SHORT COMMUNICATION

Johan Lind · Ulrika Kaby · Sven Jakobsson

Split-second escape decisions in blue tits (*Parus caeruleus*)

Abstract Bird mortality is heavily affected by birds of prey. Under attack, take-off is crucial for survival and even minor mistakes in initial escape response can have devastating consequences. Birds may respond differently depending on the character of the predator's attack and these split-second decisions were studied using a model merlin (*Falco columbarius*) that attacked feeding blue tits (*Parus caeruleus*) from two different attack angles in two different speeds. When attacked from a low attack angle they took off more steeply than when attacked from a high angle. This is the first study to show that escape behaviour also depends on predator attack speed. The blue tits responded to a high-speed attack by dodging sideways more often than when attacked at a low speed. Escape speed was not significantly affected by the different treatments. Although they have only a split-second before escaping an attack, blue tits do adjust their escape strategy to the prevailing attack conditions.

Introduction

Adult mortality in small birds is heavily affected by birds of prey (e.g. Geer 1978; Cresswell and Whitfield 1994). When hunting, many raptors rely on surprise attacks (Kenward 1978; Cresswell 1993, 1996) and, due to the small time margins, tiny mistakes in escape response by prey can result in capture (Cresswell 1993). Nevertheless, attack success rates are generally low, approximately 10% (Lindström 1989; Cresswell 1993, 1996; Cresswell and Whitfield 1994), which implies that prey birds may affect the outcome of attacks by adapting behaviourally to the prevailing attack conditions.

When attacked, the prey bird's initial phase of escape ought to be crucial to its survival. A rapid take-off, high speed and high climb rate should be at a premium (e.g.

Kenward 1978). However, birds face a trade-off between maximising linear acceleration and climb rate when flying (Witter and Cuthill 1993). When the prey is unable to attain as high a speed as the attacking predator it is advantageous to divert from the attack trajectory (Howland 1974). Such a diversion is suggested to be even more important when the pursuing predator is travelling faster or when the attack is detected later (Howland 1974; cf. Witter and Cuthill 1993).

Two studies have shown behavioural prey flexibility to different attack conditions (Cresswell 1993; Kullberg et al. 1998). In a field study, redshanks' (*Tringa totanus*) escape responses depended both on raptor species and attack strategy used (Cresswell 1993). Responses that led to escape more often from one predator species led to capture more often by another species. When great tits (*Parus major*) face experimental surprise attacks they adjust their take-off angle according to the predator's attack angle (Kullberg et al. 1998). However, robins (*Erithacus rubecula*) tested in the same experimental set-up are insensitive to different attack angles (Lind et al. 1999).

Blue tits (*Parus caeruleus*) are closely related to great tits and live in overlapping habitats. Thus, it is reasonable to assume that similar selective pressures have acted on the evolution of their escape behaviours. We studied escape tactics by subjecting blue tits to simulated predator attacks from different angles and at different speeds to investigate which factors of an attack influence split-second escape decisions.

Materials and methods

Blue tits were trapped during the winter of 2000 around Tovetorp Zoological Research Station, Sweden, and housed indoors in individual cages (90×60×95 cm). Water, sunflower seeds and suet were available ad libitum and a few mealworms (*Tenebrio molitor*) were also provided daily. Lighting followed a natural photoperiod and birds were kept on average 2.2 days (ranging from 1 to 6 days) before experiments.

Experiments were conducted indoors using a large experimental cage (2×0.7×2 m) consisting of solid walls (for a detailed de-

J. Lind (✉) · U. Kaby · S. Jakobsson
Department of Zoology, Stockholm University,
106 91, Stockholm, Sweden
e-mail: johan.lind@zoologi.su.se
Tel.: +46-8-164052, Fax: +46-8-167715

scription see Kullberg et al. 1998). One of the short-side walls was made of a mesh net and a glass screen. A 50 cm high pole with a perch was placed on the floor inside the cage by the glass screen. On the perch there was a steel wire to secure mealworms prior to each experiment. Finally, there was a curved wooden pole, with small perches attached at 15 cm intervals, at a constant distance of 1.5 m from the feeding perch.

To simulate a standardised surprise attack, a model merlin was pulled down along a line towards the perch at two different angles, 15° and 45°. Two different weights, 0.12 and 2 kg, achieved two different speeds with maxima of 2 and 5 m s^{-1}. Subsequently, four treatments were used: attack from a low angle with high (n=29) or low speed (n=10) and attack from a high angle with high (n=24) or low speed (n=16). The attacks took approximately 0.6 s at high speed and 2.2 s (ranging from 1.9 to 3.3 s) at low speed and the merlin travelled 180 cm before it stopped behind the feeding perch.

A bird was randomly chosen and subjected to an attack. An attack was launched when the bird was sitting on the feeding perch, eating a mealworm, with its back facing the merlin. After trial, the bird was ringed (to prevent it being used twice) and released in the vicinity of the station. Daily, during winter, small non-migratory birds increase in body mass by approximately 10%, but since these diurnal increases do not affect take-off ability (see Kullberg 1998; Kullberg et al. 1998; van der Veen and Lindström 2000) birds were tested throughout the day, with no experiments earlier than 45 min after full lights-on in the mornings and none later than 1 h before dusk. Escapes were assessed using Sony Digital Cameras DCR-VX1000E (25 frames/s). One camera yielded angles of ascent and speed and was placed perpendicular to the line of flight, recording through a 0.8×0.8 m window in the wall. The other camera, situated behind the feeding perch, enabled us to estimate deviations from the centre trajectory. Angles of ascent and speed were calculated after 20, 40 and 60 cm of flight (using same method as described in Kullberg et al. 1998). Birds that deviated dramatically from the centre trajectory (>30°) could not be analysed in terms of speed and angle of ascent. However, the frequency of such dodging birds in the treatments was recorded. A total of 89 males, 47 young and 42 old, were used. Ten birds could not be analysed due to flying in a zig-zag course, diving or not detecting the merlin before it stopped.

To confirm that the blue tits responded to the visual stimulus of the merlin and not to the sound, ten additional blue tits (females) were exposed, one by one, to a simulated attack from a high angle at high speed but with the merlin removed. None of them responded until the weight hit the floor, when eight of them took flight and the two others remained on the perch feeding. Hence, during the attack by the merlin, the blue tits reacted to the visual stimulus of the merlin.

Statistical analyses were performed using STATISTICA 5.5. (Statsoft).

Results

During escape flights, 65% (58 of 89) of the birds rolled and looped within the first metre of flight (Fig. 1) possibly trying to outmanoeuvre the incoming predator by flying above it in the opposite direction. Angles of ascent and escape speed increased with distance travelled in all
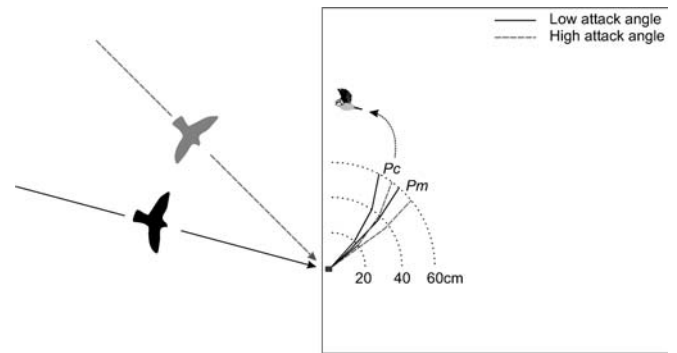

Fig. 1 Escape trajectories (angles of ascent at 20, 40 and 60 cm after take-off) for blue (*Pc*) and great tits (*Pm*) when subjected to simulated surprise attacks from a low angle and a high angle (in blue tits at high speeds). Everything except the size of the birds is drawn to scale. The *dashed line* on top indicates the common behaviour observed when blue tits escaped by taking off steeply, making half a loop, and attempted to escape by flying above the predator in the opposite direction.

treatment groups (Tables 1, 2). In addition, blue tits' escape angles were affected by attack angle; birds escaped at steeper angles when subjected to a low attack angle (Table 1, Table 2 and Fig. 1 for the high speed treatments) than to a high attack angle. However, attack speed did not affect take-off angles significantly (Tables 1, 2), and there were no significant differences in escape speed between the four treatment groups (Tables 1, 2).

Log-linear analysis revealed that a high attack speed resulted in a higher frequency of birds dodging sideways

Table 2 Summary of the 3-way ANOVA of the effect on the blue tits' angle of ascent and take-off speed. Factor 1 – attack angle, factor 2 – attack speed, factor 3 – distance after take-off (repeated measurement with three levels, i.e. the three distances 20, 40 and 60 cm from the perch) and the resultant interactions

Dependent factor	Factor	df Effect	df Error	F	P-level
Angle of ascent	1	1	48	8.8	0.005
	2	1	48	0.6	0.43
	3	2	96	388	<0.0001
	12	1	48	<0.1	0.88
	13	2	96	1.1	0.32
	23	2	96	4.6	0.01
Take-off speed	1	1	48	0.1	0.77
	2	1	48	0.5	0.50
	3	2	96	193	<0.0001
	12	1	48	0.2	0.62
	13	2	96	0.1	0.90
	23	2	96	0.1	0.87

Table 1 Speeds and angles of ascent at 20, 40 and 60 cm after take-off for each of the four treatment groups. Values are means ± SE

Treatment	Ascent angle (°)			Speed (m s^{-1})			n
	at 20 cm	at 40 cm	at 60 cm	at 20 cm	at 40 cm	at 60 cm	
Low angle–high speed	46.9±2.4	54.0±2.3	62.0±2.5	2.2±0.05	2.7±0.06	2.9±0.09	16
Low angle–low speed	50.1±2.6	57.6±2.1	63.4±1.8	2.2±0.05	2.7±0.05	3.0±0.09	10
High angle–high speed	36.9±3.2	46.3±3.5	55.1±3.8	2.3±0.07	2.8±0.06	3.1±0.09	13
High angle–low speed	41.0±3.4	48.2±3.4	54.6±3.4	2.2±0.09	2.7±0.9	2.9±0.1	13

compared with the low attack speed (χ^2=12.9, P<0.001, df=1). Attack angle did not influence dodging behaviour significantly (χ^2=2.9, P=0.09, df=1) and no interaction between angle and speed of attack was found (χ^2=2.7, P=0.10, df=1). Frequencies for low angle of attack; 13 out of 29 dodged when attacked at high speed as compared with 0 out of 10 when attacked at low speed. Frequencies for high angle of attack; 11 out of 24 dodged when attacked at high speed compared with 3 out of 16 when attacked at low speed.

Discussion

This study shows that blue tits incorporate information about a predator's surprise attack when choosing their own escape response. Blue tits adjusted their ascent angles to the merlin's attack angle. When attacked from a low angle birds ascended approximately 10° more steeply than when attacked from a high angle, a pattern consistent throughout the measured distance (Fig. 1). These results suggest that, on attack, the best strategy is not always to maximise the distance from the predator, but to divert from the attack trajectory. By diverting from the attack trajectory a slower prey can escape from a faster predator. A predator with a high speed (and usually larger body) requires a longer turning radius than a slower (and usually smaller) prey, making it impossible for the predator to turn as sharply as the prey (Howland 1974; Andersson and Norberg 1981; Hedenström and Rosén 2001). When small birds are attacked they reach a flight speed of approximately 3 m s^{-1} after about 0.6–0.7 m of flight (see Kullberg et al. 1998; Lind et al. 1999) whereas *Accipiter* hawks attack at 5–28 m s^{-1} (Goslow 1971; Hilton et al. 1999). Thus, adjusting the take-off angle may be important for birds in outmanoeuvring surprise attacking predators. Previous studies have revealed that great tits (Kullberg et al. 1998) adopt different ascent angles according to attack angles in a surprisingly similar manner to that of blue tits, whereas robins do not (Lind et al. 1999). This apparent disparity between robins and tits could depend on several reasons, which are not well understood. Different species have different escape tactics inherently and they usually prefer habitats in which their particular escape tactic is most effective (Lima 1992, 1993). Blue and great tits are closely related, forage in a similar manner and seem to share the same inherent escape tactics. Robins seldom move far away from cover and also give high priority to the safety of cover when selecting territories (Cuadrado 1997). The lack of flexibility in escape response found in robins may be linked with a more secluded life style and habitat choice.

The escape behaviour of the blue tits also depended on attack speed. Birds dodged sideways more frequently when attacked at high speed than at low speed. Thus we show, for the first time, that diversion becomes more important with increasing attack speed as suggested from theory (Howland 1974; Witter and Cuthill 1993). This is reasonable, since high attack speed enables prey birds to outmanoeuvre predators, and, when predators attack, it is advantageous to divert laterally since a steep take-off should constrain acceleration. In comparison, when attacked slowly, a prey bird may benefit more from fleeing to cover, out-climbing or delaying its initiation of outmanoeuvring the predator until it is beneficial (cf. Howland 1974; Hedenström and Rosén 2001). Dodging behaviour has also been observed in sedge warblers (*Acrocephalus schoenobaenus*) (Kullberg et al. 2000). Even though inter-specific variation in escape flights has been documented (Lind et al. 1999; Kullberg et al. 2000; van der Veen and Lindström 2000), no comparative studies have been performed and this variation is still not thoroughly understood.

That the blue tits adopted the same take-off speed in all treatments and that vertical ascent angles were independent of attack speed suggest that some elements of escape from surprise attacks follow a standard escape response, as suggested by Hedenström and Rosén (2001). One reason could be that obtaining information about attacks is time-constrained. However, this study shows that blue tits have time to adjust some aspects of their escape to the prevailing attack conditions.

Although they have just a split-second before taking off following attack, this study, together with Kullberg et al. (1998), shows that birds are able to obtain information about the prevailing attack conditions and to incorporate it into their escape. However, more studies are needed to unravel the previously mentioned inter-specific behavioural differences in escape tactics.

References

Andersson M, Norberg Å (1981) Evolution of reversed sexual dimorphism and role- partitioning among predatory birds, with a size scaling of flight performance. Biol J Linn Soc 15:105–130

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

Cresswell W (1996) Surprise as a winter hunting strategy in sparrowhawks *Accipiter nisus*, peregrines *Falco peregrinus* and merlins *F. columbarius*. Ibis 138:684–692

Cresswell W, Whitfield DP (1994) The effects of raptor predation on wintering wader populations at the Tyninghame estuary, southeast Scotland. Ibis 136:223–232

Cuadrado M (1997) Why are migrant robins *Erithacus rubecula* territorial in winter? The importance of the anti-predation behaviour. Ethol Ecol Evol 9:77–88

Geer TA (1978) Effects of nesting sparrowhawks on nesting tits. Condor 80:419–422

Goslow GE Jr (1971) The attack and strike of some North American raptors. Auk 88:815–827

Hedenström A, Rosén M (2001) Predator versus prey: on aerial hunting and escape strategies in birds. Behav Ecol 13:150–156

Hilton GM, Cresswell W, Ruxton GD (1999) Intraflock variation in the speed of escape-flight response on attack by an avian predator. Behav Ecol 10:391–395

Howland HC (1974) Optimal strategies for predator avoidance: the relative importance of speed and manoeuvrability. J Theor Biol 47:333–350

Kenward RE (1978) Hawks and doves: factors affecting success and selection in goshawk attacks on woodpigeons. J Anim Ecol 47:449–460

Kullberg C (1998) Does diurnal variation in body mass affect take-off ability in wintering willow tits? Anim Behav 56:227–233

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

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

Lima SL (1992) Strong preferences for apparently dangerous habitats? A consequence of differential escape from predators. Oikos 64:597–600

Lima SL (1993) Ecological and evolutionary perspectives on escape from predatory attacks: a survey of north American birds. Wilson Bull 105:1–215

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

Lindström Å (1989) Finch flock size and risk of hawk predation at a migratory stopover site. Auk 106:225–232

Veen IT van der, Lindström KM (2000) Escape flights of yellow-hammers and greenfinches: more than just physics. Anim Behav 59:593–601

Witter MS, Cuthill IC (1993) The ecological cost of avian fat storage. Philos Trans R Proc Lond B 340:73–92