TA could result in a bias in ETs, depending on the approach angle of the predator (Arnott et al., 1999). That is, for certain predator approach angles, these species are not able to achieve specific ETs. In contrast, prey with a range of TAs spanning at least 0–180 deg on either side of the body [e.g. many fish species (Domenici and Blake, 1997)] are potentially capable of producing ET⁰s through 360 deg, independent of the predator approach angle.

Although certain predators have a preferred direction of approach relative to the prey's body axis (e.g. 90 deg in pike *Esox lucius*), their actual range can be quite large (0–164 deg in *E. lucius*) (Webb and Skadsen, 1980), and it is conceivable that random encounters between predators and prey can yield a variety of predator approach angles. If we consider the extreme case of random predator approach direction and a narrow TA range by the prey, the resulting distribution would be random ET⁰s spanning 360 deg relative to the threat, as preferred ET⁰s (relative to the threat) would not always be achievable by animals with a narrow TA range. Therefore, a random ET pattern could result from two theoretical possibilities with respect to TA. The first possibility is that ETs are random relative to the stimulus, but related to the initial body orientation of the animal. This is possibly the case in prey such as collembolans. In this case, predators could potentially predict ETs based on the body orientation of the prey at the onset of the response. Second, ETs could, in principle, be completely random relative to both the stimulus direction and the prey's body axis. Although this pattern of response would produce maximum unpredictability, such a pattern does not seem to occur in any of the case studies reviewed in Domenici et al. (Domenici et al., 2011).

Sensory and neural constraints

In some species, preferred ETs are likely to correspond to specific orientations relative to the stimulation, as dictated by the sensory and/or the neural effector systems. For example, the multiple ET⁰s of the cockroach (Domenici et al., 2008) may be an emergent property of the various wind-hair orientations on the cerci (Dagan and Camhi, 1979) or of signal processing by the many thoracic interneurons interposed between the GIs and the leg motoneurons in the thoracic ganglia (Ritzmann and Pollack, 1990). In some cases, it has been shown that ETs are largely determined by the orientation of the sensory organs relative to the threat, a necessary outcome if continuous feedback during the escape response is needed, as in fiddler crabs (Land and Layne, 1995). Fiddler crabs can escape sideways and, therefore, are able to keep track of the threat even when escaping with an ET of 180 deg. Many species, however, do not walk sideways and have a blind zone posteriorly; therefore, escaping at 180 deg away from the threat would not allow them to keep track of the threat. Hall et al. (Hall et al., 1986) and Lazzari and Varju (Lazzari and Varju, 1990) working on fish (*Merlangius merlangus*) and assassin bugs (*Triatoma infestans*), respectively, suggested that the observed ET⁰s (approximately 135 and 120 deg, respectively) correspond to escaping just within the limits of the visual zone, thereby maximizing distance from the danger while tracking it. In fish, this strategy was observed in responses that are slower than the typical Mauthner-cell-mediated escape response (Hall et al., 1986). This kind of manoeuvre seems to be largely determined by the approaching speed of the predator and the prey's detection distance and swimming performance (Hall et al., 1986). It is therefore possible that predator-prey interactions at relatively slow predator speeds and long reaction distances yield relatively slow prey manoeuvres that allow predator tracking,

whereas more rapid responses with highly variable ETs may result when the time available for reaction is limited. Reaction times (latencies) may indeed have an effect on directional accuracy (Turesson et al., 2009) and, therefore, on the resultant ETs because long latencies may provide additional sensory processing time. Escape latencies can vary across species and largely depend on the speed of the threatening signal, the sensory channels involved and the central neural circuitry. Latencies are of the order of a few milliseconds in fast-moving animals with escape responses mediated by giant neurons, such as fish, various crustaceans and insects (Eaton, 1984), whereas they are much longer in slow-moving animals, such as most gastropods [e.g. 0.6 s in *Nassa mutabilis* (Lemmnitz et al., 1989) and 4–6.5 s in *Tritonia diomedea* (Frost et al., 1998)]. Unfortunately, latency data are not necessarily provided with directional data. Furthermore, looming visual stimuli, such as those used in many ET studies, do not allow accurate calculation of latency (Card and Dickinson, 2008). Therefore, although the possibility of an effect of latency on ET pattern cannot be excluded, a comprehensive analysis requires a more complete data set, comprising ETs and their escape latencies, than is available at present.

Context dependency

Many laboratory studies have focused on the relationship between stimulus direction, body orientation and escape direction. However, the structural context and topography around the prey can also have an important effect on ETs (Eilam, 2005). At least for some species, the presence of a refuge is a fundamental factor affecting ETs in realistic settings. Refuges affecting escape behaviour can be burrows, shade or areas of vegetation. A number of field studies have stressed the importance of the position of the refuge in escape behaviour (Clarke et al., 1993; Martin and Lopez, 2000; Woodbury, 1986; Zani et al., 2009). For many intertidal species, escape directions in a seaward direction are common (e.g. Ugolini and Pezzani, 1993), although a lot of this work did not record the direction of threat and is therefore not discussed in this review. The relative importance of refuge position in determining ET distribution is, in some cases, related to its distance from the prey (Zani et al., 2009). In addition, prey may also flee along a compromised course that takes into account both predator and refuge positions (Woodbury, 1986). Gerbils (*Meriones unguiculatus*) can compute the optimal trajectory leading to a refuge by taking into account the position of the threat, the location of a clearly visible refuge and several other contextual variables (Ellard and Eller, 2009). Familiarity with the site was also found to be a major factor regulating the time spent in finding refuges; therefore, animals in familiar sites are more likely to be able to evade predators than those in unfamiliar sites (Clarke et al., 1993). Like refuges, obstacles can affect ETs by creating an angular range that is not used by prey (Eaton and Emberley, 1991), in some cases even after the obstacle has been removed (Ingle and Hoff, 1990).

Although little work has been published in this area, it seems clear that the biotic context can also affect ETs. The presence of conspecifics can decrease the variability in ETs when compared with individuals of the same species startled while solitary, as shown in herring (Domenici and Batty, 1997). When predators approach from a number of directions, prey choose a compromised direction rather than focusing on only one of the threats (Cooper et al., 2007). Remarkably, the predator itself can steer the ET of the prey to its own advantage. As discussed by Jablonski (Jablonski, 2001), this is sometime observed in rare predators, which take advantage of their rare occurrence to exploit common

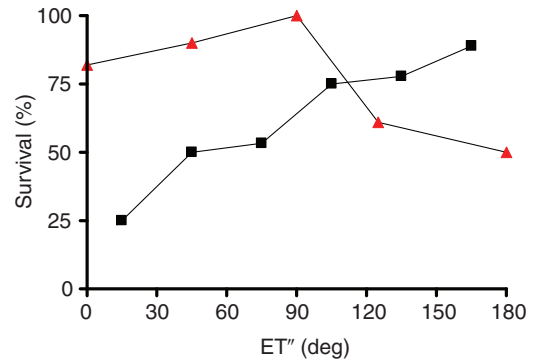


Fig. 4. Percent survival, at different values of ET°, in pike cichlid *Crenicichla alta* attacking guppies *Poecilia reticulata* [black squares; based on table 5 from Walker et al. (Walker et al., 2005)] and owl (*Tyto alba*) attacking an artificially moving prey (a dead mouse or chick) [red triangles; based on Shifferman and Eilam (Shifferman and Eilam, 2004)]. Data from Walker et al. (Walker et al., 2005) are plotted mid-way through the 30 deg range of ET°s observed (i.e. at 15 deg for the 0–30 deg ET°). Data from Shifferman and Eilam (Shifferman and Eilam, 2004) are plotted at the experimental ET° imposed on the artificial prey.

characteristics of the prey's escape behaviour that are not counteracted by evolution of alternative strategies. In other words, natural selection that shapes the escape system for avoiding the attack pattern of rare predators is weaker than the selection for avoiding more common predators (Jablonski, 1999; Jablonski, 2001). There are a few examples of rare predators taking advantage of the prey ETs by triggering the prey's escape in a direction that is favourable to the predator. The redstart, *Myioborus pictus*, preys on dipterous flies, visually triggering the flies' giant-fibre escape system (Bacon and Strausfeld, 1986) by spreading and pivoting their conspicuous tails and wings (Jablonski, 2001). These pivoting movements on one side cause flies to escape away from the predator's tail and towards the central field of vision of the predator, where the predator's stereoscopic vision makes it easier to track and intercept the prey (Jablonski, 2001; Jablonski and McInerney, 2005). Similarly, tentacle snakes (*Erpeton tentaculatum*) trigger escape responses in fish with a pressure wave caused by the motion of their body (Catania, 2009). In most cases, fish respond to this stimulation by making a C-start away from the stimulus, which, in encounters with their common predators, would result in directing fish away from the threat. However, the tentacle snake cunningly positions its mouth in anticipation for this response, and therefore away responses are actually directed towards the mouth of the predator (Catania, 2009). Anticipatory behaviours by the predator predicting prey ETs, albeit not as sophisticated as to include deliberately stimulating escape behaviour, were also observed in ctenophores (*Mnemiopsis leidyi*) preying on copepods (*Acartia tonsa* and *Oithona colcarva*), in which approximately half of the encounters showed changes in the position of the predator's oral lobes, anticipating the actual contact with the prey (Costello et al., 1999). Anticipatory responses are likely to be due to fluid disturbances created by swimming copepods. Such behaviour allows predators to reduce the escape avenues available to the prey, hence increasing capture efficiency (Costello et al., 1999).

ETs and relevance for predator–prey interactions

Most of the work on ETs has been carried out using artificial stimulation in the laboratory. In some cases, human approach has been used in fieldwork, but rarely have escape trajectories been

observed using real predators and prey (Fuiman, 1993; Walker et al., 2005). More work of this kind is needed to assess the functional survival significance of ETs. Nevertheless, some preliminary trends have emerged. Walker et al. have shown that ET $^{\circ}$ has a significant effect on survival in fish–fish interactions (Walker et al., 2005). The most successful sector of ET $^{\circ}$ s was 150–180 deg, with close to 90% survival, whereas escape towards the predator shows as little as 25% survival (Fig. 4). Similar results have been obtained in fish larvae, which show the highest escape success (76%) when escaping with an ET $^{\circ}$ within the 135–180 deg sector [<45 deg in Fuiman (Fuiman, 1993)], and the lowest when escaping towards the predator within the 0–45 deg sector of ET $^{\circ}$ [>135 deg in Fuiman (Fuiman, 1993)]. Taken together, these results suggest that ET $^{\circ}$ s in the sector ranging from approximately 130 to 180 deg may be the most successful escape sector in fish and possibly in predator–prey encounters with similar relative timing and locomotor performance. The effect of ETs on escape success is not surprising and it is in line with theoretical considerations, but it does not address the issue of the functional significance of ET variability. Although experimentally challenging, it is of fundamental importance to test the hypothesis that variability in ETs in fish and other animals results in lower vulnerability to predator attacks than does escaping at fixed angles.

The relationship between vulnerability and ETs can vary depending on the relative plane of motion of predator and prey and their functional constraints. For example, predator–prey interactions in three dimensions show a different relation between ETs and prey survival than those in two dimensions, where undercutting the predator by escaping towards it (although above or below it) is an option when attacked by predatory birds. Using an artificially moving prey (a dead mouse or a chick) and a living barn owl predator, Shiffman and Eilan showed that escaping at 180 deg resulted in lower survival than escaping at 0 deg, whereas escaping at 90 deg resulted in the highest escape success (Fig. 4) (Shiffman and Eilan, 2004). The high survival rate in escaping at 90 deg from the predator's line of approach may be due to the difficulties these predators have in tracking sideways moving prey, which requires movement of the whole head in owls. Real prey were indeed found to tend to escape sideways rather than away from or towards the predator (Ilany and Eilan, 2008).

Conclusions and future studies

The study of ETs is crucial for our understanding of predator–prey interactions, as ETs are a major factor determining prey survivability. Although species from a given taxon share a number of similarities, some characteristics of ETs appear to be related to taxon-independent animal design features and to the environmental context. Integrative work employing a number of approaches, such as behavioural and evolutionary ecology, neurophysiology and functional morphology, is needed to understand the functional and mechanistic basis of ETs in terms of their design constraints and evolutionary significance. The relationship between ETs and locomotory and sensory performance is also a crucial point that needs further attention and can gain major insights from a tight coupling with behavioural modeling along the lines of Weihs and Webb (Weihs and Webb, 1984), Arnott et al. (Arnott et al., 1999) and Domenici (Domenici, 2002). Protean variability in ETs is a common feature across taxonomic groups, and integrative studies could test the adaptive significance of such variability at the individual and population levels. Large data sets need to be gathered to provide sufficient power for determining which ET distribution shows the best fit among various hypothetical ones. More work using predators and prey is

also necessary in order to assess the survival value of escape trajectories and their associated variability. The use of a mixed approach combining interactions with model predators, and also model prey (Shiffman and Eilan, 2004), can be an effective tool for controlling experimental variables and developing predictions of the outcome of the predator–prey encounters, tested by examining real interactions in the laboratory and in the field. Although more challenging, fieldwork is crucial for putting ETs within an ecologically relevant context. Furthermore, context dependency was found to be a determinant of ETs in many species. Therefore, the interplay between habitat type, ETs and escape performance needs to be investigated further by combining field and laboratory work on a large range of species. This is the route to increase our understanding of the functional basis and adaptive features of animal ETs.

Acknowledgements

We thank two anonymous referees for useful comments on an earlier version of this manuscript.

References

- Arnott, S. A., Neil, D. M. and Ansell, A. D. (1999). Escape trajectories of the brown shrimp *Crangon crangon*, and a theoretical consideration of initial escape angles from predators. *J. Exp. Biol.* **202**, 193–209.
- Bacon, J. P. and Strausfeld, N. J. (1986). The Dipteran giant fiber pathway – neurons and signals. *J. Comp. Physiol. A Sens. Neural Behav. Physiol.* **158**, 529–548.
- Batty, R. S. (1989). Escape responses of herring larvae to visual stimuli. *J. Mar. Biol. Assoc. UK* **69**, 647–654.
- Blaxter, J. H. S. and Batty, R. S. (1985). The development of startle responses in herring larvae. *J. Mar. Biol. Assoc. UK* **65**, 737–750.
- Blaxter, J. H. S. and Batty, R. S. (1987). Comparisons of herring behavior in the light and dark-changes in activity and responses to sound. *J. Mar. Biol. Assoc. UK* **67**, 849–859.
- Bonati, B., Csermely, D., Lopez, P. and Martin, J. (2010). Lateralization in the escape behaviour of the common wall lizard (*Podarcis muralis*). *Behav. Brain Res.* **207**, 1–6.
- Bonenfant, M. and Kramer, D. L. (1996). The influence of distance to burrow on flight initiation distance in the woodchuck, *Marmota monax*. *Behav. Ecol.* **7**, 299–303.
- Booth, D., Marie, B., Domenici, P., Blagburn, J. M. and Bacon, J. P. (2009). Transcriptional control of behavior: engrailed knock-out changes cockroach escape trajectories. *J. Neurosci.* **29**, 7181–7190.
- Boothby, K. M. and Roberts, A. (1995). Effects of site of tactile stimulation on the escape swimming responses of hatching *Xenopus laevis* embryos. *J. Zool.* **235**, 113–125.
- Brackenburg, J. (1999). Regulation of swimming in the *Culex pipiens* (Diptera, Culicidae) pupa: kinematics and locomotory trajectories. *J. Exp. Biol.* **202**, 2521–2529.
- Bullock, T. H. (1984). Comparative neuroethology of startle, rapid escape and giant fiber-mediated responses. In *Neural Mechanisms of Startle Behaviour* (ed. R. C. Eaton), pp. 1–13. New York: Plenum Press.
- Camhi, J. M. (1983). *Neuroethology: Nerve Cells and the Natural Behavior of Animals*. Sunderland: Sinauer.
- Camhi, J. M. and Tom, W. (1978). The escape behaviour of the cockroach *Periplaneta americana*. 1. Turning response to wind puffs. *J. Comp. Physiol. A* **128**, 193–201.
- Cantalupo, C., Bisazza, A. and Vallortigara, G. (1995). Lateralization of predator-evasion response in a teleost fish (*Girardinus falcatus*). *Neuropsychologia* **33**, 1637–1646.
- Card, G. and Dickinson, M. H. (2008). Visually mediated motor planning in the escape response of *Drosophila*. *Curr. Biol.* **18**, 1300–1307.
- Catania, K. C. (2009). Tentacled snakes turn C-starts to their advantage and predict future prey behavior. *Proc. Natl. Acad. Sci. USA* **106**, 11183–11187.
- Clarke, M. F., Dasilva, K. B., Lair, H., Pocklington, R., Kramer, D. L. and McLaughlin, R. L. (1993). Site familiarity affects escape behavior of the eastern chipmunk, *Tamias striatus*. *Oikos* **66**, 533–537.
- Comer, C. (2009). Behavioral biology: inside the mind of Proteus? *Curr. Biol.* **19**, R27–R28.
- Comer, C. M. and Dowd, J. P. (1987). Escape turning behaviour of the cockroach. Changes in directionality induced by unilateral lesions of the abdominal nervous system. *J. Comp. Physiol.* **160**, 571–583.
- Cooper, W. E. (1997). Escape by a refuging prey, the broad-headed skink (*Eumeces laticeps*). *Can. J. Zool. Rev. Can. Zool.* **75**, 943–947.
- Cooper, W. E. (2000). Tradeoffs between predation risk and feeding in a lizard, the broad-headed skink (*Eumeces laticeps*). *Behaviour* **137**, 1175–1189.
- Cooper, W. E., Perez-Mellado, V. and Hawlena, D. (2007). Number, speeds, and approach paths of predators affect escape behavior by the Balearic lizard, *Podarcis lilfordi*. *J. Herpetol.* **41**, 197–204.
- Costello, J. H., Loftus, R. and Waggett, R. (1999). Influence of prey detection on capture success for the ctenophore *Mnemiopsis leidyi* feeding upon adult *Acartia tonsa* and *Oithona colcarva* copepods. *Mar. Ecol. Prog. Ser.* **191**, 207–216.

- Dagan, D. and Camhi, J. M. (1979). Responses to wind from the cercal nerve of the cockroach *Periplaneta americana*. II. Directional selectivity of the sensory neurons innervating single columns of filiform hairs. *J. Comp. Physiol. A* **133**, 103-110.
- Dill, L. M. (1977). Handedness in Pacific tree frog (*Hyla regilla*). *Can. J. Zool. Rev. Can. Zool.* **55**, 1926-1929.
- Dill, L. M. and Houtman, R. (1989). The influence of distance to refuge on flight initiation distance in the gray squirrel (*Sciurus carolinensis*). *Can. J. Zool. Rev. Can. Zool.* **67**, 233-235.
- Domenici, P. (2002). The visually mediated escape response in fish: predicting prey responsiveness and the locomotor behaviour of predators and prey. *Mar. Freshw. Behav. Physiol.* **35**, 87-110.
- Domenici, P. (2010). Context-dependent variability in the components of fish escape response: integrating locomotor performance and behavior. *J. Exp. Zool.* **313A**, 59-79.
- Domenici, P. and Batty, R. S. (1994). Escape manoeuvres of schooling *Clupea harengus*. *J. Fish Biol.* **45**, 97-110.
- Domenici, P. and Batty, R. S. (1997). Escape behaviour of solitary herring (*Clupea harengus*) and comparisons with schooling individuals. *Mar. Biol.* **128**, 29-38.
- Domenici, P. and Blake, R. W. (1993). Escape trajectories in angelfish (*Pterophyllum eimekei*). *J. Exp. Biol.* **177**, 253-272.
- Domenici, P. and Blake, R. W. (1997). The kinematics and performance of fish fast-start swimming. *J. Exp. Biol.* **200**, 1165-1178.
- Domenici, P., Batty, R. S. and Simila, T. (2000a). Spacing of wild schooling herring while encircled by killer whales. *J. Fish Biol.* **57**, 831-836.
- Domenici, P., Batty, R. S., Simila, T. and Ogam, E. (2000b). Killer whales (*Orcinus orca*) feeding on schooling herring (*Clupea harengus*) using underwater tail-slaps: kinematic analyses of field observations. *J. Exp. Biol.* **203**, 283-294.
- Domenici, P., Lefrançois, C. and Shingles, A. (2007). Hypoxia and the anti-predator behaviour of fishes *Philos. Trans. R. Soc. Lond. B* **362**, 2105-2121.
- Domenici, P., Booth, D., Blagburn, J. M. and Bacon, J. P. (2008). Cockroaches keep predators guessing by using preferred escape trajectories. *Curr. Biol.* **18**, 1792-1796.
- Domenici, P., Booth, D., Blagburn, J. M. and Bacon, J. P. (2009). Escaping away from and towards a threat: the cockroach's strategy for staying alive. *Commun. Integr. Biol.* **2**, 497-500.
- Domenici, P., Blagburn, J. M. and Bacon, J. P. (2011). Animal escapology II: escape trajectory case studies. *J. Exp. Biol.* **214**, 2474-2494.
- Eaton, R. C. (1984). *Neural Mechanisms of Startle Behaviour*. New York: Plenum Press.
- Eaton, R. C. and Emberley, D. S. (1991). How stimulus direction determines the trajectory of the mauthner-initiated escape response in a teleost fish. *J. Exp. Biol.* **161**, 469-487.
- Eaton, R. C., Lavender, W. A. and Wieland, C. M. (1981). Identification of Mauthner-initiated response patterns in goldfish – evidence from simultaneous cinematography and electrophysiology. *J. Comp. Physiol.* **144**, 521-531.
- Eaton, R. C., Lee, R. K. K. and Foreman, M. B. (2001). The Mauthner cell and other identified neurons of the brainstem escape network of fish. *Prog. Neurobiol.* **63**, 467-485.
- Edut, S. and Eilam, D. (2004). Protean behavior under barn-owl attack: voles alternate between freezing and fleeing and spiny mice flee in alternating patterns. *Behav. Brain Res.* **155**, 207-216.
- Eilam, D. (2005). Die hard: a blend of freezing and fleeing as a dynamic defense-implications for the control of defensive behavior. *Neurosci. Biobehav. Rev.* **29**, 1181-1191.
- Ellard, C. G. and Eller, M. C. (2009). Spatial cognition in the gerbil: computing optimal escape routes from visual threats. *Anim. Cogn.* **12**, 333-345.
- Frost, W. N., Brandon, C. L. and Mongeluzi, D. L. (1998). Sensitization of the *Tritonia* escape swim. *Neurobiol. Learn. Mem.* **69**, 126-135.
- Fuiman, L. A. (1993). Development of predator evasion in Atlantic herring, *Clupea harengus* L. *Anim. Behav.* **45**, 1101-1116.
- Godin, J.-G. J. (1997). Evading predators. In *Behavioural Ecology of Teleost Fishes*, (ed. J.-G. J. Godin), pp. 191-236. Oxford: Oxford University Press.
- Hall, S. J., Wardle, C. S. and Macleannan, D. N. (1986). Predator evasion in a fish school-test of a model for the fountain effect. *Mar. Biol.* **91**, 143-148.
- Hatta, K. and Korn, H. (1999). Tonic inhibition alternates in paired neurons that set direction of fish escape reaction. *Proc. Natl. Acad. Sci. USA* **96**, 12090-12095.
- Heuts, B. A. (1999). Lateralization of trunk muscle volume, and lateralization of swimming turns of fish responding to external stimuli. *Behav. Processes* **47**, 113-124.
- Humphries, D. A. and Driver, P. M. (1970). Protean defence by prey animals. *Oecologia* **5**, 285-302.
- Ilany, A. and Eilam, D. (2008). Wait before running for your life: defensive tactics of spiny mice (*Acomys cahirinus*) in evading barn owl (*Tyto alba*) attack. *Behav. Ecol. Sociobiol.* **62**, 923-933.
- Ingle, D. J. and Hoff, K. V. (1990). Visually elicited evasive behavior in frogs. *Bioscience* **40**, 284-291.
- Izvekov, E. I. and Nepomnyashchikh, V. A. (2008). Laterality of the initial stage of escape response in roach (*Rutilus rutilus*) upon impact of alternating electric current. *Biol. Bull.* **35**, 30-36.
- Jablonski, P. G. (1999). A rare predator exploits prey escape behavior: the role of tail-fanning and plumage contrast in foraging of the painted redstart (*Myioborus pictus*). *Behav. Ecol.* **10**, 7-14.
- Jablonski, P. G. (2001). Sensory exploitation of prey: manipulation of the initial direction of prey escapes by a conspicuous 'rare enemy'. *Proc. R. Soc. B* **268**, 1017-1022.
- Jablonski, P. G. and McInerney, C. (2005). Prey escape direction is influenced by the pivoting displays of flush-pursuing birds. *Ethology* **111**, 381-396.
- Jayne, B. C. and Lauder, G. V. (1993). Red and white muscle-activity and kinematics of the escape response of the bluegill sunfish during swimming. *J. Comp. Physiol. A Sens. Neural Behav. Physiol.* **173**, 495-508.
- Kanou, M., Ohshima, M. and Inoue, J. (1999). The air-puff evoked escape behavior of the cricket *Gryllus bimaculatus* and its compensational recovery after cerebral ablations. *Zool. Sci.* **16**, 71-79.
- Kanou, M., Konishi, A. and Suenaga, R. (2006). Behavioral analyses of wind-evoked escape of the cricket, *Gryllodes sigillatus*. *Zool. Sci.* **23**, 359-364.
- King, J. R. and Comer, C. M. (1996). Visually elicited turning behavior in Rana pipiens: comparative organization and neural control of escape and prey capture. *J. Comp. Physiol. A Neuroethol. Sens. Neural Behav. Physiol.* **178**, 293-305.
- Krause, J. and Godin, J. G. J. (1996). Influence of prey foraging posture on flight behavior and predation risk: predators take advantage of unwary prey. *Behav. Ecol.* **7**, 264-271.
- Krylov, V. V., Nepomnyashchikh, V. A., Izvekov, E. I., Izumov, Y. G. and Chebotareva, Y. V. (2008). Asymmetry of escape behavior of the roach (*Rutilus rutilus*, Cyprinidae): correlation with morphological asymmetry. *Zool. Zhurnal* **87**, 573-577.
- Land, M. and Layne, J. (1995). The visual control of behavior in fiddler crabs. 2. Tracking control-systems in courtship and defense. *J. Comp. Physiol. A Sens. Neural Behav. Physiol.* **177**, 91-103.
- Lazzari, C. and Varju, D. (1990). Visual lateral fixation and tracking in the hematophagous bug *Triatoma infestans*. *J. Comp. Physiol. A Sens. Neural Behav. Physiol.* **167**, 527-531.
- Lemnitz, G., Schuppe, H. and Wolf, H. G. (1989). Neuromotor basis of the escape behaviour of *Nassa mutabilis*. *J. Exp. Biol.* **143**, 493-507.
- Lippolis, B., Bisazza, A., Rogers, L. J. and Vallortigara, G. (2002). Lateralisation of predator avoidance responses in three species of toads. *Laterality* **7**, 163-183.
- Malashichev, Y. B. and Wassersug, R. J. (2004). Left and right in the amphibian world: which way to develop and where to turn? *BioEssays* **26**, 512-522.
- Martin, J. and Lopez, P. (1996). The escape response of juvenile *Psammmodromus algirus* lizards. *J. Comp. Psychol.* **110**, 187-192.
- Martin, J. and Lopez, P. (2000). Fleeing to unsafe refuges: effects of conspicuousness and refuge safety on the escape decisions of the lizard *Psammmodromus algirus*. *Can. J. Zool. Rev. Can. Zool.* **78**, 265-270.
- Moulton, J. M. and Dixon, R. H. (1967). Directional hearing in fishes. In *Marine Biocoustics* (ed. W. N. Tavolga), pp. 187-203. Oxford: Pergamon Press.
- Nalbach, H. O. (1990). Discontinuous turning reaction during escape in soldier crabs. *J. Exp. Biol.* **148**, 483-487.
- Preuss, T. and Faber, D. S. (2003). Central cellular mechanisms underlying temperature-dependent changes in the goldfish startle-escape behavior. *J. Neurosci.* **23**, 5617-5626.
- Ritzmann, R. E. and Pollack, A. J. (1990). Parallel motor pathways from thoracic interneurons of the ventral giant interneuron system of the cockroach, *Periplaneta americana*. *J. Neurobiol.* **21**, 1219-1235.
- Santer, R. D., Yamawaki, Y., Rind, F. C. and Simmons, P. J. (2005). Motor activity and trajectory control during escape jumping in the locust *Locusta migratoria*. *J. Comp. Physiol. A Neuroethol. Sens. Neural Behav. Physiol.* **191**, 965-975.
- Schrader, S. (2000). The function of the cerebellar sensory system in escape behavior of the cave cricket *Troglophilus neglectus* Krauss. *Pflügers Arch.* **439**, R187-R189.
- Shifferman, E. and Eilam, D. (2004). Movement and direction of movement of a simulated prey affect the success rate in barn owl *Tyto alba* attack. *J. Avian Biol.* **35**, 111-116.
- Sillar, K. T. and Roberts, A. (1988). A neuronal mechanism for sensory gating during locomotion in a vertebrate. *Nature* **331**, 262-265.
- Suchman, C. L. (2000). Escape behavior of *Acartia hudsonica* copepods during interactions with scyphomedusae. *J. Plankton Res.* **22**, 2307-2323.
- Svoboda, K. R. and Fetcho, J. R. (1996). Interactions between the neural networks for escape and swimming in goldfish. *J. Neurosci.* **16**, 843-852.
- Takeuchi, Y., Tobo, S. and Hori, M. (2008). Morphological asymmetry of the abdomen and behavioral laterality in atyid shrimps. *Zool. Sci.* **25**, 355-363.
- Tauber, E. and Camhi, J. M. (1995). The wind-evoked escape behavior of the cricket *Gryllus bimaculatus* – integration of behavioral elements. *J. Exp. Biol.* **198**, 1895-1907.
- Tureson, H., Satta, A. and Domenici, P. (2009). Preparing for escape: anti-predator posture and fast-start performance in gobies. *J. Exp. Biol.* **212**, 2925-2933.
- Ugolini, A. and Pezzani, A. (1993). Learning of escape direction in *Idotea baltica*. *Mar. Behav. Physiol.* **22**, 183-192.
- Vardi, N. and Camhi, J. M. (1982). Functional recovery from lesions in the escape system of the cockroach. 1. Behavioral recovery. *J. Comp. Physiol.* **146**, 291-298.
- Walker, J. A., Ghalambor, C. K., Griset, O. L., McKenney, D. and Reznick, D. N. (2005). Do faster starts increase the probability of evading predators? *Funct. Ecol.* **19**, 808-815.
- Webb, P. W. and Skadsen, J. M. (1980). Strike tactics of *Esox*. *Can. J. Zool. Rev. Can. Zool.* **58**, 1462-1469.
- Weih, D. and Webb, P. W. (1984). Optimal avoidance and evasion tactics in predator-prey interactions. *J. Theor. Biol.* **106**, 189-206.
- Weiss, S. A., Preuss, T. and Faber, D. S. (2009). Phase encoding in the Mauthner system: implications in left-right sound source discrimination. *J. Neurosci.* **29**, 3431-3441.
- Wohl, S. and Schuster, S. (2007). The predictive start of hunting archer fish: a flexible and precise motor pattern performed with the kinematics of an escape C-start. *J. Exp. Biol.* **210**, 311-324.
- Woodbury, P. B. (1986). The geometry of predator avoidance by the blue crab, *Callinectes sapidus* Rathbun. *Anim. Behav.* **34**, 28-37.
- Ydenberg, R. C. and Dill, L. M. (1986). The economics of fleeing from predators. *Adv. Stud. Behav.* **16**, 229-249.
- Yin, M. C. and Blaxter, J. H. S. (1987). Escape speeds of marine fish larvae during early development and starvation. *Mar. Biol.* **96**, 459-468.
- Zani, P. A., Jones, T. D., Neuhaus, R. A. and Milgrom, J. E. (2009). Effect of refuge distance on escape behavior of side-blotched lizards (*Uta stansburiana*). *Can. J. Zool. Rev. Can. Zool.* **87**, 407-414.