



Predator-induced take-off strategy in great tits (*Parus major*)

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When birds are attacked by predators the initial take-off is crucial for survival. The strategy in the initial phase of predator evasion is probably affected by factors such as body mass and presence of cover and conspecifics, but it may also be a response to the character of the predator's attack. In choosing an angle of flight, birds face a trade-off between climbing from the ground and accelerating across the ground. This is, to our knowledge, the first study investigating whether the attack trajectory of a raptor affects the take-off strategy of the prey bird. First-year male great tits (*Parus major*) adjusted take-off angle to a model predator's angle of attack. Birds attacked from a steep angle took off at a lower angle than birds attacked from a low angle. We also compared take-offs at dawn and dusk but could not find any measurable effect of the diurnal body mass gain (on average 7.9%) in the great tits on either flight velocity or angle of ascent.

Keywords: take-off strategy; predation; flight performance; great tit; *Parus major*

1. INTRODUCTION

Birds use several different escape tactics that are dependent on the structure of the birds' environment (Pulliam & Mills 1977; Lima 1993). Escape tactics described are escape into vegetation, flight into open air (either by out-running or out-climbing the predator, aerial dodging or flight in a coordinated flock), escape into water or snow or even plunging to the ground (Lima 1993). Several studies indicate that the success rate of raptor attacks is reduced if the prey gets fully airborne (cf. Rudebeck 1950; Kenward 1978; Newton 1986; Lindström 1989; Cresswell 1993). Thus, disregarding escape tactics, the initial take-off when escaping an attacking raptor seems to influence the bird's survival chances. High velocity and high rate of climb in the take-off both reduce the risk of being killed. Because a low angle of ascent allows the most rapid acceleration, the bird faces a trade-off between gaining height and accelerating across the ground (Witter & Cuthill 1993). Starlings (*Sturnus vulgaris*) took off at lower angles when carrying artificial weights while velocity was conserved, suggesting that the birds choose a lower angle to be able to maintain a high speed when heavier. Furthermore, starlings with reduced body mass due to food deprivation flew at higher angles but at the same speed as control birds (Witter *et al.* 1994). In a study on the effect of migratory fuel load on take-off ability in blackcaps (*Sylvia atricapilla*), Kullberg *et al.* (1996) found that birds with low fuel loads took off at a right angle to the model predators attack trajectory, whereas heavier birds flew at lower take-off angles. From these data we hypothesized that flying perpendicular to the predator's line of attack is

a strategy for maximizing distance to the predator, but a strategy that very heavy birds cannot pursue successfully (Kullberg *et al.* 1996). Here we present a study to investigate if birds adjust take-off strategy to the predator's attack flight. First-year male great tits (*Parus major*) were exposed to a model predator attacking from either a low (15°) or a high (45°) angle. Because several studies on take-off ability in birds have reported an effect of body mass on both velocity and angle of ascent (Witter *et al.* 1994; Metcalfe & Ure 1995; Kullberg *et al.* 1996; Lee *et al.* 1996), half of the birds were tested at dawn while the other half were tested at dusk. The body mass of the great tits increased by on average 7.9% over the day. Take-off flights of individual birds were analysed in terms of angle of ascent and velocity.

2. MATERIALS AND METHODS

First-year male great tits (*Parus major*) were trapped in cages at feeding stations during February and March 1997 in the area around Tovetorp Zoological Research Station, south-east Sweden (58°56' N, 17°08' E). The birds were banded with individual colour bands, housed in groups of three to five in holding rooms (3 m × 1.5 m and 2 m high) equipped with branches, and fed with sunflower seeds, hemp seeds, suet, water *ad libitum* and 20 g of mealworms (*Tenebrio molitor*) every day. The birds were kept in captivity for at least two days before the testing.

To compare escape strategies depending on predator attack angle and test for effects of daily body mass gain on flight ability in the great tits, we used four treatment groups: ten birds were attacked from a low angle (15°) at dawn, ten birds were attacked from a low angle (15°) at dusk, ten birds were attacked from a high angle (45°) at dawn, and ten birds were attacked from a high angle (45°) at dusk. Thus, a total of 40 birds were used in the experiment and each bird was subjected to an attack only once. In

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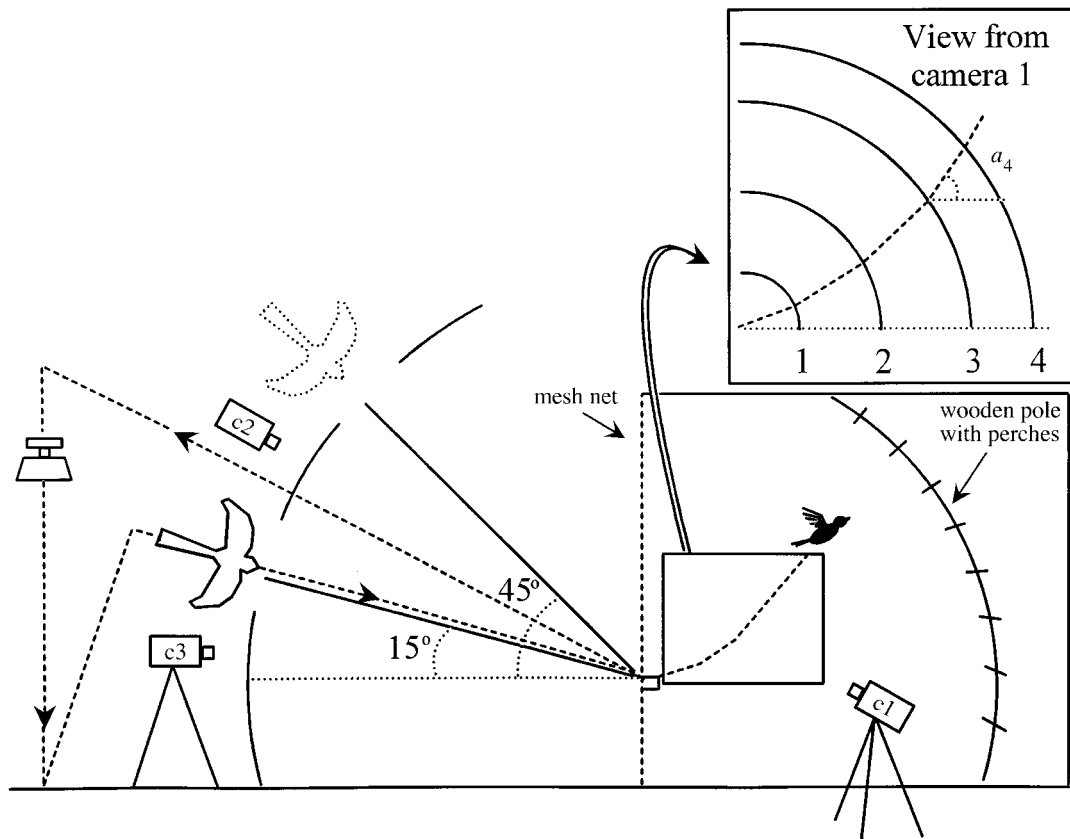


Figure 1. Experimental set-up. Two different set-ups were used: one where the model merlin attacked from a 45° angle and one where the merlin attacked from a 15° angle. The merlin was attached to a weight, pulling it down a wire in a constant velocity irrespective of angle. The take-off of each great tit was recorded by three video cameras (c1, c2 and c3). The video from camera 1 was analysed in terms of angle of ascent and velocity. The view from camera 1 was divided into four sections separated by four lines (lines 1, 2, 3 and 4). Angle of ascent was calculated in each section by using basic trigonometric functions (angle a_4 is shown in the figure).

addition, before each simulated predator attack, a control take-off, when the bird took off from the feeding tray spontaneously, without predator attack, was recorded. There was no difference between the four treatment groups concerning wing length (mean \pm s.e. = 77.05 ± 0.2 mm; ANOVA: $F_{(3,36)} = 0.63$, $p = 0.60$). One great tit at a time was taken at random from one of the holding rooms and transferred to a special experimental room. The four treatments were altered in the following way: low angle at dawn; high angle at dusk; high angle at dawn; low angle at dusk, and so on. The experimental room (2 m \times 0.7 m and 2 m high) was equipped with a curved wooden pole with 10 cm perches every 15 cm at a constant distance from the feeding tray (1.5 m). The feeding tray was placed at a height of 50 cm on one of the short sides of the experimental room where the wall consisted of a mesh net (figure 1). A cardboard model of a flying merlin (*Falco columbarius*) could be sent down along a wire towards the feeding tray at an angle of either 15° or 45° . The merlin started behind a blind 2 m from the mesh net, glided towards the feeding tray placed on the mesh net and stopped just in front of the net. By using a weight (2 kg) attached to the merlin by a closed loop of fishing line, pulling the merlin down the wire, the merlin had an average velocity of 13 km h^{-1} irrespective of attack angle (figure 1). Thus, the merlin was attacking during 0.6 s. Our aim was to simulate a surprise attack, which is a common strategy of merlins, sparrowhawks (*Accipiter nisus*) and peregrines (*Falco peregrinus*) (Cresswell 1996). By combining close appearance and a relatively low velocity of the merlin (which was necessary not

to damage the model) we tried to obtain a situation resembling a natural attack. The model merlin was released in a standardized way when the great tit was sitting on the feeding tray facing the mesh net (where the merlin appeared) and was about to take a mealworm from the feeding tray. Three video cameras recorded the take-off. A Super-VHS camera was placed perpendicular to the line of the take-off (camera c1 in figure 1), recording through a window in the wall, and two standard Video 8 cameras were placed along the line of the take-off (behind the blind where the merlin was hidden) to record side movements by the bird (cameras c2 and c3 in figure 1). Cameras 1 and 2 were connected to video screens to permit observation from outside. Directly after each 'attack trial', the body mass of the bird was recorded on a Precisa 200A scale with an accuracy of 0.01 g and the bird was released at the site of capture.

Four equidistant lines from the feeding tray (15 cm, 37.5 cm, 60 cm and 75 cm) projected onto the video screen of camera 1 (by drawing lines on the screen: lines 1, 2, 3 and 4 in figure 1) and allowed us to divide the bird's flight into four sections. The recordings from cameras 2 and 3 showed that all birds flew in a more or less straight line and no corrections were needed for sideways deviations in flight path. By analysing the video from camera 1, we measured flying velocity and angle of ascent of each bird. Flying velocity was calculated when the birds passed each of the lines 1, 2, 3 and 4 by measuring the distance between two successive frames. Because one frame covered 0.02 s, the velocity (m s^{-1}) was calculated by dividing the

Table 1. Effect of body mass and attack angle on velocity at alarmed take-off

(Summary statistics of ANOVA with attack angle (AA) and body mass (BM) (lean or heavy) as independent factors and the four measured velocities at different distances from the start (DS) as the dependent variable with repeated-measures design.)

effect	d.f. effect	d.f. error	<i>F</i>	<i>p</i>
body mass	1	36	0.2	0.7
attack angle	1	36	0.2	0.7
distance from start	3	108	315	<0.0001
interaction BM × AA	1	36	0.2	0.6
interaction BM × DS	3	108	1.7	0.2
interaction AA × DS	3	108	0.5	0.7
interaction BM × AA × DS	3	108	0.4	0.8

distance moved by 0.02 s. We measured the angle of ascent of each bird in each section by using basic trigonometric functions (angle a_4 is shown in figure 1).

To be sure that the birds actually reacted to the 'attacking' merlin and not only to the sound of the moving fishing line, another five great tits were used in control experiments where only the fishing line, without the model merlin, was pulled by the weight. Four of the birds did not leave the feeding tray until they heard the sound of the weight hitting the ground, and one bird did not react at all, but stayed at the feeding tray and continued to eat. In the attack trials the merlin stopped at the feeding tray when the weight hit the ground, and all 40 experimental birds had at that moment started their escape and were at least 20 cm from the feeding tray.

Statistical calculations were made using STATISTICA for Windows 5.1 (Statsoft Inc.).

3. RESULTS

All great tits reacted instantly to the attacking merlin by flying up towards the opposite side of the room. Once perched they began emitting alarm calls or stayed motionless for several minutes. When flying up spontaneously without disturbance, birds flew to one of the perches at 150 cm distance from the feeding tray. However, three birds did not fly directly but jumped down to the water bowl on the floor, or just remained on the feeding tray to consume the mealworm. Thus, we could record control take-offs for 37 of the 40 great tits.

Great tits were on average 7.9% heavier at dusk (mean \pm s.e. = 19.2 ± 0.19 g) than at dawn (mean \pm s.e. = 17.8 ± 0.13 g; *t*-test for independent samples: $t = -6.13$, d.f. = 38, $p < 0.0001$). This diurnal body mass increase is in the same magnitude as reported for wild great tits during winter (Lehikoinen 1987; Haftorn 1992).

There was no effect of attack angle or body mass gain on take-off velocity of the great tits at any of the four distances from the start point (table 1). Great tits adopted different take-off angles depending on the attack angle of the model predator; however, body mass gain did not affect take-off angle. This was true for all four measurements (table 2). Thus, when the predator attacked from a high angle the birds' escape trajectory was about 10° lower than when the predator attacked from a low angle

Table 2. Effect of body mass and attack angle on angle of ascent at alarmed take-off

(Summary statistics of ANCOVA with attack angle (AA) and body mass (BM) (lean or heavy) as independent factors, the four measured take-off angles at different distances from the start (DS) as the dependent variable with repeated-measures design, and velocity as the changing covariate.)

effect	d.f. effect	d.f. error	<i>F</i>	<i>p</i>
body mass	1	35	0.9	0.3
attack angle	1	35	15.6	<0.001
distance from start	3	105	9.8	<0.0001
velocity	1	35	23.6	<0.0001
interaction BM × AA	1	35	1.1	0.3
interaction BM × DS	3	105	0.1	0.9
interaction AA × DS	3	105	0.4	0.7
interaction BM × AA × DS	3	105	1.4	0.2

(figure 2). Furthermore, control take-offs were not affected by the daily body mass increase (tables 3 and 4).

Because there was no difference in the effect of attack angle on take-off flights at the four measured distances we restrict further analyses to line 4, 75 cm from the feeding tray. In take-offs provoked by the model merlin, great tits flew at a lower velocity when they chose a steeper angle of ascent, and there was a negative relationship between angle of ascent and velocity ($r^2 = 0.26$, $b = -0.018$, $n = 40$, $p < 0.001$; figure 3*a*). Even though birds escaping at a steep angle had a lower velocity than birds escaping at a low angle, the effect of angle of ascent on velocity was too small to discern a difference in velocity between the two groups of great tits attacked from a high and a low angle (*t*-test for independent samples: $t = -0.61$, d.f. = 38, $p = 0.5$). In the control take-offs, there was no relation between velocity and angle of ascent ($n = 37$, $p = 0.84$; figure 3*b*). When taking-off spontaneously, the great tits flew slower than in the predator-induced take-offs (*t*-test for paired samples: $t = 10.45$, d.f. = 36, $p < 0.0001$).

4. DISCUSSION

Birds face a trade-off between flight velocity and angle of ascent when escaping from a predator, as a low angle permits the highest acceleration (Witter & Cuthill 1993). In accordance, we found a linear relationship between take-off velocity and angle of ascent, with great tits escaping at a low angle flying faster than birds escaping at a high angle when attacked by the model predator. However, in control events, where the birds took off undisturbed, there was no need for maximum speed and thus birds flew slower and there was no correlation between angle of ascent and velocity. This indicates that birds interpreted the attack of the model predator as a real threat and took off at maximum speed for the chosen flight angle. In this study, where no cover was available, the predator's angle of attack affected the take-off strategy of the prey. Great tits took off at a lower angle when the predator attacked in a steep trajectory compared with when it attacked from a low angle. Witter & Cuthill (1993) suggested that the optimal policy

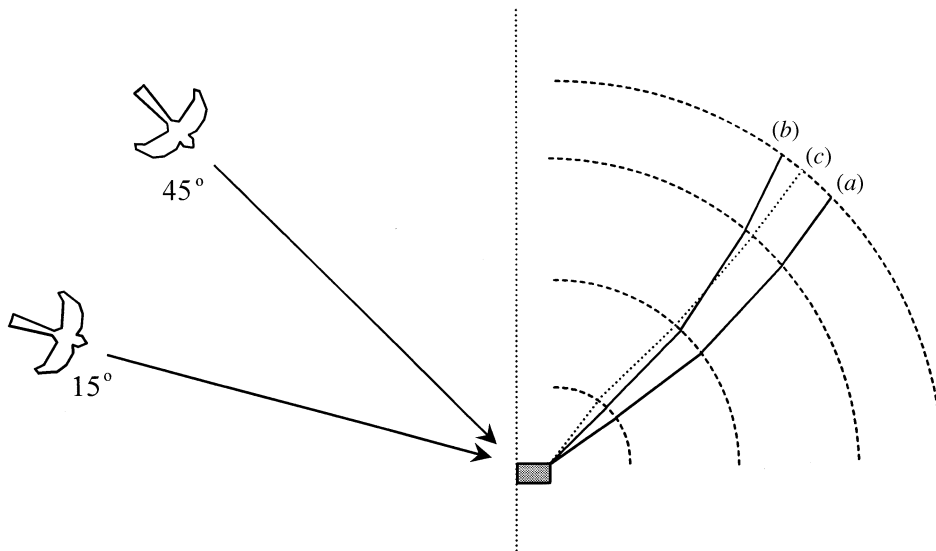


Figure 2. Average take-off angle of great tits (a) attacked from 45°, (b) attacked from 15° and (c) in control flights of all birds.

Table 3. *Effect of body mass on velocity at control take-offs*

(Summary statistics of ANOVA with body mass (BM) (lean or heavy) as the independent factor and the four measured velocities at different distances from the start (DS) as the dependent variable with repeated-measures design.)

effect	d.f. effect	d.f. error	<i>F</i>	<i>p</i>
body mass	1	35	0.4	0.3
distance from start	3	105	219	<0.0001
interaction BM × DS	3	105	3.1	0.03

between velocity and angle of ascent when a bird escapes from an attacking predator might depend on the detailed nature of the predator's attack, the proximity to cover, and the presence of conspecifics. Furthermore, the escape strategy of different species probably varies depending on the habitat to which they are adapted to (Pulliam & Mills 1977). Cresswell (1993) found that redshanks (*Tringa totanus*) responded by using different escape strategies according to the species of the attacking raptor and that correct predator identification can therefore be vital during an attack.

In the present study, we were unable to detect an effect of diurnal body mass gain on escape flight by great tits. In accordance, in a companion experiment, no effect of a 7.7% diurnal body mass gain in wintering willow tits (*Parus montanus*) could be measured (Kullberg 1998). Furthermore, in migratory blackcaps (Kullberg *et al.* 1996), take-off ability was affected heavily only at fuel loads exceeding 40%. In contrast to these studies, Metcalfe & Ure (1995) reported a large effect of diurnal variation in body mass on flight performance in the zebra finch (*Taeniopygia guttata*). The fact that no difference in velocity between heavy and light birds could be observed, either in the present study or in the study of willow tits (Kullberg 1998), suggests that heavier birds had to work harder to achieve the same flight speed as leaner birds. Furthermore, it might indicate that there exists an optimal get-away speed that the birds must achieve, and both heavy and light birds

Table 4. *Effect of body mass on angle of ascent at control take-offs*

(Summary statistics of ANCOVA with body mass (BM) (lean or heavy) as the independent factor, the four measured take-off angles at different distances from the start (DS) as the dependent variable with repeated-measures design, and velocity as the changing covariate.)

effect	d.f. effect	d.f. error	<i>F</i>	<i>p</i>
body mass	1	34	1.3	0.3
distance from start	3	102	3.5	0.02
velocity	1	34	0.2	0.6
interaction BM × DS	3	102	1.9	0.1

succeeded in attaining this velocity. Thus, the results suggest that the relatively small increases in body mass of wintering tits during a day does not affect predation risk directly by impaired predator evasion. However, the daily body mass gain in wintering tits may still increase exposure to predation owing to intensive foraging reducing the time available for vigilance (Lima 1986; Houston & MacNamara 1993; Witter & Cuthill 1993; McNamara *et al.* 1994). In accordance, some studies, both from the field and the laboratory, indicate that birds may adjust their body mass to the perceived risk of predation (Witter *et al.* 1994; Gosler *et al.* 1995; Lillien-dahl 1997; see also Cuthill & Houston 1997).

In a study of take-off ability in migratory blackcaps (Kullberg *et al.* 1996), the birds with the smallest fuel loads took off at a right angle to the predator's attack flight, whereas heavier birds (up to 59% fuel load) took off at lower take-off angles. In accordance with the suggestion by Kullberg *et al.* (1996), that a right angle to the predator's attack trajectory might be an optimal escape angle, great tits exposed to a 45° attack angle took off more-or-less perpendicular to the predator's attack (figure 2). However, when exposed to a 15° attack angle, great tits took off much lower than expected from a perpendicular take-off. When taking both velocity and angle of ascent into account, a steep take-off at a 75°

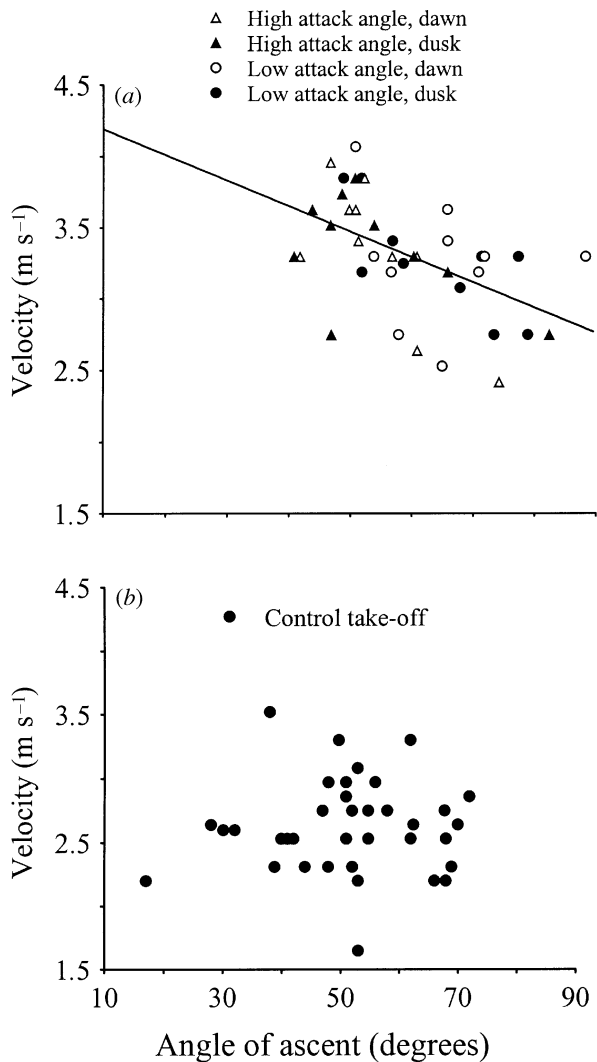


Figure 3. Take-off velocity (m s⁻¹) in relation to angle of ascent (degrees) at line 4 in (a) predator-induced take-offs ($r^2=0.26$, $b=-0.018$, $n=40$, $p<0.001$) and (b) control take-offs ($n=37$, $p=0.84$).

angle may reduce velocity too much to be efficient (according to the relationship found between take-off angle and velocity at line 4, a take-off at right angles to the 15° attack trajectory would result in a 13% lower velocity than was found). In the experiment, the model predator attacks along a constant trajectory giving the great tit no indication of changing the flight direction until the raptor stops at the feeding tray. Using the linear relationship found between angle of ascent and velocity, and elementary trigonometry, the distance (d) from the predator's extended attack trajectory can be expressed as: $d=(A+B \times C_e) \times \sin(C_a+C_e)$, where A is the intercept, B is the regression coefficient, C_e is the escape angle and C_a is the attack angle. When the predator attacks from 15°, the equation gives a maximum distance for an escape angle of 56° (compared with an average take-off angle of 64° found at line 4). However, when attacked from 45°, the calculated optimal angle is much lower than the average take-off angle found for the great tits (28° versus 54°). This may eventually be explained by the birds making a trade-off between height gained and velocity, because a low angle gives a relatively low gain in height that may be disadvantageous.

In a natural attack situation with a real raptor, the raptor will change its flight trajectory according to the movement of the prey, which may explain the birds' strategy of taking off in an accelerating curve (figure 2). Even if the purpose for a fast acceleration is obvious during an escape flight, the benefit of gaining height is not as clear. Probably, height opens up the possibility of a variety of evasive manoeuvres for reducing the risk of being caught by the raptor.

Because predation in the wild is hard to observe, there are relatively few studies on birds' escape responses in relation to predator attack. However, existing studies report dynamic predator responses in birds (for examples, see Rudebeck 1950; Morse 1973; Lima 1993; Cresswell 1993, 1996). This study provides further evidence for a flexibility in the take-off by the prey-bird in the very first moment of a predator attack. However, there is clearly a need for further empirical and theoretical work in order to gain a better understanding of how birds adjust take-off behaviour in relation to predator attacks.

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