A rare predator exploits prey escape behavior: the role of tail-fanning and plumage contrast in foraging of the painted redstart (*Myioborus pictus*)

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Escape response, triggered by an approaching predator, is a common antipredatory adaptation of arthropods against insectivores. The painted redstart, *Myioborus pictus,* represents insectivorous birds that exploit such antipredatory behaviors by flushing, chasing, and preying upon flushed arthropods. In field experiments I showed that redstarts evoke jump and flight in prey by spreading wings and tail: this display increased frequency of aerial chases by redstarts. Artificial models with spread tails also elicited escape responses more often than models with closed tails and wings. The white patches on black wings and tails additionally help: the frequency of chases decreased when the white patches were covered with black dye. Black models also tended to elicit escape response less often than black-and-white models did, at least in some situations. Hence, the prey's ability to detect birds and to flee could cause the evolution of predators specialized at using conspicuous behavior and contrast in body coloration to elicit and exploit such antipredatory responses. Redstarts constitute only a small proportion of the predatory guild, and their adaptations to exploit the prey's behavior illustrate the theoretically modeled "rare enemy" effect present in multispecies predator–prey systems. This is the first experimental study of morphological and behavioral adaptations of a rare predator that both elicits and exploits antipredator escape behavior of its prey against more common predators. Hence, the study documents a behavior that could be evolutionarily explained only if indirect interactions in predator–prey communities are taken into account. *Key words*: antipredator strategies, coevolution, escape behavior, foraging, *Myioborus pictus,* painted redstart, predator–prey relationships, warblers. *[Behav Ecol 10:7–14 (1999)]*

Coevolution of predators and prey, involving adaptations of prey to avoid predation and counteradaptations of predators to hunt prey, has been proposed as an important factor shaping the morphology and behavior of species (Abrams, 1986; Dawkins, 1983; Dawkins and Krebs, 1979; Van Valen, 1973), as well as the structure of predatory guilds (e.g., Brown and Vincent, 1992). In the classical situation of two interacting species, there exists an asymmetry: the predator exerts stronger selection on the prey's antipredator adaptations than the prey does on the predator's hunting techniques (Dawkins and Krebs, 1979). However, subsequent models have challenged this view (Abrams, 1986, 1990), and models of multispecies systems have suggested that various indirect effects can influence evolution of predators and prey (Abrams, 1992, 1995) and community complexity (Abrams and Matsuda, 1996; Matsuda et. al., 1993, 1994, 1996). For example, the selective impact of a predator that rarely encounters a particular prey species is predicted to be small, and selection for escape from such a rare predator is expected to be weak ("the rare enemy effect"; Dawkins, 1983). Although it was suggested more than 20 years ago that in such a situation a predator may evolve hunting techniques that exploit prey adaptations to avoid other predators (Charnov et al., 1976; Hamilton, 1971), to my knowledge no studies have experimentally examined such predator adaptations.

Most avian predators attack insect prey directly on the substrate on which they are found. Many insects have evolved a flight response to escape from such predators (Edmunds, 1974). However, some studies have suggested that one or two species in a guild may specialize at spreading the wings and tail to flush arthropods and, subsequently, to chase the prey in the air. Such flush-pursuers (sensu Remsen and Robinson, 1990) have been found in insectivorous guilds from Australia (Frith, 1984, Holmes and Recher, 1986; Jackson and Elgar, 1993; Osborne and Green, 1992; Recher and Holmes, 1985; Recher et al., 1983, 1985; Thomas, 1980), Central and South America (Charnov et al., 1976, Howell, 1971; Moynihan, 1962; Nocedal, 1988; Ridgley and Tudor, 1989; Sherry, 1984; Sillet, 1994), North America (Ficken and Ficken, 1962; Hailman, 1960; Keast et al., 1995; Morse, 1970; Rabenold, 1978; Robinson and Holmes, 1982, 1984; Root, 1967), Asia (Ali and Ripley, 1971, 1972, 1973a,b, 1974; Cramp, 1992; Price, 1991), and Africa (Monroe, 1964; Newman, 1980; Prozesky, 1974). Thus, the flush-pursuers are good examples of predators exploiting insect antipredatory behaviors (Charnov et al., 1976) evolved against other predators in the community.

During foraging, typical flush-pursuers such as *Myioborus* species (e.g., Moynihan, 1962; Ridgley and Tudor, 1989), *Setophaga ruticilla* (Robinson and Holmes, 1982), and most of the genus *Rhipidura* (e.g., Holmes and Recher, 1986, Recher et al., 1985) forage with constantly half-spread wings and broadly spread and half-raised tail exposing distinct bright patches in the tail and wings (e.g., *M.pictus, S ruticilla,*) or rump (e.g., *R. rufifrons*). While hopping, they move their bodies from side to side in a manner often described as twisting, twitching, or swiveling. Because contrast is important in eliciting insect escape responses (e.g., Holmqvist and Srinivasan, 1991), the evolution of the flush-pursue foraging mode has been suggested to promote selection for bright plumage in the areas exposed during wing and tail spreading (e.g., Ficken

and Ficken, 1962; Gander, 1931; Hailman, 1960; Jabłoński, 1993, 1994, 1996; Remsen and Robinson, 1990; Root, 1967). If this were the case, flush-pursuers might not only illustrate natural selection due to the ''rare enemy effect'' (Dawkins, 1983), but may also provide a rare example of the evolution of increased predator conspicuousness, instead of higher crypticity, as an adaptation to hunt prey. However, no experimental test has been conducted to evaluate the role of tail and wing display and the importance of plumage contrast in the foraging of flush-pursuers.

The painted redstart (*Myioborus pictus*) uses the flush-pursue foraging mode (Jabłoński, 1993, 1994; Ridgley and Tudor, 1989). Both sexes have predominantly black bodies, with red bellies and white patches on the dorsal surface of the wings and on the ventral and dorsal surfaces of the outer tail feathers (Peterson, 1990). This is the only bird, among roughly 20 insectivorous species typical for the oak–pine woodlands of the southwestern United States, that forages with spread tail and wings, conspicuously displaying the white patches (Ficken and Ficken, 1962; Marshall and Balda, 1974) and therefore can be treated as a ''rare enemy'' (Dawkins, 1983). As more than 50% of redstarts' prey are insects that escape from predators by flying or jumping (Jabłoński PG, Hespenheide H, in preparation; *Diptera,* 43%; *Homoptera,* 10%; *Lepidoptera,* 7%), and almost 70% of attacks on prey consist of chases after escaping arthropods (Jabłoński PG, personal observations), the movements of foraging birds are hypothesized to elicit insect fleeing response. Redstarts then chase insects flushed from branches or leaves, often above the bird.

Here I present results of field experiments that confirm that wing and tail spreading and the display of white patches help redstarts flush insects. This study suggests that a rarely encountered predator may exploit prey antipredatory behavior evolved in response to more common predators (Charnov et al., 1976, Hamilton, 1971), and it may also evolve adaptations to elicit such antipredatory behavior.

METHODS

Observations of foraging birds

In the 1992, 1993, and 1995 breeding seasons (March–July), I studied foraging behavior of painted redstarts in the area surrounding the Southwestern Research Station in Cave Creek Canyon, Chiricahua Mountains, Arizona, USA. I followed foraging birds and recorded sequences of behaviors on a tape recorder. I noted hops and whether they were accompanied by tail and wing spreading, and whether the bird kept head up looking at the branch above it or whether it looked down toward the lower surfaces of branches and twigs. I also noted all pecks (birds pecking at the substrate and handling a prey afterward) and chases. Each time, I recorded the substrate on which the bird foraged. I measured chasing frequency (number of chases/100 hops) and used it as an index of frequency of flushing insects by redstarts. In 1995 I followed birds foraging in trees (most foraging occurs in trees; other substrates are rocks in creek beds, ground on slopes of canyons, rocky canyon walls, and logs) to describe distances between an insect and the bird and the position of the insect in relation to the bird at the moment of escape.

To test the null hypothesis that chasing frequency is not increased due to tail and wing spreading during foraging, I used a one-tailed paired Student's *t* test to compare chasing frequency during foraging with spread tail and wings (number of chases that occurred after hops with spread tail and wings/100 hops with spread tail and wings) with chasing frequency during foraging with closed tail and wings (number of chases that occurred after a hop with closed tail and wings/100 hops

with closed tail and wings). For this test I used 1993 data from 19 birds with unaltered plumage, including 14 females studied in experiment described below (7 controls and 7 experimentals before painting) and 5 birds that were not used in the other experiments.

Additionally, I measured three variables that were not directly used to test the hypothesis because they were not good measures of success in flushing insects by redstarts. Changes in number of pecks/minute and number of chases/minute may be viewed as consequences of changes in chasing frequency. Number of hops with spread tail and wings/minute indicates how often birds use the display aimed at flushing insects.

Effect of dyeing bird's plumage

To test the hypothesis that white patches help redstarts to flush insects, I studied the effect of covering white patches on the spread tail and wings with black dye on the frequency of flushing insects (number of chases that occurred after hops with spread tail and wings/100 hops with spread tail and wings). Adult birds were caught at the nest, color banded, and measured at the last stage of incubation or soon after hatching of young. When nestlings were 6–8 days old, I caught the parents again and covered the white wing and tail patches of experimental birds with black permanent marker applied directly to feathers (1992; $n = 6$), or to feathers covered with a thin layer of white enamel paint (1993; $n = 7$). In the control birds, I either applied the black marker to the black feathers surrounding the white patches (1992; $n = 6$) or covered the white patches with white paint (1993; $n = 7$).

In both experiments (1992 and 1993) I observed each bird for 1–3 days after each capture, recording its foraging behavior as described above. All observations of a given individual were conducted at the same time of day to rule out effects of diurnal changes in foraging behavior. For each bird, I combined all sequences longer than 5 s for each of the two observation periods, before and after plumage alteration. I used foraging data only from twigs and branches of oaks (the preferred tree species) because these observations were sufficiently numerous (about 50% of foraging data) for all birds. The median duration of foraging data for control birds was 380 s (range: 110–910 s) in 1992 and 301 s (131–730 s) in 1993. For experimental birds the median duration was 390 s (15–1590 s) in 1992 and 465 s (58–1010 s) in 1993.

The two experiments differed in their design and the subsequent statistical analysis. In 1992, one member of each pair was the experimental and the other was the control ($n = 6$; 3 pairs with males and 3 pairs with females as controls). For each bird I calculated a difference, *D,* in chasing frequency as postpainting minus prepainting frequency. I used Wilcoxon paired one-tailed statistics to test the prediction that the difference, *D,* in the control member of a pair is smaller than in the experimental one. Such a design should have minimized the variance caused by spatio-temporal variation in food availability among territories and observation periods. However, any relationship between a bird's foraging behavior and changes in its mate's coloration might have biased the results.

Therefore, in 1993 I manipulated females only (7 experimentals and 7 controls). The frequency of chases by unaltered birds ($n = 19$ in 1993; 7 experimental and 7 controls before painting, and 5 birds that were not included in the experiment due to nest predation that occurred before they could have been painted) did not differ from a normal distribution (Kolmogorov-Smirnov, $p > .45$), and I used Student's *t* test (one tailed) for independent comparisons to test the prediction that the difference in chasing frequency was smaller in
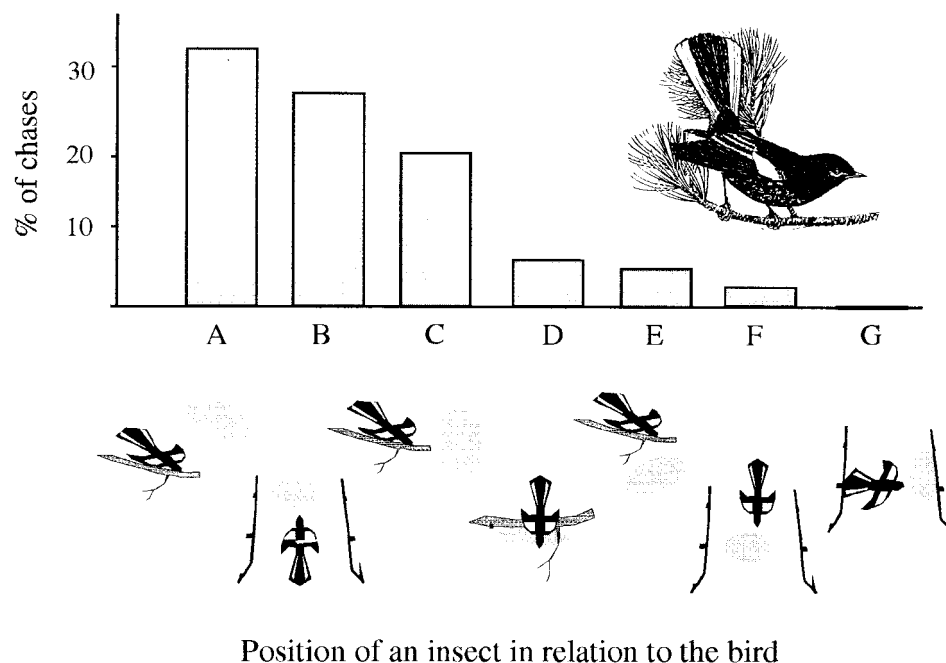
Figure 1
Frequencies of chases observed in the field in seven situations differing in the position of the insect in relation to the bird (shaded areas indicate sites from which insect initiated the escape: A, insect in front and above the bird; B, insect above the bird that is moving up the tree trunk; C, insect in front of the bird; D, insect below the bird, on the lower surface of the branch; E, insect in front and below the bird; F, insect in front of the bird that is moving down along the tree trunk; G, insect in front of the bird that is moving around the tree trunk. (Graphics by B. Swarbrick, with permission of the artist and The Tucson Audubon Society.)

experimentals than in controls. Because the experiments provided two independent (different seasons, different birds, different territories, different designs) tests of the same hypothesis, I calculated Fisher's combined test (Fisher, 1932; Rosenthal, 1991; Wolf, 1986) of the effect of plumage alteration on chasing frequency.

To test the null hypothesis that white patches do not modify the effect of wing and tail spreading on the frequency of flushing insects, I used an interaction term in a two-factor ANOVA with "tail spread versus closed" as a within-subject factor and "presence versus absence of patches" as a between-subject factor applied to chasing frequency of 14 birds after plumage alteration in 1993 (7 experimentals and 7 controls). If white patches modify the effect of tail and wing spreading on the frequency of flushing insects, I expected a significant interaction between these two factors.

To present a full picture of the effect of plumage alteration on redstart foraging behavior, I also report changes in three variables that were not directly used to test the hypotheses because they were not good measures of success in flushing insects by wing and tail spreading. Changes in number of pecks/minute and number of chases/minute may be viewed as consequences of changes in chasing frequency. Number of hops with spread tail and wings/minute indicates how often birds use the display aimed at flushing insects. For each year, I report these variables in a different way so that they fit the different statistical analyses required by different experimental designs. For each bird in 1992 I calculated the differences, $D,$ between postpainting and prepainting values of the variable. As each control bird in 1992 was mated to one experimental bird, the values of D are paired in a statistical sense. Therefore I used a paired Student's t test (two-tailed) to test the null hypothesis of no difference in D between control and experimental members of a pair. In 1993 the experimentals and controls were independent. As in 1992, the same bird was tested before and after plumage alteration, but unlike in 1992, controls and experimentals were females from different pairs. Therefore values of D are independent and Student's t test could have been used. However, I chose an alternative (and equivalent) method of analysis. Because absolute values of the foraging variables give better information about the behavior

than differences do, I reported them and used the interaction term between the within-subject factor "before versus after painting" and the between-subject factor "experimentals versus controls" in a two-way ANOVA to determine whether the effect of painting differed between experimental and control groups. The behavioral variables ($n = 19$ unaltered birds; 1993) were normally distributed (Kolmogorov-Smirnov tests, $p > .95$).

Flushing insects using bird models

As it is often impossible for a human observer on the ground to see insects that are chased by redstarts, the frequency of chases is only an approximate measure of the frequency of flushed insects. In experiments using artificial bird models to flush insects, I asked whether models with spread tail and wings and models with white patches flush insects more frequently. In 1993, I conducted field tests to flush *Lypocosma* spp. (Pyraustinae) moths from under logs, rocks, etc., and various flies and damselflies from stones in a creek bed, some of the typical places where the redstarts were seen chasing insects. I used four different types of paper models of redstarts mounted on a 2-m long, thin, black stick: (1) black and white, closed tail and wings, (2) uniformly black, closed tail and wings, (3) black and white, spread tail and wings, (4) uniformly black, spread tail and wings. In each test, I slowly placed the model about 50 cm from an insect, turned it three times to imitate a foraging redstart, then moved the model forward to about 25 cm from the insect and turned it again. Markings on the stick helped to estimate distances. When turning the model, I rapidly turned the stick 45° to the left, then 90° to the right, and to the left, back to the original position. Models were used in a random order and each insect was tested only once.

I also tested *Lypocosma* moths in a seminatural setting. I caught moths and released them in front of a vertical rock on which they often alighted (the same rock was used in all tests). No direct sunlight reached the surface of the rock during the tests. After a moth remained motionless for 2 min, I tested its escape response as in the field experiments described above.

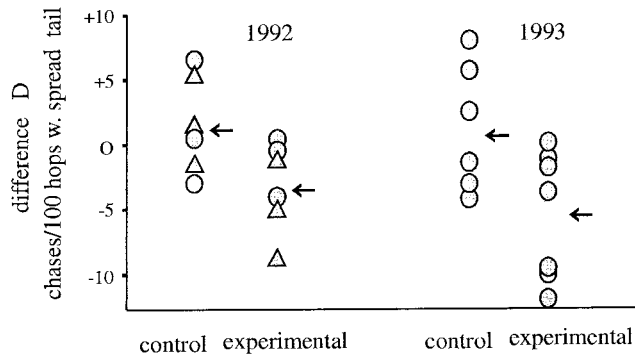I tested *Bulia deducta* (Noctuidae) moths in the laboratory.

Figure 2
The effect of plumage color manipulation on frequency of chases after prey in control and experimental birds. In 1992 the difference, *D,* in chasing frequency, calculated as postpainting minus prepainting frequency, was smaller in the experimental than in the control member of a pair (Wilcoxon paired one-tailed test, *T* = 19, *p* < .05, *n* = 6; circles, females; triangles, males). In 1993, *D* was also smaller for experimental (*n* = 7) than for control (*n* = 7) females (Student's *t* test for independent comparisons, one tailed, *t* = 2.255, *p* = .02). Arrows indicate the means.

I put each moth into a petri dish (20 cm diam, 5 cm high) with bottom raised at an angle of 60°. The moth rested on corrugated cardboard at the bottom and could see the approach of the model through the dish cover.

For each of the five experiments (three in the field, one in "seminatural" conditions, one in the laboratory), I analyzed results (2 × 2 × 2 table) by fitting a loglinear model with the backward selection procedure, starting with the full model with three factors: presence versus absence of patches (factor P), spread versus closed tail and wings (factor S), and success in flushing an insect (factor F). If both factors, P and S, influence success in flushing (F), I expected that the fitted model would be: PF, SF (i.e., the model in which interaction between factors P and F as well as interaction between factors S and F are included).

Additionally, for each experiment I calculated significance levels of each of the two interactions, PF and SF (the probabilities that the interaction excluded from the model "PF, SF" has a coefficient zero) indicating, respectively, the probabilities of the two null hypotheses: (1). there is no effect of patches on success in flushing insects, and (2) there is no effect of wing and tail spreading on success in flushing insects. I calculated sequential-Bonferroni corrections of significance levels for these five experiments. The experiments can be considered as independent tests of the hypothesis because they were conducted in different sites, different light conditions, and on different insects (except for the two different experiments on *Lypocosma*). Therefore, for all five experiments, I used Fisher's combined tests to test the null hypothesis of no effect of patches and, separately, to test the null hypothesis of no effect of wing and tail spreading on success in flushing insects. The Fisher's combined tests use the original, not the corrected, significance levels, and I report those also.

RESULTS

Observations of foraging individuals with unaltered plumage

When watching birds in trees, I observed 52 chases in which I could describe the relative position of the insect with respect to the bird before flushing. In 89% of these cases the insect was flushed from in front of or above the bird (Figure 1). My general impression from observations (1992–1995) of birds foraging on other substrates (rocks in creek bed, ground on
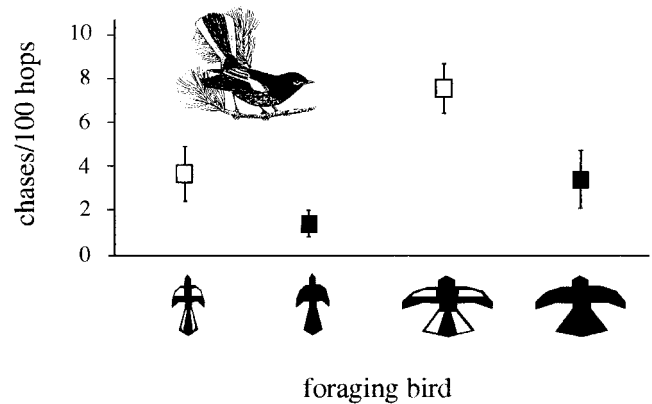

Figure 3
The effect of spreading tail and wings and the effect of white patches on chasing frequency by altered birds (*n* = 14: 7 white- and 7 black-painted females; squares indicate means; bars are SEs). Effect of white patches on chasing frequency (*F* = 7.96, df = 1, *p* = .015) is independent (interaction term *F* = 0.83, df = 1, *p* = .38) from the effect of tail and wing spreading (*F* = 10.19, df = 1, *p* = .008). (Graphics by B. Swarbrick, with permission of the artist and The Tucson Audubon Society.)

slopes of canyons, rocky canyon walls, logs) was that many prey items were flushed from above and in front of the bird. Thus, most of the flushed insects must have been able to see the upper surface of the raised and spread tail as well as the surface of the spread, drooped wings of the redstart. In almost half of the chases (44%) the insect tried to escape when the bird was at a distance of 1–2 redstart body lengths, that is, about 14–28 cm. One-third (32%) of the insects were flushed at a distance not larger than the redstart body length (about 14 cm). The remaining 22% of insects were flushed from a distance larger than 30 cm, but only about 9% from a distance larger than 45 cm. Most of the chases (74%) were quick dives. My impression from these observations, as well as from some slow-motion video-recorded foraging sequences, was that the birds do not detect these insects until after they are flushed.

While foraging with spread wings and tail, birds chased prey (mean ±SE; 6.9 ± 1.2 chases/100 hops), more often (Student's paired, one-tailed test; *t* = 2.66, *n* = 19, *p* = .016) than during foraging with closed wings and tail (3.1 ± 1.0 chases/100 hops). This indicates that spreading of the wings and tail helps to startle insects and/or that redstarts spread their tails and wings more often in places with a high abundance of insects that are easy to flush . When the birds were looking at the branches above them, with their heads up, they spread wings and tails (85.9 ± 5.9% of hops) more often (Wilcoxon ranks test, *z* = 3.60, *p* = .0003) than during other foraging sequences (47.0 ± 5.9% of hops). This suggests that the birds use the tail and wing spreading when they scan a substrate above them where insects, if present, are able to see the white-and-black pattern of the upper surface of the redstart's body and open tail and wings.

Pecking frequency was lower (*t* = −3.48, *n* = 19, *p* = .002) during foraging with spread (0.9 ± 0.2 pecks/100 hops) than during foraging with closed (2.7 ± 0.5 pecks/100 hops) tail and wings. This suggests either that some arthropods flushed by the display of spread tail and wings are preyed upon by pecking when a bird is foraging with closed tail and wings, or that redstarts spread their tails and wings more often in places with low abundance of insects that are easy to peck.

Effect of dyeing bird's plumage

The frequency of aerial chases (i.e., number of chases that occurred after hops with spread tail and wings/100 hops with

Table 1

Effect of plumage color alteration on the difference in foraging behavior between postpainting and prepainting observations (D = post-minus prepainting) in 1992

	Difference, D		t (p)	Bonferroni-corrected p
	Control ($n = 6$)	Experimental ($n = 6$)		
Chasing rate (chases/min)	0.48 (0.48)	−0.84 (0.56)	−1.357 (.24)	.65
Pecking rate (pecks/min)	−0.18 (0.30)	−0.02 (0.50)	0.289 (.78)	.95
Tail-fanning rate (hops with tail fanned/min)	4.22 (3.87)	6.04 (4.14)	0.115 (.91)	.91

Means and SEs (in parentheses) of the difference are shown. As each control bird was mated to one experimental bird, the values of D are paired in a statistical sense. The paired Student's t tests (two-tailed) of differences between values of D are calculated and the p values are sequential-Bonferroni corrected ($k = 3$).

tail and wings spread) in both years of the study decreased after covering the white patches with black dye (Figure 2). Results from both experiments combined showed that the presence of white patches improves the ability of redstarts to flush insects (Fisher's combined test $\chi^2 = 13.82$, df = 4, $.005 < p < .01$).

Analysis of the postpainting data ($n = 14$; 7 experimental and 7 control birds after plumage alteration in 1993) showed that the presence of white patches did not modify the effect of spread tail and wings on chasing frequency (Figure 3).

Interestingly, but irrelevant to hypothesis testing, the chasing rate decreased (significantly in 1993 only), probably as a consequence of a decrease in chasing frequency after covering the white patches with black dye (Tables 1 and 2). The pecking rate, as well as the rate of spreading wings and tail were not affected by the experimental treatment (Tables 1 and 2).

Flushing insects using bird models

In the field experiment, both open wings and tail and the presence of white patches (marginally significant after Bonferroni correction) in models increased efficiency of flushing *Lypocosma* moths from their shady resting sites under rocks and logs (Table 3, Figure 4; loglinear model fitted to the data: PF, SF, $G = 1.76$, $p = .42$). The responses of flies and damselflies, often resting in sunny sites, in a creek bed (where redstarts also forage) were affected by spreading of wings and tail but not by the presence of white patches (Table 3; flies: model SF, $G = 2.47$, $p = .65$; damselflies: model SF, $G = 1.29$, $p = .73$). Tests conducted in a seminatural setting using *Lypocosma* moths showed that only the effect of spread wings and tail was important (Table 3; model SF, $G = 0.60$, $p = .90$). Laboratory tests on *Bulia deducta* did not show significant effects (Table 3; model F, $G = 0.83$, $p = .93$).

All five experiments combined showed a significant effect of the spread tail and wings and a marginally significant effect of white patches on success in flushing insects (Table 3; Fisher's combined tests).

DISCUSSION

This study documents that painted redstarts use wing and tail spreading and the display of white patches to flush insects and subsequently chase them in the air. This suggests that selection for efficiency of such flush-pursue foraging might have caused evolution of wing and tail spreading as well as the presence of bright patches in the plumage of the painted redstart.

The importance of white patches in experiments using models was only marginally significant, either due to imperfect imitation of a foraging redstart or to the possibility that white patches are effective only when a model is presented against a dark background (Jabłoński PG, Strausfeld NJ, in preparation). In accordance with the latter suggestion, white patches seemed effective in flushing *Lypocosma* moths in shady sites, but not in flushing flies and damselflies in sunny sites. It remains to be tested whether particular prey species are more easily flushed independent of light conditions or whether in shady conditions white patches help in flushing all kinds of insects. Hence, just as habitat darkness may affect evolution of bright, aggressive intraspecific signals in warblers (Marchetti, 1993), this system may offer an interspecific context to study the role of physical properties of habitats in the evolution of signaling (e.g., Endler, 1992).

Selection for wing and tail spreading may be related to flush-pursue foraging in at least eight other species of insectivorous birds for which flushing insects from trees and bushes with spread tail and wings has been explicitly mentioned: *Myioborus sulphureipygius* (Howell and Webb, 1995; Sherry,

Table 2

Effect of plumage color manipulation on foraging behavior in 1993

Behavioral variables	Controls		Experimentals		ANOVA interaction, p (Bonferroni-corrected p)
	Before alteration	After alteration	Before alteration	After alteration	
Chasing rate (chases/min)	2.1 (0.4)	2.7 (0.3)	2.4 (0.3)	1.5 (0.2)	.002 (.006)
Pecking rate (pecks/min)	0.5 (0.1)	0.7 (0.3)	0.9 (0.2)	0.8 (0.4)	.600 (.600)
Tail-fanning rate (hops with tail fanned/min)	23.1 (4.6)	30.0 (4.3)	21.7 (4.6)	25.0 (5.8)	.590 (.832)

Means and SEs (in parentheses) are shown. As three separate ANOVAs were performed, the sequential-Bonferroni-corrected p values were calculated with $k = 3$. As in 1992, the same bird was tested before and after plumage alteration, but unlike in 1992, controls and experimentals are birds from different pairs, so they are not paired in a statistical sense. Therefore, I could use the interaction term between the within-subject factor "before versus after painting" and the between-subject factor "experimentals versus controls" in a two-way ANOVA to determine whether the effect of painting differed between experimental and control groups. The behavioral variables of all observed birds ($n = 19$) were normally distributed (Kolmogorov-Smirnov tests, $p > .95$).

Table 3
The effect of tail and wing spreading and of white patches on success in flushing insects with models presented in Figure 4

Experiment	Effect of spread tail and wings			Effect of white patches		
	G	p	Corrected p[a]	G	p	Corrected p
Moths in field	9.689	.002	.006	5.513	.020	.091
Moths on rock	7.639	.006	.011	4.584	.045	.168
Moths in petri dish	0.281	.596	.596	0.513	.474	.810
Flies in field	23.010	.000	.000	0.014	.905	.905
Damselflies in the field	59.487	.000	.000	0.636	.425	.723
Fisher's combined test[b] (df = 10)	$\chi^2 = 69.851, p \ll .001$			$\chi^2 = 17.544, .05 < p < .10$		

[a] As five analyses were performed to estimate each effect, the sequential Bonferroni correction was calculated with $k = 5$.

[b] The Fisher's combined test uses the original, not the corrected, p values.

1984), *M. miniatus* and *M. torquatus* (Moynihan, 1962), *Rhipidura albicollis* and *R. aureola* (Ali, 1977; Ali and Ripley, 1973; Fleming et al., 1979), *R. brachyrhyncha* (Beehler et al., 1986), *R. leucophrys* (Pizzey, 1980), *Setophaga ruticilla* (Ficken and Ficken, 1962; Robinson and Holmes, 1982). Similar selective factors may have played a role in the evolution of wing/tail movements in at least two species of ground foragers: Northern mockingbirds *Mimus polyglottos* (Hailman, 1960) and Willie wagtails *Rhippidura leucophrys* (Jackson and Elgar, 1993). In addition, six species of bush and tree foragers have been reported to use quick wing/tail movements to flush arthropods: *Muscicapa rubelculoides* (Ali and Ripley, 1973), *Muscicapella hodgsoni* (Ali, 1962, 1977; Ali and Ripley, 1973a; MacKinnon and Philips, 1993), *Phylloscopus inornatus, P. nitidus,* and *P. trochiloides* (Ali and Ripley, 1973; Cramp, 1992) and *Terenotriccus erythrurus* (Sherry, 1984; Ridgley and Tudor, 1989). Many such species have bright patches on the wings and/or on the tail. Because these various flush-pursuers often belong to different evolutionary lineages (Sibley and Ahlquist, 1990), many of these adaptations to foraging result from convergent evolution. However, even though an analysis of a set of 10 *Phylloscopus* warblers suggested that bright patches might have evolved to help in flushing the prey (Jabłoński,

1996), a more detailed comparative analysis of another set of *Phylloscopus* warblers revealed that selection for such patches may be stronger in the context of aggressive signaling than in foraging (Marchetti and Price, 1997). There is no doubt that many conspicuous plumage characters evolved as intraspecific signals, and there is no reason to disregard the possibility that bright patches in flush-pursuers also function as aggressive signals.

Why do flush-pursuers use wing and tail spreading to flush prey? If escape response depends on the distance to the predator or the predator's size, birds that spread tails and wings could exploit insect escape response by sending false information about being closer or being larger than they really are. Accordingly, the escape responses in flies are elicited more often and from a larger distance by larger approaching objects than by smaller ones (Holmqvist and Srinivasan, 1991). Insects may judge distance on the basis of the apparent size or changes in the apparent size (Schwind, 1989) of the predator in the field of view. In such a situation, spreading of wings and tail would simulate a close approach of a predator and would elicit an escape response from a greater distance. This could be beneficial to birds because it allows them to detect more insects trying to escape. Additionally, by being farther away from
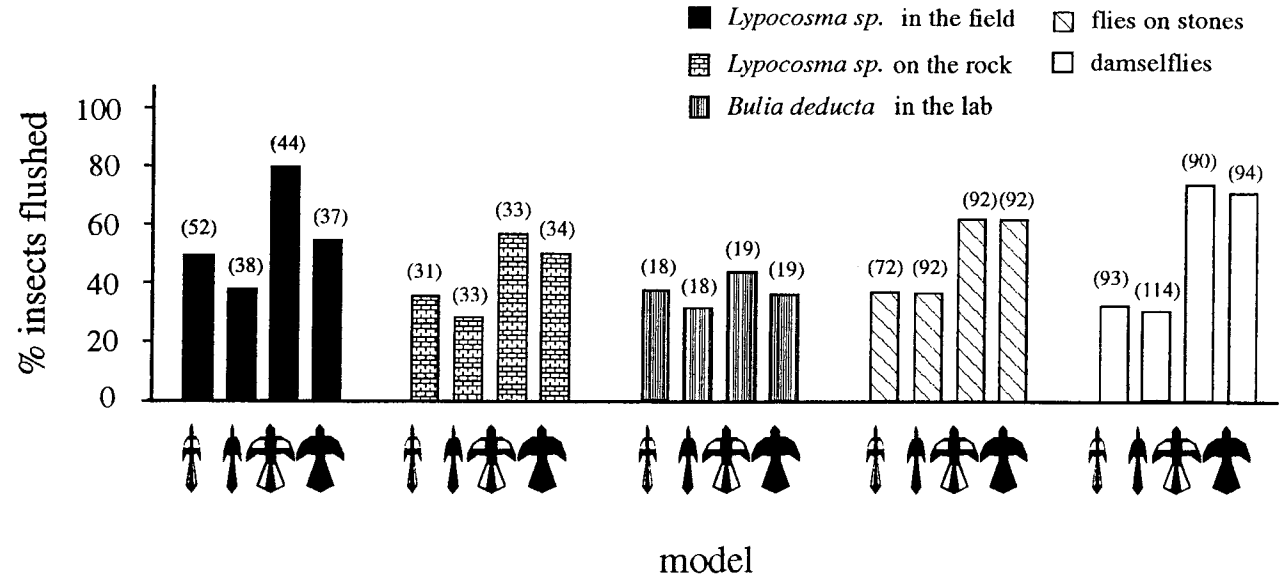

Figure 4
The effect of spreading tail and wings and the effect of white patches on frequency of flushing insects using models. Tail and wing spreading significantly affected the frequency of flushes, but the effect of white patches was marginally significant and seen only for *Lypocosma* moths in shady sites (see Table 3).

the insect, the bird decreases the angular speed of the prey's image on the bird's retina and decreases the chances that the prey disappears from the bird's field of view. These factors may assist in tracking the prey's escape trajectory and intercepting the prey, as suggested in studies of flies and humans (Collet and Land, 1978; Land, 1992; McBeath et al., 1995). In a bird specializing in chasing prey in the air, such benefits from increased distance to escaping prey may outweigh the negative effects due to possible increase in pursuit length. None of these hypothetical costs and benefits of flushing insects by birds have been studied.

Why might contrast in the plumage increase success in flushing insects? An approaching dark object seen against a light background is the best elicitor of the escape response in house flies (Holmqvist and Srinivasan, 1991). A light disk presented against a dark background also elicited escape responses (Holmqvist and Srinivasan, 1991). Hence, the ideal flush-pursuer should appear black if seen against a light background, and white if seen against dark background. Therefore, a flush-pursuer that has both dark and bright plumage colors may hypothetically exploit insect escape responses in various situations.

Differences among populations of *Dalbulus maidis* cicadas (Homoptera) in sensitivity to stimuli triggering the escape response (Heady and Nault, 1985) suggest that in insects there exists a variation upon which selection for lower sensitivity may work. Hence, there seems to be a potential for insects to evolve lower sensitivity to flushing by birds as a defense against flush-pursuers. Why do insects continue to be exploited by flush-pursuers? Flush-pursuers constitute a relatively small proportion of each guild (one or two species constituting, on average, 15% and occasionally up to 30% of the guild; data from 12 guilds described by Frith, 1984; Howell, 1971; Morse, 1970; Nocedal, 1988; Osborne and Green, 1992; Price, 1991; Rabenold, 1978; Recher and Holmes, 1985; Recher et al., 1983; Robinson and Holmes, 1982; Sillett, 1994; Thomas, 1980). Because flush-pursuers constitute only a small fraction of any predatory guild, insects appear to be under stronger selection pressure to avoid other birds (and other nonavian predators) than the prey-flushing members of a guild. Hence, foraging based on exploitation of insect escape responses might have evolved due to the rarity of the flush-pursuing predators, an effect predicted by Hamilton (1971) and others. This illustrates how prey escape responses to common predators may enable diversification of hunting strategies among predators (Charnov et al., 1976; Matsuda et al., 1993, 1994, 1996) .

REFERENCES

Abrams PA, 1986. Adaptive responses of predators to prey and prey to predators: the failure of the arms race analogy. Evolution 40:1229–1247.

Abrams PA, 1990. The evolution of antipredator trait in prey in response to evolutionary change in predators. Oikos 59:147–156.

Abrams PA, 1992. Predators that benefit prey and prey that benefit predators: unusual effects of interacting foraging adaptations. Am Nat 140:573–600.

Abrams PA, 1995. Implications of dynamically variable traits for identifying, classifying, and measuring direct and indirect effects in ecological communities. Am Nat 146:112–134.

Abrams PA, Matsuda H, 1996. Positive indirect effects between prey species that share predators. Ecology 77:610–616.

Ali S, 1962. The birds of Sikkim. Madras, India: Oxford University Press.

Ali S, 1977. Field guide to the birds of the eastern Himalayas. Delhi: Oxford University Press.

Ali S, Ripley SD, 1971. Handbook of the birds of India and Pakistan, vol. 6. Cuckoo-shrikes to babaxes. Bombay: Oxford University Press.

Ali S, Ripley SD, 1972. Handbook of the birds of India and Pakistan, vol. 7. Laughing thrushes to the Mangrove whistler. Bombay: Oxford University Press.

Ali S, Ripley SD, 1973a. Handbook of the birds of India and Pakistan, vol. 8. Warblers to redstarts. Bombay: Oxford University Press.

Ali S, Ripley SD, 1973b. Handbook of the birds of India and Pakistan, vol. 9. Robins to Wagtails. Bombay: Oxford University Press.

Ali S, Ripley SD, 1974. Handbook of the birds of India and Pakistan, vol. 10. Flowerpeckers to buntings. Bombay: Oxford University Press.

Beehler BM, Pratt TK, Zimmerman DA, 1986. Birds of New Guinea. Princeton, New Jersey: Princeton University Press.

Brown JS, Vincent TL, 1992. Organization of predator-prey communities as an evolutionary game. Evolution 46:1269–1283.

Charnov EL, Orians GH, Hyatt K, 1976. Ecological implications of resource depression. Am Nat 110:247–259.

Collet TS, Land MF, 1978. How hoverflies compute interception courses. J Comp Physiol 125:191–204.

Cramp S (ed), 1992. Handbook of the birds of Europe, the Middle East and North Africa. The birds of the western Palearctic, vol. VI. Warblers. Oxford: Oxford University Press.

Dawkins R, 1983. The extended phenotype. Oxford: Oxford University Press.

Dawkins R, Krebs JR, 1979. Arms races between and within species. Proc R Soc Lond B 205:489–511.

Edmunds M, 1974. Defence in Animals. A survey of anti-predator defences. Harlow, Essex: Longmann Ltd.

Endler JA, 1992. Signals, signal conditions, and the direction of evolution. Am Nat 139:S125-S153.

Ficken MS, Ficken WR, 1962. The comparative ethology of the wood warblers: a review. Living Bird 2:103–122.

Fisher RA, 1932. Statistical methods for research workers. London: Oliver and Boyd.

Fleming RL Sr, Fleming RL Jr, Bangdel LS, 1979. Birds of Nepal. Katmandu: Banks P.P. Avalok Publishers.

Frith DW, 1984. Foraging ecology of birds in upland tropical rain forest in North Queensland. Aust Wildl Res 11:325–347.

Gander FF, 1931. May the color pattern of the Mockingbird's wings aid in finding insect food. Wilson Bull 43:146.

Hailman JP, 1960. A field study of the mockingbird's wingflashing behavior and its association with foraging. Wilson Bull 72:346–357.

Hamilton WD, 1971. Geometry of the selfish herd. J Theor Biol 31:295–311.

Heady SE, Nault LR, 1985. Escape behavior of *Dalbulus* and *Baldulus* leafhoppers (Homoptera: Cicadellidae). Environ Entomol 14:154–158.

Holmes RT, Recher HF, 1986. Search tactics of insectivorous birds foraging in an Australian eucalypt forest. Auk 103:515–530.

Holmqvist MH, Srinivasan MV, 1991. A visually evoked escape response of the housefly. J Comp Physiol A 169:451–459.

Howell SNG, Webb S, 1995. A guide to the birds of Mexico and Northern Central America. Oxford: Oxford University Press.

Howell TR, 1971. An ecological study of birds of the lowland pine savanna and adjacent rain forest in northeastern Nicaragua. Living Bird 10:185–242.

Jabłoński P, 1993. Why painted redstarts fan their tails. SWRS News. Southwestern Research Station, The American Museum of Natural History 8:4–5.

Jabłoński P, 1994. Adaptive significance of colour patterns in painted redstart. J Ornithol 135 (suppl. 147).

Jabłoński P, 1996. Dark habitats and bright birds: warblers may use wing patches to flush prey. Oikos 75:350–352.

Jackson J, Elgar M, 1993. The foraging behavior of the willie wagtail *Rhipidura leucophrys*: why does it wag its tail? Emu 93:284–286.

Keast A, Pearce L, Saunders S, 1995. How convergent is the American redstart (*Setophaga ruticilla,* Parulinae) with flycatchers (Tyrannidae) in morphology and feeding behavior? Auk 112:310–325.

Land MF, 1992. Visual tracking and pursuit: humans and arthropods compared. J Insect Physiol 38:939–951.

MacKinnon J, Phillips K, 1993. A field guide to the birds of Borneo, Sumatra, Java and Bali. Oxford: Oxford University Press.

Marchetti K, 1993. Dark habitats and bright birds illustrate the role of the environment in species divergence. Nature 362:149–152.

Marchetti K, Price T, 1997. The adaptive significance of colour patterns in the Old World leaf warblers genus *Phylloscopus*. Oikos 79: 410–412.

Marshall JD, Balda RP, 1974. The breeding ecology of the painted redstart. Condor 76:89–101.

Matsuda H, Abrams PA, Hori M, 1993. The effect of adaptive antipredator behavior on exploitative competition and mutualism between predators. Oikos 68:549–559.

Matsuda H, Hori M, Abrams PA, 1994. Effects of predator-specific defence on community complexity. Evol Ecol 8:628–638.

Matsuda H, Hori M, Abrams PA, 1996. Effects of predator-specific defence on biodiversity and community complexity in two-trophic-level communities. Evol Ecol 10:13–28.

McBeath MK, Shaffer DM, Kaiser MK, 1995. How baseball outfielders determine where to run to catch fly balls. Science 268:569–573.

Monroe BL Jr, 1964. Wing-flashing in the red-backed scrub-robin, *Erythropygia zambesiana*. Auk 81:91–92.

Morse DH, 1970. Ecological aspects of some mixed species foraging flocks in birds. Ecol Monogr 40:119–168.

Moynihan M, 1962. The organization and probable evolution of some mixed species flocks of neotropical birds. Smithsonian Misc Collection 143:1–140.

Newman K, 1980. Birds of Southern Africa. 1 Kruger National Park. Johannesburg: Macmillan South Africa.

Nocedal J, 1988. Resource partitioning in a guild of foliage gleaners in an oak-pine woodland of southern Mexico. Int Ornithol Congr 19:2318–2327.

Osborne WS, Green K, 1992. Seasonal changes in composition, abundance and foraging of birds in the Sunny Mountains. Emu 92:93–105.

Peterson RT, 1990. A field guide to western birds. Boston: Houghton Mifflin.

Pizzey G, 1980. A field guide to the birds of Australia. Sydney: Collins.

Price T, 1991. Morphology and ecology of breeding warblers along an altitudinal gradient in Kashmir, India. J Anim Ecol 60:643–664.

Prozesky OPM, 1974. A field guide to the birds of Southern Africa. London: Collins.

Rabenold KN, 1978. Foraging strategies diversity and seasonality in bird communities of Appalachian spruce-fir forests. Ecol Monogr 48:397–424.

Recher HF, Gowing G, Kavanagh R, Shields J, Rohan-Jones W, 1983. Birds, resources and time in tablelands forest. Proc Ecol Soc Aust 12:101–123.

Recher HF, Holmes RT, 1985. Foraging ecology and seasonal patterns of abundance in forest avifauna. In Birds of eucalypt forests and woodlands: ecology, conservation, management (Keast A, Recher HF, Ford H, Saunders D, eds). Royal Australasian Ornithologists Union and Surrey Beatty & Sons; 79–96.

Recher HF, Holmes RT, Schulz M, Shields J, Kavanagh R, 1985. Foraging patterns of breeding birds in eucalypt forest and woodland of southwestern Australia. Aust J Ecol 10: 399–419.

Remsen JV, Robinson SK, 1990. A classification scheme for foraging behavior of birds in terrestrial habitats. Stud Avian Biol 13:144–160.

Ridgley RS, Tudor G, 1989. The birds of South America, vol. I. The oscine ppasseriformes. Austin: University of Texas Press.

Robinson SK, Holmes RT, 1982. Foraging behavior of forest birds: the relationships among search tactics, diet and habitat structure. Ecology 63:1918–1931.

Robinson SK, Holmes RT, 1984. Effects of plant species and foliage structure on the foraging behavior of forest birds. Auk 101:672–684.

Root RB, 1967. The niche exploitation pattern of the Blue-grey Gnatcatcher. Ecol Monogr 37:315–350.

Rosenthal R, 1991. Meta-analytic procedures for social research. Newburry Park, California: Sage Publications.

Schwind R, 1989. Size and distance perception in compound eyes. In: Facets of vision (Stavenga DG, Hardie RC, eds). Berlin: Springer-Verlag; 425–444.

Sherry TW, 1984. Comparative dietary ecology of sympatric, insectivorous neotropical flycatchers (Tyrannidae). Ecol Monogr 54:319–338.

Sibley CG, Ahlquist JE, 1990. Phylogeny and classification of birds. New Haven, Connecticut: Yale University Press.

Sillett TS, 1994. Foraging ecology of epiphyte searching insectivorous birds in Costa Rica. Condor 96:863–877.

Thomas HR, 1980. The bird community of Tasmanian temperate forest. Ibis 122:298–306.

Van Valen L, 1973. A new evolutionary law. Evol Theor 1:1–30.

Wolf FM, 1986. Meta-analysis. Quantitative methods of research synthesis. Beverly Hills, California: Sage Publications.