# REVIEW

# Animal escapology II: escape trajectory case studies

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## Summary

**Escape trajectories (ETs; measured as the angle relative to the direction of the threat) have been studied in many taxa using a variety of methodologies and definitions. Here, we provide a review of methodological issues followed by a survey of ET studies across animal taxa, including insects, crustaceans, molluscs, lizards, fish, amphibians, birds and mammals. Variability in ETs is examined in terms of ecological significance and morpho-physiological constraints. The survey shows that certain escape strategies (single ETs and highly variable ETs within a limited angular sector) are found in most taxa reviewed here, suggesting that at least some of these ET distributions are the result of convergent evolution. High variability in ETs is found to be associated with multiple preferred trajectories in species from all taxa, and is suggested to provide unpredictability in the escape response. Random ETs are relatively rare and may be related to constraints in the manoeuvrability of the prey. Similarly, reports of the effect of refuges in the immediate environment are relatively uncommon, and mainly confined to lizards and mammals. This may be related to the fact that work on ETs carried out in laboratory settings has rarely provided shelters. Although there are a relatively large number of examples in the literature that suggest trends in the distribution of ETs, our understanding of animal escape strategies would benefit from a standardization of the analytical approach in the study of ETs, using circular statistics and related tests, in addition to the generation of large data sets.**

Key words: escape trajectory, insect, crustacean, mollusc, lizard, fish, amphibian, bird, mammal.

## Introduction

Escape trajectories (ETs) have been studied in a wide variety of animal groups, using a large number of methodologies. Various types of startling stimuli have been used, including real and model predators as well as acoustic, visual, mechanical and tactile artificial stimuli. Furthermore, various analytical and statistical methods have been applied, and different definitions of escape trajectories have been employed. A companion paper (Domenici et al., 2011) discusses theory, identifies theoretical ET distributions (e.g. unimodal, multimodal and random) that may emerge and compares these with the main trends in experimental ET distributions. A key aspect of Domenici et al. (Domenici et al., 2011) is the issue of unpredictability both for directionality (i.e. the direction of the initial escape turn being away or towards the threat) and for ETs relative to the threat; unpredictability in directionality and ETs may prevent predators from learning a simple escape pattern.

Here we review a large number of case studies, mainly from the past two decades of laboratory and field research, and provide a comparative analysis of ETs across many animal taxa. By focusing on locomotory escape responses, and not discussing withdrawal or other types of aversive responses, we examine how prey from different taxa escape their predators while keeping a certain degree of unpredictability in their response, as expected on theoretical grounds (Domenici et al., 2011). Studies of escape behaviour have adopted a wide range of perspectives, including biomechanics, neurophysiology, ecomorphology and behavioural ecology. From these quite disparate perspectives, we identify common escape strategies adopted by animals from

different taxa. These findings should be of value to neurobiologists examining the neural basis of escape behaviour and to behavioural ecologists studying the adaptive value of different escape strategies.

Given the heterogeneity of methodology and definitions used by various authors, we begin by discussing some methodological issues that are of fundamental importance for the comparative analysis of the literature on this topic.

### A major methodological issue: linear *versus* circular analysis of ETs

Unlike goal-oriented displacements, which are commonly analyzed using circular statistics (Batschelet, 1981), ETs have traditionally been analyzed using linear statistics of escape angle ($y$-axis) as a function of stimulus angle ($x$-axis) (e.g. Camhi and Tom, 1978; Eaton et al., 1981; Stern et al., 1997) (Fig. 1A). This type of analysis is based on testing the significance of the regression line of $y$ *versus* $x$. Although, graphically, it may be possible to qualitatively assess the dependence of escape angle on the stimulus angle, the testing of regression through points that are mainly located in two Cartesian sectors ($-x$ and $y$; $x$ and $-y$) may result in significance even in the absence of a significant relationship within each Cartesian sector. A more meaningful test of the relationship between escape angle and stimulus angle is to analyse each Cartesian sector separately, superimposing responses to left and right stimuli in a single graph (e.g. Eaton and Emberley, 1991). However, neither option allows interpretation of the escape behaviour in terms of the various circular patterns of ETs that are theoretically possible [fig. 2 in Domenici et al. (Domenici et al.,
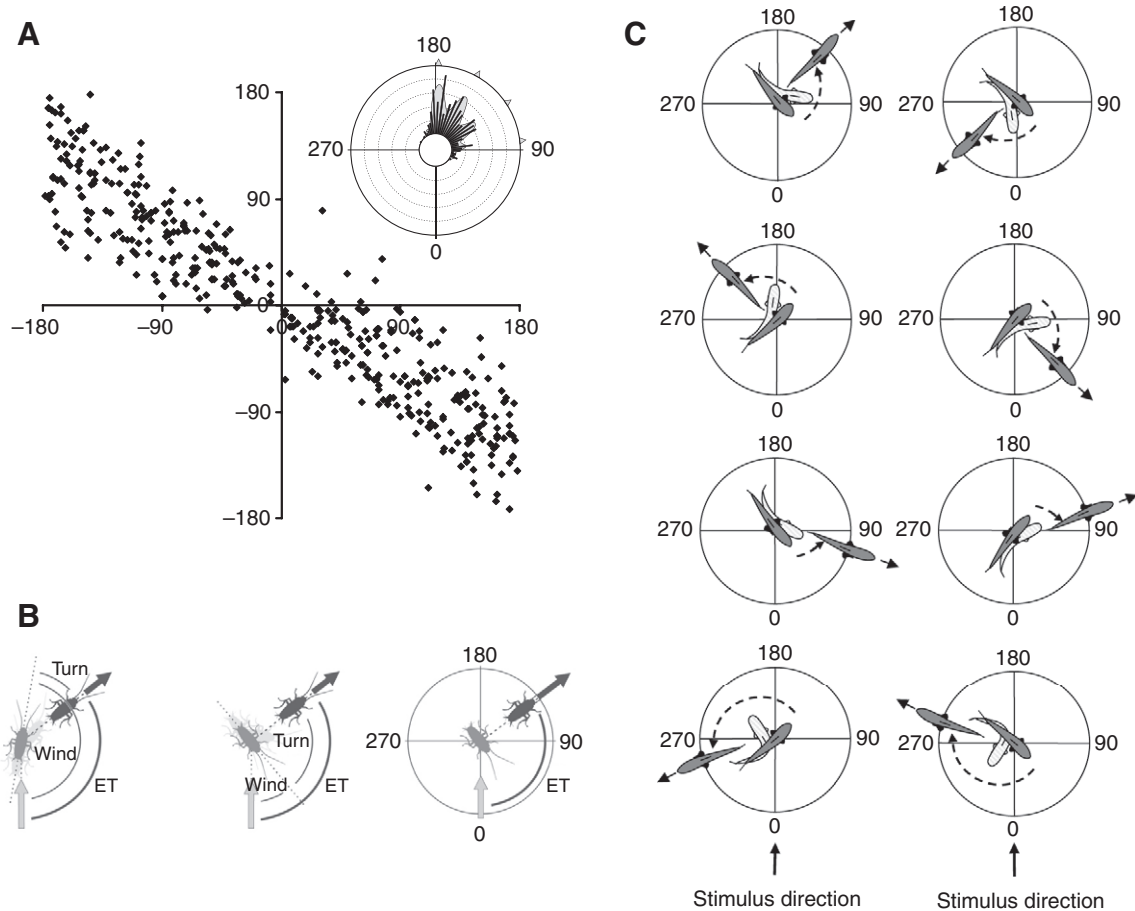
Fig. 1. (A) Cartesian representation of the relationship between response angle (*y*-axis) and stimulus angle (*x*-axis). By convention, stimuli from and responses to the right are plotted as positive values whereas stimuli from and responses to the left are plotted as negative values [cockroach *Periplaneta americana*, data set 5i; *N*=431; unpublished figure based on data from Domenici et al. (Domenici et al., 2008)]. Inset: circular representation of the data using the convention shown in B. Responses are plotted as if the stimulus is always coming from the right of the animal. Concentric circles represent a frequency of 10. Bin frequency is 5 [reprinted from Current Biology, fig. 2A from Domenici et al. (Domenici et al., 2008) with permission from Elsevier]. (B) Definitions of escape trajectory angles in towards (left panel) and away (central panel) responses. Towards and away responses are escapes in which the turn angle achieved during the initial rotation is directed towards or away from the stimulus, respectively. In this example from the cockroach, the arc labelled 'wind' is the stimulus angle, the arc labelled 'turn' is the turn angle and the thick arc is the final escape trajectory ($ET^0$). Away and towards responses may have the same $ET^0$ (shown in the right panel) [based on fig. 5 from Booth et al. (Booth et al., 2009) reproduced with permission of the Journal of Neuroscience]. (C) The resultant $ET^0$s may span 360 deg. In this example of escaping fish, all four 90 deg sectors can be reached by both away (left panels) and towards (right panels) responses [fig. 1 from Domenici (Domenici, 2002a) reproduced with permission from John Wiley & Sons Ltd Publisher]. Stimuli from the right and from the left are pooled as if from the right. In all circular plots in A, B and C, the threat is positioned at 0 deg.

2011)]. In addition, linear regression is arguably not an appropriate tool if, for any given value of *x*, the values of *y* are not normally distributed (Domenici, 2002a; Zar, 1984), as is likely to be the case for multiple ETs.

In contrast to the linear approach, Domenici and Blake (Domenici and Blake, 1993) used circular statistics to analyze ETs in angelfish; this methodology has subsequently been used in studies of various species (e.g. Arnott et al., 1999; Domenici et al., 2008; Martin and Lopez, 1996). The ET is defined as the angle between the stimulus (positioned at 0 deg) and the escape path of the animal once the rotation is completed (Domenici et al., 2008) or at a specific kinematic stage such as the second axial bend [i.e. stage 2 (Domenici and Blake, 1997)] in the fish escape response (Domenici and Blake, 1993). The ET corresponds to the angular sum of the stimulus angle and the turn angle, in which the turn angles of the away and towards responses (i.e. responses in which the initial body rotation is away from or towards the threat, respectively; Fig. 1B) bear a positive and a negative sign, respectively (Fig. 1B). Escape trajectories in which

the stimulus remains on the side of the original stimulation (e.g. coming from the left of the animal) at the end of the escape response, are considered to be in the semicircle 0–180 deg, whereas those in which the stimulus ends up on the opposite side of the original stimulation are considered to be in the semicircle 180–360 deg (Fig. 1C). This type of ET measurement will be denoted as $ET^0$ in this review, to distinguish from two other ways of measuring trajectories, i.e. ET′ and ET″ (see below), whereas the abbreviation ET will be used in the context of escape trajectories in general.

By using this method, peaks in $ET^0$s that are not apparent from the *x*–*y* plot can be revealed (Fig. 1A, inset). $ET^0$ is effectively a circular variable as it can span 360 deg relative to the stimulus (Domenici, 2002a) (Fig. 1C). This approach allows the determination of which of the possible $ET^0$ strategies [i.e. distributions shown in fig. 2 of Domenici et al. (Domenici et al., 2011)] is adopted by a particular animal. The distribution of recorded $ET^0$s can be tested using standard circular statistics against various model distributions

such as random, circular normal (von Mises) (as would be expected if the animals had a single optimum $ET^0$) and even multi-modal distributions (Domenici et al., 2008). In addition, the possibility that prey escape angles could be fixed relative to their body axis can be analyzed by testing the distribution of their turn angles (Domenici et al., 2008; Domenici et al., 2009).

Provided there are no differences between responses to left and right stimuli due to animal asymmetry, statistical analysis of $ET^0$s is simplified by pooling responses to stimuli to the right of the animal (i.e. 0–180 deg to its right) and stimuli to its left (0–180 deg to its left). By this convention, trajectories are pooled as if stimuli are on the right (Domenici and Blake, 1993). This convention will be used for all circular plots presented here when based on available $x$–$y$ plots of stimulus angle *versus* escape angles (Figs 1, 2). These original data were ditigized using Image J software. In the digitization process, some data points may have been missed because of data overlaps in the original figures. Where applicable and available, $N_o$ (the number of data points in the original published figures) is given in the figure legend, in addition to $N_d$ (the number of data points obtained through digitization). Where our figures represent data that were previously published and did not need to be re-digitized, only one $N$ is provided. In addition to this convention for measuring ET, two other main methods have been used to analyze ETs (Fig. 2). Although in many cases these two other conventions do yield the same values as the ET defined above, they do emphasise different properties of the ETs, and will therefore be distinguished here as $ET'$ and $ET''$.

Some previous studies have used a convention that does not distinguish between keeping and not keeping the stimulus on the original side of the stimulation, as it simply records the final escape trajectories measured relative to the predator positioned at 0 deg. Responses with ETs <180 and >180 deg are considered to be directed, respectively, right and left of the line directly away from the predator, and independent of whether the prey was startled on its left or right side (Fig. 2). This convention will be denoted as $ET'$.

In some cases, escape trajectories were calculated using values ranging only from 0 deg (i.e. towards the threat) to 180 deg (i.e. away from the threat), thereby using only one semicircle regardless of whether the prey reached a given trajectory (e.g. 135 deg) by making a small turn (Fig. 2A,C), or by making a larger turn (Fig. 2B,D) and ending up with the threat on its opposite side. This convention will be denoted as $ET''$.

The relevance of each of these methods of calculating ET may be related to the type of predator–prey interactions involved and the goal of the experimenter in terms of the information the data are supposed to convey. In a system assumed to be bilaterally symmetrical, the basic $ET^0$ measurement conveys more information than $ET'$ or $ET''$. Nevertheless, the general pattern of ETs found by the different methods are largely comparable because the overall specific pattern is affected only in certain situations, e.g. trajectories symmetrical about the 0–180 deg axis may result in a single trajectory when using $ET''$, compared with the two other methods (e.g. in Fig. 2, $ET''$ yields 135 deg in all cases, as opposed to $ET'$ and $ET^0$). The main difference between $ET^0$ and $ET'$ is that the former yields different angles when the prey shifts its orientation (relative to stimulus) from one semicircle (e.g. the left one) to the other (e.g. the right one), yielding, for example, an $ET^0$ of 225 deg (Fig. 2D) in contrast to when it escapes within the same semicircle within which it was oriented at the onset of the response (yielding an $ET^0$ of 135 deg in Fig. 2C); $ET'$ measurements do not record this difference, but yield different angles based on whether the final trajectory is in the right ($ET'$ of 135 deg) or left ($ET'$ of
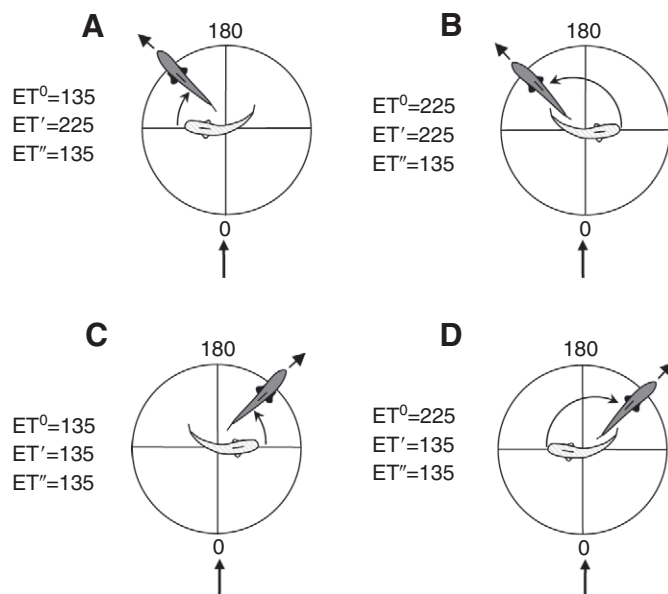


Fig. 2. Different conventions used in the literature for analysing escape trajectories in prey with various stimulus and response angles. The corresponding values of $ET^0$, $ET'$ and $ET''$ are indicated on each plot. In all plots, the threat is positioned at 0 deg. $ET^0$: the angle of the escape trajectory as illustrated in Fig. 1B; it corresponds to taking the angle in the semi-circle 0–180 or 180–360 deg based on whether the threat remains on the side of the original stimulation or ends up on the opposite side of it, respectively. (By convention, ETs are plotted as if the stimulus is always coming from the right.) $ET'$: the escape angle is calculated regardless of whether the prey is stimulated on the left or right side. Trajectories <180 deg are directed to the right of the predator's attack line whereas trajectories >180 deg are directed to the predator's left. $ET''$: the escape angle spans 0–180 deg only, as it is calculated as the angle between 0 deg and the direction of escape, regardless of the initial orientation of the prey.

225 deg) semicircle relative to the threat that is located at 0 deg (compare Fig. 2A with 2C). All of these conventions allow the main general hypotheses described above to be tested, albeit with somewhat different angular characteristics. Furthermore, in some studies described in this review, such as those in which animals are startled by tactile stimulation, the trajectory of escape is measured simply as the 'turn angle', i.e. the angle of the escape movement relative to the initial body orientation, rather than relative to the position of the predator. In this review, in all theoretical and general considerations we use the expression ET. For the experimental examples described, we use the expression $ET^0$ only when angular measurements are taken, or can be derived, that correspond to Fig. 1C, which is the main method discussed in this review. Otherwise we specifically use the expressions $ET'$ and $ET''$.

The effect of the stimulus orientation on $ET^0$s can be tested using circular linear correlation [a rank correlation test (Batschelet, 1981)]. Ideally, stimulus orientation should be standardized by using a uniform distribution of stimulus angles in order to avoid any differences in $ET^0$ distributions that may arise from the use of different stimulus orientations (Domenici et al., 2008). When using circular statistics analysis, $ET^0$ is the circular variable (varying from 0 to 360 deg) and the initial orientation is the linear variable as it spans a limited arc (0–180 deg) (Batschelet, 1981). The effect of initial orientation on $ET^0$s can be further tested by dividing stimulus orientations into angular sectors [e.g. 30 deg sectors in Domenici et al. (Domenici et al., 2008)]. Randomly generated $ET^0$s may give
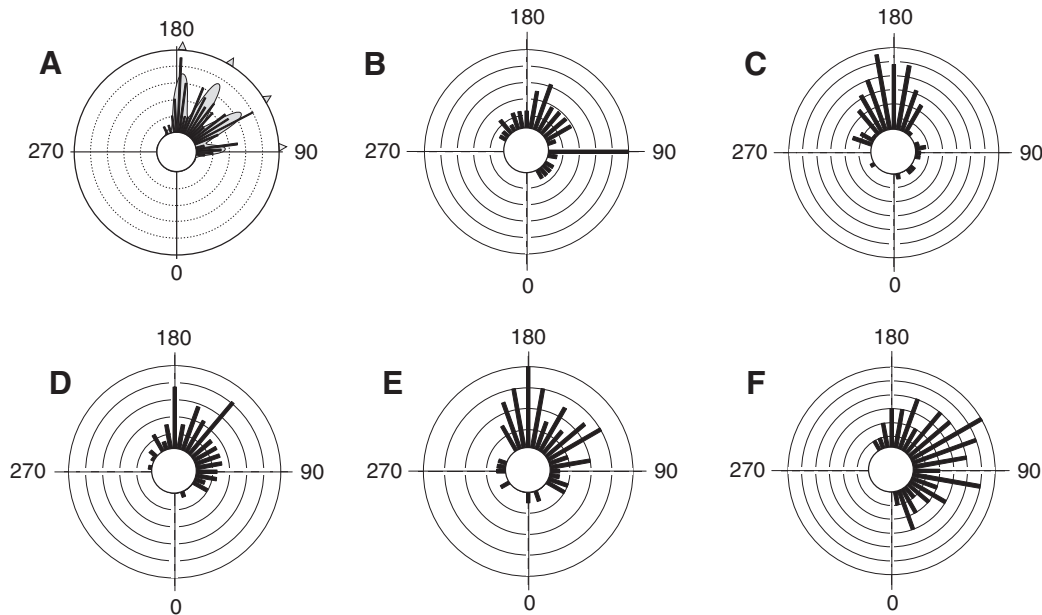
Fig. 3. Escape trajectories in cockroaches, crickets and locusts. Stimulus direction corresponds to 0 deg. (A) ET⁰s in the cockroach *Periplaneta americana* stimulated by wind (*N*=86) [reprinted from Current Biology, fig. 2B from Domenici et al. (Domenici et al., 2008) with permission from Elsevier]. Frequency distributions are shown by bars. Bin intervals are 5 deg; concentric circles represent a frequency of 2. Best-fit distributions at 90, 120, 150 and 180 deg are shown as multimodal curves. Arrowheads indicate peaks, defined as those that contribute at least 5% to the best-fit curve. (B) ET⁰s in the cricket *Gryllus bimaculatus* startled using wind stimulation [$N_d$=46, $N_o$=46; bin intervals are 10 deg; concentric circles represent a frequency of 1.6; data transformed from *x–y* plot in fig. 4A in Tauber and Camhi (Tauber and Camhi, 1995)]. (C) ET⁰s in *G. bimaculatus* startled using wind stimulation [$N_d$=93, $N_o$=93; bin intervals are 10 deg; concentric circles represent a frequency of 2.5; data transformed from *x–y* plot in fig. 3 in Kanou et al. (Kanou et al., 1999)]. (D) ET⁰s in the cave cricket *Troglophilus neglectus* startled using wind stimulation [$N_d$=95; bin intervals are 10 deg; concentric circles represent a frequency of 3.2; data transformed from *x–y* plot in fig. 1 in Schrader (Schrader, 2000)]. (E) ET⁰s in the cricket *Gryllodes sigillatus* startled using wind stimulation [$N_d$=68; bin intervals are 10 deg; concentric circles represent a frequency of 2; data transformed from *x–y* plot in fig. 2C in Kanou et al. (Kanou et al., 2006)]. (F) ET⁰s in the locust *Locusta migratoria* startled using a looming stimulus [$N_d$=60, $N_o$=70; bin intervals are 10 deg; concentric circles represent a frequency of 2; data transformed from *x–y* plot in fig. 1B in Santer et al. (Santer et al., 2005)].

rise to apparent preferred clusters of ET⁰s, particularly if the sample size is low. Therefore, large sample sizes should ideally be used to provide sufficient power for testing the goodness-of-fit of various hypothetical distributions such as uniform and von Mises (Batschelet, 1981). Confidence in the pattern of ET⁰ distribution can be further gained by comparing the frequency distributions in different individuals stimulated repeatedly and monitoring whether the same pattern appears when data are subdivided into left and right stimulation (Domenici et al., 2008).

If the ET⁰ distribution is neither random nor von Mises, a goodness-of-fit of multiple peaks can be assessed by fitting curves based on mixtures of multiple Gaussian distributions to the unbinned ET⁰ data using a maximum likelihood method. Computation of the corrected Akaike's information criterion enables the determination of the best-fit curve (i.e. that which balances a maximization of the likelihood against the minimization of the number of parameters) (Domenici et al., 2008).

### Case studies

Drawing mainly from invertebrate and lower vertebrate taxa, a number of case studies examining patterns of ETs are discussed below. Variability in escape trajectories is examined in terms of its ecological significance and morpho-physiological constraints. Various taxonomic levels are included, from whole phyla (e.g. molluscs) to the species level in those cases where a large number of studies has been carried out on the escape response of certain animals, e.g. cockroaches. This species is presented first, as cockroach ETs arguably provide the most comprehensive available

data set, and its discussion highlights issues that inform consideration of behavioural studies in other taxa. Plankton, not representing a taxon but an ecological group, are discussed together because they share a number of basic properties and constraints.

### Insects

#### Cockroaches

One of the best-known model species for escape response is the cockroach *Periplaneta americana*, which is startled by wind stimulation to simulate the attack of a predator (Camhi, 1983). Work on cockroach escape responses extends from sensory physiology to behaviour and biomechanics (e.g. Camhi and Tom, 1978; Comer and Dowd, 1987; Rinberg and Davidowitz, 2000; Stierle et al., 1994; Westin, 1979). Hairs on their abdominal cerci detect the direction of wind produced by an approaching real or simulated threat (Camhi and Tom, 1978; Kondoh et al., 1991; Thompson et al., 1992; Westin, 1979). The directional sensory wind information from these hairs is transmitted to giant interneurons (GIs) in the terminal ganglion (Kolton and Camhi, 1995). Each ascending GI has a specific directional selectivity to wind, and therefore directional information is transmitted to the interneurons and motorneurons in the thoracic ganglia, which generate the appropriate commands for the body turns (Kolton and Camhi, 1995).

Earlier work on the cockroach escape response has mainly utilized linear statistics (Fig. 1A) to show that escape angle tends to increase with stimulus angle, although with high variability (e.g. Camhi and Tom, 1978; Comer and Dowd, 1987). Recent work employing circular statistics of ET⁰s relative to the stimulus

direction shows that $ET^0$s in cockroaches are neither random nor unimodal, but instead are clustered in preferred directions that were suggested to provide unpredictability in the escape response (Fig. 1A inset, Fig. 3A) (Domenici et al., 2008). These preferred $ET^0$s are not the result of fixed turn angles (relative to the body axis), as turn-angle distribution was found to be uniform (Domenici et al., 2008). Preferred $ET^0$s were found both in single individuals stimulated repeatedly and in 86 individuals, each stimulated once only (Domenici et al., 2008). Hence, preferred $ET^0$s are not due to different individual preferences within the population but are a shared characteristic of the laboratory population investigated. Interestingly, circular reanalysis of previous work that had been presented in linear $x$–$y$ mode (Camhi and Tom, 1978; Comer and Dowd, 1987) also revealed preferred $ET^0$s (Domenici et al., 2008), although with peaks at slightly different angles, possibly because of population or methodological differences (e.g. different distributions of stimulus angles used) (Domenici et al., 2008) between studies. Furthermore, similar $ET^0$s are produced by both towards and away responses (Domenici et al., 2009). Wind direction has an effect on the distribution of $ET^0$s used. This is because most escape responses are a turn away from the stimulus and, therefore, the angular magnitude of $ET^0$ is almost always larger than that of wind angle (Domenici et al., 2008). The observed $ET^0$s are mainly within the 90–180 deg sector, in line with theoretical predictions (Arnott et al., 1999; Domenici, 2002b; Weihs and Webb, 1984). $ET^0$s greater than 180 deg (i.e. due to overturning as in Fig. 2B) are rarely used, suggesting that using the 90–180 deg sector provides sufficient unpredictability while minimizing the time needed to complete the body rotation.

The neural mechanism for generating these multiple $ET^0$s is unknown. However, the fact that ETs of adult cockroaches (with 440 cercal sensory hairs) are almost identical to those of early-stage juveniles (with only 80) strongly suggests that it is centrally located (Booth et al., 2009). Domenici et al. (Domenici et al., 2008) suggest that the ET-generating mechanism could involve the many thoracic interneurons that are interposed between the ventral GIs and the motor neurons (Ritzmann and Pollack, 1990; Westin et al., 1988) or perhaps also the dorsal GIs. Alternatively, the possibility that the preferred directions of pliancy of the sensory hairs (Dagan and Camhi, 1979) may control $ET^0$s cannot be ruled out. In addition, the cockroach escape response has provided a model (using dsRNAi in a reverse-genetic approach) to understand how molecular genetic information is used to construct circuits of neurons and thereby mediate behaviour (Booth et al., 2009). The transcription factor Engrailed (En), expressed only in the medially borne sensory neurons, acts as a positional determinant of sensory neuron identity, controlling the patterns of synaptic connections to the GIs (Marie et al., 2000). Booth et al. showed that En knock-out significantly perturbs the animals' perception of posterior wind, altering the choice of $ET^0$s to those more appropriate for anterior wind (Booth et al., 2009).

The finding of preferred ETs underscores the need to revisit the neural mechanisms controlling escape directions in the cockroach and other similar animal models. In addition, as argued by Domenici et al. (Domenici et al., 2008), it is unlikely that there is any particular ecological significance (in terms of limiting predator capture performance) for any specific ET, for example escaping at 120 or 150 deg but not at 135 deg. Irrespective of how the multiple ETs are generated, it seems possible that their protean unpredictability is adaptive, producing a selective advantage in predator avoidance compared with a repeated, and hence predictable, single ET (Domenici et al., 2011).

## Other insects

In addition to cockroaches, the escape behaviour of some other insect species with wind-sensitive filiform hairs borne on posterior cerci has been investigated. A few indicative examples are reported here. The cricket *Gryllus bimaculatus* responds to a wind stimulus with either a turn, a jump or a turn followed by a jump (Tauber and Camhi, 1995). The body and leg movements producing the turns are similar to those observed in cockroaches (Tauber and Camhi, 1995). In contrast, jumps are based on energy-storing mechanisms in the posterior legs (Bennet-Clark, 1975). Although jumps are evoked only when crickets are stimulated posteriorly, the directions of escape in the three types of response show considerable overlap (Tauber and Camhi, 1995). Data originally analyzed as $x$–$y$ plots of stimulus angles *versus* turn angles are presented here as circular plots and reveal two apparent peaks of $ET^0$, at 90 and 170 deg (Fig. 3B), although the low sample size (46) does not allow exclusion of the possibility that these peaks are due to random noise. Work on the same species (Kanou et al., 1999), reanalyzed here using circular plots (Fig. 3C), show less $ET^0$ variability, clustered around 180 deg; this could be due to either real inter-population differences or methodological differences, as noted by Domenici et al. (Domenici et al., 2008) in cockroaches. In *G. bimaculatus*, as in the case of *P. americana* (Domenici et al., 2008), the different $ET^0$ distribution found in these two different studies may be related to the different stimulus angles used in the two experiments. The mean stimulus angles calculated based on the original figures are 57.6±6.5 deg (mean ± s.e.m.; $N$=46) and 104.6±5.5 deg ($N$=93) for Tauber and Camhi (Tauber and Camhi, 1995) and Kanou et al. (Kanou et al., 1999), respectively. These differences are significant, based on a $t$-test ($t$=5.22, d.f.=137, $P$<0.001). Because most escape responses tend to be a rotation away from the stimulus, the predominant use of large stimulus angles (i.e. posterior stimulation, with angles >90 deg) by Kanou et al. (Kanou et al., 1999) may explain why the predominant $ET^0$ peak at 90 deg in Fig. 3B [data from Tauber and Camhi (Tauber and Camhi, 1995)] is not apparent in Fig. 3C [data from Kanou et al. (Kanou et al., 1999)]. We cannot, however, exclude the possibility that these different $ET^0$ patterns are due to other differences in populations and methodologies.

Relatively high variability, with some apparent peaks in the distribution of $ET^0$s, is also found in circular plots of data (originally analyzed with an $x$–$y$ plot of stimulus *versus* response angle) of the cave cricket *Troglophilus neglectus* startled by wind (Schrader, 2000) (Fig. 3D). $ET^0$s of the cricket *Gryllodes sigillatus* also show high variability with some clustering at peaks (Kanou et al., 2006) (Fig. 3E). In contrast, mechanical stimulation of the posterior legs of another cricket species (*G. bimaculatus*) causes $ET^0$s that are directed forward. Forward jumping is the most effective escape strategy in this case because it is mediated by simultaneous movement of the fore and hindlegs, quickly moving the body forward and away from the threat (Hiraguchi and Yamaguchi, 2000).

Escape responses in jumping insects such as locusts and grasshoppers can be triggered visually. Circular reanalysis of these escape jumps in the locust *Locusta migratoria* (Fig. 3F) shows high variability in $ET^0$s in a range similar to the wind-elicited escapes discussed above, despite the fact that the animal could not produce a body turn of more than approximately 50 deg and, therefore, could only produce $ET^0$s <90 deg when the locusts was stimulated head-on (Santer et al., 2005). In contrast to this variability of $ET^0$s, locusts (*Schistocerca gregaria*) and grasshoppers (*Phaulacridum vittatum*) are able to accurately aim
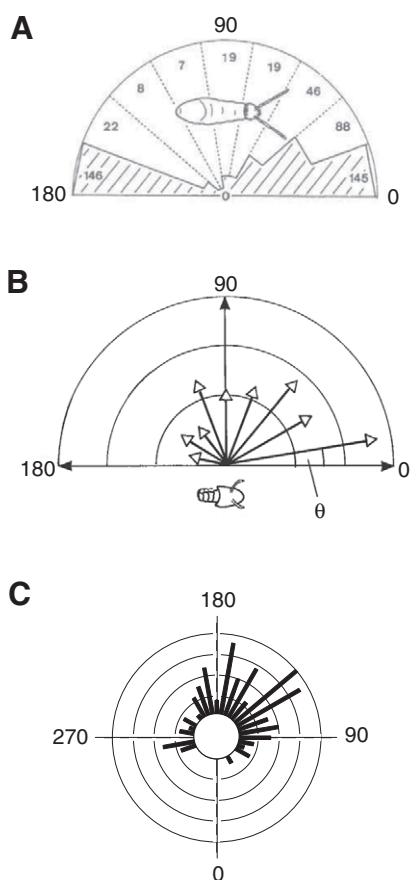
Fig. 4. Escape angles relative to the body axis (head pointing at 0 deg, tail at 180 deg) in mechanically stimulated (A) *Heteromurus nitidus* (Collembola) [*N*=500; reprinted from Zoologische Jahrbuch, fig. 19 from Von Christian (Von Christian, 1978) with permission from Elsevier] and (B) *Culex pipiens* pupae [concentric circles represent *N* of 15, 25 and 35; fig. 1B reproduced with permission from Brackenbury (Brackenbury, 1999)]. (C) ET$^0$s (in this case measured as the displacement of the centre of mass) relative to a looming visual stimulus in *Drosophila melanogaster* [$N_d$=89, $N_o$=91; data transformed from *x*–*y* plot in fig. 1E in Card and Dickinson (Card and Dickinson, 2008)]. Following the convention for ET$^0$ measurement adopted for the reanalysis of previously published data in this review, data are replotted as if stimulus is coming from the right – the original data of Card and Dickinson were plotted as if the stimulus is always coming from the left. Bin intervals are 10 deg; concentric circles represent a frequency of 2.5. In C, the threat is positioned at 0 deg.

at specific targets when jumping voluntarily (Collett and Paterson, 1991; Eriksson, 1980). However, these jumps usually follow peering motions and long axis adjustments so that locusts end up facing the goal (Collett and Paterson, 1991; Eriksson, 1980). Santer et al. suggest that locusts jump rapidly when threatened, at the expense of accuracy, compared with 'voluntary' jumps (Santer et al., 2005). Another plausible (and non-conflicting) explanation for the high variability observed in locust ETs is that is makes the escape response relatively unpredictable, as suggested for the cockroach model (Domenici et al., 2008). When the threatening stimulus to a grasshopper was an approaching human, Cooper found that ETs were quite variable, but most ET″ values were between 80 and 120 deg (Cooper, 2006). However, the low angular resolution recorded has not allowed our further evaluation of specific ETs.

A number of other insect species possess energy-storage jumping mechanisms similar to those described above. In collembolan springtails (*Heteromurus nitidus*), the energy for jumping is not stored in the legs but in the abdominal sclerites (furca). Releasing the furca from flexion catapults the animal off the ground (Brackenbury and Hunt, 1993), mainly forwards or backwards relative to the body axis (Fig. 4A) (Von Christian, 1978). Although these escape directions were not analyzed as ETs relative to the stimulus direction, these data do show two preferential escape directions relative to the body axis, presumably resulting from the mechanical constraints of the jumping mechanism (Brackenbury, 1999; Von Christian, 1979). Although fixed relative to the body axis, this jumping escape behaviour could appear unpredictable to a predator because the resulting ETs might be in random directions if predators attack from various angles relative to the prey's body axis. Mechanically stimulated *Culex pipiens* pupae show a similar tendency to escape in a fixed direction relative to the body axis (mainly forward), albeit with relatively high variability (Fig. 4B) (Brackenbury, 1999). Using this strategy [described as *D* in fig. 2 of Domenici et al. (Domenici et al. (2011)], ETs are random relative to the stimulus (but in this particular case fixed relative to the body orientation). This escape strategy is probably determined by functional constraints in the manoeuvrability of the prey, resulting from the angular sector within which the spring can effectively work.

Fruit flies *Drosophila melanogaster* can use visual information to plan a jump in a direction away from a looming threat (Card and Dickinson, 2008). Approximately 200 ms prior to take-off, flies begin a series of postural adjustments that determine the direction of their escape; they position their centre of mass so that leg extension will push them in a direction approximately away from the expanding visual stimulus (Card and Dickinson, 2008). Nevertheless, the ET$^0$s of *D. melanogaster* show some degree of variability, which, when plotted using circular histograms relative to the stimulus direction, clusters as multiple ET$^0$ peaks, mainly in the 120–170 deg range (Fig. 4C).

*Triatoma infestans* bugs turn away from a vertical rotating black stripe by keeping the stimulus at a fixed angle relative to their body (Lazzari and Varju, 1990). This behaviour has been interpreted as an escape response by which *T. infestans* maximizes the distance from the threat while keeping it at a fixed angle (ET″) of 120 deg – well within the limit of its 140 deg visual field (Lazzari and Varju, 1990). This escape behaviour seems to be an example of sensory tracking of the threat, although it does not provide much unpredictability.

Some insect species (e.g. the locust *L. migratoria*) show hiding behaviour when sitting in an elevated position on a stem as a response to looming or moving visual stimuli. When these animals are threatened while perched, their forelegs and middle legs perform lateral tilting movements while the hindlegs slide laterally and guide the rotation of the posterior body behind the stem (Hassenstein and Hustert, 1999). Strictly speaking, these are not escape responses involving locomotion, but can be considered as a form of avoidance response. Interestingly, locusts often stopped before reaching an 'optimal' hiding position (i.e. <180 deg from the stimulus), perhaps to allow tracking of the stimulus from behind the supporting rod using the ipsilateral eye (Hassenstein and Hustert, 1999).

In summary, insects show high variability in ETs, which in some cases can be ascribed to multiple preferred ETs. However, in some species, we do note evidence of fixed turn angles relative to the body axis, which may yield random ETs, and examples where fixed ETs seem to enable sensory tracking.
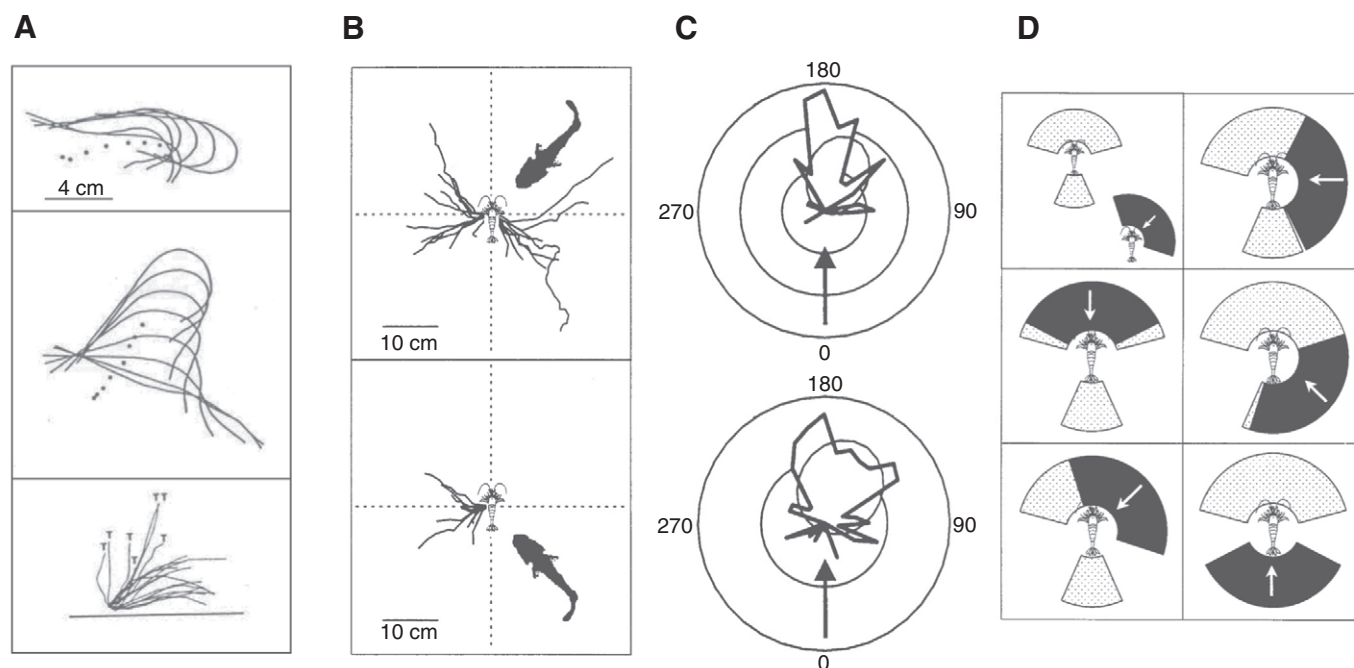
**A**    **B**    **C**    **D**



Fig. 5. ETs resulting from crustacean tail flips. (A) Tail flip escape responses in the lobster *Nephrops norvegicus*. Top and centre: superimposed outlines of sequential body positions seen from the side, showing flexion movement and the relative displacement of the centre of mass indicated by the dot, in escapes triggered by stimuli touching the rostrum (backward flip, top panel) and the telson (upward flip, centre panel). Bottom: trajectories of the centre of mass observed in different animals stimulated at the rostrum (unmarked) and the telson (T), relative to the ground (horizontal line) [fig. 4 reproduced with kind permission from Springer Science+Business Media, fig. 4A,B,D from Newland and Neil (Newland and Neil, 1990a)]. (B) Superimposed escape motions in the horizontal plane of *Crangon crangon* attacked by cod from the anterior right (top) and posterior right (bottom) quadrants [fig. 4 reproduced with permission from Arnott et al. (Arnott et al., 1999)]. (C) Circular frequency plots of ET$^0$s of *C. crangon* attacked by cod, indicated by the stimulus direction (arrow at 0 deg). Two discernible ET$^0$ peaks are seen at 130 and 180 deg. Top: all responses ($N$=76); bottom: away response only [$N$=47; bin intervals are 10 deg; concentric circles represent a relative frequency of 5%; fig. 6 reproduced with permission from Arnott et al. (Arnott et al., 1999)]. (D) Top left panel shows the exclusion envelope – the angular range spanning 63 deg either side of the direction of the approaching predator (arrow) that was never used by the escaping prey (black shaded area) – and the escape envelope – the unfilled sectors 75–156 deg to the left and right of the prey. The stippled regions in front and behind the body were never used by the shrimp. The other five panels show the interaction between the exclusion and the escape envelopes for different attack directions (the predator's attack line is indicated by the white arrow), leaving one or two empty sectors within which ET$^0$s were observed [fig. 8 reproduced with permission from Arnott et al. (Arnott et al., 1999)].

## Crustaceans
### Crayfish, lobsters, shrimp and mysids

When startled, many species of malacostran crustaceans, such as various decapods and mysids, show a typical tail-flip response. The decapod tail-flip escape response has been studied extensively, and can include three-dimensional components. As has been suggested (Neil and Ansell, 1995), these are more conveniently discussed separately because either the horizontal or vertical component may predominate, depending on the species and the type of stimulation.

Decapod tail-flip escapes, triggered by tactile stimuli, fall into two main turn angles (measured relatively to the body axis) in the vertical plane [in crayfish *Procambarus clarkii* (Wine and Krasne, 1972)]. Telson-triggered escapes tend to be directed upwards [with mean turn angle relative to the ground in the vertical plane being 71 deg in the lobster *Nephrops norvegicus* (Newland and Neil, 1990a)] whereas rostrum-triggered responses are directed mainly backwards [mean turn angle 15 deg (Newland and Neil, 1990a)]. Although the trajectories of the two types of response do not overlap, a relatively large range of turn angles can be observed for each response type (Fig. 5A). These responses are short-latency escapes mediated by medial giant neurons for frontal attacks and lateral giant neurons for posterior attacks. Non giant-fibre escapes with longer latencies were also observed as a reaction to threats that develop gradually (in

crayfish *P. clarkii*) (Wine and Krasne, 1972; Edwards et al., 1999), and can result in straight escape, pitching or even somersaulting (in crayfish *Cherax destructor*) (Cooke and Macmillan, 1985). The longer latencies for non-giant escapes are more variable and have been attributed to the 'voluntary' nature of the tail-flips in which crayfish make decisions about the direction and angle of the response before the response is executed (Herberholz et al., 2004; Reichert and Wine, 1983; Wine and Krasne, 1972).

Hence, rapid (giant-neuron mediated) responses as a reaction to sudden stimulation are less variable than the slower responses, which occur as a reaction to more gradual stimulation. This response delay might result from the neural computation required for flexible behaviour (Edwards et al., 1999). The two giant-neuron-mediated response patterns are distinct because cephalothorax stimuli just above threshold for median giant neurons cause a backward response even in the presence of below-threshold abdominal stimulation, and the reverse pattern causes vertical responses (Edwards et al., 1999). In contrast, non-giant neurons control a wide variety of response patterns, which vary, probably continuously, as a function of the stimulus characteristics (Edwards et al., 1999).

Work using real predators confirms that attacks to the front of the crayfish triggered backwards-directed tail-flips mediated either by the medial giant neuron or by non-giant circuitry, whereas

attacks to the rear elicited upwards-directed tail-flips mediated by the lateral giant neurons (Herberholz et al., 2004). In all these cases, the swimming trajectory in the vertical plane is mainly determined by the direction of the propulsive thrust generated by the tail flip. However, some degree of steering action can be provided in various decapod species by antennal scales (Jacklyn and Ritz, 1986), uropods (Newland and Neil, 1990b) and swimmerets (Newland et al., 1992a). Reichert and Wine showed that although the first giant tail flip in *P. clarkii* is stereotypical, subsequent flips can be steered (Reichert and Wine, 1983). In contrast, Newland et al. showed that in *Nephrops norvegicus*, even the first giant-fibre-mediated tail flip can be steered as a response to directional stimuli, providing the potential for some variability in swimming trajectory (Newland et al., 1992b).

The horizontal component of escapes has mainly been examined in responses triggered by lateral stimulation. Tactile stimuli delivered laterally cause rotation of the abdomen and asymmetric positioning of the uropods, which results in movement away from the stimulus (Newland et al., 1992b). *Nephrops nephrops* escape in variable directions from a simulated moving trawl net, all in the semicircle away from the threat (Newland and Chapman, 1989). When startled by approaching predators (cod *Gadus morhua*), small decapods (*Crangon crangon*) exhibit variability in the horizontal escape plane with an initial 90 deg rotation of the whole body about the longitudinal axis, ensuring that thrust is produced mainly in the horizontal plane (Arnott et al., 1999; Neil and Ansell, 1995).

*Crangon crangon* tends to escape in a direction away from a lateral stimulus, and turns left or right when attacked frontally or posteriorly. Their resultant $ET^0$s are quite variable (Fig. 5B) and a circular representation shows two discernible peaks of $ET^0$s at 130 and 180 deg (Fig. 5C), although the distribution is not different from a von Mises distribution (Arnott et al., 1999). Arnott et al. also noted that the shrimp never escaped in specific angular regions anterior and posterior to their body axis (Fig. 5D), and suggested that the boundaries between these regions may be determined by anatomical constraints on the shrimp (Arnott et al., 1999). For example, the length of the abdomen relative to the body places a constraint on the forces that rotate the shrimp rostrally during body flexion (Daniel and Meyhofer, 1989), limiting the initial body turn angle that can be achieved. The lack of escapes directly backwards differs from the escape pattern shown by some other decapod crustaceans (Newland and Neil, 1990a; Wine and Krasne, 1972). This may be due to differences in the escape mechanics, which, in *C. crangon* startled by a real predator, involve mainly the anterior region of the abdomen, whereas in other species it invokes telson-to-cephalothorax flexion (Arnott et al., 1999). To summarize, the $ET^0$s of *C. crangon* can be understood to lie within a range that combines the angular sectors available for escape relative to its body axis, combined with an exclusion envelope (defined as the angular region measured relative to the attack that is never used by the shrimp) spanning approximately 120 deg in the direction of the attack (Fig. 5D) (Arnott et al., 1999).

Using a different pair of predator and prey (stickleback *Spinachia spinachia* and mysids *Neomysis integer*, respectively), Kaiser et al. found that mysids use two main ET″s relative to the predator attack path (Kaiser et al., 1992); approximately 70% of the responses showed an ET″ directed at 90 deg and approximately 30% of the responses showed an ET″ directed at 180 deg [0 deg in Kaiser et al. (Kaiser et al., 1992)]. A 90 deg ET″ relative to the predator attack line moves the mysid out of the swimming path of the predator and is effective because it is executed at the last

moment, not allowing the predator to redirect the attack (Kaiser et al., 1992). The adoption of two main ET″s by mysids in response to a stickleback attack could be an effective strategy to increase unpredictability.

Two morphological types were found in a population of atyid shrimp (*Neocaridina denticulata*), with opposite abdominal asymmetries that were related to a behavioural asymmetry in the escape direction (back left or back right) (Takeuchi et al., 2008). Because the two morphs coexist in nature, this is an example in which a relatively unpredictable escape direction is related to the presence of different morphs in the population.

To summarize, decapod crustaceans such as shrimp and lobster show two main patterns of tail flips in the vertical plane: backwards from front stimuli and upwards from posterior stimuli. In contrast, high variability of ETs in the horizontal plane was found, notwithstanding constraints in the turn angles relative to the body axis.

## Crabs

Most crab species walk sideways, and therefore they may be able to escape directly away from a threat while tracking it visually. Work by Oliva et al. investigated the escape trajectories of crabs *Chasmagnathus granulatus* startled by a looming visual stimulus from different directions (Oliva et al., 2007). The crabs escaped sideways to the left or right with equal probability when stimulated in their dorsal visual field, but escaped in a single direction away from a stimulus presented in the horizontal plane (Fig. 6A). Lateral stimulation triggered a sideways response with little body rotation or ET′ variation. Frontal stimulation caused the largest rotational components, because frontally stimulated crabs need to rotate in order to escape in a direction away from the stimulus while walking sideways (Oliva et al., 2007). Furthermore, ET′s triggered by frontal stimulation were also highly variable (approximate range 90–230 deg; Fig. 6A). This may be the result of minimizing the time spent for the rotation, which increases the ET′ variability (Fig. 6A).

The directional component of the visually mediated escape response of the fiddler crab *Uca pugilator* is known to be controlled by continuous visual feedback (Land and Layne, 1995a; Land and Layne, 1995b). Work in a laboratory setting (i.e. open loop with crabs walking on a styrofoam ball) has shown that fiddler crabs react, with some variability, with ETs of approximately 180 deg (Land and Layne, 1995b). Escapes were based on a combination of translation and rotations: in translation, the crab walks directly away (180 deg) from the visual stimulus, whereas a rotational movement turns the crab so that the visual stimulus is visually tracked and kept at approximately 90 deg to the body axis (Land and Layne, 1995b). Translation resulted in a range of $ET^0$s from approximately 140 to 230 deg [based on digitization of data in fig. 8a of Land and Layne (Land and Layne, 1995b)]. Land and Layne suggested that this variability could be caused by measurement errors and the crab's difficulty in manipulating the ball on which it was walking (Land and Layne, 1995b), although it cannot be excluded that this angular range may also be an expression of adaptive unpredictability in ETs. In the soldier crab *Mictyris longicarpus*, relatively high variability in $ET^0$s was observed (Domenici and Blake, 1993; Nalbach, 1990). Unlike most shore crabs such as those described above, soldier crabs walk forwards. Nalbach (Nalbach, 1990) compared the following alternative hypotheses: (1) crabs move in a fixed direction (180 deg) away from the visual stimulus and (2) crabs move within a fixed range of turn angles relative to the initial body orientation (Fig. 6B).
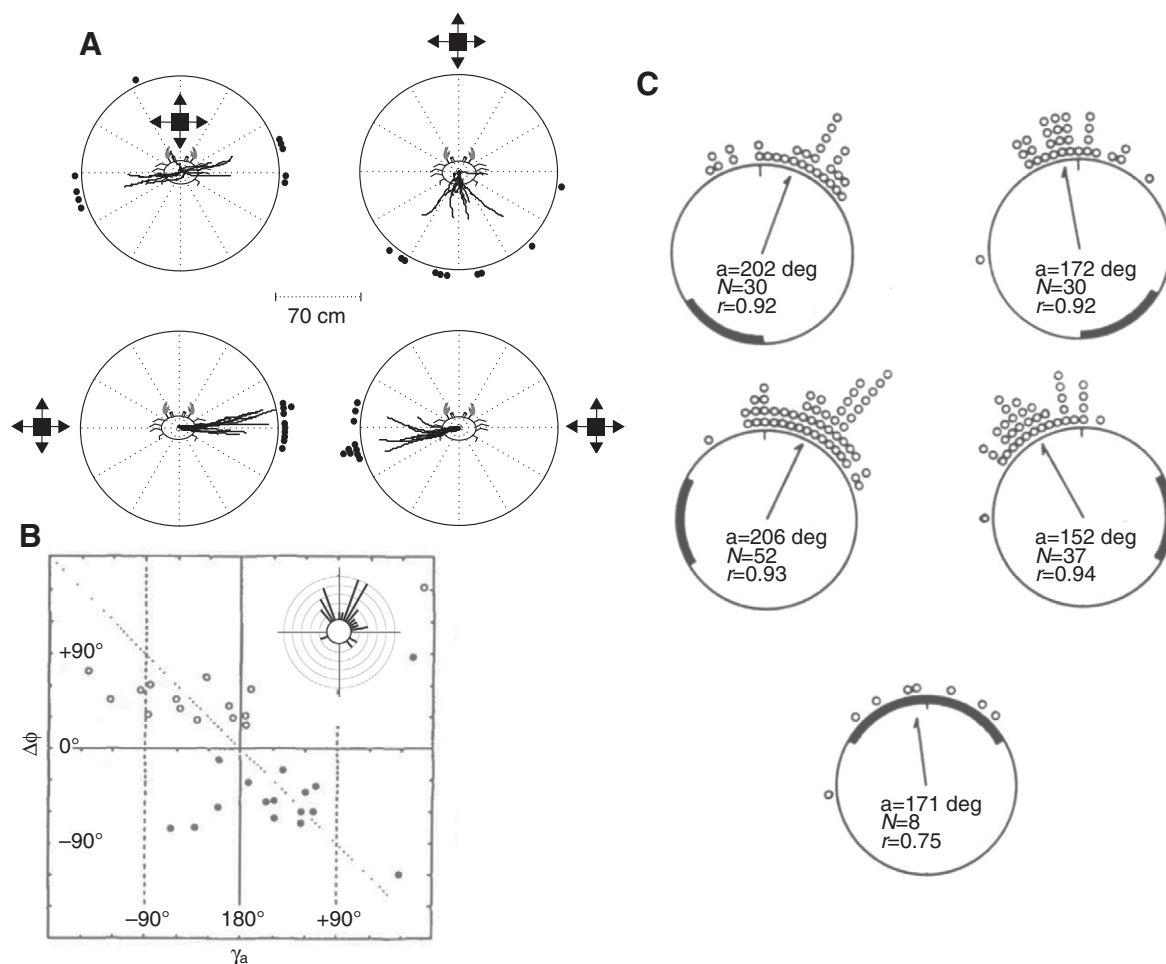
Fig. 6. (A) ETs in the crab *Chasmagnathus granulatus* triggered by a looming visual stimulus (black square). Upper left panel, stimulus from above; upper right panel, frontal stimulus; lower left panel, stimulus from the left; lower right panel, stimulus from the right [fig. 6A reproduced with permission from Oliva et al. (Oliva et al., 2007)]. (B) *x–y* plot of stimulus *versus* response angle in visually stimulated escape responses of the crab *Mictyris longicarpus*. The variance is smaller when calculated around a mean escape angle of 56.8 deg than when calculated relative to the 45 deg negative slope representing escape directed 180 deg away from the stimulus [$N_d$=31, $N_o$=31; fig. 2 reproduced with permission from Nalbach (Nalbach, 1990)]. Inset: circular frequency distribution based on reanalysis of the *x–y* plot shown in B. Peaks of $ET^0$s can be seen at 150 and 210 deg. Bin intervals are 10 deg; concentric circles represent a frequency of 2; the threatening stimulus is positioned at 0 deg. (C) ET′s caused by a human approaching the blue crab *Callinectes sapidus*. The 30 deg angular sector of the human approach is indicated by the darkened arc. The seaward heading is indicated by 180 deg. The resultant escape trajectory is a compromise between escaping away from the threat and towards the refuge of deeper water. In the directly conflicting situation (lower panel), a seaward direction of escape is chosen [reprinted from Animal Behaviour, fig. 5 from Woodbury (Woodbury, 1986) with permission from Elsevier]. Open circles represent single events.

Because the variance was smaller for the latter alternative, Nalbach concluded that soldier crabs turn by a stimulus-independent angle of approximately 20–80 deg, relative to their body axis (mean 56.8 deg) (Nalbach, 1990). However, a circular plot shows a bimodal pattern of $ET^0$s, with symmetric peaks on either side of 180 deg (150 and 210 deg) (Domenici and Blake, 1993) (Fig. 6B, inset). Although most responses are away from the stimulus, towards responses can occur, particularly in response to posterior visual stimulation, and result in trajectories similar to those of away responses (i.e. at 150 deg). As in some other taxa (fish, *Marlangius merlangus*; insects, *Triatoma infestans*) (Hall et al., 1986; Lazzari and Varju, 1990), these preferred ETs may correspond to particular limits imposed by the crab's sensory organs (Domenici and Blake, 1993) because soldier crab eyes have a limited field of view, which may be extended by the rotation of their eye stalks (Nalbach and Nalbach, 1987).

Field work on the fiddler crab *Uca vomeris* showed that distance to refuges (burrows) affects escape speed (Hemmi, 2005) and that escape responses were executed in multiple stages at different distances from the burrow (i.e. an early phase consisting of a home-run towards the burrow, and a late phase during which the crab entered the burrow), which were triggered by different types of visual cues (Hemmi and Pfeil, 2010). Because the presence/absence of a refuge nearby affects escape behaviour in crabs, it is also likely to have an important effect on their ETs. The importance of the refuge was also demonstrated by another field study on the blue crab, *Callinectes sapidus*, in which both a threatening stimulus and a refuge site were provided (Woodbury, 1986). The response of a swimming blue crab startled by human approach was a compromise between escaping away from the threat and escaping in a seaward direction (i.e. towards a refuge) (Fig. 6C) (Woodbury, 1986). In the case of directly conflicting drives, i.e. a threat coming from the sea,

A



B

*Acartia tonsa* males
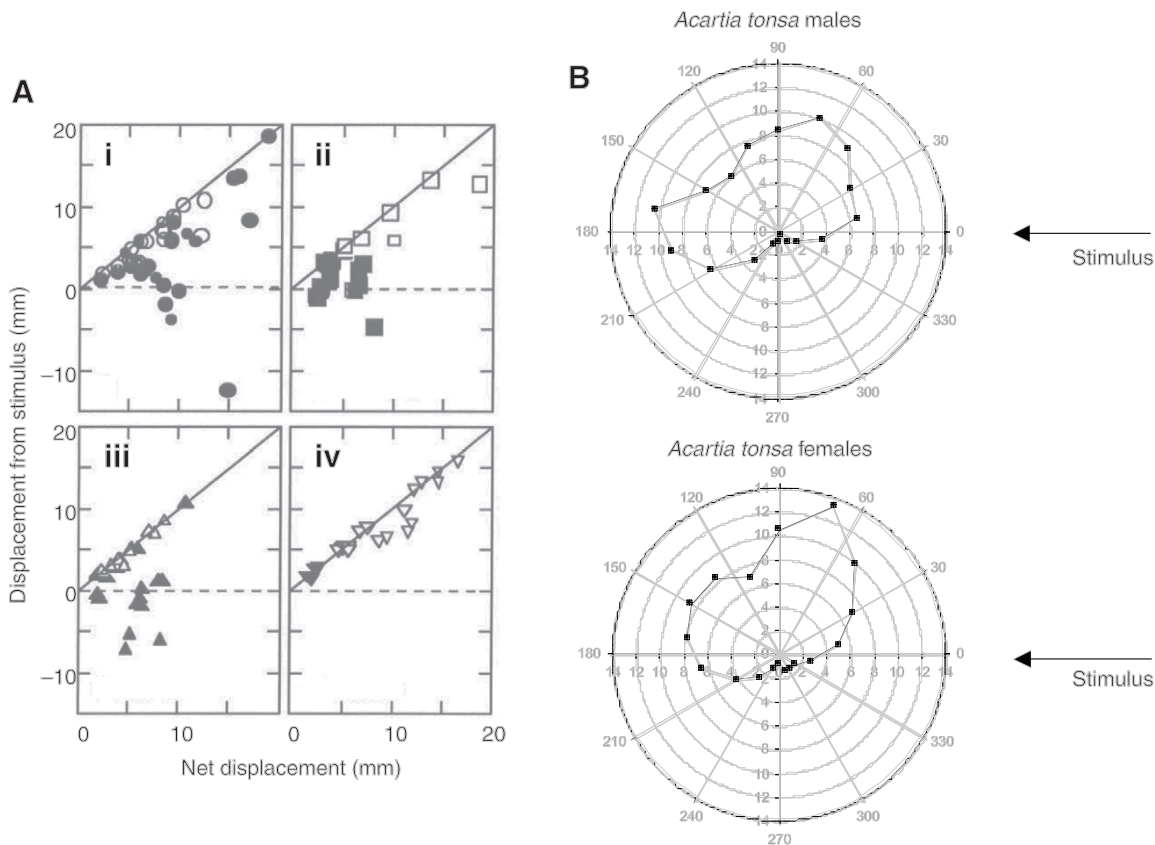
*Acartia tonsa* females

Fig. 7. (A) The relationship between displacement from the stimulus *versus* net displacement in four species of copepod: (i) *Tortanus discaudatus*, (ii) *Centropages hamatus*, (iii) *Acartia hudsonica* and (iv) *Temora longicornis*. The line at 45 deg represents the maximum distance from the stimulus, i.e. escaping with an ET of 180 deg. Escape responses elicited by a water current tend to be directed at 180 deg, i.e. they are mainly aligned with the 45 deg line (open symbols), whereas those elicited by a vibrating stimulus (filled symbols) show high variability [reprinted with permission from Limnology and Oceanography, fig. 8 from Burdick et al. (Burdick et al., 2007); © 2007 by the American Society of Limnology and Oceanography, Inc.]. (B) ET's in the vertical plane in the copepod *Acartia tonsa*. Top panel, adult males; bottom panel, adult females. Relative frequencies (%) divided into 20 deg bins are plotted. 0, 90 and 270 deg correspond to stimulus direction, upward-directed escapes and downward-directed escapes, respectively; concentric circles represent a frequency of 2 [reproduced with kind permission from Marine Ecology Progress Series, fig. 6 from Buskey et al. (Buskey et al., 2002)].

the crabs tended to swim offshore, showing that this drive was stronger than escaping away from the threat (Woodbury, 1986).

In conclusion, the crab species investigated to date react mainly with ETs that allow them to track the threat, although their ETs can also be affected by their surroundings.

### Plankton – protists and planktonic crustaceans

Although plankton is not a taxonomic group, various plankton species will be treated together as they share similar life-history and environmental characteristics, stimulus and escape patterns. ETs of planktonic prey (these range from protists to larval crustaceans) have been investigated using a number of stimulus types, such as suction, vibration and shadow. Plankton escapes can be complex three-dimensional trajectories, and previous work has often considered these ETs both relative to the stimulus and the vertical plane (i.e. negative geotactic behaviour). Many marine planktonic predators create water currents to entrain and capture prey. Prey entrained within such feeding currents often show rheotactic escape reactions. If the direction of escape is away from the feeding current, the prey may avoid predation, whereas if it is towards the centre of the feeding current, the prey will be re-directed towards its predator and may be captured (Fields and Yen, 1997; Jakobsen, 2002).

Jakobsen studied ET″s of protists (the ciliate *Strobilidium* sp. and two flagellates, *Chrysochromulina simplex* and *Gymnodinium* sp.) reacting to a water flow that simulated suction from a predator (Jakobsen, 2002). ET″s were non-random and had a negative geotactic component. According to Jakobsen, an escaping ciliate startled by the suction flow of a filtering predator orients its swimming trajectory at an angle to the flow to escape the predator's reach (Jakobsen, 2002). An optimal angle in this case may therefore be moving perpendicularly from the flow field of the predator (i.e. at 90 deg), maximizing distance from the flow (Jakobsen, 2002). Data from three different species show mean ET″s of 53, 82 and 97 deg (Jakobsen, 2002). Any pattern of frequency distribution of ET″s cannot, however, be assessed because only means were reported. Two possible mechanisms underlying these observed ET″s were discussed by Jakobsen (Jakobsen, 2002): (1) differential activation of mechanoreceptors embedded in the cell membrane or (2) passive orientation of the ciliate cellular body relative to the flow field of the predator (Visser and Jonsson, 2000). In another planktonic organism, Fields and Yen (Fields and Yen, 1997) found that *Acartia hudsonica* copepod nauplii threatened by similar flow suction mechanisms had only a limited ability to alter their initial orientation to effect an escape once entrained in the flow-field of the predatory calanoid copepod *Euchaeta rimana*, and their turning

angles (the angle between their body orientation before and after stimulation) were limited to approximately ±10 deg.

Titelman and Kiorboe examined anti-predation strategies in relation to motility patterns for early and late nauplii of six species of copepods (*Acartia tonsa*, *Calanus helgolandicus*, *Centropages typicus*, *Eurytemora affinis*, *Euterpina acutifrons* and *Temora longicornis*) (Titelman and Kiorboe, 2003). ET″s showed negative geotaxis (as in the previous example) and were mainly directed away from the flow line, although within a relatively large angular range (approximately 60 deg in most cases) (Titelman and Kiorboe, 2003). Burdick et al. found that the escape responses of four species of calanoid copepods (*A. hudsonica*, *Centropages hamatus*, *T. longicornis* and *Tortanus discaudatus*) tested using suction flow as a startling stimulus were directed away from the source of suction, although the responses elicited by vibration did not necessarily maximize distance between the animal and the stimulus (Burdick et al., 2007). These authors did not measure escape trajectories directly, but measured the relationship between distance from the stimulus (suction flow or vibration) and net displacement of the prey. Points along the marked slope of 1 correspond to prey escaping at 180 deg (Fig. 7A). They found that for escapes in response to water current, the relationship between distance from the stimulus and net displacement of the prey quite closely matched the slope, implying a single ET directed at 180 deg, whereas in escape responses to vibration, the relationship was highly variable, implying a high variability in trajectory of escape, which may increase the effectiveness of the escape by generating unpredictability (Fig. 7A) (Burdick et al., 2007).

ET′s in the vertical plane of free-swimming adult males and females of the copepods *A. tonsa* and *Acartia lilljeborgii*, in response to a vibrating stimulus, showed high variability, but were mainly in the 60–180 deg range, with ET′ peaks at approximately 70 and 170 deg, where 180 deg corresponds to a direction away from the stimulus and 90 deg corresponds to a negative geotactic response. Similar peaks were observed in males and females (Fig. 7B) (Buskey et al., 2002).

Buskey and Hartline studied the escape response of the copepod *A. tonsa* to shadow stimulation (Buskey and Hartline, 2003). Here it can be hypothesized that horizontally oriented escape trajectories should be more effective than vertically oriented ones, which would tend (by negative geotaxis) to propel the copepod towards the shadow-casting predator above. Copepods adapted to higher light intensities indeed tended to escape laterally, with peaks of ET′s at approximately 10 and 150 deg relative to the horizontal axis, although individuals adapted to low light intensities showed mainly upwards-oriented ET′s. A possible explanation for upwards-oriented ET′s in these copepods, which are found near the seabed during the day, is that they may act as a defence against shadow-generating benthic predators such as bottom-feeding fish (Buskey and Hartline, 2003). Observations using a real predator (a scyphomedusa) showed that the copepod *A. hudsonica* displays variable escape behaviour, including responses away, towards and parallel to the predator (Suchman, 2000). This high escape variability may be the best strategy for copepods faced with predation pressure from a wide variety of predators (Suchman, 2000).

In summary, escape trajectories in plankton are highly variable. A common feature for response to flow (suction) is a tendency to escape in a direction away from the axis of the flow generated by the predator. In response to vibration, the pattern of escape trajectories is similar to that of many other taxa with high variability, mainly within the 90–180 deg quadrant. In addition, many species show a negative geotactic component.

## Molluscs

Although escape responses in cephalopods have been studied extensively from neurobiological and biomechanical perspectives (e.g. Otis and Gilly, 1990; Packard, 1969), relatively little is known about their ETs. The escape response in the squid *Loligo opalescens* can be elicited by visual, acoustic or chemical stimuli (Otis and Gilly, 1990). It is generated by jet propulsion, which moves the animal in a direction opposite to the jet. Squid can control the orientation of the funnel, which provides a remarkable steering ability (Ward, 1972), and previous observations suggest that the siphon may change orientations during squid escape responses (Otis and Gilly, 1990). Therefore, squid should be able, potentially, to swim in various directions relative to their body orientation at the time of stimulation, and thus escape at ETs that are relatively fixed with respect to the stimulus, as is the case for other taxa. However, this question remains to be answered. Similarly, despite a large number of studies on scallop escape responses (Ansell et al., 1998; Bailey and Johnston, 2005; Cheng et al., 1996; Himmelman et al., 2009; Perez et al., 2009; Schmidt et al., 2008; Stephens and Boyle, 1978; Thomas and Gruffydd, 1971), little is known about their ETs. Analysis of the escape response in the vertical plane shows it comprises three phases: take-off, level swimming and sinking (Ansell et al., 1998). Analysis of the escape response of the scallop *Chlamys hastata* in the horizontal plane, startled by the sea star *Pycnopodia helianthoides*, found that mechanical stimuli applied to the anterior mantle consistently resulted in an anticlockwise rotation during the initial escape whereas posterior stimulation resulted in a clockwise rotation (Brown, 2009).

Slower forms of escape responses have also been examined in various gastropod species. Laboratory and field work on the sea slug *Tritonia diomedea* shows that they escape downstream away from an upstream predator, the sea star *P. helianthoides*, by either turning and then crawling or by swimming and then drifting downstream (Wyeth and Willows, 2006; Wyeth et al., 2006). This escape behaviour is most likely triggered by a combination of chemical cues and water flow, resulting in ET′s oriented away from the predator position (Wyeth and Willows, 2006; Wyeth et al., 2006). Laboratory observations show that the mean heading of their ET′ was 192 deg away from the predator, with a range from approximately 135 to 240 deg (i.e. with the edges of the distribution approximately symmetric with respect to 180 deg) (Wyeth et al., 2006). The ET′s of the periwinkle *Littoraria irrorata* were not affected by the position on its body where predator mucus was applied (Dix and Hamilton, 1993). This contrasts with observations on response in other gastropods, such as *Strombus maculatus*, *Melagraphia aethiops*, *Tegula funebralis*, *Fasciolaria tulipa* and *Nassarius vibex*, which tend to escape away from (usually at aproximately 90 or 180 deg) the direction of predator contact (Berg, 1974; Clark, 1958; Feder, 1963; Snyder and Snyder, 1971; Gore, 1966).

According to Dix and Hamilton, the most adaptive response of the periwinkle *L. irrorata* may be to crawl quickly in the direction it is already facing, in order to encounter a plant stem (found in high density in the periwinkle's habitat) as quickly as possible (Dix and Hamilton, 1993). Therefore, differences in escape trajectory distribution among gastropods may reflect different habitats, types of predator or anatomical constraints (Dix and Hamilton, 1993). The limpet *Siphonaria sirus* tends to escape with ET′s at

approximately 120 and 240 deg (i.e. symmetric with respect to 180 deg) relative to the predator attack of the muricid snail *Thais calvigera* (Iwasaki, 1993). Iwasaki suggests that fleeing in a direction almost perpendicular to that of the attack may be more effective than fleeing away or towards the predator, because it may allow prey to get further away from the predator within a shorter time, and reduce the probability of a second attack (Iwasaki, 1993). In the sea slug *Pleurobranchaea californica*, appetitive or aversive chemotactile stimuli applied to the chemosensory oral veil triggered orienting and aversive turns, respectively, and the turn angles were linearly related to where the stimulus was applied to the animal's body (Yafremava et al., 2007). As in some other animals, e.g. the frog (King and Comer, 1996), orienting turns tend to be relatively precise whereas avoidance turns are more variable, with turn angles of 30–250 deg, which are sufficient to redirect the animal's locomotion quickly away from the stimulus (Jing and Gillette, 2003). This high variability is consistent with the idea of making ETs unpredictable.

In summary, although more work may be needed in order to test the escape-trajectory strategies of fast-moving molluscs such as cephalopods, many gastropods tend to escape within the semi-sector away from the predator, with an ET′ range that is symmetric with respect to the predator's line of attack. Because most work on gastropod has used ET′ as a metric, it would be interesting to test whether using $ET^0$ would provide additional insights into the variability of the response with respect to the prey's initial orientation at the onset of the response.

### Fish

Fish escape behaviour has mostly been investigated in the laboratory using artificial stimuli, although a few predator–prey studies have also been carried out. ETs are variable, but are most frequent between 90 and 180 deg. Domenici and Blake (Domenici and Blake, 1993) and Domenici and Batty (Domenici and Batty, 1997) found that mechanically stimulated single fish (herring *Clupea harengus* and angelfish *Pterophyllum eimekei*, respectively) tend to escape with peaks of $ET^0$s at approximately 130 and 180 deg (Fig. 8A,E), which suggests that these two trajectories may correspond to either keeping the stimulus within the sensory discriminating zone or maximizing distance from the threat, respectively. Work using visual stimulation of fish shows a similar range of $ET^0$s (Meager et al., 2006). Preferred ETs in a similar range to that found by Domenici and Blake (Domenici and Blake, 1993) are apparent in reanalysis of previous data sets (Eaton and Emberley, 1991; Walker et al., 2005) (Fig. 8F,G, respectively). Eaton and Emberley (Eaton and Emberley, 1991) used mechanical stimulation to startle single goldfish and the data reported include only away responses unobstructed by walls, as proximity to the wall can affect ETs. Walker at al. (Walker at al., 2005) investigated the escape response of the guppy *Poecilia reticulata* attacked by real predators, the pike cichlid *Crenicichla alta*. Guppies used ET″s mainly in the range of 80–180 deg, with apparent peaks at the edges of the distribution. Escape success was highest with ET″s of 150–180 deg (Walker et al., 2005). *Polypterus senegalensis*, mechanically stimulated as single individuals (Tytell and Lauder, 2002), also showed high variability in $ET^0$s, with a range spanning approximately 90–270 deg and peaks on either side of 180 deg in similar positions to those of other species tested as single fish (Fig. 8H).

Away and towards responses yield different $ET^0$s in single fish (Domenici and Batty, 1997; Domenici and Blake, 1993) (Fig. 8A,B), whereas in schools (Fig. 8C,D), fish appear to correct their swimming path to the extent that the $ET^0$s of away and towards responses do not differ significantly, perhaps as a result of their tendency to maintain school cohesion (Domenici and Batty, 1997). In addition, schooling fish were found to show relatively uniform $ET^0$s (approximately 150 deg), unlike solitary individuals of the same species, presumably as a result of interactions among neighbours (Domenici and Batty, 1997). Similarly, avoidance responses in schooling whiting, *Merlangius merlangus*, were found to show ET″s of approximately 135 deg, which was interpreted as prey keeping the threat within the limits of their visual field (Hall et al., 1986). Such avoidance responses are, however, slower than Mauthner-initiated escape responses. Cowtail stingrays, *Pastinachus sephens* (both groups and individuals), were found to escape at 135 deg from the approaching stimulus; these ET′s were also interpreted as a way to keep the stimulus within the visual field (Semeniuk and Dill, 2005). In addition, when measured relative to the shore, ET′s in cowtail stingrays were always directed 45 deg away from the shore; hence their escape strategy might also be related to avoiding the threat while seeking refuge in deeper water, a conclusion similar to those from a study on blue crabs (Woodbury, 1986). A unimodal distribution of ET′s within the range of 90–270 deg (ET′=180 deg is denoted as 0 deg in the original figure) was found when roach *Rutilus rutilus* were startled using infrasound (Karlsen et al., 2004) (Fig. 8I). Fish were tested when in groups of seven to eight individuals; therefore, a unimodal ET is in line with observations of herring schools (Domenici and Batty, 1997).

Larval fish produce escape trajectories outside the 90–180 deg range. Herring (*C. harengus*) larvae attacked by predators (cod *G. morhua*) show a bimodal distribution of ET″, with peaks at approximately 30 and 160 deg (calculated relative to the approach path of the predator) (Fuiman, 1993) (Fig. 8J,K). These ET″ correspond to 150 and 20 deg if measured relative to a stimulus positioned at 0 deg at the onset of the response. However, direct comparison of escape trajectories relative to a moving predator nearby and relative to an artificial stationary stimulus is difficult because a moving predator at a close distance changes its angular position considerably relative to the prey (Fig. 8J). In these observations, responses were most successful when directed away (79% survival) from the predator rather than towards (57%), although this was not statistically significant, possibly because of the low sample size (Fuiman, 1993). Skajaa and Browman found that cod larvae showed highly variable ET″, with a unimodal distribution (Skajaa and Browman, 2007). These trajectories were measured as vertical and horizontal angles relative to the attack path of the predator, simulated by water suction into a pipette (Fig. 8L,M). ET″ tended to be directed away from the threat, and the vertical angles also depended on the position of the larvae relative to the suction plume at the start of the stimulus (Skajaa and Browman, 2007). Of all the responses shown in Fig. 8, only those based on data by Eaton and Emberley (Eaton and Emberley, 1991) (Fig. 8F) can be assumed to be Mauthner-neuron mediated, because the data were taken from a previous study in which one of the two Mauthner neurons had been electrophysiologically recorded during the escape (Eaton et al., 1981). Although lower ET variability might be expected in Mauthner-neuron-mediated responses, as is the case for the giant *versus* non-giant neuron response of crayfish (Edwards et al., 1999), no specific comparison of ETs in Mauthner-neuron-mediated *versus* non-Mauthner-neuron-mediated responses is possible with the data available. We do note, however, that variability in the ETs of these Mauthner-neuron-mediated escape
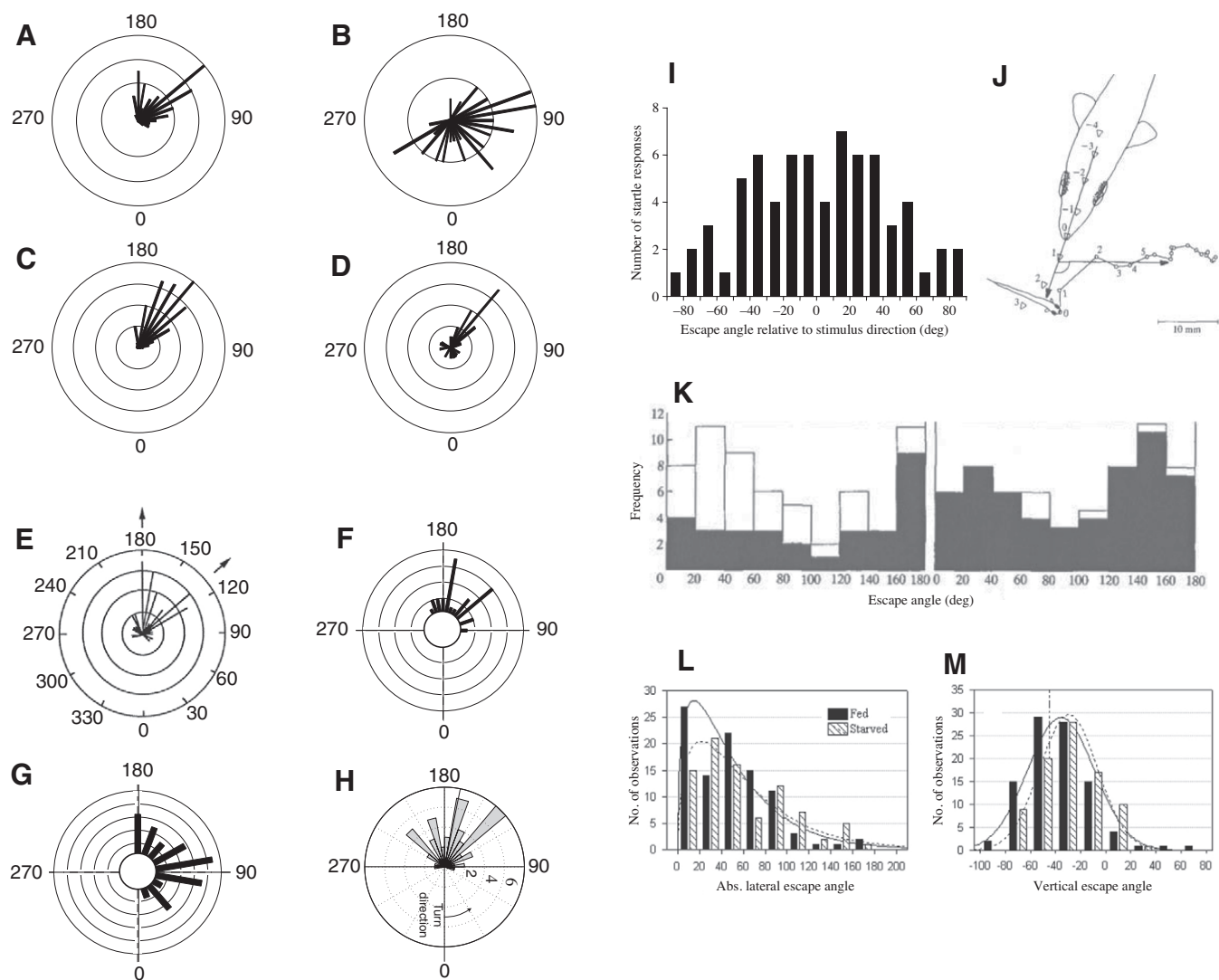
Fig. 8. ETs in fish. In all circular plots, the threatening stimulus is positioned at 0 deg. (A–D) ETs in herring *Clupea harengus*. (A) Away response in single fish (*N*=75). Bin intervals are 10 deg; concentric circles represent a frequency of 4. (B) Towards response in single fish (*N*=42). Bin intervals are 10 deg; concentric circles represent a frequency of 2. (C) Away responses in schooling fish (*N*=223; bin intervals are 10 deg; concentric circles represent a frequency of 10). (D) Towards responses in schooling fish (*N*=30; bin intervals are 10 deg; concentric circles represent a frequency of 2) [reproduced with kind permission from Springer Science+Business Media, fig. 3 from Domenici and Batty (Domenici and Batty, 1997)]. (E) ETs (away responses only) in the angelfish *Pterophyllum eimekei* (*N*=46; bin intervals are 10 deg; concentric circles represent a frequency of 2) [fig. 6B reproduced with permission from Domenici and Blake (Domenici and Blake, 1993)]. (F) ETs in the goldfish *Carassius auratus* (only away responses unobstructed by walls) [*N*$_d$=28; *N*$_o$=28; bin intervals are 10 deg; concentric circles represent a frequency of 2; data are based on an *x–y* plot from fig. 6B of Eaton and Emberley (Eaton and Emberley, 1991)]. (G) ET″s in the guppy *Poecilia reticulata* [*N*=55; data were originally divided into 20 deg bins; concentric circles represent a frequency of 2.5; based on table 4A from Walker et al. (Walker et al., 2005)]. (H) ETs in bichir *Polypterus senegalensis* [*N*=65; bin intervals are 10 deg; concentric circles represent a frequency of 2; fig. 6B reproduced with permission from Tytell and Lauder (Tytell and Lauder, 2002)]. (I) ET′s in roach, *Rutilus rutilus* [*N*=71; 0 deg corresponds to escaping directly away from the stimulus; bin intervals are 10 deg; fig. 3 reproduced with permission from Karlsen et al. (Karlsen et al., 2004)]. (J) Diagram illustrating the angle of ET″s (calculated relative to the attack path of the predator, see main text) in herring *C. harengus* larvae attacked by cod *Gadus morhua* for the data shown in K [reprinted from Animal Behaviour, fig. 2 from Fuiman (Fuiman, 1993) with permission from Elsevier]. (K) ET″s in herring larvae (*N*=59). Left panel: attacks; right panel: false alarm (defined as responses to predator motion by individuals that were not in immediate danger). Both small larvae (filled bars) and large larvae (open bars) are shown. Bin intervals are 20 deg [reprinted from Animal Behaviour, fig. 5C,D from Fuiman (Fuiman, 1993) with permission from Elsevier]. (L,M) ET″s in cod larvae (L, horizontal angles; M, vertical angles), with 0 deg representing a response away from the threat. Responses from fed (filled bars) and unfed (striped bars) larvae are shown. Bin intervals are 20 deg [reprinted from the Journal of Experimental Marine Biology and Ecology, fig. 4A,D from Skaaja and Browman (Skaaja and Browman, 2007) with permission from Elsevier].

responses appears to be relatively high (with ETs from approximately 90 to 180 deg; Fig. 8F).

In summary, fish show a high degree of variability in ETs as a result of wide unimodal distributions (e.g. in schooling fish) or preferred (bimodal) ETs observed in single individuals of some species in response to various kinds of stimulation. The mechanisms producing these ETs are unknown, and the possibility that they correspond to maximizing distance from the predator or keeping the threat within the limits of the angular field to allow continuous sensory tracking should be further explored. Regardless
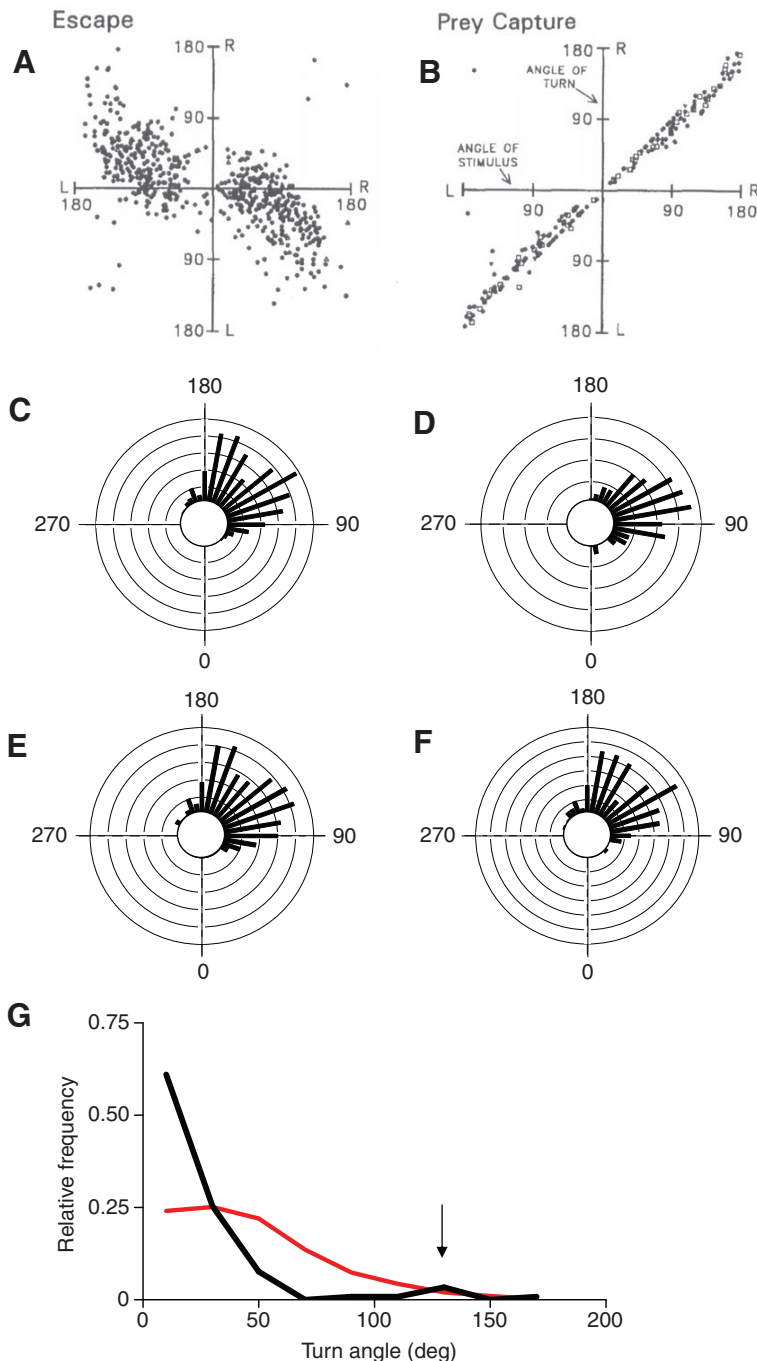
Fig. 9. Escape responses and prey capture in frogs (*Rana pipiens*). (A) *x–y* plots (response turn angle *versus* stimulus angle) of escape responses (*N*=564) and (B) prey capture behaviour (*N*=184) [reproduced with kind permission from Springer Science+Business Media, fig. 8 from King and Comer (King and Comer, 1996)]. Note the low variability in the relation between *x* and *y* in B compared with A. (C) $ET^0$s in away responses ($N_d$=391), (D) $ET^0$s in towards responses ($N_d$=118), (E) $ET^0$s in away responses from left stimuli ($N_d$=191), (F) $ET^0$s in away responses from right stimuli ($N_d$=200). For plots C–F, bin intervals are 10 deg and concentric circles represent a frequency of 5 in all plots except C (frequency is 10). Plots C–F are based on data shown in A. In all circular plots, the threat is positioned at 0 deg. (G) Relative frequency distributions of turn angles in away (red line) and towards responses (black line). Most towards responses are small turns (<50 deg), except for occasional 'overshooting turns' (*sensu* Domenici et al., 2009; indicated by the arrow – these are responses that start out as towards responses, move through a position facing head on to the threat, and end up as away responses), which appear as turns ranging from 100 to 150 deg.

of how they are mediated, multiple trajectories do increase the unpredictability of the response, which is a common feature of escape behaviour observed in the other taxa.

### Larval amphibians and frogs

Many larval amphibians possess a mechanism of neural control that triggers escape responses, similar to that found in fish, that involves Mauthner neurons (Will, 1991). A tactile stimulus directed to the head (but not at the tail or the trunk) of *Xenopus laevis* embryos triggered an escape response with a bimodal distribution of turn angles measured relative to the body axis, possibly as a result of low directionality and variability in the direction of the second muscular flexion (Boothby and Roberts, 1995). These authors

suggest that this variability in turn angles may increase the unpredictability of the response. Tactile stimulation was used to startle the larval and adult salamander *Eurycea bislineata* (Azizi and Landberg, 2002). Although it is not known whether *E. bislineata* possesses Mauthner neurons, they have been described in larvae and adults of other salamander species (Azizi and Landberg, 2002). The escape responses triggered by tactile stimulation applied at right angles to the body (towards the forelimb or the pectoral region of the salamander) were directed at approximately 90 deg from the body axis (and therefore at approximately 180 deg from the stimulus), with larger variation in larvae (Azizi and Landberg, 2002). Such anti-predator behaviour would position the tail closest to and the head furthest from the
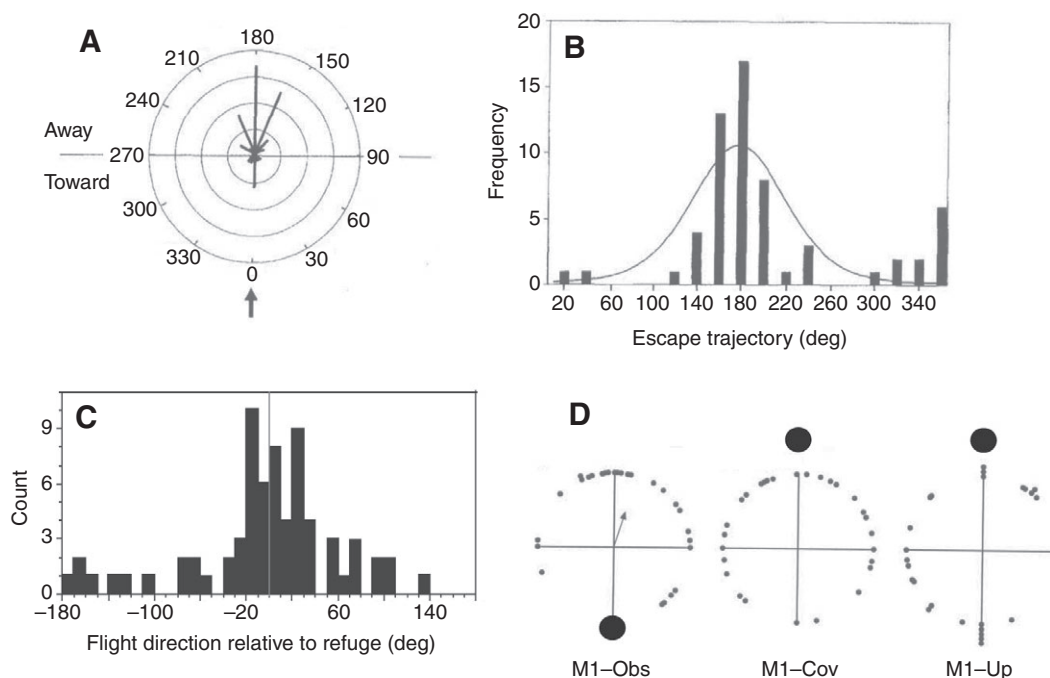
Fig. 10. Escape responses in lizards. (A) ET$^0$s in *Psammodromus algirus* (*N*=60). Bin intervals are 20 deg; concentric circles represent a frequency of 5; the threatening stimulus is at 0 deg. ET$^0$s are different from a von Mises distribution, shown as the curve in B [fig. 1 from Martin and Lopes (Martin and Lopes, 1996) © 1996 by the American Psychological Association; reproduced with permission]. (C) ET's relative to a refuge (cliff, at 0 deg) of the 70 side-blotched lizard (*Uta stansburiana*), showing non-random ET's toward the refuge [fig. 3A from Zani et al. (Zani et al., 2009) © 2008 NRC Canada or its licensors; reproduced with permission]. (D) ET's in *Uma scoparia* (*N*=28). Left: ET's relative to the approaching threat, whose position is indicated by the filled circle on the bottom. Centre: the same ET's measured relative to the nearest vegetation cover (position indicated by the filled circle at the top). Right: the same ET's measured relative to the steepest uphill path indicated by the filled circled at the top. Only the distribution of ET's in the left plot shows a significant difference from a random distribution. Small filled circles represent single events [reprinted from Animal Behaviour, fig. 3 from Jayne and Ellis (Jayne and Ellis, 1998), with permission from Elsevier].

stimulus, in line with observations that tadpoles and salamanders often suffer tail damage when attacked by predators (Whiteman and Wissinger, 1991).

Work on frog escape responses is mainly based on visual stimulation. When stimulated at 45 deg above the horizontal plane, frogs (genus *Craugastor*) escaped away from the stimulus at various angles relative to their body axis (Cooper et al., 2008). Although the escape trajectories were not calculated, the frogs were usually stimulated when they were at approximately right angles to the stimulus, hence their mean response angle of 44.4 deg corresponds to an ET″ of approximately 135 deg. Although ET″s tended to be away from the threat when it was approaching at 45 deg, they were random with respect to the frog's initial orientation for threats approaching from above, contributing to the unpredictability of the response (Cooper et al., 2008).

The escape system of frogs, responding to visual stimulation, is highly adaptable. Frogs were able to remember obstacles that had been removed from an arena up to 60 s later; they avoided jumping in the direction where the obstacle had been previously located (Ingle and Hoff, 1990). Frogs can compensate for changes in their own body orientation and remember barrier locations in real-world coordinates (Ingle and Hoff, 1990). In addition, frogs tend to modulate their ETs by seeking dark areas representing potential refuges. ET's, in response to frontal stimuli positioned at 45 deg from the body axis, range from approximately 90 to 180 deg, with peaks at approximately 90 and 135 deg (Ingle and Hoff, 1990).

The escape directions of frogs (*Rana pipiens*) startled using a looming black square visual stimulus, show high variability in the *x–y* plots of escape angle *versus* stimulus direction, in stark contrast to the low variability observed in *x–y* plots of attacks angles *versus* stimulus angles reported for prey capture behaviour (King and Comer, 1996) (Fig. 9A,B). According to King and Comer (King and Comer, 1996), escape variability may be a fundamental component in the strategy of predator avoidance in these frogs, and could be an intrinsic property of the neural pathways controlling escapes. Given the higher speed of escape when compared with attacks, it was suggested that escape turning optimizes the speed of execution whereas attacks maximize spatial accuracy (King and Comer, 1996). Reanalysis of the original *x–y* escape data as circular plots shows two peaks of ET$^0$s, at approximately 110 and 160 deg. As found in cockroaches (Domenici et al., 2009), the frogs' towards responses show similar ET$^0$s as the away responses, with the exception of the largest ET$^0$ (i.e. thus escaping at 110 deg but not at 160 deg) (Fig. 9C,D). Preferred trajectories are apparent in both left and right turns (Fig. 9E,F), suggesting that they are not the result of random fluctuation in the system. In addition, the turn angles (i.e. angles measured relative to the body axis) of towards responses are relatively small compared with those of away responses (<50 deg; Fig. 9G). These small turns of the towards responses occur mainly when the stimulus direction is >90 deg, thus they enable frogs to reach ET$^0$s >90 deg. Large turns (>100 deg) are all overshooting responses *sensu* Domenici et al. (Domenici et al., 2009), i.e. escapes that start out as towards responses but end up as away responses. This variability in ETs may serve to increase

protean unpredictability (Comer, 2009; Domenici et al., 2011), and contrasts with the high precision in jump direction of the same frogs when aiming at prey (King and Comer, 1996). It seems possible that the presence of the two main peaks of $ET^0$s may result from the need to keep either of the vertical edges of the visual stimulus at the same angular position of the visual field. More work using stimuli of different sizes would be needed to test this.

The treefrog *Hyla regilla*, stimulated head-on by an approaching model predator, showed an $ET''$ of approximately 70 deg with high variability, the highest values in the frequency distribution being at approximately 45 and 90 deg (Dill, 1977). A more recent study on three species of Trinidadian frogs (the stream frog *Mannophryne trinitatis* and the treefrogs *Trachycephalus venulosus* and *Hypsiboas geographicus*) using a mechanical stimulation (a tap on the grid close to the frog) showed that $ET'$s were highly variable, and some evidence of bimodality was suggested for *M. trinitatis* and *H. geographicus* (Royan et al., 2010). Lateral stimulation in *M. trinitatis* elicited $ET'$s of approximately 60 and 135 deg, and the latter $ET'$ was suggested to correspond to the limits of the visual zone (Royan et al., 2010).

To summarize, ETs in amphibians show a relatively high variability, and bimodality was observed in some frog species. Generally speaking, the ETs of amphibians appear to share a number of characteristics with those of fish, both in terms of ET distribution patterns and the factors modulating them.

### Lizards

Work on lizard escape behaviour is quite extensive and includes numerous field observations using human approach as the stimulus. Cooper et al. used different combinations of approaching single and multiple human 'predators' and found that the lizard *Podarcis lilfordi* modulates its $ET''$s depending on the number of predators attacking from different directions and their speed (Cooper et al., 2007). When attacked by a single predator, $ET''$s were approximately 120 deg [i.e. 60 deg away from the predator's attack path in fig. 2 of Cooper et al. (Cooper et al., 2007)] for slow attacks and approximately 160 deg for fast attacks. These authors suggested that $ET''$ in response to fast attacks may serve to maximize distance from the predator whereas those stimulated by slow attacks may serve to keep predators within the visual field. Using combinations of predator attacks, it was found that prey escape with $ET''$s of approximately 90 deg when attacked by predators from opposite directions, and with $ET''$s of approximately 45 deg when attacked by predators at 90 deg from each other (Cooper et al., 2007). Lizards therefore seem to be able to produce a compromise $ET''$ when attacked by two predators, rather than focusing on escaping away from one of them (Cooper et al., 2007). A laboratory study of the lizard *Psammodromus algirus* found that it uses two main $ET^0$s (clustered around 180 deg and a few at 0 deg). $ET^0$s at 180 deg are used when the initial body orientation is already away from the incoming predator, but when the initial body orientation is facing the predator prior to the attack, the lizards produce $ET^0$s at both 0 deg and approximately 180 deg, making their response relatively unpredictable (Martin and Lopez, 1996) (Fig. 10A,B).

In the field, lizard escape trajectories appear to be largely influenced by refuges and topography (Cooper, 1997; Zani et al., 2009). Zani et al. showed that the $ET'$s of the lizard *Uta stansburiana* were randomly oriented with respect to the approaching model predator, but oriented non-randomly with respect to the nearest cliff (refuge) (Fig. 10C), though they only seemed to escape towards the cliff when startled at <15 m from it (Zani et al., 2009). Similarly, the
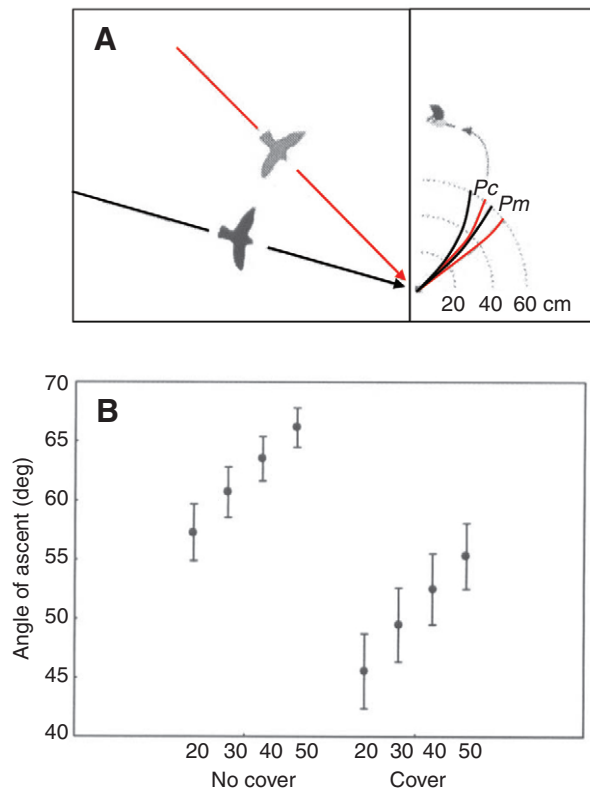


Fig. 11. Escape trajectories in birds, in the vertical plane. (A) The angle of attack of the predator determines the angle of ascent of the prey in blue tits (*Parus caeruleus*, Pc) and great tits (*Parus major*, Pm). Both species escape by taking off in a direction away from the predator, make a half-loop and attempt to escape by flying above the predator in a direction opposite to the predator's approach. Prey tend to ascend more steeply (black lines) when attacked at lower angles than when attacked at high angles (red lines) [reproduced with kind permission from Springer Science+Business Media, fig. 1 from Lind et al. (Lind et al., 2002)]. (B) The effect of cover on the angle of ascent at 20, 30, 40 and 50 cm along the escape flight of great tits. Birds tend to take off at steeper angles in the absence of cover [reproduced with kind permission from Springer Science+Business Media, fig. 2 from Kullberg and Lafrenz (Kullberg and Lafrenz, 2007)].

probability that *Leiocephalus carinatus* entered a refuge after being threatened was found to be inversely related to refuge distance (Cooper, 2007). The lizard *P. algirus* escaped with random trajectories relative to the attack (Martin and Lopez, 2000). However, their direction of escape ($ET''$ <90 deg or >90 deg) was affected by the type of refuge available, suggesting that in the field this species does not necessarily maximize the distance between itself and the predator, but produces $ET''$s dependent on the type of refuges nearby (Martin and Lopez, 2000). In contrast, *Uma scoparia* was observed to escape with non-random $ET'$s relative to the threat (Fig. 10D) but with random $ET'$s relative to cover and topography when examined in the field (Jayne and Ellis, 1998).

In summary, these results show that both refuges and threat position can affect escape trajectories in lizards, and the relative importance of their effect may be dependent on the particular species, refuge distance and environmental context.

### Birds

Studies of escape trajectories in birds has focused mainly on trajectories in the vertical plane, i.e. take-off angle, which appears
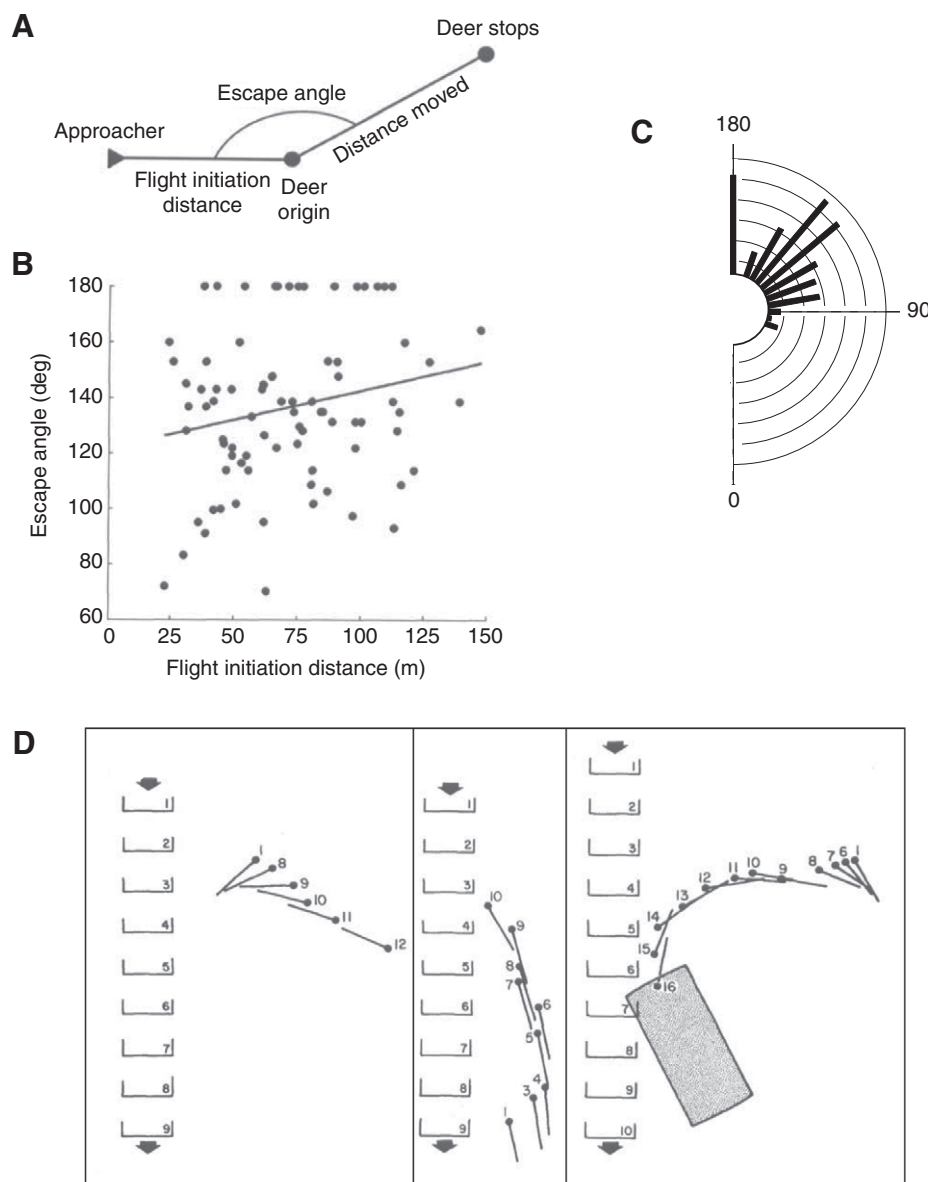
**A**



**B**



**C**



**D**



Fig. 12. (A) Escape variables in black-tailed deer (*Odocoileus hemionus columbianus*). Flight initiation distance (reaction distance) is the distance between the approaching threat and the deer at the onset of the escape response. Escape angle (ET″) is the angle between the line of flight initiation distance and the line of distance moved (between deer origin and deer stops) [reproduced with permission from Oxford University Press, fig. 1 from Stankowich and Coss (Stankowich and Coss, 2007)]. (B) The relationship between flight initiation distance and escape angle in deer [reproduced with permission from Oxford University Press, fig. 2 from Stankowich and Coss (Stankowich and Coss, 2007)]. (C) Reanalysis of the data shown in B as a semi-circular plot of ET″s ($N_o$=82, $N_d$=79; bin intervals are 10 deg; concentric semi-circles represent a frequency of 2.5; threatening stimulus at 0 deg). (D) Escape responses in gerbils (*Meriones unguiculatus*) attacked by a moving stimulus [reproduced with kind permission from Springer Science+Business Media, fig. 4A–C from Ellard and Goodale (Ellard and Goodale, 1988)]. The positions of the stimulus are represented by the descending series of numbered three-sided boxes. The stimulus moves from top to bottom. The successive positions of the body axis of the gerbil are represented by the numbered segments, where the snout is represented by the dot at the end of each segment. Numbers correspond to video frames shot at 60 Hz. Left: the gerbil makes an escape response in a direction away from a peripherally presented stimulus. Centre: the gerbil makes an escape response in a direction towards the trajectory of a centrally presented stimulus. Right: when escape responses are elicited in the presence of a refuge, gerbils escape towards the entrance of that refuge (grey rectangle).

to be a fundamental determinant of prey survival in birds (Cresswell, 1993; Kullberg et al., 1998; Kullberg and Lafrenz, 2007). Predator–prey interactions beyond the initial prey startle response have also been examined, taking into account the relative locomotor performance (e.g. speed and manoeuvrability) of predator and prey (Hedenstrom and Rosen, 2001; van den Hout et al., 2010), but discussion of such work is beyond the scope of this review. The final direction of escape in terms of habitat type (e.g. herbaceous vegetation, woody vegetation, air) is largely taxon and life-history specific (Lima, 1993). The strategy in the initial phase of predator evasion is probably affected by factors such as body mass, proximity to cover and the presence of conspecifics (Kullberg and Lafrenz, 2007; Witter and Cuthill, 1993). The type of anti-predator response, such as crouching, creek diving or flying, may depend on the predator species and the pattern of attack (Cresswell, 1993). Take-off angle can be affected by a number of factors. When attacked from a low attack angle, great and blue tits take off more steeply (Fig. 11A) than when attacked from a higher angle [great tits *Parus major* (Kullberg et al., 1998); blue tits *Parus caeruleus* (Lind et al., 2002)]. Typically, these escaping birds

initially fly away from the predator and then make a half loop, attempting to escape by flying above the predator (Lind et al., 2002) (great tits; Fig. 11A).

Body mass affects take-off angle (Lind et al., 1999). The take-off angles of starlings (*Sturnus vulgaris*) carrying small lead weights are lower than in controls (Witter et al., 1994), and gravid females take off at lower angles than post-laying females (Lee et al., 1996). Also, take-off angles were greater for *Parus* spp. that detected a predator at a shorter distance (Lind et al., 2003). Habitat type can also have an effect on take-off angle; in starlings, this was close to the ground when escaping in long grass, perhaps because tall clumps were hindering take-off or such clumps were used as protective cover, whereas on short grass their take-off angle was much steeper (>45 deg) (Devereux et al., 2008). Similarly, great tits being attacked by predators in the absence of cover took off at a 10 deg higher angle compared with prey that took off in the presence of cover (Kullberg and Lafrenz, 2007) (Fig. 11B).

Less information is available on bird escape trajectories in the horizontal plane. Kullberg et al. subjected sedge warblers (*Acrocephalus schoenobaenus*) to a simulated predator attack by a

model merlin (*Falcus columbarius*) (Kullberg et al., 2000). Half escaped by taking off in a straight line away from the predator model, whereas 43% darted sideways at an ET″ of almost 90 deg from the model (Kullberg et al., 2000). Although escaping away from the predator could be a strategy aimed at maximizing distance from the threat, Kullberg et al. suggest that escaping at 90 deg from the predator's line of attack may be adaptive because the probability of disappearing from the predator's view is high in the dense vegetation of the sedge warbler's habitat (Kullberg et al., 2000). Devereux et al. showed that a starling tends to move away from an approaching hawk predator with an angular variation of approximately 90 deg (Devereux et al., 2008). Blue tits that detect a predator late in its high-speed attack tend to dodge sideways more often than when attacked at slow speed (Lind et al., 2003). These authors suggest that this outmanoeuvring strategy is used by prey when attacked by predators approaching with a high-speed attack flight, and in these cases it is advantageous to divert laterally rather than taking off at a steep angle, because the latter would reduce acceleration (Witter and Cuthill, 1993). In contrast, when attacked by slower predators, the prey bird may benefit more from escaping to cover, and out-climbing the predator (Lind et al., 2002).

In summary, birds show a variety of escape trajectories, both in the vertical and horizontal planes, which are largely context dependent. Some bird species appear to show two main alternative ET strategies, which are largely determined by the predator attack speed: taking off initially away from the predator to then climb back over it (Fig. 11A) or darting sideways at approximately 90 deg from the predator's rapid line of attack.

## Mammals

Work on mammal ETs includes laboratory investigations on small rodents and a few field studies on larger mammals such as ungulates. Field observations show that the escape angle (ET″) of black-tailed deer (*Odocoileus hemionus columbianus*), reacting to human approach, increases with reaction distance (i.e. flight initiation distance; Fig. 12A,B) (Stankowich and Coss, 2007). These results were interpreted as deer using relatively small escape angles to hinder pursuit when the threat is close, whereas they flee directly away from the approaching threat when the latter is further away. Stankowich and Coss suggested that taking an escape angle that does not maximize the absolute distance between the predator and prey (i.e. ET″ <180 deg) might signal to the predator that the prey can easily maintain a lead during a pursuit, thereby deterring further chase (Stankowich and Coss, 2007). In addition, stotting behaviour allows deer to rapidly change direction during escapes at large ET″ angles (Geist, 1981), which forces the predator to change direction during approach and may allow the prey to put more distance between itself and the predator (Stankowich and Coss, 2007). A semi-circular frequency distribution plot of the escape angles from Stakowich and Coss (Stankowich and Coss, 2007) shows two ET″ peaks, i.e. at 140 and 180 deg (Fig. 12C). Although the narrow range of angles around 180 deg may be explained by limitation in the angular resolution, we cannot exclude the possibility that this apparent bimodal distribution may be an expression of the kind of adaptive escape variability seen in some other taxa.

In the same study, continuous threatening behaviour by an approaching human led to longer durations of escape behaviour (inducing trotting and stotting), and deer tended to escape uphill and into taller vegetation, using these habitat features as a refuge (Stankowich and Coss, 2007). The effect of habitat characteristics on escape behaviour may, however, be different even in closely

related species of deer. When approached by coyotes, mule deer (*Odocoileus hemionus*) escape uphill and towards slopes whereas white-tailed deer (*Odocoileus virginianus*) flee downhill and away from slopes (Geist, 1981; Lingle, 2002). These two species also differ in their initial response to a threat. Mule deer tend to look directly at the approaching threat whereas white-tailed deer tend to flee or to look in a direction different from the threat's direction. Mule deer may detect predators earlier than white-tailed deer as an adaptation to their more open habitats, or because they need more time to coordinate subsequent anti-predator defences (Lingle and Wilson, 2001). Fieldwork on reindeer, *Rangifer tarandus tarandus*, startled by approaching humans found that escape direction was largely influenced by terrain and wind direction; reindeer escaped more often uphill and into the wind than on level ground, downhill or in other directions relative to the wind (Reimers et al., 2006).

Escape responses of small rodents have mainly been studied in the laboratory. By moving a dead mouse, Shifferman and Eilam (Shifferman and Eilam, 2004) found that the barn owl, *Tyto alba*, was more successful at capturing the prey when the mouse was moved directly away from the owl compared with when it was moved sideways. Other work using live prey showed that spiny mice did indeed tend to escape in those directions in which owls had a lower success in catching the simulated prey, i.e. sideways (Ilany and Eilam, 2008). This accords with geometrical models (Domenici, 2002b; Weihs and Webb, 1984) that show that it makes sense to escape sideways when predators are faster than their prey. In these experiments, failure to catch prey that move sideways may also be due to constraints in postural head movements in aerial predators (e.g. the barn owl) that cannot move the eyes but rather move the entire head when tracking prey (Shifferman and Eilam, 2004). These authors also found that escaping towards the predator was safer than away from the predator. This may be related to the different planes of motion in predators compared with prey, bird in the air and mouse on the ground, which would clearly not apply in situations in which predators and prey are moving on one single plane – prey moving towards a predator may well end up in the predator's mouth.

These results are similar to studies on gerbils *Meriones unguiculatus* escaping in response to an aerial attack by a simulated model predator. When the testing arena contained a refuge, gerbils usually ran towards the refuge (Ellard and Goodale, 1988) (Fig. 12D). If no refuge was available, gerbils showed two main escape strategies: they either undercut the stimulus (with an initial ET″ of approximately 0 deg) or they ran away from it (with an initial ET″ of approximately 120 deg), depending on the relationship between the orientation of the gerbil's body at the time of stimulation and the stimulus itself (Ellard and Goodale, 1988) (Fig. 12D). Because of the high approach velocity of many aerial predators, this undercutting behaviour may provide the gerbil with enough time to escape successfully (Ellard and Goodale, 1988). However, if the gerbil is already partially turned away from the predator, it may be advantageous to keep running without spending time in a turn towards the predator (Ellard and Goodale, 1988). Regardless of the influence of the initial orientation, the occurrence of alternative escape tactics increases unpredictability in the escape response of these small mammals when attacked by aerial predators. This protean unpredictability of the response, beyond the initial reaction, is further enhanced by erratic movements such as zigzagging and stop-and-go running and freezing behaviours (Edut and Eilam, 2004; Eilam, 2005). Although further work suggests that the main determinant of escape route by gerbils, when escaping from a threat, is the position of a safe refuge rather than the

approaching trajectory of the threat, there is still a marked tendency for the path of the threat to affect escape trajectory, especially during the early phase of the response (Ellard, 1993; Ellard and Eller, 2009; Ellard and Goodale, 1988).

To summarize, mammals show a number of possible alternative strategies in their initial escape response. However, the complexity of their response is modulated by many external factors related to the presence of refuges and barriers as well as the type of terrain and familiarity with it (Clarke et al., 1993; Ellard and Eller, 2009; Vlasak, 2006).

## Conclusions

It appears that certain escape strategies (single ETs and highly variable ETs within a limited angular sector, often associated with multiple peaks) are found across most taxa, suggesting that these escape trajectory patterns may be the result of convergent evolution. The precise determination of which of these strategies is used by any particular species has rarely been tested statistically in the examples reviewed here, and indeed in many cases the sample sizes are too small to draw rigorous conclusions about the ET distribution pattern. A number of examples do show relatively high variability within a limited angular sector (mainly 90–180 deg), which may correspond to either preferred ETs or random ETs within a given sector. $ET^0$s >180 deg are rarely used; hence it is possible that variability with the 90–180 deg sector provides sufficient unpredictability while minimizing the time needed to complete the body rotation. A distribution with multiple preferred ETs is suggested in at least one example in each of the animal groups reviewed here {insects (Domenici et al. 2008); swimming crustaceans (Kaiser et al. 1992); crabs (Domenici and Blake, 1993); plankton (Buskey et al., 2002); molluscs (Iwasaki, 1993); fish (Domenici and Blake, 1993); frogs (Royan et al., 2010); lizards (Martin and Lopez, 1996); birds (Kullberg et al., 2000); and mammals [Fig. 12C, based on data from Stankowich and Coss (Stankowich and Coss, 2007)]}. Given that high variability is a common feature of ETs across many taxa, in line with the theoretical expectation that high variability provides desirable unpredictability in the prey's response (Domenici et al., 2011), systematic experimental observations on real predators and prey would provide important data on the actual survival value of such variability.

A unimodal pattern of ETs was found in most taxa reviewed here, and was in some cases related to stimulus tracking (e.g. Lazzari and Varju, 1990). It is possible that in these species, tracking the threat from a distance has a higher survival value than escaping in an unpredictable fashion. Further work is needed to conclusively disentangle the various possible ET patterns of distribution by using large sample sizes and statistical tools that test the goodness-of-fit of the alternative distributions.

Random ETs appear to be relatively rare (e.g. Branckenbury, 1999), and they may be related to constraints in the manoeuvrability of the prey, typical of some insect species (Domenici et al., 2011). Similarly, published reports of refuge effects are relatively uncommon and are mainly confined to lizards and mammals, to which can be added the intermediate strategy (i.e. resulting in a trajectory that is intermediate between escaping towards a refuge and away from a threat) found in some fish (Semeniuk and Dill, 2005) and crabs (Woodbury, 1986). The effect of refuge is, however, likely to be a more common occurrence than is indicated by the small number of examples reviewed here. Many other animal groups, e.g. birds (Lima, 1993), are heavily influenced by the presence of refuges. It is likely that the paucity of refuge effect in

the literature may be related to the preponderance of laboratory studies in which refuges were not provided. The effects of animal design constraints and environmental context on ETs are discussed in depth in Domenici et al. (Domenici et al., 2011).

In conclusion, although there are a relatively large number of examples in the literature that suggest trends in ET patterns, work in the field of comparative 'animal escapology' would benefit from a standardization of the analytical approach using circular statistics and related tests as suggested here, in addition to the use of large data sets. Experimentally testing the effect of the presence of refuges could provide a more realistic scenario for predicting the outcome of escape behaviour in nature. Furthermore, the hypothesized adaptive value of high variability in ETs needs to be tested by observing real encounters between prey and predators.

## References

**Ansell, A. D., Cattaneo-Vietti, R. and Chiantore, M.** (1998). Swimming in the Antarctic scallop *Adamussium colbecki*: analysis of in situ video recordings. *Antarct. Sci.* **10**, 369-375.

**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.

**Azizi, E. and Landberg, T.** (2002). Effects of metamorphosis on the aquatic escape response of the two-lined salamander (*Eurycea bislineata*). *J. Exp. Biol.* **205**, 841-849.

**Bailey, D. M. and Johnston, I. A.** (2005). Scallop swimming kinematics and muscle performance: modelling the effects of "within-animal" variation in temperature sensitivity. *Mar. Freshw. Behav. Physiol.* **38**, 1-19.

**Batschelet, E.** (1981). *Circular Statistics in Biology*. New York: Academic Press.

**Bennet-Clark, H. C.** (1975). Energetics of jump of locust *Schistocerca gregaria*. *J. Exp. Biol.* **63**, 53-83.

**Berg, C. J.** (1974). Comparative ethological study of strombid gastropods. *Behaviour* **51**, 274-322.

**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 hatchling *Xenopus laevis* embryos. *J. Zool.* **235**, 113-125.

**Brackenbury, J.** (1999). Regulation of swimming in the *Culex pipiens* (Diptera, Culicidae) pupa: kinematics and locomotory trajectories. *J. Exp. Biol.* **202**, 2521-2529.

**Brackenbury, J. and Hunt, H.** (1993). Jumping in springtails-mechanism and dynamics. *J. Zool.* **229**, 217-236.

**Brown, J. W.** (2009). Directionally mediated escape swimming in the scallop. *Integr. Comp. Biol.* **49**, E206-E206.

**Burdick, D. S., Hartline, D. K. and Lenz, P. H.** (2007). Escape strategies in co-occurring calanoid copepods. *Limnol. Oceanogr.* **52**, 2373-2385.

**Buskey, E. J. and Hartline, D. K.** (2003). High-speed video analysis of the escape responses of the copepod *Acartia tonsa* to shadows. *Biol. Bull.* **204**, 28-37.

**Buskey, E. J., Lenz, P. H. and Hartline, D. K.** (2002). Escape behavior of planktonic copepods in response to hydrodynamic disturbances: high speed video analysis. *Mar. Ecol. Prog. Ser.* **235**, 135-146.

**Camhi, J. M.** (1983). *Neuroethology: nerve cells and the natural behavior of animals*. Sunderland, MA: Sinauer.

**Camhi, J. M. and Tom, W.** (1978). The escape behaviour of the cockroach *Periplaneta americana*. I. Turning response to wind puffs. *J. Comp. Physiol. A* **128**, 193-201.

**Card, G. and Dickinson, M. H.** (2008). Visually mediated motor planning in the escape response of Drosophila. *Curr. Biol.* **18**, 1300-1307.

**Cheng, J. Y., Davison, I. G. and DeMont, M. E.** (1996). Dynamics and energetics of scallop locomotion. *J. Exp. Biol.* **199**, 1931-1946.

**Clark, W. C.** (1958). Escape responses of herbivorous gastropods when stimulated by carnivorous gastropods. *Nature* **181**, 137-138.

**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.

**Cooke, I. R. C. and Macmillan, D. L.** (1985). Further-studies of crayfish escape behavior. I. The role of the appendages and the stereotyped nature of nongiant escape swimming. *J. Exp. Biol.* **118**, 351-365.

**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.** (2006). Risk factors and escape strategy in the grasshopper *Dissosteira carolina*. *Behaviour* **143**, 1201-1218.

**Cooper, W. E.** (2007). Escape and its relationship to pursuit-deterrent signalling in the cuban curly-tailed lizard *Leiocephalus carinatus*. *Herpetologica* **63**, 144-150.

**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.

**Cooper, W. E., Caldwell, J. P. and Vitt, L. J.** (2008). Escape responses of cryptic frogs (Anura: Brachycephalidae: Craugastor) to simulated terrestrial and aerial predators. *Behaviour* **145**, 25-38.

**Cresswell, W.** (1993). Escape responses by redshanks, *Tringa totanus*, on attack by avian predators. *Anim. Behav.* **46**, 609-611.

**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.

**Daniel, T. L. and Meyhofer, E.** (1989). Size limits in escape locomotion of carridean shrimp. *J. Exp. Biol.* **143**, 245-265.

**Devereux, C. L., Fernandez-Juricic, E., Krebs, J. R. and Whittingham, M. J.** (2008). Habitat affects escape behaviour and alarm calling in common starlings *Sturnus vulgaris. Ibis* **150**, 191-198.

**Dill, L. M.** (1977). Handedness in Pacific tree frog (*Hyla regilla*). *Can. J. Zool. Rev. Can. Zool.* **55**, 1926-1929.

**Dix, T. L. and Hamilton, P. V.** (1993). Chemically mediated escape behavior in the marsh periwinkle *Littoraria irrorata* Say. *J. Exp. Mar. Biol. Ecol.* **166**, 135-149.

**Domenici, P.** (2002a). Escape trajectory, ecological. In *Encyclopedia of Environmetrics*, Vol. 2 (ed. A. H. El-Shaarawi and W. W. Piegorsch), pp. 708-711. Chichester: John Wiley & Sons.

**Domenici, P.** (2002b). 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. 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.** (1997). The kinematics and performance of fish fast-start swimming. *J. Exp. Biol.* **200**, 1165-1178.

**Domenici, P. and Blake, R. W.** (1993). Escape trajectories in angelfish (*Pterophyllum eimekei*). *J. Exp. Biol.* **177**, 253-272.

**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 I: theoretical issues and emerging trends in escape trajectories *J. Exp. Biol.* **214**, 2463-2473.

**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.

**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.

**Edwards, D. H., Heitler, W. J. and Krasne, F. B.** (1999). Fifty years of a command neuron: the neurobiology of escape behavior in the crayfish. *Trends Neurosci.* **22**, 153-161.

**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.** (1993). Organization of escape movements from overhead threats in the Mongolian gerbil (*Meriones unguiculatus*). *J. Comp. Psychol.* **107**, 242-249.

**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.

**Ellard, C. G. and Goodale, M. A.** (1988). A functional-analysis of the collicular output pathways-a dissociation of deficits following lesions of the dorsal tegmental decussation and the ipsilateral collicular efferent bundle in the Mongolian gerbil. *Exp. Brain Res.* **71**, 307-319.

**Eriksson, E. S.** (1980). Movement parallax and distance perception in the grasshopper (*Phaulacridium vittatum* (Sjöstedt)). *J. Exp. Biol.* **86**, 337-340.

**Feder, H. M.** (1963). Gastropod defensive responses and their effectiveness in reducing predation by starfishes. *Ecology* **44**, 505-512.

**Fields, D. M. and Yen, J.** (1997). The escape behavior of marine copepods in response to a quantifiable fluid mechanical disturbance. *J. Plankton Res.* **19**, 1289-1304.

**Fuiman, L. A.** (1993). Development of predator evasion in Atlantic herring, *Clupea harengus* L. *Anim. Behav.* **45**, 1101-1116.

**Geist, V.** (1981). Behavior: adaptive strategies in mule deer. In *Mule and Black-Tailed Deer of North America* (ed. O. C. Wallmo), pp. 156-223. Lincoln, NE: University of Nebraska Press.

**Gore, R. H.** (1966). Observations on escape response in *Nassarius vibex* (Say) (Mollusca: Gastropoda). *Bull. Mar. Sci.* **16**, 423-434.

**Hall, S. J., Wardle, C. S. and Maclennan, D. N.** (1986). Predator evasion in a fish school-test of a model for the fountain effect. *Mar. Biol.* **91**, 143-148.

**Hassenstein, B. and Hustert, R.** (1999). Hiding responses of locusts to approaching objects. *J. Exp. Biol.* **202**, 1701-1710.

**Hedenstrom, A. and Rosen, M.** (2001). Predator versus prey: on aerial hunting and escape strategies in birds. *Behav. Ecol.* **12**, 150-156.

**Hemmi, J. M.** (2005). Predator avoidance in fiddler crabs: I. Escape decisions in relation to the risk of predation. *Anim. Behav.* **69**, 603-614.

**Hemmi, J. M. and Pfeil, A.** (2010). A multi-stage anti-predator response increases information on predation risk. *J. Exp. Biol.* **213**, 1484-1489.

**Herberholz, J., Sen, M. M. and Edwards, D. H.** (2004). Escape behavior and escape circuit activation in juvenile crayfish during prey–predator interactions. *J. Exp. Biol.* **207**, 1855-1863.

**Himmelman, J. H., Guderley, H. E. and Duncan, P. F.** (2009). Responses of the saucer scallop *Amusium balloti* to potential predators. *J. Exp. Mar. Biol. Ecol.* **378**, 58-61.

**Hiraguchi, T. and Yamaguchi, T.** (2000). Escape behavior in response to mechanical stimulation of hindwing in cricket, *Gryllus bimaculatus. J. Insect Physiol.* **46**, 1331-1340.

**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.

**Iwasaki, K.** (1993). Analyses of limpet defense and predator offense in the field. *Mar. Biol.* **116**, 277-289.

**Jacklyn, P. M. and Ritz, D. A.** (1986). Hydrodynamics of swimming in scyllarid lobsters. *J. Exp. Mar. Biol. Ecol.* **101**, 85-99.

**Jakobsen, H. H.** (2002). Escape of protists in predator-generated feeding currents. *Aquat. Microb. Ecol.* **26**, 271-281.

**Jayne, B. C. and Ellis, R. V.** (1998). How inclines affect the escape behaviour of a dune-dwelling lizard, *Uma scoparia. Anim. Behav.* **55**, 1115-1130.

**Jing, J. and Gillette, R.** (2003). Directional avoidance turns encoded by single interneurons and sustained by multifunctional serotonergic cells. *J. Neurosci.* **23**, 3039-3051.

**Kaiser, M. J., Gibson, R. N. and Hughes, R. N.** (1992). The effect of prey type on the predatory behavior of the 15-spined stickleback, *Spinachia spinachia* (L.). *Anim. Behav.* **43**, 147-156.

**Kanou, M., Ohshima, M. and Inoue, J.** (1999). The air-puff evoked escape behavior of the cricket *Gryllus bimaculatus* and its compensatory recovery after cereal 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.

**Karlsen, H. E., Piddington, R. W., Enger, P. S. and Sand, A.** (2004). Infrasound initiates directional fast-start escape responses in juvenile roach *Rutilus rutilus. J. Exp. Biol.* **207**, 4185-4193.

**King, J. R. and Comer, C. M.** (1996). Visually elicited turning behavior in *Rana pipiens*: comparative and neural control of escape and prey capture. *J. Comp. Physiol. A Neuroethol. Sens. Neural Behav. Physiol.* **178**, 293-305.

**Kolton, L. and Camhi, J. M.** (1995). Cartesian representation of stimulus direction: parallel processing by two sets of giant interneurons in the cockroach *J. Comp. Physiol. A* **176**, 691-702.

**Kondoh, Y., Arima, T., Okuma, J. and Hasegawa, Y.** (1991). Filter characteristics of cercal afferents in the cockroach. *J. Comp. Physiol. A* **169**, 653-662.

**Kullberg, C. and Lafrenz, M.** (2007). Escape take-off strategies in birds: the significance of protective cover. *Behav. Ecol. Sociobiol.* **61**, 1555-1560.

**Kullberg, C., Jakobsson, S. and Fransson, T.** (1998). Predator-induced take-off strategy in great tits (*Parus major*). *Proc. R. Soc. Lond. B* **265**, 1659-1664.

**Kullberg, C., Jakobsson, S. and Fransson, T.** (2000). High migratory fuel loads impair predator evasion in sedge warblers. *Auk* **117**, 1034-1038.

**Land, M. and Layne, J.** (1995a). The visual control of behavior in fiddler crabs. I. Resolution, thresholds and the role of the horizon. *J. Comp. Physiol. A Sens. Neural Behav. Physiol.* **177**, 81-90.

**Land, M. and Layne, J.** (1995b). The visual control of behavior in fiddler crabs. II. 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.

**Lee, S. J., Witter, M. S., Cuthill, I. C. and Goldsmith, A. R.** (1996). Reduction in escape performance as a cost of reproduction in gravid starlings, *Sturnus vulgaris. Proc. R. Soc. Lond. B* **263**, 619-623.

**Lima, S. L.** (1993). Ecological and evolutionary perspectives on escape from predatory attack-a survey of North American birds. *Wilson Bull.* **105**, 1-47.

**Lind, J., Fransson, T., Jakobsson, S. and Kullberg, C.** (1999). Reduced take-off ability in robins (*Erithacus rubecula*) due to migratory fuel load. *Behav. Ecol. Sociobiol.* **46**, 65-70.

**Lind, J., Kaby, U. and Jakobsson, S.** (2002). Split-second escape decisions in blue tits (*Parus caeruleus*). *Naturwissenschaften* **89**, 420-423.

**Lind, J., Hollen, L., Smedberg, E., Svensson, U., Vallin, A. and Jakobsson, S.** (2003). Detection distance influences escape behaviour in two parids, *Parus major* and *P. caeruleus. J. Avian Biol.* **34**, 233-236.

**Lingle, S.** (2002). Coyote predation and habitat segregation of white-tailed deer and mule deer. *Ecology* **83**, 2037-2048.

**Lingle, S. and Wilson, W. F.** (2001). Detection and avoidance of predators in white-tailed deer (*Odocoileus virginianus*) and mule deer (*O. hemionus*). *Ethology* **107**, 125-147.

**Marie, B., Bacon, J. P. and Blagburn, J. M.** (2000). Double-stranded RNA interference shows that Engrailed controls the synaptic specificity of identified sensory neurons. *Curr. Biol.* **10**, 289-292.

**Martin, J. and Lopez, P.** (1996). The escape response of juvenile *Psammodromus 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 *Psammodromus algirus. Can. J. Zool.* **78**, 265-270.

**Meager, J. J., Domenici, P., Shingles, A. and Utne-Palm, A. C.** (2006). Escape responses in juvenile Atlantic cod *Gadus morhua* L.: the effects of turbidity and predator speed. *J. Exp. Biol.* **209**, 4174-4184.

**Nalbach, H. O.** (1990). Discontinuous turning reaction during escape in soldier crabs. *J. Exp. Biol.* **148**, 483-487.

**Nalbach, H. O. and Nalbach, G.** (1987). Distribution of optokinetic sensitivity over the eye of crabs-its relation to habitat and possible role in flow-field analysis. *J. Comp. Physiol. A Sens. Neural Behav. Physiol.* **160**, 127-135.

**Neil, D. M. and Ansell, A. D.** (1995). The orientation of tail-flip escape swimming in decapod and mysid crustaceans. *J. Mar. Biol. Assoc. UK* **75**, 55-70.

**Newland, P. L. and Chapman, C. J.** (1989). The swimming and orientation behavior of the Norway lobster, *Nephrops norvegicus* (L.), in relation to trawling. *Fish. Res.* **8**, 63-80.

**Newland, P. L. and Neil, D. M.** (1990a). The tail flip of the Norway lobster, *Nephrops norvegicus*. I. Giant fiber activation in relation to swimming trajectories. *J. Comp. Physiol. A Sens. Neural Behav. Physiol.* **166**, 517-527.

**Newland, P. L. and Neil, D. M.** (1990b). The tail flip of the Norway lobster, *Nephrops norvegicus*. II. Dynamic righting reactions induced by body tilt. *J. Comp. Physiol. A Sens. Neural Behav. Physiol.* **166**, 529-536.

**Newland, P. L., Cattaert, D., Neil, D. M. and Clarac, F.** (1992a). Steering reactions as adaptive components of the tail-flip in the spiny lobster *Jasus lalandii. J. Exp. Biol.* **164**, 261-282.

**Newland, P. L., Neil, D. M. and Chapman, C. J.** (1992b). Escape swimming in the Norway lobster. *J. Crust. Biol.* **12**, 342-353.

**Oliva, D., Medan, V. and Tomsic, D.** (2007). Escape behavior and neuronal responses to looming stimuli in the crab *Chasmagnathus granulatus* (Decapoda: Grapsidae). *J. Exp. Biol.* **210**, 865-880.

**Otis, T. S. and Gilly, W. F.** (1990). Jet-propelled escape in the squid *Loligo opalescens* – concerted control by giant and non-giant motor axon pathways. *Proc. Natl. Acad. Sci. USA* **87**, 2911-2915.

**Packard, A.** (1969). Jet propulsion and giant fibre response of Loligo. *Nature* **221**, 875-877.

**Perez, H. M., Janssoone, X., Cote, C. and Guderley, H.** (2009). Comparison between in vivo force recordings during escape responses and in vitro contractile capacities in the sea scallop *Placopecten magellanicus. J. Shellfish Res.* **28**, 491-495.

**Reichert, H. and Wine, J. J.** (1983). Coordination of lateral giant and non-giant systems in crayfish escape behavior. *J. Comp. Physiol.* **153**, 3-15.

**Reimers, E., Miller, F. L., Eftestol, S., Colman, J. E. and Dahle, B.** (2006). Flight by feral reindeer *Rangifer tarandus tarandus* in response to a directly approaching human on foot or on skis. *Wildl. Biol.* **12**, 403-413.

**Rinberg, D. and Davidowitz, H.** (2000). Do cockroaches 'know' about fluid dynamics? *Nature* **405**, 756.

**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.

**Royan, A., Muir, A. P. and Downie, J. R.** (2010). Variability in escape trajectory in the Trinidadian stream frog and two treefrogs at different life-history stages. *Can. J. Zool.* **88**, 922-934.

**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.

**Schmidt, M., Philipp, E. E. R. and Abele, D.** (2008). Size and age-dependent changes of escape response to predator attack in the queen scallop *Aequipecten opercularis. Mar. Biol. Res.* **4**, 442-450.

**Schrader, S.** (2000). The function of the cereal sensory system in escape behavior of the cave cricket *Troglophilus neglectus* Krauss. *Pflugers Arch.* **439**, R187-R189.

**Semeniuk, C. A. D. and Dill, L. M.** (2005). Cost/benefit analysis of group and solitary resting in the cowtail stingray, *Pastinachus sephen. Behav. Ecol.* **16**, 417-426.

**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.

**Skajaa, K. and Browman, H. I.** (2007). The escape response of food-deprived cod larvae (*Gadus morhua* L.). *J. Exp. Mar. Biol. Ecol.* **353**, 135-144.

**Snyder, N. F. R. and Snyder, H. A.** (1971). Pheromone-mediated behaviour of *Fasciolaria tulipa. Anim. Behav.* **19**, 257-286.

**Stankowich, T. and Coss, R. G.** (2007). Effects of risk assessment, predator behavior, and habitat on escape behavior in Columbian black-tailed deer. *Behav. Ecol.* **18**, 358-367.

**Stephens, P. J. and Boyle, P. R.** (1978). Escape responses of queen scallop *Chlamys opercularis* (L.) (Mollusca: Bivalvia). *Mar. Behav. Physiol.* **5**, 103-113.

**Stern, M., Ediger, V. L., Gibbon, C. R., Blagburn, J. M. and Bacon, J. P.** (1997). Regeneration of cercal filiform hair sensory neurons in the first-instar cockroach restores escape behavior. *J. Neurobiol.* **33**, 439-458.

**Stierle, I. E., Getman, M. and Comer, C. M.** (1994). Multisensory control of escape in the cockroach *Periplaneta americana*. I. Initial evidence from patterns of wind-evoked behaviour. *J. Comp. Physiol.* **174**, 1-11.

**Suchman, C. L.** (2000). Escape behavior of *Acartia hudsonica* copepods during interactions with scyphomedusae. *J. Plankton Res.* **22**, 2307-2323.

**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.

**Thomas, G. E. and Gruffydd, L. D.** (1971). Types of escape reactions elicited in scallop *Pecten maximus* by selected sea-star species. *Mar. Biol.* **10**, 87-93.

**Thompson, K. S. J., Blagburn, J. M., Gibbon, C. R. and Bacon, J. P.** (1992). Correlation of filiform hair position with sensory afferent morphology and synaptic connections in the second instar cockroach. *J. Comp. Neurol.* **320**, 213-227.

**Titelman, J. and Kiorboe, T.** (2003). Motility of copepod nauplii and implications for food encounter. *Mar. Ecol. Prog. Ser.* **247**, 123-135.

**Tytell, E. D. and Lauder, G. V.** (2002). The C-start escape response of *Polypterus senegalus*: bilateral muscle activity and variation during stage 1 and 2. *J. Exp. Biol.* **205**, 2591-2603.

**van den Hout, P. J., Mathot, K. J., Maas, L. R. M. and Piersma, T.** (2010). Predator escape tactics in birds: linking ecology and aerodynamics. *Behav. Ecol.* **21**, 16-25.

**Visser, A. W. and Jonsson, P. R.** (2000). On the reorientation of non-spherical prey particles in a feeding current. *J. Plankton Res.* **22**, 761-777.

**Vlasak, A. N.** (2006). The relative importance of global and local landmarks in navigation by Columbian ground squirrels (*Spermophilus columbianus*). *J. Comp. Psychol.* **120**, 131-138.

**Von Christian, E.** (1978). The jump of springtails. *Naturwissenschaften* **65**, 495-496.

**Von Christian, E.** (1979). Der Sprung der Collembolen. *Zool. Jb.* **83**, 457-490.

**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.

**Ward, D. V.** (1972). Locomotory function of squid mantle. *J. Zool.* **167**, 487-499.

**Weihs, D. and Webb, P. W.** (1984). Optimal avoidance and evasion tactics in predator–prey interactions. *J. Theor. Biol.* **106**, 189-206.

**Westin, J.** (1979). Responses to wind recorded from the cercal nerve of the cockroach *Periplaneta americana*. I. Response properties of single sensory neurons *J. Comp. Physiol. A* **133**, 97-102.

**Westin, J., Ritzmann, R. E. and Goddard, D. J.** (1988). Wind-activated thoracic interneurons of the cockroach: I. Responses to controlled wind stimulation. *J. Neurobiol.* **19**, 573-588.

**Whiteman, H. H. and Wissinger, S. A.** (1991). Differences in the antipredator behavior of three plethodontid salamanders to snake attack. *J. Herpetol.* **25**, 352-355.

**Will, U.** (1991). Amphibian Mauthner cells. *Brain Behav. Evol.* **37**, 317-332.

**Wine, J. J. and Krasne, F. B.** (1972). The organization of escape behaviour in the crayfish. *J. Exp. Biol.* **56**, 1-18.

**Witter, M. S. and Cuthill, I. C.** (1993). The ecological costs of avian fat storage. *Philos. Trans. R. Soc. Lond. B* **340**, 73-92.

**Witter, M. S., Cuthill, I. C. and Bonser, R. H. C.** (1994). Experimental investigations of mass-dependent predation risk in the European starling, *Sturnus vulgaris. Anim. Behav.* **48**, 201-222.

**Woodbury, P. B.** (1986). The geometry of predator avoidance by the blue crab, *Callinectes sapidus* Rathbun. *Anim. Behav.* **34**, 28-37.

**Wyeth, R. C. and Willows, A. O. D.** (2006). Field behavior of the nudibranch mollusc *Tritonia diomedea. Biol. Bull.* **210**, 81-96.

**Wyeth, R. C., Woodward, O. M. and Willows, A. O. D.** (2006). Orientation and navigation relative to water flow, prey, conspecifics, and predators by the nudibranch mollusc *Tritonia diomedea. Biol. Bull.* **210**, 97-108.

**Yafremava, L. S., Anthony, C. W., Lane, L., Campbell, J. K. and Gillette, R.** (2007). Orienting and avoidance turning are precisely computed by the predatory sea-slug *Pleurobranchaea californica* McFarland. *J. Exp. Biol.* **210**, 561-569.

**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.* **87**, 407-414.

**Zar, J.** (1984). *Biostatistical Analysis*. Englewood Cliffs, NJ: Prentice Hall.