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Movement and direction of movement of a simulated prey affect the success rate in barn owl *Tyto alba* attack

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The present study was aimed at testing a novel idea, that rather than maximizing their distance from a predator during close-distance encounters, prey species are better off moving directly or diagonally toward the predator in order to increase the relative speed and confine the attack to a single available clashing point. We used two tamed barn owls *Tyto alba* to measure the rate of attack success in relation to the direction of prey movement. A dead mouse or chick was used to simulate the prey, pulled to various directions by means of a transparent string during the owl's attack. Both owls showed a high success rate in catching stationary compared with moving food items (90% and 21%, respectively). Success was higher when the prey moved directly away, rather than towards the owls (50% and 18%, respectively). Strikingly, these owls had 0% success in catching food items that were pulled sideways. This failure to catch prey that move sideways may reflect constraints in postural head movements in aerial raptors that cannot move the eyes but rather move the entire head in tracking prey. So far there is no evidence that defensive behavior in terrestrial prey species takes advantage of the above escape directions to lower rates of predator success. However, birds seem to adjust their defensive tactics in the vertical domain by taking-off at a steep angle, thus moving diagonally toward the direction of an approaching aerial predator. These preliminary findings warrant further studies in barn owls and other predators, in both field and laboratory settings, to uncover fine predator head movements during hunting, the corresponding defensive behavior of the prey, and the adaptive significance of these behaviors.

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In the arms race between predator and prey species, aerial raptors utilize various hunting strategies (Cresswell 1996), while prey species make behavioral adjustments in order to avoid encounter with the predator. From the prey perspective, defensive tactics are typically based on fleeing or freezing (Blanchard and Blanchard 1989, Lima and Dill 1990). 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). This and other studies in passerine birds have implicitly assumed that the correct response of a prey is to escape directly away from the oncoming aerial predator by taking off and ascending at a steep angle (Cresswell 1993, Kullberg et al. 2000, van der Veen and Lindstrom 2000, Kullberg et al. 2002). While escaping away is probably aimed at increasing the distance between predator and prey, the steep take-off reduces that distance, indicating that defense is not as simple as merely maximizing distance between prey and predator (Lind et al. 1999). Moreover, about 50% of sedge warblers *Acrocephalus schoenobaenus* responded to an "attacking" cardboard model of a merlin by darting sideways at an angle of almost 90° from the model (Kullberg et al. 2000). These behavioral responses raise the question of their adaptive value, assuming that prey species are expected to take the most appropriate defensive response (Cresswell 1993, Parmigiani et al. 1999, van der Veen and Lindstrom 2000, Edut and Eilam 2003, Furuichi 2002). Uncovering the hunting capacities of predators is therefore a prerequisite when attempting to understand defensive behavior.

In this study we approached the raptor-prey encounter from the predator's perspective, by comparing the success of barn owls *Tyto alba* in catching stationary prey with prey that moved in various directions during close encounters. We simulated the movement of the prey by dragging a food item (dead chick or mouse) in various directions, and measured the corresponding success of the barn owls. Owls utilize various hunting patterns, ranging from continuous active pursuit to perch and pounce ambushing. When perching, owls remain motionless, merging into the background with the camouflage colors of their feathers, and when hunting on the wing they fly silently by virtue of the unique structure of their wings and feathers, which suppress the sound of airflow over the wings (Graham 1934, Thorpe and Griffin 1962). However, the maneuvering abilities of owls and the ways in which a prey may respond to these abilities have not yet been examined.

We assume that when a prey is moving away from an owl, the owl will have more time to maneuver and catch it. In contrast, when owl and prey are moving toward one another, their relative speed will be higher than the owl's individual speed and there will be only a single available clashing point where the owl can catch the prey. If it misses a prey that is moving toward it, the owl will then need to execute fast and sharp maneuvering, limited by its higher speed and larger body mass (Hendenström 1992). These considerations are also applicable to the vertical domain, when prey birds try to outclimb diving raptors by taking off and ascending at a steep angle (van der Veen and Lindstrom 2000, Kullberg et al. 2002). In view of these constraints, we expected that the rate of success in catching a food item (simulated prey) would be higher with a prey moving away from the owl, and lower with a prey moving toward it. We also expected that it would be easier for the owl to catch a stationary, rather than a moving prey.

Methods

Study Animals

Barn owls *Tyto alba* are efficient hunters that feed mainly on rodents. The initial detection of prey location relies on the barn owl hearing the sounds generated by prey movement, and is followed by visually pinpointing the prey with sharp vision. It then swoops down on the prey from a perch or on the wing, catching it with its sharp talons and killing it in seconds (Taylor 1994, Konig et al. 1999). Two eggs were collected from captive barn owls and incubated for a period of about 20 days (Miracle Therbo-9900 AC incubator Appingrdam, NL, set to 37.5° and 55% humidity). The two hatchlings were hand-reared and tamed, and then trained first to fly and catch food items placed in various locations. Food items were then tied to a transparent string and pulled in various directions to train the owls in catching moving food items. The two owls were about one year old when used in this study. The long rearing and training period made it logistically impractical to use a larger number of owls in the present study.

Apparatus

The owls were introduced into a circular (6 m diameter) white arena and were stationed on a roost (2 m height) adjacent to the perimeter. The height of the roost represented the range of 1–3 m height at which barn owls typically hunt (Taylor 1994). The simulated 'prey' was a dead chick or a dead mouse ('food item') placed in the center of the arena, initially concealed from the owl by a plate and attached to a transparent string that was invisible against the white background of the arena. The string was connected through a pulley mechanism to an experimenter outside the arena. A video camera with a built-in VITC time code generator (*Panasonic* S-VHS NV-M9500) was placed outside the arena, opposite the owl's roost, and operated by a second experimenter who tracked the flight of the owl. Each food item was pulled in one of eight experimental directions, spaced at intervals of 45°, in order to simulate a moving prey (Fig. 1).

Procedure

To the best of our knowledge, no other test of this kind has been carried out previously. Before testing, the two tamed owls were trained for several weeks to receive their food in the center of the test apparatus, and only then underwent the present study. Each of the owls was placed on the post for five minutes of habituation before the experimenter removed the plate to uncover the food item. As soon as the owl took-off from the post to swoop down on the food item, this was either left stationary or pulled away via the transparent string in a direction that followed a random sequence of numbers between 0–8 as generated by 'Microsoft Excel'. Each number in this sequence was assigned to one pulling direction (8 pulling directions and one for stationary food item). Behavior was videotaped, commencing at exposure of the food item and continuing until a successful catch was made. The speed of the moving food item was calculated from the videotapes to be 2.3 ± 0.1 m/s (mean ± SEM), approximating that of a fast moving mouse. This small variation in speed of the moving food item indicates that it was similar in all the various directions and that there

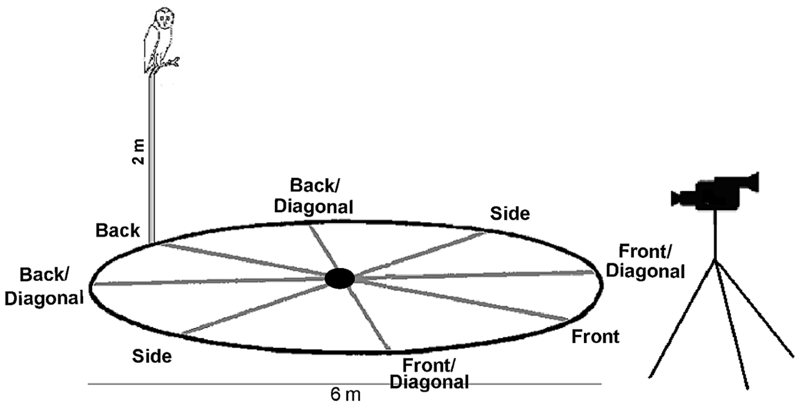

Fig. 1. The test apparatus comprised a circular white arena (6 m diameter; 0.4 m high walls). The owl roost was located opposite a video camera. The food item was placed in the center (black circle) of the arena concealed from the owl by a plate and attached to a transparent string for pulling in one of the 8 predefined directions depicted in the figure by lines. The string was invisible against the background.

was no directional bias in prey movement between treatments. Both owls were tested 2–3 days/week, with all testing sessions taking place 90 minutes before dusk, using the two owls in a random order in each session. There were up to two trials/day (one for each owl). If an owl did not swoop on the food, we covered and re-exposed it repeatedly, until the owl swooped on it. If it failed to swoop within 15 min, it was tested again only on the next test day. Accordingly we obtained 46 and 29 trials for the two owls respectively. The rate of success, however, was similar in both owls, as shown in the 'Results'.

Data acquisition

Data were scored during frame-by-frame (25 frames = 1 s) playback of the videocassettes. A time-code translator (Telcom Research T-900, Burlington, Canada) allowed reading the VITC time-code to a computer program (Excel, by Microsoft, Israel). We scored the timing of food item pulling, of onset of an attack, and of a successful catch or landing on the ground, as well as additional information such as the direction of pulling, the distance flown by the owl, and the distance traversed by the food item.

Statistics

Considering that the sample in this study was limited to two subjects only, the presented statistical tests are not meant to indicate the level of confidence regarding inferences from this sample to the general population, but rather to convey some measure of consistency in the performance of the two owls tested.

Results

As shown in Table 1, the rate of success in catching moving and stationary food items was very similar for the two barn owls, and their data were therefore combined in subsequent analyses. Similarly, data for the two hemispheres of the arena (left and right, in reference to the owl) were pooled together due to the low occurrence of successful trials (Table 1). These data show that the success rate in stationary trials was significantly higher than the rate for trials with moving food item (90% and 21%, respectively). In other words, the owls had a four-fold higher success in catching stationary, compared with moving food items.

The owls showed a high success rate in certain directions and a low success rate in other directions of simulated prey movement. Specifically, success was high in the front and front/diagonal directions, low in the back and rear/diagonal directions, and nil in the sideways directions (Table 2 and Fig. 2). Thus, the owls constantly failed to catch any simulated prey that was pulled sideways.

The duration of owl flight in failed attacks was significantly shorter than the duration in successful attacks (two-tailed t-test, $t_{14} = 3.63$, $P < 0.003$). Flight duration in both successful and failed attacks was significantly shorter when the food item was pulled in

Table 1. Number of trials, incidence of successful captures, and individual and combined rates of success for the two owls, shown for moving versus stationary prey.

	Trials			Success			Rate		
	Owl I	Owl II	Both	Owl I	Owl II	Both	Owl I	Owl II	Both
Total – moving	46	29	75	10	6	16	0.22	0.21	0.21
Total – stationary	6	4	10	6	3	9	1.00	0.75	0.90

Table 2. Number of trials, incidence of success, and success rate for the different directions of prey movement. The duration columns indicate mean duration of owl flight from take-off to landing either on the ground (failure) or on the food item (success).

Direction	Trials	Success	Success/Trials (%)	Duration of owl flight in s (mean ± SEM)	
				Successful trials	Failed trials
Front	10	5	50	1.400	1.213
Front/diagonal	18	7	39	1.496	1.220
Side	16	0	0	–	1.288
Back/diagonal	20	2	10	1.880	1.000
Back	11	2	18	2.640	0.977
Total	75	16	21	1.623 ± 0.123	1.146 ± 0.046

the back and diagonal/back directions (forward and diagonal/forward: 1.35 ± 0.06 s; sideways: 1.29 ± 0.09 s; back and back/diagonal: 1.13 ± 0.11 s; two-tailed t-test: $t_{40} = 2.18$, $P < 0.05$). The reaction time of the owls, as measured between exposure to prey and flight take-off, did not differ between successful and failed trials (mean ± SEM: 1.16 ± 0.25 and 1.15 ± 0.17 s, respectively). Similarly, the reaction time of the owls as measured between the beginning of prey movement and the beginning of flight-course correction did not differ between successful and failed trials (mean ± SEM: 0.20 ± 0.04 and 0.20 ± 0.01 s, respectively). Therefore, these latencies did not seem to affect the rate of success obtained in the different sectors. Additionally, the different durations of attacks (mean ± SEM: 1.15 ± 0.01 and 1.49 ± 0.08 s, two-tailed t-test, $t_{18} = 2.7$, $P = 0.014$, for successful and failed trials, respectively) did not seem to affect the rate of success (see, however, note in 'Methods' on the above statistical comparisons).

A correction in the direction of flight, with the owl adjusting its direction of attack according to the direction of movement of the food item, slightly affected the success rate: 23% success in trials with correction compared with 18% success in trials without correction. The overall duration of attack from owl take-off to capture (including a failure in the first attack) was just 1.23 ± 0.05 s (mean ± SEM). Finally, the owls demonstrated no improved success rates over the course of the experiment, indicating that there was no learning or practice effect (Fig. 3).

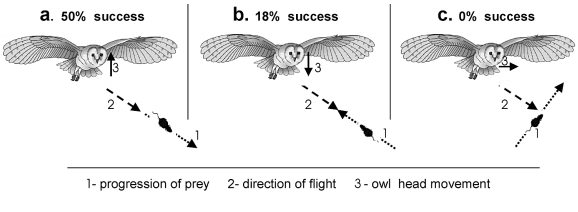

Fig. 2. The relation between rate of success and direction of movement for a food item that was pulled forward (a), backward (b) and sideways (c). Direction of prey progression – dotted arrow (1), direction of owl flight – dashed arrow (2), and direction to which the owl had to move its head or trunk-solid arrow (3). Owl picture taken from Knudsen E., Nature 2002, 417:322–328, with permission from the author and publisher.

Discussion

In the present study, two tamed barn owls were challenged to catch a food item (dead mouse or chick) that was dragged away when they launched their attack. The rationale was to simulate prey movement and test the rate of owl success in catching a moving *vs.* stationary prey, as well as to assess the possible impact of the direction of prey movement. The results reveal that the owls had a 90% success rate with stationary prey compared with a 21% success rate with moving food items. They also had higher success with food items that were dragged directly away (50%) or diagonally away (39%) from them, compared with food items dragged straight toward them (18%) or diagonally toward them (10%). Finally, both owls had 0% success in catching food items that were dragged sideways. In the following discussion we first suggest plausible constraints that may have imposed these differential rates of success, and then

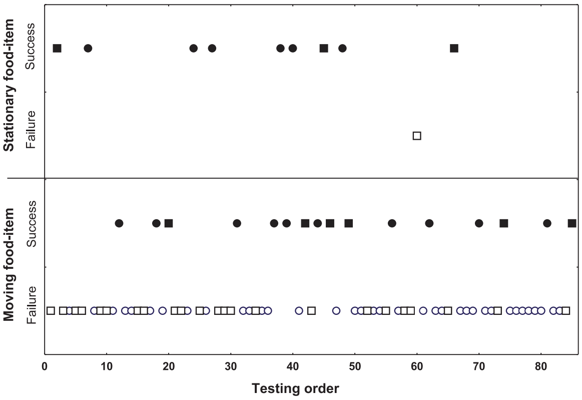

Fig. 3. Success (● – owl 1, ■ – owl 2) and failure (○ – owl 1, □ – owl 2) trials for stationary (top) and moving (bottom) food items, depicted in the temporal order of testing (x-axis), indicate that if some form of learning across trials does take place, it is subtle.

interpret the adaptive significance of defensive responses in prey species according to the present results.

Kinematic considerations of moving toward rather than away from a predator

The lower success rate in catching food items that were dragged toward the owl, compared with those dragged straight away from it, confirmed our assumption that when a predator and a prey move toward each other: i) their combined relative speed is higher than that of each individually; and ii) there is only a single clashing point available where the predator can catch the prey, unless the predator is able to execute fast and sharp maneuvering. However, maneuvering is limited by the higher speed of the predator, which implies a higher momentum of inertia, making it harder to change the current direction of progression. Indeed, in this experiment the owls typically made minor corrections, and when missing the dragged food item, they typically landed on the ground near the expected clashing point, and then took off to re-attack. In contrast, when the prey moves straight away from the owl, their combined relative speed is lower than that of the owl itself, and the owl may thus have more time to follow the prey and can swoop down on it with only minor adjustments.

Similar considerations are applicable to the vertical domain, shedding light on why prey birds take-off and ascend at a steep angle in response to a diving aerial predator (van der Veen and Lindstrom 2000). By flying at a low angle (i.e. parallel to the ground), a prey bird could gain longer distance from the predator and higher speed, but it trades these for the steeper and more energy-demanding ascent (Kullberg 1998, Lind et al. 1999, Kullberg et al. 2000, Kullberg et al. 2002). 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.

Overall, the present results illustrate that a simple physical constraint may make it advantageous for a prey to move toward rather than straight away from a nearby predator, and that maximizing the distance to the predator is not necessarily the safest tactic in close encounters (Lind et al. 1999).

Perceptual flaw may account for the failure to catch food items that move sideways

In light of the above physical considerations, it could be expected that success in catching a food item dragged sideways would be higher than with a food item moving toward the owl and lower than with one moving straight away from it. However, this was not the case since both owls entirely failed to catch any food items that were pulled sideways. When tracking a prey, birds make head movement rather than the eye movements that are common in mammals (Land 1999). Among birds, owls have large eyes that are set close together, providing binocular vision and excellent depth perception (Martin 1977, Martin 1982). However, this arrangement of the eyes also narrows the frontal visual field to a range of only 70°, causing tunnel vision. Nonetheless, lateral tracking is achieved by the owl’s ability to rotate its head rapidly and in large amplitudes of up to 270°, providing a binocular visual field of 360° with stationary trunk (Taylor 1994, Konig et al. 1999). Head swivel has been shown in roosting owls with trunk in an upright posture and the head looking forward. During flight, however, the head faces forward and the swivel is irrelevant. Rather, a lateral movement of the head and/or the trunk is required in order to track an object that moves laterally (Fig. 2). In the present study, the owls were forced to make such lateral movement of the head and/or body during flight since the food item was pulled sideways immediately after the owl took off. The failure to catch laterally moving food items may therefore indicate that this movement is slower or harder than the up or down movement required when tracking food moving along the mid-saggital (longitudinal) axis of flight. It would be interesting to determine this in further studies, by tracking raptor head movements in relation to the movement of prey. It should be noted that diurnal raptors are also required to make head movements when tracking prey (Land 1999, Tucker 2000, Tucker et al. 2000), and their successful captures may also be limited by prey movement in certain directions.

Prey tactics: differential success of predators may be reflected in the direction of prey movement

One implication of the present results is that if a prey chooses to flee, predation risk may be reduced by fleeing in the direction of the predator or sideways rather than straight away. In terrestrial animals this seems to contradict the intuitive response to flee away from threat, and therefore must remain hypothetical until shown in the behavior of prey under predator attack. In prey birds, however, these results highlight the importance of the vertical, compared with the horizontal, component of escape flight. Past studies have described escape flight directly away from the oncoming raptor, implying an attempt to maximize the distance to the predator, with ascent angle considered indicative of flight ability (Cresswell 1993, Kullberg 1998, Lind et al.

1999, van der Veen and Lindstrom 2000, Kullberg et al. 2002). In light of the present results it is suggested that the highly energy-consuming steep ascent may also have anti-predatory benefit for the kinematic considerations described above. Furthermore, the finding that darting sideways at an angle of almost 90° from an oncoming raptor model of merlin is common in sedge warblers (Kullberg et al. 2000), calls for testing whether this is an ordinary defense tactic that takes advantage of the raptors' inability to track sideways, and whether diurnal raptors are similarly disadvantaged in catching prey that move sideways.

The fundamental difference between the success rates for stationary prey and moving prey, as established in the present preliminary results, may suggest that a prey will dramatically decrease predation risk by fleeing rather than freezing when encountering a barn owl. However, freezing also eliminates the auditory and visual cues that owls use in pinpointing prey (Mikkola and Willis 1983) and if a prey freezes before being spotted, the owl may not be able to locate it (Kaufman 1974). Since upon noticing an owl, the prey might not know whether or not it has already been spotted, it may alternate between freezing and fleeing, combining disappearance through freezing with not being a stationary target if freezing fails (Edut and Eilam 2003). Defensive response, however, depends not only on motor and perceptual constraints of the predator and prey, but also on other features such as habitat structure, direction of the approaching predator, and location of shelter (Kramer and Bonenfant 1997, van der Veen and Lindstrom 2000). Nevertheless, it may prove to be of interest to search for examples of sideways escape when studying predator-prey encounters in the wild.

Concluding remark

While the present results are preliminary and based on only two tamed owls, they provide a novel perspective of predator-prey encounters from the predator's perspective and raise questions that deserve consideration in future studies on hunting and defensive behavior.

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