



## Review

# Die hard: A blend of freezing and fleeing as a dynamic defense— implications for the control of defensive behavior

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Freezing, fleeing or fighting back are general defensive responses in many taxa. These defenses are mutually exclusive, since a prey cannot simultaneously flee and fight, or freeze and flee. Each of these defenses by itself is rudimentary and probably cannot provide a completely effective means to elude predation. Freezing is efficient only if employed before the prey is spotted by the predator, otherwise the prey becomes a stationary, easy to catch target. In fleeing, the prey can move directly away and maximize its distance from the predator, move toward the predator to confine it to a single clashing point, or dodge sideways to evade the attack. Prey can also run in a straight path that is efficient against slow or distant predators, or in a zigzag path that is efficient when a raptor is close or fast. In all, freezing and fleeing constitute together a complex and flexible defensive response, and are probably controlled by different motor systems that are interconnected to allow fast switching between these behaviors, as required for an effective and versatile response.

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**1. Prologue**

Predation generates profound changes in behavior (Eilam et al., 1999), in its controlling mechanisms (Canteras, 2002), in vital activities such as foraging (Kotler et al., 1992, 1994; Otter, 1994) and reproduction (Vasilieva et al., 2000), in local population changes (Berger, 1991; Wooster and Sih, 1995), and ultimately in ecosystem change

due to shifting the balance between prey and predator populations (Abrams, 1995; Turner, 1997). The primer in this cascade of changes is the individual response of the prey and the controlling mechanisms of this behavioral response. Indeed, modulated by the strong selective pressure of predation, defensive behaviors converge to three categories that cross the entire animal kingdom: freezing, fleeing, and fighting (defensive attack). These defenses are highly structured, reflecting the ultimate output of brain mechanisms. Indeed, the neural systems that underlie the different defensive behaviors have been extensively investigated, and anatomical differentiations found among these systems at both forebrain and midbrain levels support the view that they represent independent biobehavioral systems, albeit

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originating from a common evolutionary focus on defense against danger (see Neuroscience and Biobehavioral Reviews, Vol. 21 (6) for several reviews on the different perspectives of defensive behavior). However, in order to study biobehavioral mechanisms, it is necessary to standardize and stabilize the stimulus and the response, and a standard (or general) response as ‘freezing’ or ‘fleeing’ may not provide the prey with sufficient defensive means in the arms race against predators. Moreover, the same prey species (e.g. voles), may be hunted by several species of predators with different hunting strategies (e.g. owls, foxes, snakes), forcing the prey to execute flexible and versatile defensive responses. The following survey illustrates that while both freezing and fleeing are common across vertebrates, they are integrated into a species-specific blend that varies among individuals that are directly exposed to a predator. The result is an unpredictable defensive gambit of either eluding the attacking predator or fading from its attended space. The concluding remarks of this survey discuss the implications of such a dynamic blend of defenses for the controlling brain mechanisms of defensive behavior.

## 2. Generality of defensive responses

In response to life threat, prey species may be expected to take different defensive strategies and develop differentiating mechanisms that lead to the most appropriate response. For example, under risk of owl attack, wild rodents forage near shrubs and avoid open spaces in which owls hunt, but under risk of snake predation, the same rodents forage in the open, moving away from shrubs where snakes hunt (Abramsky et al., 1996; Kotler et al., 1992). Vervet monkeys (*Cercopithecus aethiops*) emit alarm calls that vary according to the presence of a terrestrial or an aerial predator, which in turn elicit appropriate defensive behavior in other members of the troop (Seyfarth and Cheney, 1980, 1986). It has been shown that domestic chickens (*Gallus gallus*) too produce alarm calls that may be differentiated along the same lines (Collias, 1987; Evans et al., 1993; Geyer et al., 1987). Thus, prey species are renowned for their capacity to recognize potential predators and to produce a defensive strategy that is appropriate to the hunting strategy of that particular predator. The types of prey response to a predator threat converge to three defensive behaviors: freezing, fleeing, and fighting. In freezing, the prey remains immobile in order to evade the attention of the predator (Desy et al., 1990; Hendrie and Weiss, 1994; Hendrie et al., 1998; Ronkainen and Ylonen, 1994; Whishaw and Dringenberg, 1991). In fleeing, the prey gallops in order to remove itself from the vicinity of the predator (Bolles, 1970; Driver and Humphries, 1988; King, 1985). In fighting (or defensive threat), the prey heads on toward the predator in order to dissuade it and prevent predation. Defensive fighting occurs

only when the prey has no possibility of freezing and fleeing and must face the predator.

Freezing and fleeing were described in a variety of prey species, from hermit crab (Scarratt and Godin, 1992) to deer (Smith, 1991). Obviously, a prey cannot freeze and flee at the same time and, therefore, these defenses are generally considered as mutually exclusive. The dichotomy has been described in different species. For example, the white-tailed deer (*Odocoileus virginianus*) typically flees flagging its tail (Smith, 1991) whereas the jerboa (*Jaculus jaculus*, a small bipedal rodent) crouches motionless hiding its white ventral fur and exposing its yellowish dorsal fur to match the desert sand (Hendrie et al., 1998). This dichotomy may also occur in different individuals of the same species under similar conditions. For example, voles exposed to the silhouette of hawk either freeze, or increase locomotion in order to escape (Fentress, 1968). Freezing or fleeing may be also observed in the same individual animal under different circumstances. For example, woodmice (*Apodemus mystacinus*) either freeze or leap when exposed to stoats (*Mustela ermina*) (Erlinge et al., 1974) but scamper away when exposed to other predators (Bolles, 1970; King, 1985). The response also varies with age, as young white-tailed deer tend to freeze when exposed to a predatory risk, whereas adults typically flee (Smith, 1991). A dichotomy to freezing or fleeing in the face of threat was also revealed in another study of voles, demonstrating that when exposed to recorded owl calls, some voles remained motionless (‘freeze’ pattern) while others dashed through the arena and leapt up the walls as if trying to escape (‘flee’ pattern; Eilam et al., 1999). Finally, freezing and fleeing may occur in succession in the same individual. For example, robins (*Erithacus rubecula*) reacted to an approaching predator model by taking off toward the opposite side of the cage where they hovered against the wall for a short while before flying down to the floor and remaining motionless (Lind et al., 1999). These examples demonstrate that freezing and fleeing are general forms of defensive behavior across species and individuals. The question remains, however: what makes an animal decide to freeze or flee?

## 3. Fright or flight? Differentiating mechanisms

Three hypotheses have been posited to explain what makes an animal freeze or flee: (1) individual differences; (2) distance from the predator; and (3) access to shelter. The first hypothesis implies that freeze and flee responses reflect individual differences that may also be echoed in other behavioral factors such as baseline activity and social rank. Accordingly, it may be possible to predict the response of an individual by studying its ongoing behavior prior to exposure to predatory threat. For example, the behavioral response of voles to owl calls was directly linked to their baseline behavior: voles with low basal activity froze, whereas voles with high basal activity fled (Fig. 1, based on

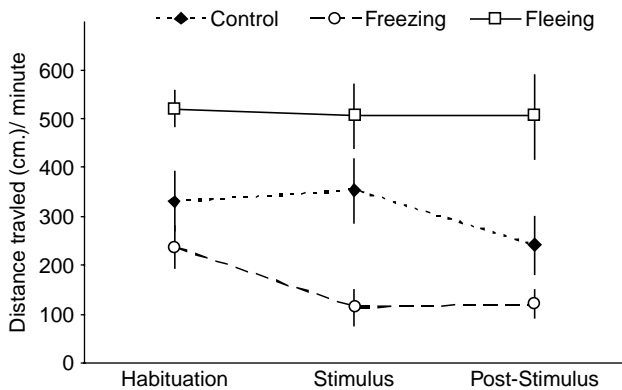


Fig. 1. (Based on data from Table 1 in Eilam et al., 1999). Continuity between activity before and after threat. Distance traveled is shown for three groups of voles that were tested in the 'call box' (Hendrie et al., 1998). This apparatus is a 40×40×40 cm box with a loudspeaker on top. A vole was placed into the box and habituated for 3 min to a human voice reading monotonically. This was followed by 2-min of stimulus, in which it was exposed to playback of tape-recorded owl calls. A post-stimulus period of 5 min silence followed. Level of activity was measured by the distance traveled per minute for each phase of the test. Voles exposed to owl calls were divided into freezing and fleeing groups (see Eilam et al., 1999 for further details on this division). A control group was not exposed to owl calls, but continued to hear the human voice. As shown, voles that fled (□) displayed high activity before their exposure to owl calls ('Habituation'), and kept this high activity in the stimulus and post-stimulus periods. Voles that froze (○) had a low level of activity during 'Habituation', and further reduced their activity in the subsequent phases. Controls (◆) did not significantly change their activity.

Eilam et al., 1999). Alternatively, these individuals may have had an innate predisposition for a certain type of behavior. If such a difference between individuals exists, then it will be possible to predict the pattern of response.

To further test the link between baseline behavior of voles and their response to owl calls, twenty voles (*Microtus socialis*) were exposed for three consecutive days to human voice (5 min of exposure to playback of tape-recorded human voice, followed by 5 min silence). These three consecutive repetitions were aimed at revealing the behavioral profile for each vole. On day 4, each vole underwent the same procedure, but this time it was also exposed to playback of tape-recorded owl calls (3 min human voice, then 2 min owl call, followed by 5 min silence). As shown in Fig. 2, most of the voles followed the same pattern of changes in activity: they reduced activity from first to second day and then sharply increased activity from the second to the third day. On the fourth day, when exposed to owl calls, activity in all voles decreased sharply. These changes occurred regardless of the initial level of activity, which varied among voles. In Fig. 2, the similarity in response is represented by the same shape but different values of each line (line=individual vole). This result further corroborates the data shown in Fig. 1, indicating that voles with demonstrated low levels of activity remain at lower levels when under threat, while those with high activity preserve it. Freezing and fleeing in these voles is therefore an extension of their various normal behaviors, and not necessarily different defensive responses. Shyness-boldness gradient, gender, age, and seasonal differences, were also shown to be involved in shaping the individual defensive response (Blanchard et al., 1991a,b; Borowski, 2002; Norrdahl et al., 2004; Perrot-Sinal et al., 1999; Shepherd et al., 1992; Wilson et al., 1994); however, the hypothesis that freezing or fleeing in response to the same stimulus is a mere property of the individual animal and relatively independent of the stimulus needs to be further

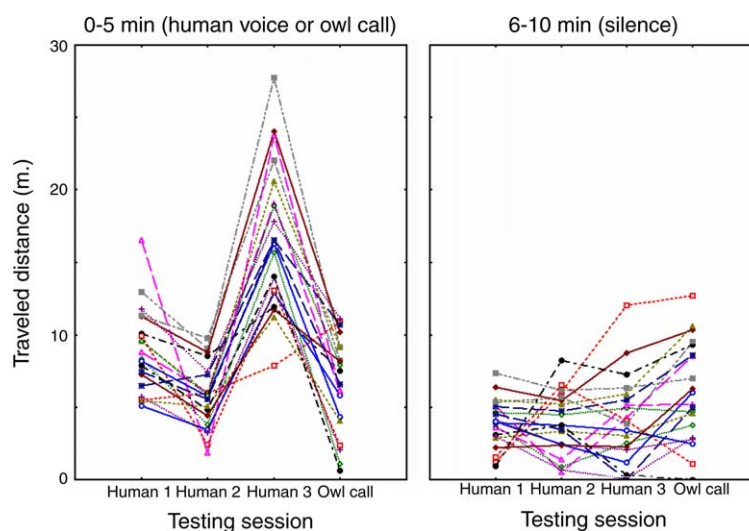


Fig. 2. The response of 20 voles to four consecutive exposures to playback of tape-recorded sounds (1 exposure/day). In the first three days, each vole was exposed to 5-min playback of a human voice followed by 5 min silence. On day 4, all 20 voles were exposed to 3 min of human voice followed by 2 min of owl calls, and then 5 min silence. Left inset shows the distance travelled during the sound pitch (min 0–5), and right inset shows the distance travelled during the silence (6–10 min). As shown, during the sound pitch, many of the lines (individual voles) followed the same pattern of change regardless of the level of activity (altitude of the line). In the silence pitch, all lines (individual scores) overlapped.

tested with other species and stimuli. Even then, further research is required in order to isolate accurate predictors of the pattern of response to predatory risk.

The second hypothesis is that freeze and flee responses are directly related to the distance between the predator and prey, and are therefore relatively independent of the ongoing behavior of the prey. In accordance, there is a 'distance-dependent defense hierarchy'; (Gallup, 1974; Ranter, 1977) a distant predator induces freezing and a closer predator induces a flee pattern. When the predator is even closer, the final (perhaps unavoidable) act of defense may be to fight the predator. To test this hypothesis, an apparatus that controls the distance and intensity of predatory threat was designed—the Mouse-Defense-Test-Battery (MDTB), introduced by R.J. Blanchard and D.C. Blanchard (Blanchard et al., 1997). A modification of this testing procedure was applied here in order to reveal how stimulus intensity shapes defensive response in rodents. The MDTB comprised an oval runway with two straight segments (2 m long) joined by curved segments at each end. The apparatus was marked at intervals for measurement of distances, and the behavior was videotaped through the transparent walls of the runway. A test rodent

was placed onto the runway and its behavior was videotaped through the following stages. (1) *Habituation*—started with introducing the rodent onto the runway and comprised 3-minutes of habituation. (2) *Approach*—started at the end of habituation, when the experimenter entered the room carrying a bird cage with an owl. The initial distance from the owl to the rodent on the runway was four meters, and the experimenter with the owl progressed directly towards the rodent at a speed of 0.5 m/s. The average duration of the approaching stage was 1 min. (3) *Adjacency*—started when the caged owl was placed inside the runway for 5 min during which the rodent could approach the owl. The owl cage was made of wire-mesh (5×8 cm) that prevented the owl from approaching the rodent, but allowed the rodent to even enter the owl cage. Two controls were used: (i) empty cage; and (ii) caged fowl (young *Gallus gallus bankiva*). The empty cage control was used to assess the effect of the approaching experimenter with the cage, and the caged-fowl control was used to discriminate the specificity of the response to owls from general response to fowl.

Two wild rodent species were tested in this runway: social voles (*Microtus socialis*) and common spiny mice

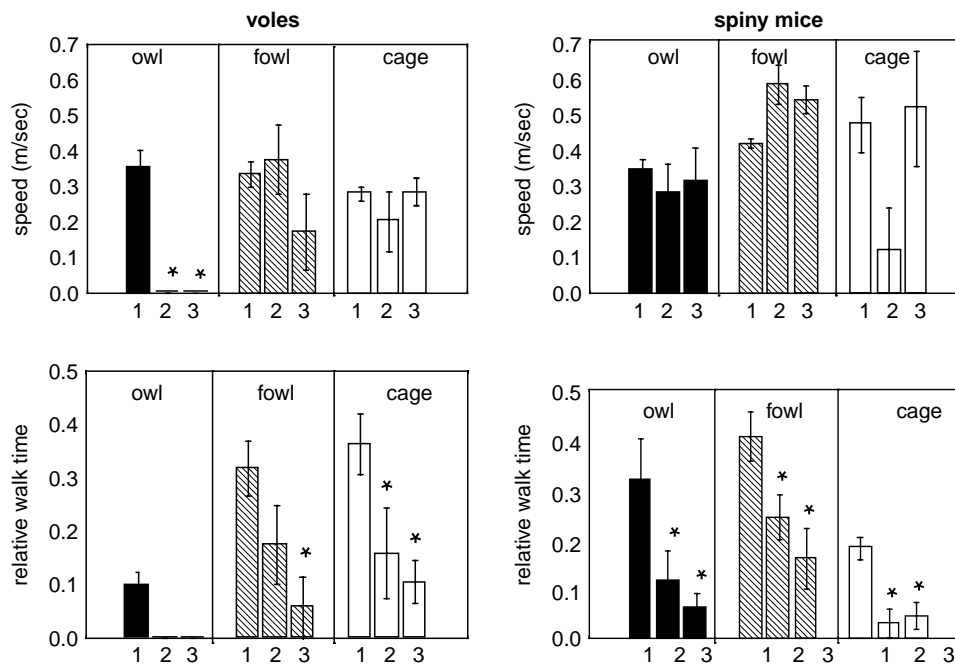


Fig. 3. Speed (m/s; top) and proportion of time spent locomoting out of the total duration of observation (bottom) for voles (left) and spiny mice (right). In each inset graph, data are shown for a test group (owl) and two control groups: a cage with fowl (chicken) and an empty cage. X-axis in each inset describes the three phases of the experiment: 1—Habituation, 2—Approaching, 3—Adjacency. Statistical analysis (Two-way ANOVA with repeated measures) revealed a significant difference in speed between the groups ( $F_{2,12}=4.8$ ;  $P=0.028$ ), between the three phases of the experiment ( $F_{2,24}=8.9$ ;  $P<0.01$ ) and significant interaction of the test groups and experimental phases ( $F_{4,24}=6.4$ ;  $P<0.01$ ). In the time spent locomoting there was a significant difference between groups (Owl, Fowl, Cage;  $F_{2,12}=5.5$ ;  $P=0.02$ ), and between the three phases of the experiment (1,2,3;  $F_{2,24}=22.8$ ;  $P<0.01$ ), but the interaction was not significant. The lower level measured during the habituation period in voles which were then exposed to owls is puzzling since the voles could not know they were going to be exposed to an owl, but should have displayed the habituation of voles in the other groups. However, it is possible that the voles were somehow able to sense the approaching owl even before it was introduced into the testing room and its vicinity. Both voles and spiny mice also responded to control stimuli. However, while this response in voles was weaker compared with the response to owl, spiny mice seemed to react similarly to control stimuli or owl. This resembles previous studies with spiny mice (Eilam et al., 1999; Hendrie et al., 1998), and may be explained by the tendency of spiny mice not to freeze but only to flee when threatened.



(*Acomys cahirinus*). Voles were selected since they are heavily preyed upon by owls and comprise 40–70% (sometimes over 90%) of barn owl (*Tyto alba*) and tawny owl (*Strix aluco*) diet (Martin and Busby, 1990; Mendelsohn and Yom-Tov, 1999; Mikkola and Willis, 1983; Selaas, 1993). In a previous study, voles displayed a conspicuous freeze and flee response when exposed to owl calls (Eilam et al., 1999). In contrast, spiny mice were selected because, surprisingly, they did not appear to react to recorded owl calls (Hendrie et al., 1998). These two rodent species thus reflect two extremes in the defensive response to owl calls.

As shown in Fig. 3, the behavior of the voles underwent a dramatic change when the owl was introduced into the testing room, a change that was not revealed in control groups. In the habituation stage, voles in test and control groups locomoted at a similar speed; but speed then declined to almost nil in voles encountering the owl, compared with no change in speed in those facing the fowl or an empty cage. When the caged owl was placed inside the runway during the adjacency stage, voles in this experiment maintained at least 1 m distance from it, but approached the cage and entered it when a fowl or empty cage were placed on the runway. The defensive response was thus specific to presence of the owl, and was not distance-dependent, at least not within 4 m. As mentioned above, spiny mice did not change their ongoing behavior when exposed to tape-recorded owl calls. However, when tested in the runway, they exhibited the same patterns of response seen in voles. As shown in Fig. 3, spiny mice did not change their speed during the different phases of the experiment, but locomoting time was reduced under exposure to an approaching owl, and was further decreased when the caged owl was left in their proximity. These decreases in response to an owl resembled the decreased response observed in controls, but with greater magnitude, supporting the finding that response to an approaching owl was not distance-dependent, at least not within 4 m.

A third, and more integrative, explanation regarding what makes an animal freeze or flee suggests that features of the threat stimulus and the situation in which it is encountered modulates the specific defensive behavior (Blanchard et al., 1991a,b). Specifically, the presence of an escape route or a refuge will promote flight to the safer area (Blanchard, 1997; Blanchard and Blanchard, 1989; Blanchard et al., 1991a,b). If these environmental features are not available, freezing will be the dominant response, while defensive threat and attack will transpire when contact with the threat source becomes imminent. Accordingly, a discrete and localizable threat source, such as a visible predator, will promote flight and defensive threat/attack, while an amorphous/difficult to locate threat source will promote freezing and risk assessment. Risk assessment (Blanchard et al., 1991a,b) involves gathering information regarding the threat in order to produce an optimal response. Based on observations mainly on laboratory rats (Blanchard and Blanchard, 1989;

Blanchard et al., 1989) and mice (Griebel et al., 1995a; 1995b) tested in a runway with doors to lock the rodent in a dead-end straight alley, R.J. Blanchard and D.C. Blanchard proposed the following continuum of defensive behaviors:

1. When approached by a potential predator in an escapable situation, the predominant reaction is to flee, which occurs at a relatively consistent (according to type of predator) distance.
2. When approached by a potential predator in an inescapable situation, the predominant reaction is to orient toward the predator, and to freeze (in rats). Mice may also freeze, but may also approach the predator.
3. The number of jumps and their average amplitude increase in rats as the prey–predator distance decreases. Mice also show jumps (jump attack or jump escape) as contact nears.
4. In rats, freezing declines abruptly at about 0.5 m distance, as defensive threat and attack become imminent. Freezing is, however, near maximal when the predator is 1–3 m distant from the subject. In contrast, if the situation involves a clear escape route, flight occurs at about the same distances.
5. Defensive threat involves sonic vocalization (screams or squeaks) while defensive attack typically involves jumps toward the oncoming predator, often accompanied by bites.
6. Although orientation to the predator is a dominant response when the subject is not fleeing, rats show little active risk assessment (i.e. approaching the predator) compared to mice. The latter may even pause while fleeing, and turn toward the chasing predator.

This behavioral continuum represents an advantage of the ‘Mouse Defense Test Battery’ (Blanchard et al., 1991a, b) over other models: it allows fine tuning of the intensity of the stimulus (i.e. threat stimulus to subject distance) and of the physical structure of the environment in order to elicit a relatively consistent defensive response in each of the various subtests of the test battery. This continuum is the basis for the expanded diagram that summarizes this survey (Fig. 7, below).

#### 4. A time to run, a time to freeze

While the above explanations refer to the occurrence of freezing and fleeing, they disregard the potential significance of freezing and fleeing under more natural circumstances that may affect the adaptive and survival value of these defenses. Of these circumstances, timing is crucial for the survival value of the freezing response. For example, by freezing before being spotted by an owl, a vole eliminates the auditory and visual cues that owls use in pinpointing prey (Mikkola and Willis, 1983). The vole then relies on the camouflage of its brown fur that matches the color of the

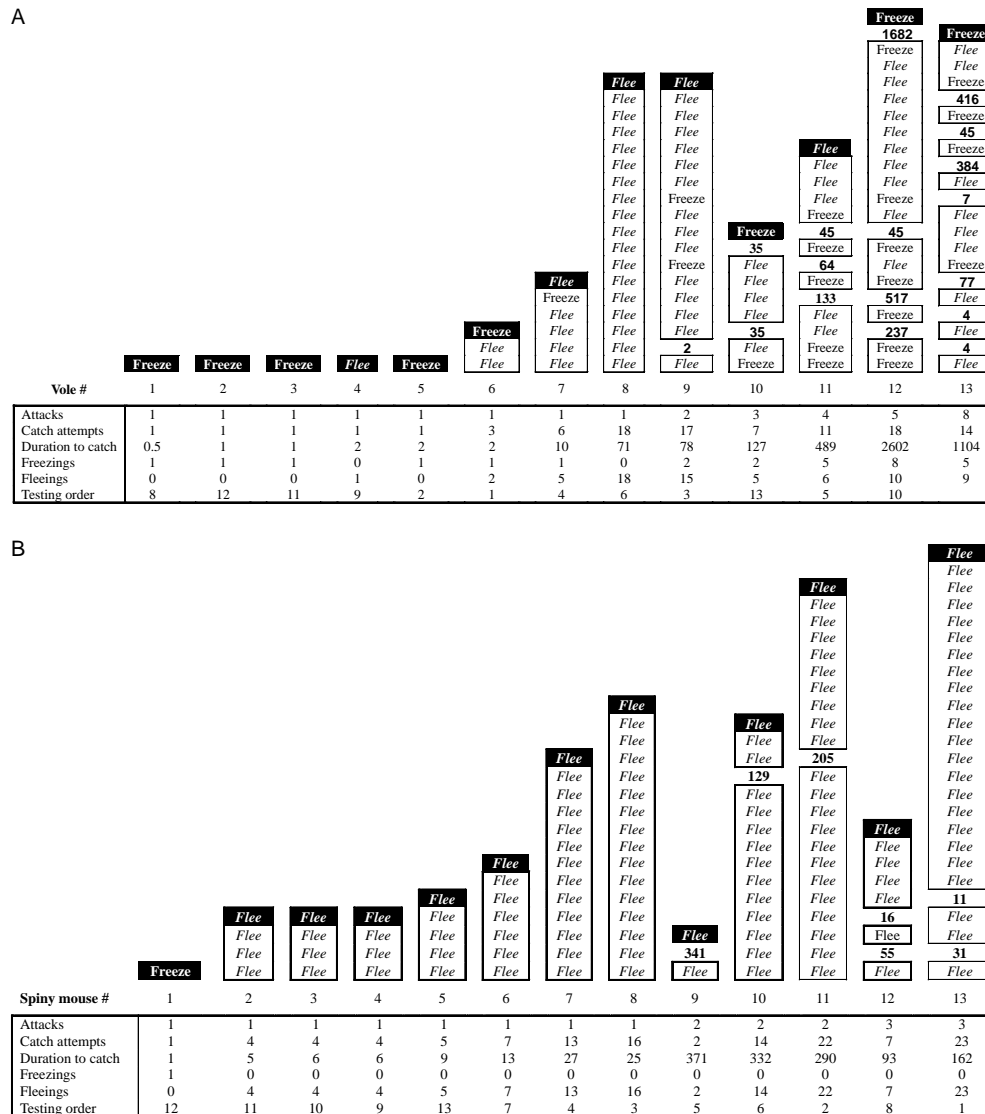


Fig. 4. (taken from Edut and Eilam, 2004). Thirteen encounters between a barn owl and voles (A) and 13 encounters between a barn owl and spiny mice (B). In voles (4A), each column represents the sequence of one vole, with the response of that animal to capture attempt of the owl arranged from bottom to top and depicted as 'freeze' or 'flee'. Capture attempts executed in the same attack (while the owl was in the vole's vicinity and had not left the rodent enclosure) are enclosed in frames (blocks). Time elapsed between successive attempts is depicted (in seconds) between attacks (blocks). Data at the bottom of each column summarize the interactions. Data on spiny mice are given in the same format as for voles. As shown, voles switched between freezing and fleeing whereas spiny mice mainly fled. The behavior of the owl also differed, frequently leaving the vicinity of the voles (indicated by more blocks compared with spiny mice). The owl then launched a new attack from a far roost. Data for encounters between the owl and spiny mice (4B) are arranged in the same structure as for voles (4A), illustrating that the owl spent more time near spiny mice (fewer blocks in spiny mice shown in 4B compared with voles shown in 4A), executing more repeated short-distance catching attempts as indicated by more defensive responses in each block of spiny mice (4B), compared with the blocks of voles (4A). See also the attached videoclip.

heavy soil it inhabits. However, if seen by the owl before freezing, the vole becomes a stationary target that an owl will not miss. Indeed, owls show a high success rate in catching immobile compared to moving food items (90 and 21%, respectively; Shifferman and Eilam, 2004). A vole cannot know whether or not it was spotted by the owl, and this duality probably leads it to use both freezing and fleeing defenses under owl attack (Fig. 4). Alternating between freezing and fleeing seems to be the optimal response, combining disappearance by freezing together with not

being a stationary target if freezing fails. As illustrated in Fig. 4, there is also variability in the defensive response of different voles: only freezing (voles 1–3, and 5); only fleeing (voles 4 and 8); switching several times between freezing and fleeing (voles 6, 7, 9, and 10); and alternating frequently between these responses (voles 11–13). Thus, voles respond in a spectrum of combinations of freezing and fleeing, and their response should neither be considered as just freezing or fleeing (Eilam et al., 1999; Hendrie et al., 1998) nor be defined according to the initial response (Edut and Eilam,

2003). In all, while previous studies have assumed that freezing and fleeing are mutually exclusive, Fig. 4 illustrates a blend of these two defenses into unpredictable sequences. Freezing and fleeing are thus building blocks in a more general defensive pattern that prevents the predator from predicting the next stage of the prey's response.

### 5. Running for your life? Assess the direction, path shape and habitat

The convention that by fleeing the prey aims to remove itself from the vicinity of the predator has been challenged (Dugatkin and Godin, 1992; Lind et al., 1999; Shiffman and Eilam, 2004). A counterintuitive response, of approaching a predator upon its detection was described in a wide variety of taxa and termed predator inspection (Dugatkin and Godin, 1992; Fishman, 1999; Randall and Boltas, 2001). It was suggested that this behavior is performed: (i) when threat is ambiguous and approaching may provide further information about the threat; (ii) to inform others about the threat; (iii) to discourage the predator from attacking; and (iv) to advertise the quality of the approacher to its potential mates (Dugatkin and Godin, 1992). Another hypothesis is that moving toward a predator is not for inspection or display purposes, but an eluding tactic. Specifically, prey species might be better off moving directly or diagonally toward the predator in order to increase their relative speed and confine the attack to a single available clashing point rather than maximizing the distance to the predator (Shiffman and Eilam, 2004). To test this hypothesis, prey movement was simulated by a dead mouse or chick that was dragged in various directions during barn owl attack. Owl success was higher when the simulated prey was dragged straight away, rather than towards the owls (50 and 18%, respectively). Strikingly, owls had 0% success in catching food items that were pulled sideways (Shiffman and Eilam, 2004). The lower success rate in catching simulated prey that were dragged toward the owl may be explained by: (i) their combined relative speed is higher than that of each individually; and (ii) there is only a single clashing point where the owl can catch the prey, unless the owl is able to execute fast and sharp maneuvering. However, maneuvering is limited by the high speed of the predator, making it harder to change its current direction of progression. In contrast, when the simulated prey was pulled straight away from the owl, the owl had more time to follow and swoop down on it, with only minor adjustments. To date, much of the work on mammalian prey approaching predators is either anecdotal or non-experimental (Dugatkin and Godin, 1992). However, a methodical study demonstrated that kangaroo rats approach, display foot drumming, and kick sand toward a snake, but it is not clear why they risk remaining within the snake's strike distance (Randall and Boltas, 2001). Thus, there is no evidence that mammals attempt escape by

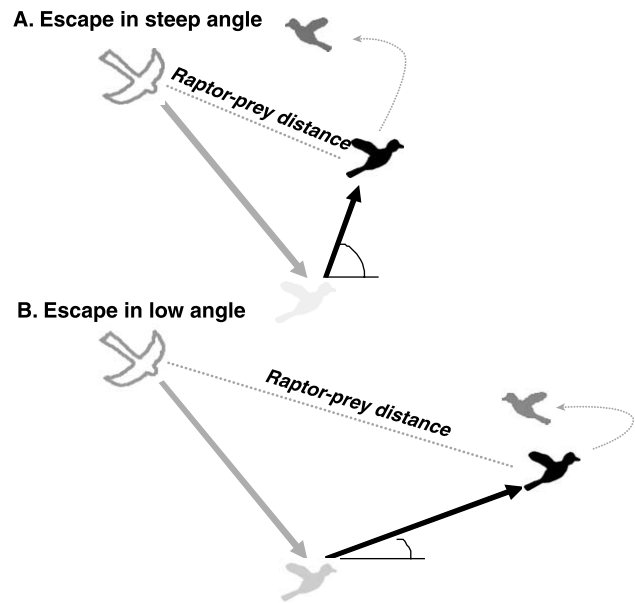


Fig. 5. Escape in passerine birds when approached by aerial raptor. Typically the prey bird takes off and ascends at a steep angle (A), and then turns to out-climb the diving raptor. In this example the prey moves diagonally toward the raptor rather than maximizing the distance to it. Birds that ascend at low angle (B), for example females that are heavy before laying their eggs or birds after migration that are energy depleted, maximize the distance to the raptor but are more vulnerable since the raptor can easily chase and pounce on them.

moving straight or diagonally toward the predator. Nevertheless, such defensive strategy is common in passerine birds that take-off and ascend at a steep angle in response to a diving aerial predator (van der Veen and Lindstrom, 2000). The prey bird could gain longer distance from the predator and higher speed by flying at a low angle (i.e. parallel to the ground), but it trades these for the steeper and more energy-demanding ascent (Kullberg, 1998; Kullberg et al., 2000, 2002; Lind et al., 1999; Fig. 5). Consequently, it flies in a path diagonal to that of the predator, presumably for the same reasons described above in the horizontal domain; namely, to increase the relative speed between itself and the predator, reducing the period it can be chased, and limiting it to a single clashing point which it tries to evade by 'outclimbing' the diving raptor and flying above it (Lind et al., 1999).

The failure of owls to catch food items that were dragged sideways is probably the incentive for another common defense in prey birds: dodging sideways when attacked by aerial raptors (Lima, 1993). For example, under high-speed attack, blue tits (*Parus caeruleus*) dodge sideways more often than when attacked at a low speed, and about 50% of sedge warblers (*Acrocephalus schoenobaenus*) respond to an 'attacking' model of a merlin by darting sideways at an angle of 90° from the model (Kullberg et al., 2000). Therefore, defense is not as simple as maximizing distance between oneself and predator (Lind et al., 1999), and running away may not pay (Hochachka, 2004) since under

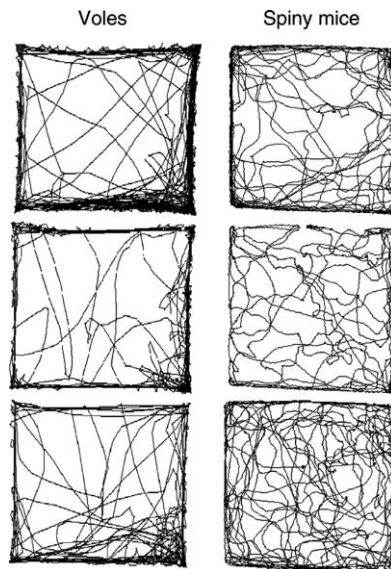


Fig. 6. (based on Eilam, 2004). Trajectories of locomotion of three voles (left) and three spiny mice (right) in a  $2 \times 2$  m arena. Each square shows one rodent. As shown, voles crossed the center in a relatively straight path whereas spiny mice moved through the center in a convoluted path, frequently changing the direction of progression.

certain circumstances it is better to move toward or sideways in relation to the attacking predator.

When tested in an open field (arena with walls), rodents generally avoid the open center of the arena and cling to the security provided by the walls (Eilam, 2003). Avoiding the center of an open field has been attributed to the higher predatory risk and lack of shelter in open spaces. Fig. 6 depicts the trajectories of locomotion in a vole and a spiny mouse, illustrating the tendency of voles to cross the center in relatively straight segments that extend from wall to wall, in contrast with spiny mice that cross the center in a winding path (Eilam, 2004). These forms of progression are in agreement with a mathematical model on the trajectories of flight from a predator (Furuichi, 2002). The model proposes that a straight trajectory is advantageous in facing a distant or relatively slow predator, whereas a zigzag trajectory is advantageous when encountering a close or fast predator. This theoretical inference may explain why in open spaces, spiny mice, which are agile rodents, favor moving continuously along a convoluted path, whereas voles, which are clumsy rodents, favor moving along straight trajectories, alternating between freezing and progressing (Edut and Eilam, 2004). Thus, having made the decision to flee in a specific direction, the prey should also consider the appropriate path shape.

Orienting to the predator is another defensive behavior that is embedded in fleeing. During flight, spiny mice tend to frequently stop and turn to the chasing owl, as if assessing its distance and intentions, and planning their next move (Edut and Eilam, 2004). Orienting is pointless in freezing since such a movement may expose the prey to the predator. Indeed, when voles freeze they do so abruptly, regardless of

their posture and position relative to the owl (Edut and Eilam, 2004).

Finally, habitat structure is another factor that is involved in defensive behavior. Spiny mice are nimble (Eilam, 1997; Oron et al., 1998), living and foraging in crevices and spaces between and under boulders, spending only little of their time in the open (Kronfeld-Schor and Dayan, 1999). Voles are clumsier than spiny mice, with basic gaits (Eilam, 1997) and slow locomotion (Ylonen et al., 1992). In addition, they live in relatively open spaces (Mendelssohn and Yom-Tov, 1999) where, once outside their burrows, they are less likely to escape an attacking owl. When attacked by a barn owl, spiny mice fled in a convoluted path whereas voles alternated between freezing and fleeing (Edut and Eilam, 2004). In other words, agility, fast running, and nearby shelters make fleeing the more appropriate response, whereas limited motor capacity and open habitat might account for alternating between freezing and fleeing. A similar dependence of defensive response on motor capacities and habitat structure was described in deer species (Lingle and Pellis, 2002). White-tailed deer (*Odocoileus virginianus*) that inhabit forests and are fast runners tend to flee when encountering coyotes (*Canis latrans*), whereas mule deer (*Odocoileus hemionus*) that live in relatively open spaces and are moderate runners tend to freeze or hold their ground while fighting the predator (Lingle and Pellis, 2002). Thus, as in spiny mice and voles, better motor capacities and habitat structure that provides nearby shelter encourage a flight response, while limited speed and open habitat conduce to freezing and/or fleeing.

At the conceptual level, freezing may be regarded as fading from the attention of the opponent, whereas fleeing may be regarded as an eluding gambit. The same concept applies to hunting, where predators utilize various hunting patterns, ranging from sit and wait ambush to continuous active pursuit. For example, tawny owls (*Strix aluco*) usually hunt in a 'perch and pounce' pattern of waiting motionless on a fixed perch and then swooping down on a nearby prey, whereas barn owls (*Tyto alba*) often hunt on the wing (Martin and Busby, 1990). Ambushing therefore resembles freezing, while chasing is reminiscent of fleeing. All in all, predator-prey interactions converge to two strategies: in one the opponents continuously attempt to avoid the attention of each other, and in the second both predator and prey continuously move while maintaining awareness of each other's location (Edut and Eilam, 2004).

## 6. Epilogue: implications on the controlling brain mechanisms of defensive behavior

In order to unveil the controlling brain mechanisms of defensive behavior it is first necessary to 'standardize' the response and to control its releasing stimuli. For this, a simple defensive response (e.g.- orienting toward the predator) that is elicited by a single stimulus such as scent



or vocals of predators, is highly appropriate. Another useful approach is to control the intensity of the threatening stimuli, as illustrated above in the mouse-defense test battery.

Such methods confine defenses into relatively simple behavioral categories like freezing, fleeing or orienting, and provide a substrate for typifying the neural mechanisms that control these defenses. For example, since an animal cannot freeze and flee at the same moment, it is clear that these defenses are mutually exclusive and therefore controlled by different motor systems (Barros et al., 2004; Blanchard et al., 2003; Brandao et al., 2003; Canteras, 2002; Comoli et al., 2003; Lamprea et al., 2002). Indeed, freezing in mice involves neural activity in the lateral ventral septum and several medial and periventricular hypothalamic nuclei, whereas fleeing in mice involves more neural activity in cortical, amygdalar and striatal motor areas, the dorsolateral posterior zone of the hypothalamus, and the vertical limb of the diagonal band (Mongeau et al., 2003). Various defensive responses such as flight, defensive fight, freezing, avoidance reactions, submissive postures, tonic immobilization, hypoalgesia and autonomic arousal are mediated via projections of the central nucleus of the amygdala to the midbrain periaqueductal gray, and the hypothalamus and the brainstem (Misslin, 2003). One study has illustrated the effect of 5HT on orienting and other defensive behaviors

elicited by stimulating the superior colliculus in rats (Dringenberg et al., 2003), while another study has highlighted the role of the hypothalamus in defensive behaviors (Canteras, 2002). The known connections between these structures suggest ways in which the brain mediates the balance between these defensive behaviors (Mongeau et al., 2003). For example, inhibitory interactions between the structures mediating these defenses allow rapid switching between defensive modes as the threatening situation varies (Fanselow, 1994). Recently, it was suggested that defensive behavior is two-dimensional. One dimension is the defensive distance (see ‘distance dependent hierarchy’, above), which is mapped to neural levels with the shortest defensive distances involving the lowest neural level (periaqueductal gray) and the largest defensive distances the highest neural level (prefrontal cortex) (McNaughton and Corr, 2004). The second defensive dimension extends from fear to anxiety, and is mapped to separate parallel streams that run across the levels of the first dimension so that fear and anxiety are represented at all neural levels, resulting in a series of distinct neural modules, each with typical symptoms of stress disorders such as panic, phobia, obsession, etc. (McNaughton and Corr, 2004). All in all, defensive behaviors, and specifically freezing and fleeing, are not mutually exclusive responses that knock out each other when activated. Rather, they are

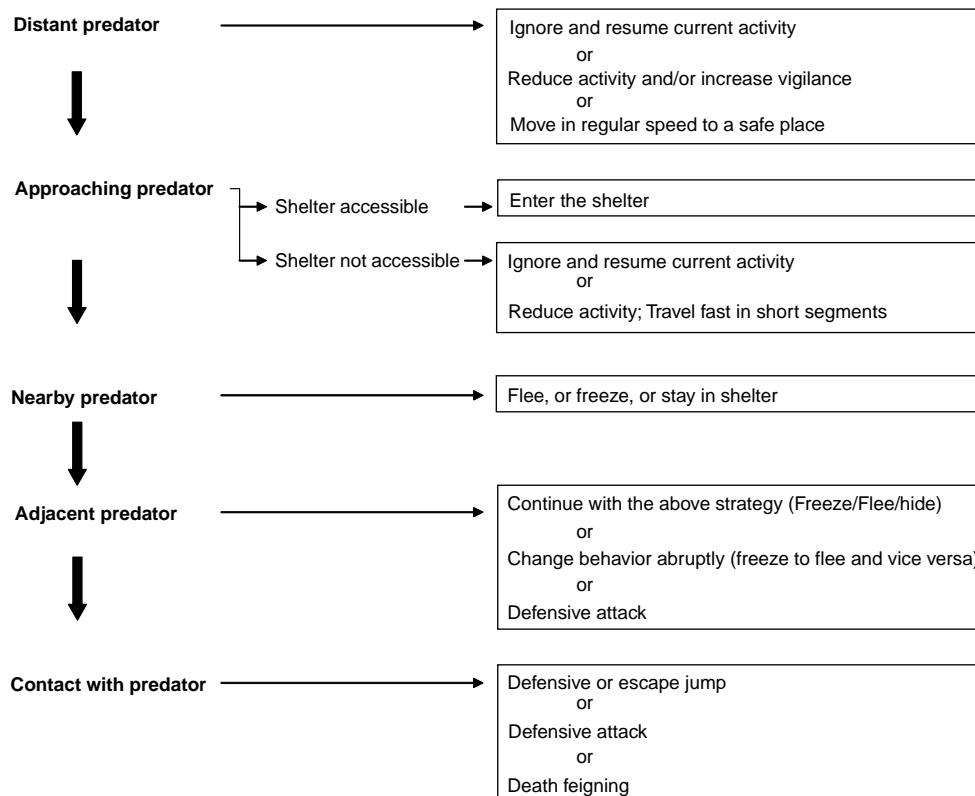


Fig. 7. Diagram of defensive behavior under increasing threat (e.g. an approaching predator), illustrating the multiple defensive responses at each stage and the many transitions that may occur between these defenses. Such versatility is vital in the arms race between predator and prey, in order to prevent predators from learning the defensive response.

integrated into a more complex and flexible, distance-dependent defensive response, as illustrated in Fig. 7.

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## Supplementary data

Supplementary data associated with this article can be found, in the online version, at [doi:10.1016/j.neubiorev.2005.03.027](https://doi.org/10.1016/j.neubiorev.2005.03.027)

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