

Sensory exploitation of prey: manipulation of the initial direction of prey escapes by a conspicuous 'rare enemy'

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The painted redstart (*Myioborus pictus*) represents a group of non-cryptic predators, the flush pursuers, who visually trigger prey escapes by spreading and pivoting their conspicuously patterned tails and wings. The prey are then chased in aerial pursuits. Such an exploitation of prey may be possible because the predation risk from redstarts is smaller than that from the predatory guild of insectivores and their neural pathways are adapted to helping prey avoid common predators rather than 'rare enemies'. I propose that the pivoting movements of flush pursuers direct insect escapes across the central field of vision of a predator, where it is easier to track and intercept the prey. Eighty per cent of chases by wild redstarts were in a direction suggesting that prey were entering the birds' area of stereoscopic vision. The redstart's fanned and raised tail creates a stronger visual stimulus than a redstart's head. Flies escaped away from the section of the fly's field of vision in which the model's tail was located and towards the area where the predator's stereoscopic vision is likely to be located, in front of a bird's forehead. The experiments suggested that redstarts may not only exploit the sensitivity of typical neural escape pathways, which are non-directionally sensitive, but that they may also exploit the sensitivity of some directionally sensitive neural pathways in prey.

Keywords: sensory exploitation; predator–prey interactions; signalling; escape pathways; *Myioborus pictus*

1. INTRODUCTION

Sensory exploitation occurs when a signaller evolves stimuli that tap into a receiver's existing sensitivity, which has evolved in contexts other than sensory exploitation signalling or might be a coincidental product of neural architecture (Ryan *et al.* 1990; Proctor 1991; Basolo 1995; Phelps & Ryan 1998). Most studies on sensory exploitation have concerned sexually selected, intra-specific signals, which typically evolve in males in order to exploit sensory properties in females. Two questions may arise. Are females really being exploited? Do they pay costs of responding to the 'exploitative' rather than 'non-exploitative' signals of males? Sometimes it may be difficult to establish whether the evolution of characters regarded as exploitative signals has pre-dated the evolution of the hypothetically exploited sensitivity in receivers. The present study concerns a predator-to-prey exploitative, interspecific signalling system where the costs paid by the receivers are clear and where the architecture of the neural networks that are being exploited is well defined and undoubtedly pre-dates the evolution of the exploitative signalling.

Certain insectivorous birds that include a high proportion of dipterans in their diet exploit the visual sensitivity of escape pathways in flies by flushing the prey from the substrate and then chasing it in the air where the prey offers visual contrast (Jabłoński 1994, 1996, 1999; Barber *et al.* 2000). Unlike typical leaf-gleaning warblers, the flush pursuers (Remsen & Robinson 1990) forage with half-spread wings and a broadly spread and half-raised tail, thereby exposing contrasting bright patches on the

tails, wings or rump. These displays are well tuned to the simple sensory characteristics of the prey escape networks (Jabłoński & Strausfeld 2000; P. G. Jabłoński and N. J. Strausfeld, unpublished data). The presence of these escape pathways in prey is a prerequisite for the evolution of flush–pursue displays; these displays cannot effect the escapes of insects without such pathways (P. G. Jabłoński and N. J. Strausfeld, unpublished data).

There are several reasons why flush pursuers are interesting subjects for evolutionary studies. First, like cuckoos and cowbirds (see the reviews in Kilner *et al.* 1999; Winfree 1999), they are ideal examples of evolution through sensory exploitation because, unlike the sensory exploitation of females choosing a mate, there is no doubt that the prey is being exploited when it is killed. However, unlike exploitative signalling of cuckoos to hosts where hosts can evolve recognition abilities in order to reject the parasitic eggs (see the review in Winfree 1999), the extreme simplicity of insect escape networks imposes a clear constraint on prey abilities to identify the exploiting predator (Hatsopoulos *et al.* 1995; Rind & Simmons 1999; P. G. Jabłoński and N. J. Strausfeld, unpublished data). Second, the evolution of flush-pursuing birds occurred 10–30 million years ago (Sibley & Ahlquist 1986, 1990). This is more than 70 million years after the appearance of modern families of Diptera (Shaw 1989). This suggests an undoubtedly earlier existence of the neural escape pathways in prey than the exploitative signals in predators. Third, flush pursuers exemplify an evolutionary paradox of how selection for conspicuous rather than cryptic coloration in predators helps in foraging. Finally, Jabłoński (1999) proposed that flush

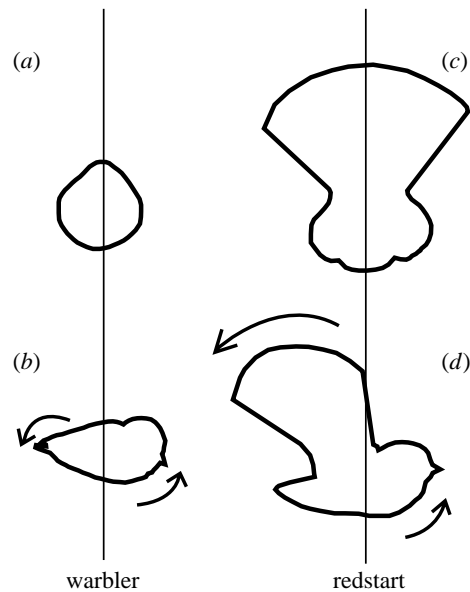


Figure 1. Schematic silhouettes of birds as seen by prey located in the predator's path (marked by a line). (a) Warbler at the start of a pivot in the counter-clockwise direction, (b) warbler at the end of a pivot in the counter-clockwise direction, (c) redstart at the start of a pivot in the counter-clockwise direction and (d) redstart at the end of a pivot in the counter-clockwise direction. Arrows indicate the direction of pivoting movements.

pursuers serve as a good empirical example of a 'rare enemy effect' (*sensu* Dawkins 1983), which is an evolutionary consequence of interactions in theoretical, multi-species predator-prey systems (Matsuda *et al.* 1993, 1994). According to theory, exploitation of prey by flush pursuers might occur because the natural selection that shapes the sensitivity of the escape networks for avoiding a rare predator (the flush-pursuing species) is weaker than such a selection for avoiding other common predators (Jabłoński 1999; Jabłoński & Strausfeld 2000). While the presence of specific escape pathways in prey may explain the form of the conspicuous displays (Jabłoński & Strausfeld 2000; P. G. Jabłoński and N. J. Strausfeld, unpublished data), the rare enemy effect could explain the evolutionary stability of those displays (Jabłoński 1999). However, it would not explain what the selective advantages of the evolution of flush pursuing are to birds.

How do flush-pursuing birds benefit from using conspicuous displays? In response to conspicuous displays by the painted redstart (*Myioborus pictus*), which is a typical flush-pursuing species, prey initiate escapes at greater distances from the predator (Jabłoński 1999; Jabłoński & Strausfeld 2000). Consequently, the number of insects flushed and conspicuously available for birds to chase may be increased (Jabłoński 1999). I suggest a new hypothesis. I propose that redstarts' displays confuse insects with regard to the direction of predator approach and the area of the predator's visual attention.

2. HYPOTHESIS

Visually elicited escape responses in arthropods are directed away from stronger visual stimulation (Woodbury 1986; Nalbach 1990), which usually indicates an

approaching predator. When an approaching redstart pivots its spread tail, a different pattern of visual stimulation is created than that produced by substrate-gleaning warblers. The visual stimuli created by foraging warblers contain pivoting movements when a bird switches position on a branch during hopping. This pivoting is not associated with conspicuous spreading of the half-raised tail, which is characteristic of redstarts. In the present paper, I ask whether the effect of pivoting on prey escape direction is different for redstart-specific foraging (with a spread and half-raised tail) than for warbler-like foraging (with tail and wings closed and not raised). When a bird turns to the left during a pivot (counter-clockwise when seen from above) (figure 1), the prey in front of a bird receives visual stimulation from the bird's head turning left (right from the perspective of prey facing the bird) and from the bird's tail moving right (left from the prey's perspective). Because the visual stimulus from a closed tail moving behind a warbler's body (i.e. far from an insect) is weaker than the visual stimulus from the warbler's head moving near an insect, the right side of the insect's field of view subtending the bird will be stimulated more strongly than the left side (figure 1*a,b*). If an insect escapes away from the stronger stimulation it will fly to the warbler's right side, that is away from the frontal field of vision in a bird and away from the area on which the bird's attention may be focused. Redstarts spread their tails broadly and keep them half-raised during pivoting. Because the visual stimulus from an open tail moving above a redstart's body (the tail is raised) is stronger than the visual stimulus from the redstart's head, the left side of insect's field of view will be stimulated more strongly than the right (figure 1*c,d*). Therefore, an insect will fly to the left (from the bird's perspective), that is across the frontal field of a redstart's vision. I test the hypothesis that, by pivoting of a spread and raised tail, redstarts direct the escapes of their dipteran prey into the zone of the predator's stereoscopic vision, where it is easier to track and intercept escaping prey.

3. METHODS

(a) Observations of birds

I videotaped unbanded and individually indistinguishable birds from 14 different non-adjacent territories. Pivoting movements were estimated from the screen with an approximate accuracy of 5–10°, depending on the quality of the picture and the position of the bird. Each frame in 14 separate sequences of 45.7 ± 7.7 frames (mean \pm s.d.) (which were most probably taken from 14 different birds) was classified with respect to the angle of the redstart's body and its tail to the horizontal. This provided information about how often a redstart's upper body surface was directed towards a potential prey above and in front of the bird.

I extracted 30 chases after insects from slow-motion playback of the video recordings of foraging redstarts (34 chases were found in the video and four chases that were directly along the path of a bird's approach were excluded) in which I classified the escape direction as either the same or opposite the direction of head movement due to pivoting immediately preceding the chase. All pivots were accompanied by spread and half-raised tails and spread wings. I used a binomial test (Zar 1999) in order to test the null hypothesis that chases were equally frequent in the two directions.

Table 1. *Effect of raised and spread tails in pivoting models on escape directions of flies*

(Probabilities p were sequential, Bonferroni-corrected p_b for multiple ($k=3$) comparisons. The following factors were used in the contingency tables: escape type (lateral versus directly away), escape direction (same versus opposite the head movements), model type (tail closed in the manner of a warbler versus tail raised and open in the fashion of redstarts) and fly category.)

fly category	percentage of escapes in the lateral direction among all escapes (n)		G -test (p and p_b): model type × escape type for 2×2 table	percentage of escapes in the direction of model's head turn among all lateral escapes (n)		G -test (p and p_b): model type × escape direction for 2×2 table
	warbler	redstart		warbler	redstart	
<i>Musca</i> sp.	67.3 (55)	69.0 (58)	0.25 (0.881 and 0.881)	10.8 (37)	72.5 (40)	32.77 (0.000 and 0.000)
<i>Thricops</i> sp.	72.9 (59)	67.8 (59)	0.37 (0.833 and 0.972)	23.3 (43)	67.5 (40)	17.00 (0.000 and 0.000)
Calliphoridae	81.0 (116)	77.8 (126)	0.39 (0.531 and 0.896)	42.6 (94)	63.3 (98)	8.27 (0.004 and 0.004)

(b) *Simulations of bird approaches to prey*

I compared the frequency distributions of the escape directions of flies found in redstart territories in response to two models: (i) a taxidermic model of a redstart with a closed tail and wings, and (ii) a taxidermic model of a redstart with a spread and half-raised tail and with half-spread wings. Because the aim was to test the effect of redstart-specific posture during pivoting rather than the effect of redstart-specific body coloration, I used taxidermic redstart models that did not visibly differ in their coloration and the patterning of the black and white plumage presented towards insects. Any slight, non-visible differences between the models should not have affected escapes because fly responses to unavoidably spectrally different paper models of redstarts have been shown to be non-significantly different from responses to taxidermic models (Jabłoński & Strausfeld 2000).

For each test, a model was moved towards the front of a fly along a straight path while imitating hops with pivots. Each individual fly was tested once only by an experimenter in camouflaged cloths standing *ca.* 1.5 m in front of the fly. In order to test the effect of redstart-specific body posture alone, both models were pivoted in the same way. A pivot was performed during each hop around a centre located approximately one-third of the body length from the model bird's beak. The speeds of the model movements were within the range recorded for birds (for details see Jabłoński & Strausfeld 2000). I noted the direction of the model's head movement during a pivot that caused a fly to escape. Model head movement was defined as the movement of frontal parts of the model body during pivoting. The escapes were classified into two escape types: away or lateral. Escapes of an initial direction that was within $\pm 20^\circ$ from the line of model approach were classified as away from the model because they were not clearly directed at either side of the model's path. The remaining responses, which are termed here as lateral escapes, were categorized into two escape directions, namely either the same or opposite the direction of the movement of the model's head during pivoting that caused the escape. During pivoting redstarts mostly look forwards along the main body axis (Jabłoński 1999; P. G. Jabłoński, personal observation). I used a G -test and multiway log-linear contingency table analysis (with a backward stepwise procedure for choosing the simplest model that fitted the data) in order to test the null hypothesis of no differences in escape direction distributions between warbler-like and redstart-like treatments. The third factor in the contingency tables was fly category with three classes, as in table 1. Representatives of these classes are

found in the redstart diet (P. G. Jabłoński, H. Hespeneide, S. Gadi and J. P. Cygan, unpublished data).

(c) *Simulations of single pivots*

The same two models as described in §3(b) were used. A fly was chosen for each test and a model was very slowly moved to within *ca.* 20 cm of it, with the frontal part of the model's head facing the front of the fly's body. Such a distance is commonly observed in redstarts that are flushing insects (Jabłoński 1999). The model was then pivoted once to either the right or left, thereby imitating a single pivot of a redstart around a pivoting centre located approximately one-third of the body length from the bird's beak. I tested two families of Diptera: Sarcophagidae (with most probably one unidentified genus) and Muscidae (*Thricops* sp.). Each individual fly was tested once only. In approximately half the tests, a glass partition (which is transparent in near ultraviolet light) was carefully moved between the model and the fly before model movement. This transparent partition prevented air currents produced by pivoting from reaching the fly. By looking at the effect of partition I estimated a possible role of non-visual stimuli in affecting the direction of escape. I used a G -test and contingency table analysis in order to test the null hypothesis of no differences in escape direction distributions between warbler-like and redstart-like treatments.

(d) *Effect of the direction of stimulus movement on escape direction*

In addition to the hypothetical effect of the spread tail due to asymmetry of the stimulation in the visual field (figure 1), I tested whether the direction of movement itself affected the initial direction of an escape. Flies react in a similar way to simple geometrical models and to bird-like models (P. G. Jabłoński and N. J. Strausfeld, unpublished data). I tested the responses of *Thricops* sp. flies (Muscidae) found in redstart territories in the field to horizontally, silently moving (left or right), black-and-white vertical stripes located 20 cm in front of a fly. The stimulus consisted of a 20 cm × 50 cm striped board moved horizontally by an observer behind an 80 cm × 100 cm grey board with a rectangular 6 cm × 11 cm window through which the moving striped board was viewed by a test fly located 20 cm from the grey board. The speed of movement was within the speeds of pivots recorded in redstarts (Jabłoński & Strausfeld 2000). Hence, a fly was stimulated with a horizontally moving, vertically striped pattern within a fixed window in the fly's frontal field of vision. The stimulus window was located either symmetrically or asymmetrically with respect to the centre of

the fly's field of vision. Either the centre or the vertical edge of the window faced the fly at the centre of its field of vision (directly in front of a fly). When the window was positioned asymmetrically (the left and right areas of the fly's field of view were chosen in a randomized fashion) the horizontal movement was performed in the direction towards the centre of the fly's field of view. Fly escapes were categorized as the same or opposite the direction of stimulus movement. Escapes that were directly away, i.e. those within $\pm 20^\circ$ from the straight line pointing perpendicularly to the model surface, were excluded.

If the direction of stimulus movement alone affects escape direction the proportion of the number of same escapes to the number of opposite escapes in the symmetrical treatment should differ from the expected ratio of 1:1 (which was tested using a binomial test) (Zar 1999). If the location of the window in the fly's field of vision influences escape direction then the effect of movement direction in asymmetrical treatment should be different than in symmetrical treatment. A transparent (including near ultraviolet light) glass partition present between the model and the fly that prevented air currents produced by the board movements reaching the fly was used in 90 tests, while in 70 other tests the partition was absent. By looking at the effect of the partition I estimated a possible role of non-visual stimuli in affecting the direction of escape. I analysed the data in a contingency table with three factors: stimulus location (symmetrical or asymmetrical), fly escape direction (same or opposite), and glass partition (present or absent).

4. RESULTS

(a) *Bird behaviour*

Redstarts held their bodies horizontally for the majority of foraging (figure 2). Occasionally a bird would hold its body tilted down (head down, in *ca.* 30% of frames in foraging sequences) or up (head up, in *ca.* 20% of frames). Birds' tails were raised up for *ca.* 60% of foraging time and sometimes the angle to the horizontal was large (more than 60°) (figure 2). In such positions, the conspicuous contrasting pattern of redstarts' upper body surfaces could easily be seen by any potential prey above and in front of a foraging redstart. The typical movements of foraging redstarts seen in the video recording consisted of *ca.* 10-cm-long hops frequently associated with or followed by pivots of the whole body of up to 180° around its point of support (detailed description in Jabłoński & Strausfeld 2000). Foraging redstarts chased insects in the direction of the head movement during pivoting immediately preceding the chase more often (80%) than in the opposite direction (20%) ($n=30$) (binomial test, $p < 0.005$).

(b) *Simulations of bird approaches*

The proportion of flies escaping laterally did not differ significantly between insect families or model types (table 1) (the best-fit model in the three-factor contingency table included no interactions) (escape type and fly category, $G_8=7.711$ and $p=0.462$). In accordance with expectations, laterally escaping flies flew more frequently in the direction of a bird's head turn in response to imitations of displaying redstarts than in response to the models of approaching warblers (table 1). This effect of model type was significant for each of the three categories of flies tested (table 1). However, the effect differed between test

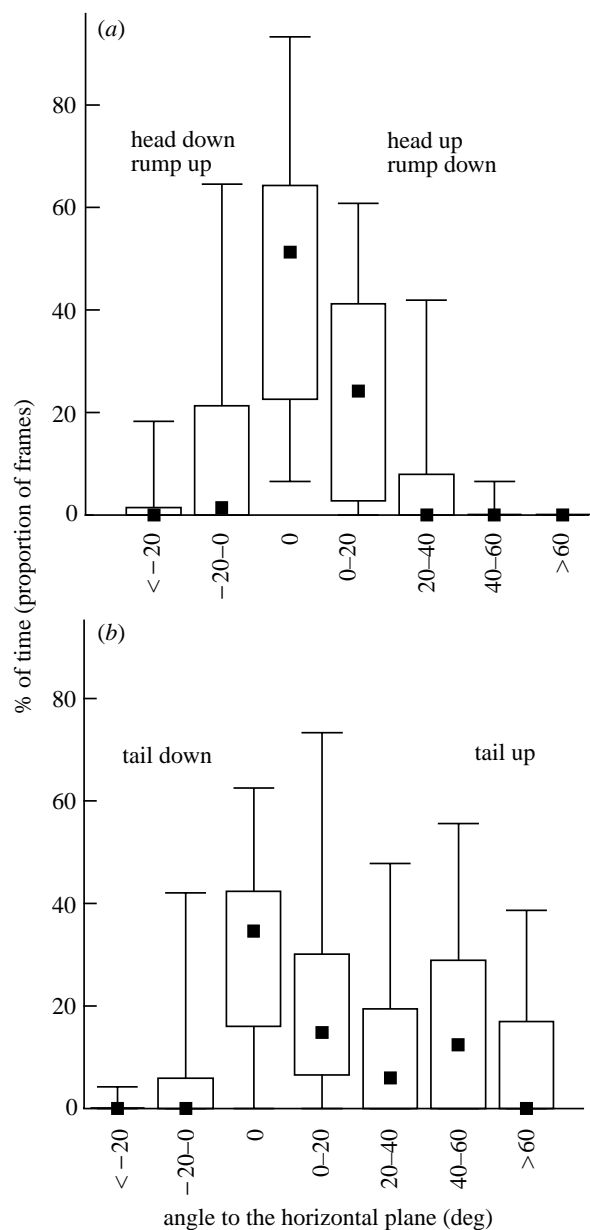


Figure 2. Positions of (a) the body and (b) the tail of foraging redstarts ($n=14$ sequences). The medians (black squares), upper and lower quartiles (boxes) and maximum and minimum values (lines) are shown.

flies, which was indicated by the contingency table analysis in which only the statistical model with three-factor interactions (fly category \times model type \times escape direction) fitted the data (criterion $p > 0.05$).

(c) *Single pivots*

The proportion of lateral escapes of *Thricops* flies did not depend on model type or the presence of a glass partition, because the best-fit statistical model (escape type and glass partition, $G_5=4.700$ and $p=0.454$) (table 2) did not contain any interaction effect. Flies escaped in the direction of a bird's head turn more often in response to a single pivot of the redstart-like taxidermic model than they did in response to a pivot of the warbler-like taxidermic model (table 2). The statistical model fitted to the data for laterally escaping *Thricops* sp. included the effect of model type but did not include the effect of the

Table 2. Effect of raised and spread tails in models on escapes of flies in response to single pivots

(The effect of a glass partition between the model and flies (*Muscidae*) is also shown for *Thricops* sp.)

fly family	glass partition	percentage of escapes in the lateral direction among all escapes (<i>n</i>)		percentage of escapes in the direction of model's head turn among all lateral escapes (<i>n</i>)	
		warbler	redstart	warbler	redstart
<i>Muscidae</i> (<i>Thricops</i> sp.)	present	79.7 (69)	79.2 (72)	47.3 (55)	66.7 (57)
	absent	68.4 (98)	69.6 (102)	31.8 (66)	58.8 (68)
<i>Sarcophagidae</i>	absent	44.9 (49)	52.2 (46)	40.9 (22)	66.7 (24)

presence of a glass partition on escape direction (the fitted statistical model: bird model type \times escape direction, $G_4 = 5.710$ and $p = 0.222$) (table 2). In tests without the glass partition, three-factor contingency table analysis resulted in the statistical model which included the effect of model type but did not include the effect of fly family on escape direction (the fitted statistical model obtained by a forward or backward fitting procedure: bird model type \times escape direction and fly family, $G_3 = 0.588$ and $p = 0.899$), indicating that in both families of flies the redstart-like pivots increased the frequency of escapes in the direction of the model's head turn during pivoting (table 2).

(d) Effect of movement direction

In most of the symmetrical tests the flies escaped in the direction opposite the direction of stimulus movement (table 3) (binomial $p \ll 0.001$) and this was independent of the presence of the glass partition (effect of glass partition on escape direction, $G_1 = 0.512$ and $p = 0.474$). The location of the window in which the stimulus was presented influenced the escape direction by increasing the frequency of escapes away from the area of the field of vision where the window was located. The statistical model fitted to the data did not contain the effect of the glass partition, but included the effect of the symmetry of stimulus presentation on escape direction (table 3) (fitted model: stimulus location escape direction, $G_4 = 6.368$ and $p = 0.173$). However, despite this effect, in asymmetrical treatment flies more often flew against than with the direction of the stimulus movement, even though this was towards the area of stronger visual stimulus in a fly's field of vision (table 3).

5. DISCUSSION

The results showed that visual stimuli from pivoting and raising an opened tail by flush pursuers may increase the frequency of prey escapes in the direction which is likely to be the centre of a bird's field of view at the moment of prey escape. When models did not have raised and opened tails, the effect of pivoting was reversed and the prey escaped more often in the direction away from the centre of a bird's field of view. Such a sensitivity of prey escape pathways may be adaptive because it leads to avoidance of the area where warblers are likely to focus their visual attention, i.e. in front of a bird in the zone of stereoscopic vision. By changing the character of the visual stimulus (figure 1), redstarts may exploit prey by evoking prey escapes in a direction that is maladaptive

Table 3. Effect of the location of moving a striped stimulus board in the field of vision on the escape directions of *Thricops* sp. flies (*Muscidae*)

glass partition	percentage of escapes opposite the stimulus movement among all lateral escapes (<i>n</i>)	
	symmetrical stimulus location	asymmetrical stimulus location
present	92.9 (42)	70.8 (48)
absent	87.5 (24)	60.9 (46)

from the prey point of view but beneficial for redstarts, i.e. an escape across a redstart's central field of vision.

The centre of a bird's field of view contains a narrow area of stereoscopic vision (Martin 1986; Martin & Katzir 1999). Having prey in this area at the moment of prey escape should help redstarts track prey in three-dimensional space and intercept the prey escape trajectory in aerial chases. Observations of foraging redstarts confirmed this hypothesis: birds chased insects in the direction that coincided with the direction of their stereoscopic vision. However, this result may have been additionally influenced by factors other than the direction of prey escapes. It is likely that, for mechanistic reasons, it is easier to chase prey in the same direction in which a bird's body is being turned at the moment preceding the chase. I was unable to estimate the extent of this effect on chase direction in the present study.

This study also showed that redstarts may exploit two aspects of the visual sensitivity of prey: sensitivity to the location of the stimulus in the prey's visual field and sensitivity to the direction of stimulus movement. Escape in flies starts by activation of the left and right tergo-trochantal muscles (TTMs) through the left and right giant descending neurons (GDNs), which are activated by visual inputs. TTMs control middle leg extension during an initial jump followed by flight powered by flight muscles (Bacon & Strausfeld 1986; Milde & Strausfeld 1990; Holmqvist & Srinivasan 1991). Thus, the direction of escape may be influenced at the moment of escape by asymmetrical activation of the two GDNs due to asymmetrical distribution of the stimulus in the prey's visual field. However, it is more likely that the direction of escape is influenced in flight. The action of flight muscles is controlled by various descending neurons, which, unlike GDNs, are directionally sensitive to visual stimuli

(Egelhaf *et al.* 1988). Therefore, these neurons might have reacted directionally to a moving experimental stimulus immediately after initiation of the escape. Accordingly, experiments by P. G. Jabłoński and C. McInerney (unpublished) using paper models rather than taxidermic ones showed that initial escape direction was also more frequently against than with the pivot direction for flies that viewed the approaching model laterally. In this situation asymmetry of the stimulation of right and left GDNs cannot explain the directionality of escape behaviour.

In summary, the present experiments showed that conspicuous tail fanning by birds may exploit their prey's anti-predatory responses and make prey capture easier. The results suggested that, in addition to recently studied exploitation of non-directionally sensitive escape pathways (GDNs in flies), some directionally sensitive pathways in prey may be exploited by flush-pursuing birds.

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REFERENCES

- Bacon, J. P. & Strausfeld, N. J. 1986 The dipteran 'giant fibre' pathway: neurons and signals. *J. Comp. Physiol.* **B158**, 529–548.
- Barber, M. B., Barber, D. R. & Jabłoński, P. G. 2000 Painted redstart (*Myioborus pictus*). In *The birds of North America*, no. 528 (ed. A. Poole & F. Gill). Philadelphia, PA: Academy of Natural Sciences and Washington, DC: American Ornithologists' Union.
- Basolo, A. L. 1995 Phylogenetic evidence for the role of pre-existing bias in sexual selection. *Proc. R. Soc. Lond.* **B259**, 307–311.
- Dawkins, R. 1983 *The extended phenotype*. Oxford University Press.
- Egelhaf, M., Hausen, K., Werner, R. & Wehrhahn, C. 1988 Visual course control in flies relies on neuronal computation of object and background motion. *Trends Ecol. Evol.* **11**, 351–358.
- Hatsopoulos, N., Gabbiani, F. & Laurent, G. 1995 Elementary computation of object approach by a wide-field visual neuron. *Science* **270**, 1000–1003.
- Holmqvist, M. H. & Srinivasan, M. V. 1991 A visually evoked escape response of the house fly. *J. Comp. Physiol.* **A169**, 451–459.
- Jabłoński, P. G. 1994 Adaptive significance of colour patterns in painted redstart. *J. Ornithol.* **135**(Suppl.), 147.
- Jabłoński, P. G. 1996 Dark habitats and bright birds: warblers may use wing patches to flush prey. *Oikos* **75**, 350–352.
- Jabłoński, P. G. 1999 A rare predator exploits prey escape behavior: the role of tail-fanning and plumage contrast in foraging of the painted redstart (*Myioborus pictus*). *Behav. Ecol.* **10**, 7–14.
- Jabłoński, P. G. & Strausfeld, N. J. 2000 Exploitation by a recent avian predator of an ancient arthropod escape circuit: prey sensitivity and elements of the displays by predators. *Brain Behav. Evol.* **56**, 94–106.
- Kilner, R. M., Noble, D. G. & Davies, N. B. 1999 Signals of need in parent-offspring communication and their exploitation by the common cuckoo. *Nature* **397**, 667–672.
- Martin, G. R. 1986 The eye of a passeriform bird, the European starling (*Sturnus vulgaris*): eye movement amplitude, visual fields and schematic optics. *J. Comp. Physiol.* **159**, 545–557.
- Martin, G. R. & Katzir, G. 1999 Visual fields in short-toed eagles, *Circus gallicus* (Accipitridae), and the function of binocularly in birds. *Brain Behav. Evol.* **53**, 55–66.
- Matsuda, H., Abrams, P. A. & Hori, M. 1993 The effect of adaptive anti-predator behavior on exploitative competition and mutualism between predators. *Oikos* **68**, 549–559.
- Matsuda, H., Hori, M. & Abrams, P. A. 1994 Effects of predator-specific defence on community complexity. *Ecol. Ecol.* **8**, 628–638.
- Milde, J. J. & Strausfeld, N. J. 1990 Cluster organization and response characteristics of the giant fiber pathway of the blowfly *Calliphora erythrocephala*. *J. Comp. Neurol.* **294**, 59–75.
- Nalbach, H. O. 1990 Visually elicited escape in crabs. In *Frontiers in crustacean neurobiology* (ed. K. Wiese, W. D. Krenz, J. Tautz, H. Reichert & B. Muloney), pp. 165–171. Basel, Switzerland: Birkhäuser.
- Phelps, S. M. & Ryan, M. J. 1998 Neural networks predict response biases of female tungara frogs. *Proc. R. Soc. Lond.* **B265**, 279–285.
- Proctor, H. C. 1991 Courtship in the water mite *Neumania papillator*: males capitalize on female adaptations for predation. *Anim. Behav.* **42**, 589–598.
- Remsen, J. V. & Robinson, S. K. 1990 A classification scheme for foraging behavior of birds in terrestrial habitats. *Studies Avian Biol.* **13**, 144–160.
- Rind, F. C. & Simmons, P. J. 1999 Seeing what is coming: building collision-sensitive neurones. *Trends Neurosci.* **22**, 215–220.
- Ryan, M. J., Fox, J. H., Wilczynski, W. & Rand, A. S. 1990 Sexual selection for sensory exploitation in the frog *Physalemus pustulosus*. *Nature* **343**, 66–67.
- Shaw, R. S. 1989 The retina-lamina pathway in insects, particularly Diptera, viewed from an evolutionary perspective. In *Facets of vision* (ed. D. G. Stavenga & R. C. Hardie), pp. 186–212. New York: Springer.
- Sibley, C. G. & Ahlquist, J. E. 1986 Phylogeny and classification of New World subsocial passerine birds (Passeriformes: Oligomyodi: Tyrannides). *Ornithol. Monogr.* **36**, 396–405.
- Sibley, C. G. & Ahlquist, J. E. 1990 *Phylogeny and classification of birds. A study in molecular evolution*. Yale University Press.
- Winfrey, R. 1999 Cuckoos, cowbirds and the persistence of brood parasitism. *Trends Ecol. Evol.* **14**, 338–343.
- Woodbury, P. B. 1986 The geometry of predator avoidance by the blue crab, *Callinectes sapidus* Rathbun. *Anim. Behav.* **34**, 28–37.
- Zar, J. H. 1999 *Biostatistical analysis*. Englewood Cliffs, NJ: Prentice Hall, Inc.