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ARE CONSPICUOUS BIRDS UNPROFITABLE PREY? FIELD EXPERIMENTS WITH HAWKS AND STUFFED PREY SPECIES

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ABSTRACT.—The unprofitable-prey hypothesis predicts that birds of prey, when given a choice, should more often attack a cryptic than a conspicuous bird if conspicuousness is a signal of unprofitability. We tested this prediction by exposing pairs of stuffed birds to migrating birds of prey. In experiment 1, we paired the conspicuous White Wagtail (*Motacilla alba*) with the cryptic Meadow Pipit (*Anthus pratensis*). In experiment 2, we paired the conspicuous female Great Spotted Woodpecker (*Dendrocopos major*) with the cryptic female Blackbird (*Turdus merula*). Automatic cameras documented attacks by birds of prey, mostly accipiters, on the mounts. The numbers of attacks on wagtails and pipits were similar, whereas Blackbirds were attacked much more often than woodpeckers. Experiment 2 thus supports the prediction of the unprofitable-prey hypothesis. Using photographs of the experimental situation, we examined detectability of mounts by human observers. Wagtails and pipits were equally easy to detect from a distance, but woodpeckers usually were easier to detect than Blackbirds. Thus, wagtails and pipits did not differ in "long-distance conspicuousness," which may explain the result of experiment 1. To analyze reasons for unprofitability, we presented flesh from woodpeckers and Blackbirds to captive falcons, but found no evidence that woodpeckers are distasteful. Other explanations for why woodpeckers were rarely attacked are discussed. *Received 26 April 1993, accepted 17 August 1993.*

THE PLUMAGE of diurnal birds exhibits striking variation in color patterns, from dull, cryptic patterns in some species to bright red, yellow, or black-and-white in others. The evolution of conspicuous colors in birds has been debated since Darwin (1871) proposed his theory of sexual selection to explain the bright colors of many male birds. Darwin's idea of selection through female choice of bright males was discussed by Hingston (1933), who argued that contest competition among males primarily selected for conspicuous colors (review in Butcher and Rohwer 1989). Several studies have supported both the idea of female choice (e.g. Höglund et al. 1990, Norris 1990, Hill 1991) and male-male competion (Røskaft and Rohwer 1987, Rohwer and Røskaft 1989).

Avian coloration is also related to risk of predation. Cryptic plumages in birds such as nightjars and female ducks suggest an important role for predation. Conspicuous plumages may be antipredator adaptations as well. Certain brightly colored birds are distasteful to hornets, cats, and people and, therefore, may be aposematic (Cott 1947, Cott and Benson 1970, Götmark 1994a). Recently, two or three apparently

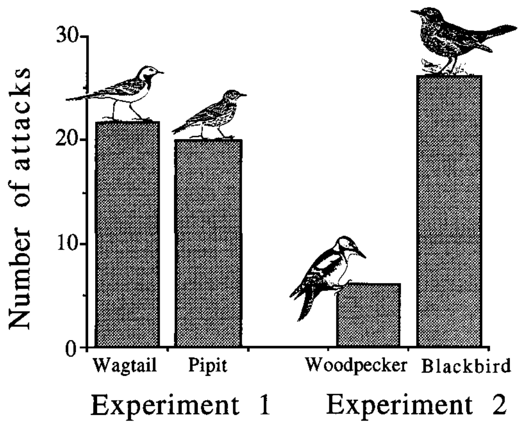

Fig. 1. Attacks by birds of prey on mounts of four prey species (White Wagtail, Meadow Pipit, Great Spotted Woodpecker, and Blackbird). The wagtail, pipit, and woodpecker were exposed in the field in approximate position shown in diagram; the Blackbird had its tail down (resting position).

poisonous, brightly colored birds were discovered in New Guinea (Dumbacher et al. 1992). Moreover, Baker and Parker (1979) suggested that conspicuous birds signal to predators that they are unprofitable prey. They assumed that bright birds are agile or vigilant and, therefore, difficult to catch. Below, we consider the unprofitable-prey hypothesis in a broad sense, including any mechanism that makes conspicuous birds unprofitable. The hypothesis suggests that unprofitability to predators is a major explanation of conspicuousness in birds (Cott 1947, Baker and Parker 1979). A central prediction of the hypothesis is that experienced predators, when given a choice, should more often attack a cryptic than a conspicuous bird, even if the former is more difficult to detect.

This prediction has been difficult to test. Comparative studies of color patterns, ecological factors, and mortality rates of birds support the prediction (Baker and Parker 1979, Baker and Hounsome 1983), but the results are open to alternative explanations (Krebs 1979, Andersson 1983, Reid 1984, Lyon and Montgomerie 1985, see also Baker 1985). In addition, these comparative analyses have methodological problems (Harvey and Pagel 1991). More recent studies (Butcher 1984, Baker and Bibby 1987, Flood 1989) found no, or weak, support for antipredator functions of conspicuous plumages, but the prediction of differential attacks was not addressed.

Birds of prey are the major predators of smaller birds and, therefore, should be appropriate in testing the prediction. We studied predation on small birds by exposing mounted specimens to migrating birds of prey at concentration points along the migration route. Caldwell (1986) used a similar method, exposing model herons to hawks in Panama, which were attracted to the models, but did not attack them. In an earlier study, Götmark (1992) found that Sparrowhawks (*Accipiter nisus*) more often attacked mounts of cryptic females than mounts of conspicuous males of the Pied Flycatcher (*Ficedula hypoleuca;* see also Götmark 1993). Here we examine the prediction of the unprofitable-prey hypothesis that predators prefer to attack cryptic species over conspicuous species (Lyon and Montgomerie 1985). We selected pairs of species, one cryptic and one conspicuous, for field experiments. We also assessed conspicuousness of these species in the experimental situation, and studied possible antipredator adaptations of the species.

METHODS

Choice of prey species.—For experiment 1, we chose the conspicuous White Wagtail (*Motacilla alba*) and the cryptic Meadow Pipit (*Anthus pratensis*). For experiment 2, we chose the conspicuous female Great Spotted Woodpecker (*Dendrocopos major*) and the cryptic female Blackbird (*Turdus merula*). The two conspicuous species are black, gray and white (the female woodpecker also has red undertail coverts); the cryptic ones are mostly brown or brown-streaked (for general plumage patterns, see Fig. 1).

The wagtail and pipit occur in open habitats, are of similar size, and are closely related (Cramp 1988). The wagtail seems agile and is not shy; it is known to pursue Sparrowhawks in flight, uttering a "mobbing song" (Bergmann and Helb 1982, Cramp 1988). The pipit is less conspicuous and does not mob Sparrowhawks in the same way as the wagtail (Cramp 1988). The woodpecker and Blackbird are solitary woodland species of similar size, and place their nests in trees (the woodpecker in holes). These two species are not closely related. However, the unprofitable-prey hypothesis predicts a general correlation between conspicuousness of birds and their unprofitability to predators (Baker and Parker 1979, Lyon and Montgomerie 1985). Therefore, one may compare species that are less related, but seem to differ in unprofitability to predators. The woodpecker has a powerful bill, which might be used in defense. Moreover, the woodpecker, but not the Blackbird, has been reported to be distasteful (Cott 1947:472) and to attack hawk models (Cramp 1985:866).

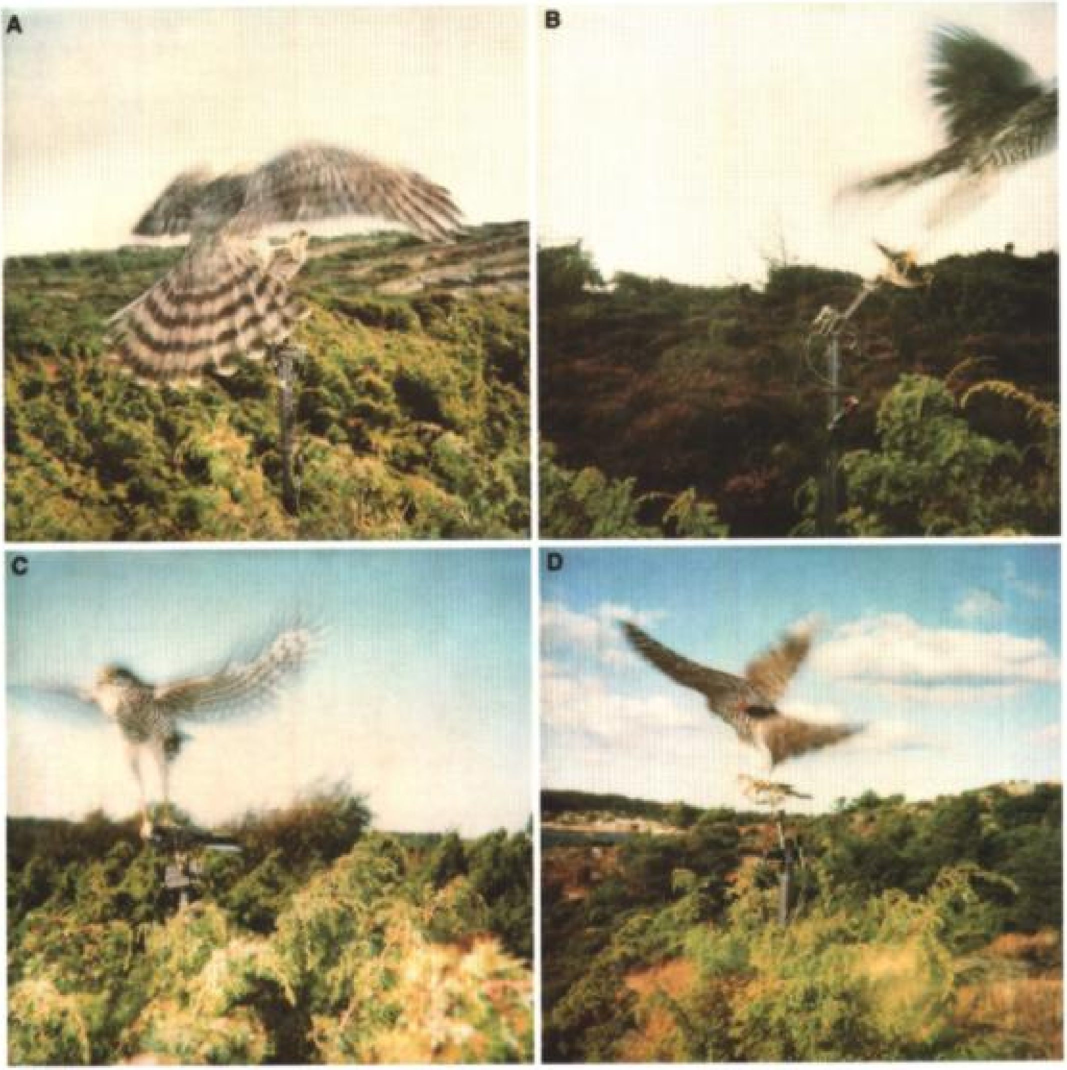

Fig. 2. Photographs taken by automatic Polaroid camera, triggered during attacks on mounted prey species. (A, B, D) Sparrowhawks seizing Meadow Pipit mounts in flight (hawk in photo A was a juvenile, based on light fringes of wing coverts); (C) Sparrowhawk seizing a White Wagtail mount in flight.

Mounted specimens, in resting but upright position, were bought from taxidermists in Sweden. Adult male and female wagtails are similar in plumage, but males have a more distinct black crown (nape) than females. Most of the 18 wagtails we used were probably adult males. In the pipit (18 mounts), males, females, and juveniles are all similar in plumage. Adult female Blackbirds vary in plumage from mainly brown to brown-black (all with diffuse streaks on the breast). We used eight mounts of brown females and seven of brown-black females. In the woodpecker, the adult male, adult female, and juvenile are similar. We used eight adult females, four adult males, and three juveniles; the small red spot on the head of adult males, and the red crown of juveniles, were painted black with Indian ink, so that they resembled black-headed females. All mounts were sprayed with an impregnating agent ("Woly 3 × 3," Lever Sutter AG, Münchwilen) so that they would better withstand the rain.

Exposure of mounts and experimental design.—Mounted specimens were exposed at Hållsundsudde, Sweden (a coastal peninsula 50 km south of Göteborg) in the autumn of 1991. Sparrowhawks start migrating in mid-August, and later, many other birds of prey and other bird species migrate in a southerly direction along the coast (Götmark et al. 1979).

We attached mounts to cryptically painted aluminum poles set into the ground. About 1.1 m south or north of each mount pole we placed another pole with a box (24 × 18 × 16 cm) containing a Polaroid 635 CL camera. The box was camouflaged with vegetation. About 8 cm below the bird on the mount pole was a trigger mechanism for the camera, consisting of two horizontal plates (4 × 6 cm) that divided the pole (Fig. 2B). On the lower plate, we placed a glued printed circuit card with a small Hall-effect sensor (TL 172; Texas Instruments, USA). On the upper plate, a magnet was attached above the sensor. The camera was released by movements of the upper plate/magnet, allowing current to pass through the sensor (the piece with mount, perch, and upper plate was removed in attacks, but not lost; it was attached with a wire). Cables on the ground joined the trigger mechanism and the camera, which was driven by six-volt batteries. The system was sensitive to movement of the mount (upper plate) and, in windy weather, the plates were tied together with rubber bands. Photographs, taken with flash, were delivered by the camera into the box. In about 90% of all attacks, the predator could be identified (Fig. 2). Predators lost the mount in flight (Fig. 2) and probably did not learn that it was inedible. Daily maintenance of the camera system was required, and was combined with checks for attacks.

The study area is rocky and open, dominated by heather (*Calluna vulgaris*), patches of low junipers (*Juniperus communis*), and isolated low trees or groves of trees (mostly pine [*Pinus sylvestris*], birch [*Betula* spp.], willow [*Salix* spp.], and rowan [*Sorbus aucuparia*]). In mid-August, we selected 15 sites for 15 pairs of mounts in an area of about 1 km^2. Nearest-neighbor distances between sites varied from 50 to 225 m ($\bar{x}$ = 150 m). The same sites were used for experiments 1 and 2. At 10 sites, mount and camera poles were placed among juniper bushes; at two sites, among pines; at two sites, among willows; and at one site, among birches. At each site, we selected two bushes of similar size with similar surroundings; equipment was placed in a similar manner in each bush. The distance between the two bushes varied from 10 to 22 m ($\bar{x}$ = 15 m). The mounted birds were about 1.6 m above the ground. If two mounts are placed 1 to 2 m apart, only one camera is needed for surveillance (Götmark 1993); if both mounts are attacked on the same day, the photographs make clear which mount was attacked first.

The plumages of the pipit, woodpecker and Blackbird do not change from the breeding to the nonbreeding season. The mounted wagtails were in breeding plumage. In August-September, wagtails molt into a winter plumage (Cramp 1988). Therefore, in order to match appropriate season and plumage, we started experiment 1 first (on 23 August). We placed one wagtail and one pipit at each of the 15 sites, drawing random numbers to determine in which bush to place each mount. All mounts faced west, a predominant wind direction. After an attack at a site (=one trial), mounts were shifted between bushes. After the next attack, mounts were removed, and experiment 2 (Blackbird and woodpecker) was started (from 23 September onwards). At three sites, no attack was recorded and we ended experiment 1 on 24 September; at other sites, only one attack was recorded and we exposed mounts longer in the hope of a second attack (see below). For experiment 2, 12 sites were used from late September to 30 October. Compared to Blackbird mounts, woodpecker mounts were placed in a more upright position, typical of perching woodpeckers. Attack rate was generally higher than in experiment 1, and most mounts were shifted between bushes several times. Mounts could often be reused between attacks, but sometimes had to be repaired or changed. During rain storms, mounts became wet and looked unnatural, but once dry again they were easy to restore (almost no attacks were recorded in bad weather).

To obtain a larger sample, we repeated experiment 1 between 25 and 31 August 1992. In the same study area, we selected 15 sites for 15 pairs of mounts (eight sites were new and seven had been used in 1991; all were in similar habitat). In August, there are no migrating owls or raptors, except Sparrowhawks. From results in 1990 and 1991, we were confident that only Sparrowhawks would attack mounts, and did not use cameras to document attacking species; otherwise, the methods were the same as in 1991.

Conspicuousness of prey species.—In selecting species, we assessed plumage conspicuousness in the same way as most earlier workers. One may define it as appearance "at close quarters to a potential predator once the latter had either distinguished the bird from its surroundings or had accidently arrived so close to the bird that the latter was at risk of immediate capture once noticed" (Baker and Parker 1979:78). By this definition of close-quarter conspicuousness, one may subjectively assess conspicuousness of birds from pictures in a field guide, as Baker and Parker (1979) did for each of nine parts of the bird body, using scores from 0 (minimum conspicuousness) to 5 (maximum). For female Great Spotted Woodpeckers, adult White Wagtails, Meadow Pipits, and female Blackbirds, the averages of the nine scores were 3.4, 3.1, 1.3, and 0.9, respectively (R. R. Baker and A. F. Read pers. comm.; for scoring of species, see Baker and Parker 1979:79). We asked 10 Swedish ornithologists (who were unaware of our hypotheses) to score overall close-quarter conspicuousness of the species, from 0 (minimum conspicuousness) to 5 (maximum), by using field guides and personal experience. The resulting average values (order of species as above) were 4.0 ± SD of 0.8, 3.7 ± 0.5, 0.9 ± 0.6, and 1.0 ± 0.7.

Conspicuousness in the sense of detectability of distant prey in natural habitats is also important (below called long-distance conspicuousness, or detectability; Guilford and Dawkins 1991). This component of conspicuousness has rarely been quantified in studies of bird coloration. Detectability of birds depends on many factors, such as background, light conditions, and vision in predators (Endler 1978, Burtt 1986). Visual acuity in birds of prey is probably about the same or somewhat better than that of humans (Reymond 1985, 1987). Many, if not all diurnal birds perceive colors (Bowmaker 1988); although birds of prey have not been studied, they likely "have a colour system in the retina not too different from that of other diurnal birds" (J. K. Bowmaker pers. comm.). In this study, we used humans to assess long-distance conspicuousness of mounts by presenting photographs of them with the major backgrounds and light conditions of the experiments. One problem is that humans may differ from birds in perception of colors (Jacobs 1981). However, this is probably not a serious problem in our tests with white, gray, brown, and black species; these "colors" are likely to be perceived in approximately the same way by humans and birds of prey.

We examined four backgrounds (see below) and two light conditions (sunny and cloudy weather). Photographs were taken of mounts at 10 experimental sites (the ones where most attacks were recorded), using 10 different mounts of each species (one at each site). We randomly selected one of the two bushes at each site (surroundings of the two bushes were similar). For each background, we selected the patch that was closest to the bush. For each light condition and background, we took one photograph of a cryptic species (mount) and one of a conspicuous species (mount). The mounts were placed in the same position, with exactly identical background and identical light condition, and photographs were taken with a 50-mm lens from a distance of about 6 m (somewhat closer for the smaller wagtails and pipits, so that all birds on the photographs were of approximately same size). The distance between mount and background was about 0.5 m. We photographed mounts in sideway, frontal, and backward (only woodpecker and Blackbird) position. In sunlight, the sun's position was perpendicular to the line between camera and mount. Such sidelight increases contrast in the background, compared to sunlight coming from behind the camera, which more resembles the situation with an overcast sky (for direct sunlight, see below). Mounts photographed from the side in sunlight faced the sun.

On developed color photographs (10 × 15 cm), the size of the mount was about 1 cm. For each person (trial), two photographs, either of a wagtail and a pipit, or of a woodpecker and a Blackbird, were positioned on a board next to each other. The board was first presented at a distance from which he or she could not detect mounts (about 7 m). The person was asked to try to find a bird and to search repeatedly back and forth on the pictures. We then approached the person slowly, pausing at about every 50 cm, until he or she detected a mount. Ten trials with different persons were conducted for each paired species and background comparison (recall that photographs were taken at 10 experimental sites). Some persons were tested twice, each time with different species.

There were four main background colors, corresponding to four vegetation or ground types: light yellow (dry grass); brown (heather, deciduous trees without leaves, or with brown leaves); green (coniferous trees and juniper bushes); and gray (rock, often partly covered with lichens). We estimated percentage cover of each color type at the 15 sites by first randomly selecting one bush at each site. In a circle with a 10-m radius, with the bush in the center, cover of each color type was estimated by eye. Standing at the bush, we also quantified the distant background, below the horizon but above the limit of the circle around the bush. For this "area" of 360°, percentage cover of colors was also estimated by eye. This work, and all photography, were conducted after experiment 2 ended. Backgrounds, thus, were studied when most deciduous trees had lost their leaves. In September–October, backgrounds would contain some more yellow-brown or red-brown and less pure brown color, whereas in August–September, there would be some more green, and less brown colors. Close to mounts (within 10 m) there were few deciduous trees or bushes (mounts were mostly placed in conifers), and little change in colors. The open habitat with a low density of deciduous trees meant that seasonal change affected measurements and conclusions to a minor extent only.

Antipredator adaptations in prey species.—A low wing loading implies high maneuverability in flight (Norberg 1990) and, thus, improved escape capacity for prey (Witter and Cuthill 1993). Wing loading is measured by the formula mg/S, where m is mass (kg), g is gravitational acceleration (9.81 m/s), and S is wing area (m^2; Norberg 1990). We measured mass and wing area of seven wagtails, eight pipits, six Blackbirds, and six woodpeckers using dead but fresh (frozen) specimens obtained from taxidermists and bird stations. We took photographs of specimens with wings held perpendicular to the body axis on paper with a grid in millimeters. Wing area includes the body surface between wings (Norberg 1990).

To examine palatability of prey species, we presented flesh from them to 14 pairs of captive Peregrine Falcons (*Falco peregrinus*) at a breeding center near Göteborg. The falcons had earlier been fed chickens, and tended to avoid any new type of food for a day or two after it had been introduced (T Järås pers. comm.). To avoid this problem, a piece of flesh (a flight muscle) was placed in the body of a dead one-day-old chicken. The falcons perceived these chickens as being normal and so we could observe them consuming the added meat piece. Sometimes the falcons discarded the meat piece (see below), perhaps because it was unfamiliar, or perceived as intestines (which they normally discard). We recorded the behavior of the falcons from presentation of a chicken until about 1 h after consumption of a meat piece. This test was conducted for the species in experiment 2 (which differed in attack frequency; see below) using six Blackbirds and six woodpeckers. For each carcass, we used both flight muscles, obtaining 12 pieces of meat for each species and, in total, 24 presentations of meat to falcons.

RESULTS

ATTACKS BY BIRDS OF PREY ON MOUNTS

Experiment 1. White Wagtail vs. Meadow Pipit.—At each of eight experimental sites in 1991, one of the two mounts was attacked. At each of these sites, we shifted the mounts between bushes, and one mount was attacked again at all sites, resulting in a total of 16 trials. As placement was controlled for by shifting mounts, and as different individuals probably attacked mounts (see below), we considered trials to be statistically independent. In 10 trials, White Wagtail mounts were attacked first; in 6 trials, Meadow Pipit mounts were attacked first (two-tailed sign test, $P = 0.38$). At five experimental sites, only one attack was recorded. When we added these five trials, wagtails were attacked first in 13 and pipits attacked first in 8 trials ($P = 0.45$). In one trial, both mounts were attacked on the same day (not included above).

For an alternative statistical analysis, we calculated attack rate (i.e. number of attacks on mounts per day and site). For experimental sites where mounts were shifted, mean attack rates for wagtails and pipits were similar: 0.10 ± 0.08 ($n = 8$) and 0.08 ± 0.09 ($n = 8$), respectively (Wilcoxon matched-pairs test, $P = 0.18$). When we added the five remaining trials, the corresponding figures were 0.17 ± 0.27 ($n = 13$) and 0.08 ± 0.09 ($n = 13$), respectively ($P = 0.40$).

We could recognize the attacking species in 23 cases. Sparrowhawks (13 attacks; Fig. 2) predominated; we also recorded three attacks by Goshawks (*A. gentilis*), three by Merlins (*F. columbarius*), one by a Great Gray Shrike (*Lanius excubitor*), one by a Long-eared Owl (*Asio otus*), one by a Short-eared Owl (*A. flammeus*), and one by a Tawny Owl (*Strix aluco*). The plumage of eight Sparrowhawks indicated that they were juveniles (young of the year; Fig. 2B), whereas two probably were adults. Two Goshawks were juveniles, and two Merlins were females or juveniles. The owls attacked mounts at night, whereas other birds of prey attacked in daylight; 9 (39%) of the latter attacks were under overcast sky, and 14 (61%) in sunshine.

At eight sites in 1992, one of the two mounts was attacked. At each of these sites, the mounts were shifted between bushes, and one mount was attacked again at all sites (we then ended the trials at these sites). In eight trials, the wagtail was attacked first, and in eight other trials the pipit was attacked first. At five sites, only one attack was recorded. When we added these trials, the wagtail was attacked first in 9 trials and the pipit first in 12 trials ($P = 0.66$). In addition, both mounts at the experimental site were attacked on the same day in four cases. The attack rates per day and site were similar for the two species: wagtail, 0.13 ± 0.17 ($n = 13$); and pipit, 0.17 ± 0.15 ($n = 13$; $P = 0.68$).

If the two years are pooled, the wagtail was attacked first in 22 trials and the pipit in 20 (Fig. 1). If three attacks by owls are excluded, the corresponding figures are 21 and 18 trials, respectively. The results suggest that birds of prey did not avoid the White Wagtail, but readily attacked both species.

Experiment 2. Great Spotted Woodpecker vs. Blackbird.—At 10 sites, mounts were shifted between attacks one to three times, resulting in two to four trials per site. At two sites, only one attack (one trial) was recorded. All 32 trials were pooled and considered independent (see below). In 6 trials, Great Spotted Woodpeckers were attacked first and in 26 the Blackbirds were attacked first (two-tailed sign test, $P = 0.0006$; Fig. 1). In three trials, both mounts were attacked on the same day (not included above).

Most mounts were probably attacked by different individuals, but two individuals probably attacked several mounts (see below; only their first attack was included in the test above). The alternative analysis of number of attacks per day and site reduces any existing pseudoreplication, as it was based on sites instead of trials. The mean attack rate was lower for woodpecker mounts (0.03 ± 0.03, $n = 12$) than for Blackbird mounts (0.17 ± 0.14, $n = 12$; Wilcoxon matched-pairs test, $P = 0.01$). Thus, birds of prey attacked mainly the Blackbird, as predicted by the unprofitable-prey hypothesis.

For 30 of 38 attacks, the attacking species could be recognized. The Goshawk predominated (14 attacks); we also recorded three attacks by Sparrowhawks, four by Common Buzzards (*Buteo buteo*), three by Eagle Owls (*Bubo bubo*), two by Short-eared Owls, two by Long-eared Owls, one by a Tawny Owl, and one by a *Strix/Asio* owl. Birds of prey were likely involved also in the remaining attacks; there was no indication that other birds attacked mounts. Ten Goshawks could be recognized as juveniles (young of the year; Fig. 2); two Goshawks and one Sparrowhawk were adults. Some birds wore bands or other marks, and we established that at least five different Goshawks (three juveniles, two adults) attacked mounts. Furthermore, two different Common Buzzards and two Long-eared Owls were identified. In total, at least 12 individuals attacked mounts. Two individuals likely made repeated attacks. A Common Buzzard (with distinctive plumage) attacked a Blackbird, and five days later a Blackbird and a woodpecker at the same site. An Eagle Owl (a rare bird) attacked a woodpecker, and five days later a Blackbird and a woodpecker at a different site. The owls (and one Goshawk) attacked at night, and the other birds in daylight. Four attacks (Goshawk plus three undetermined predators) were at dusk or dawn. Of 25 attacks in daylight (including dusk and dawn), 19 (76%) were under overcast skies and 6 (24%) in sunshine.

Diurnal birds (hawks, Common Buzzard) attacked 18 Blackbirds and 3 woodpeckers ($P < 0.0005$); nocturnal birds (owls) attacked 4 Blackbirds and 5 woodpeckers. Thus, avoidance of woodpeckers was due to prey (mount) selection in diurnal birds of prey. Juvenile hawks predominated, but the three individuals identified as adults (one Sparrowhawk, two Goshawks) all attacked Blackbirds.

Background and Conspicuousness of Mounts Under Experimental Conditions

Close to mounts (<10 m), brown colors predominated, followed by greens (together 69% of ground cover; Table 1). Farther away from mounts (>10 m), brown and green colors predominated (68% of ground cover), followed by grays. We also calculated coverage of color types for each experiment, where means were weighted by the number of attacks (0–4) at each site. The result was similar; means for individual backgrounds differed only 0 to 2.5 units from the values in Table 1.

TABLE 1. Background colors (corresponding to vegetation or ground types) of mounts at sites ($n = 15$ for each background color) used in experiments 1 and 2; surroundings of one bush at each site were examined.

	Percent cover ($\bar{x} \pm$ SD)	
Background color	Circle around bush[a]	Distant horizontal circle[a]
Brown (heather, trees)	40 ± 10	35 ± 7.6
Green (junipers, trees)	29 ± 12	33 ± 6.2
Gray (rock)	18 ± 12	22 ± 6.8
Light yellow (dry grass)	12 ± 9.8	9.7 ± 6.4

[a] For definitions, see Methods.

In detectability tests with humans, pipit and wagtail mounts photographed in profile did not differ significantly in long-distance conspicuousness for any background or light condition; each species was detected first about equally often (Table 2). The two bird species differ in breast coloration (the wagtail has a black "bib"), and we compared detectability of mounts photographed in frontal position, but found no significant differences (Table 3). Thus, for humans, the two species were about equally easy to detect when approached in the experimental situation.

For green and brown backgrounds, especially under overcast skies, woodpecker mounts were easier to detect than Blackbird mounts when in the sideways position (Table 2). For light yellow and gray backgrounds, especially under overcast sky, Blackbirds tended to be easier to detect than woodpeckers. In frontal and backward po-

TABLE 2. Assessment of detectability (10 trials with humans per category) of mounts in sideway position on paired photographs: Blackbird (B) versus Great Spotted Woodpecker (GSW); and Meadow Pipit (MP) versus White Wagtail (WW).

	B first/ GSW first		MP first/ WW first	
Background	Over-cast	Sun-shine	Over-cast	Sun-shine
Brown (heather, trees)	0/10**	2/8	6/4	5/5
Green (junipers, trees)	0/10**	1/9*	6/4	5/5
Gray (rock)	9/1*	8/2	4/6	7/3
Light yellow (dry grass)	9/1*	6/4	6/4	5/5

*, $P = 0.02$; **, $P = 0.002$. Two-tailed sign test to evaluate tendency for a species to be detected first.

TABLE 3. Assessment of detectability (10 trials with humans per category) of mounts in frontal or backward position on paired photographs: Blackbird (B) versus Great Spotted Woodpecker (GSW); and Meadow Pipit (MP) versus White Wagtail (WW).

Background	B first/ GSW first[a]		MP first/ WW first[b]
	Frontal	Backward	Frontal
Brown (heather, trees)	See text		7/3
Green (junipers, trees)	See text		5/5
Gray (rock)	7/3	2/8	4/6
Light yellow (dry grass)	3/7	10/0**	2/8

**, $P = 0.002$ (two-tailed sign test).
[a] Photographed under overcast sky.
[b] Photographed in sunshine.

sitions, we assumed (after six preliminary trials) that black-and-white woodpeckers were easier to detect than Blackbirds against dark (brown and green) backgrounds. For light yellow and gray backgrounds, we also examined frontal and backward positions. Detectability of mounts in these cases varied both with position and background (Table 3). Because green and brown colors predominated in the background, the results suggest that in most cases woodpeckers were easier to detect from a distance. In direct sunlight, a number of photographs showed that mounts appeared as silhouettes, about equally easy to detect (recall that most attacks [76%] on woodpeckers and Blackbirds were under overcast sky).

ANTIPREDATOR ADAPTATIONS IN PREY SPECIES

Wagtails and pipits did not differ significantly in wing loading (in newton/m^2; N/m^2); mean values were 16.9 ± 1.2 and 15.5 ± 1.9 N/m^2, respectively (two-tailed Mann-Whitney U-test, $P = 0.13$). Woodpeckers, however, had significantly lower wing loading than Blackbirds; mean values were 25.3 ± 1.1 and 29.8 ± 1.3 N/m^2, respectively ($P < 0.01$).

In the feeding experiment, 19 falcons tasted chickens with meat of either a Blackbird or woodpecker. As explained above, some falcons did not eat the added meat piece. Four of 12 Blackbird pieces and 5 of 12 woodpecker pieces were discarded by the falcons. Five Blackbird pieces and seven woodpecker pieces were seen to be eaten by falcons (of the remaining three Blackbird pieces, falcons either did not eat the chicken or were hidden when eating). All falcons ate the meat pieces without hesitation, like they did the rest of the chicken. They showed no signs of sickness after consuming the meat. In addition, we presented a dead but intact woodpecker and a Blackbird in similar condition to a captive Goshawk, which opened both carcasses and ate meat from them. Thus, Blackbirds and woodpeckers do not seem to differ greatly in palatability.

DISCUSSION

Predation risk in relation to prey conspicuousness.—In selecting species, we used Baker and Parker's (1979) definition of conspicuousness at close quarters (for similar approaches, see Weatherhead et al. 1991, Johnson 1991). We assessed conspicuousness from field guides, where the species usually have similar background. Certain colors or combinations of colors (e.g. blue, pink, red, yellow, black, and white) often are assumed to be inherently conspicuous as they do not match the predominantly green, brown, and gray natural habitats (but see Burtt 1986). However, earlier workers have rarely studied backgrounds in nature. Species considered conspicuous may instead by cryptic, even at close quarters. For instance, in Sweden the White Wagtail often nests along stony shores of lakes and streams, where a contrasting white, gray and black plumage may be cryptic. Conspicuousness should also be measured in nature, and one important component is long-distance conspicuousness. For at least two reasons, birds that signal unprofitability to predators should benefit from being detected early. First, high detectability should increase speed of learning in predators, as more individual unprofitable prey are detected per time unit (Endler 1991). Second, birds of prey are usually unsuccessful in their attacks (Rudebeck 1950–1951, Lindström 1989) and attack many potential prey for each one caught. *Accipiter* hawks attack suddenly and usually catch their prey by surprise (Rudebeck 1950–1951, Kenward 1982, Newton 1986, Lindström 1989). In such situations, high detectability of unprofitable prey should minimize misidentifications and misdirected attacks in the predators (Guilford 1990a, Endler 1991) and, therefore, should benefit both unprofitable prey and predators (Hasson 1991).

It seems unlikely, however, that long-distance conspicuousness alone is favored in unprofitable birds. Birds are highly mobile and, although cryptic species are camouflaged most of the time, they sometimes occur on backgrounds where they are easily detected from a distance (a female Blackbird on dry, light yellow grassland is one example; see Tables 2 and 3). Cryptic prey normally eaten by predators would be at risk in such situations; it is unlikely that predators avoid them because they become more conspicuous. Unprofitable prey, therefore, need recognition marks so that predators can distinguish them from cryptic prey that happen to be detectable. This is probably why certain colors predominate in aposematic species; "bright red, black-and-yellow alternating stripes, and white spots on a black ground" may be signals with "memory-stimulating qualities" (Rothschild 1984). Predators may avoid or learn to avoid distinctive, simple color patterns (Sillén-Tullberg 1985, Guilford 1990a, Endler 1991).

With regard to long-distance conspicuousness, we found no difference between the wagtail and the pipit, and predators attacked them about equally often. This indicates that the wagtail plumage is not a long-distance signal of unprofitability. The result also suggests that it is important to measure detectability of birds in the wild in studies of plumage conspicuousness. The woodpecker was in most cases detected earlier than the Blackbird, and was less often attacked by birds of prey, suggesting that its plumage may be used as a signal of unprofitability by predators.

With regard to close-quarter conspicuousness, or more precisely, color patterns that might be used as recognition marks, this and earlier studies (Götmark 1992, 1993) showed lower predation on two species with similar plumage. Both male Pied Flycatcher and Great Spotted Woodpeckers are black-and-white, and have black upper parts with large white spots. Because the upper parts more often will be directed at predators, they might be used in signals to them. Cott (1947) found the most marked distastefulness among species that were contrastingly black-and-white on upper parts and underparts (wheatears [*Oenanthe* spp.], Pied Kingfisher [*Ceryle rudis*], Masked Shrike [*Lanius nubicus*], and Hoopoe [*Upupa epops*]). The few poisonous, aposematic birds that are known are mostly black and orange (Dumbacher et al. 1992). However, preliminary results suggest that the black-and-white plumage of the Black-billed Magpie (*Pica pica*) does not reduce the risk of predation, but instead seems costly with regard to predation (Götmark unpubl. data).

The wagtail was also considered conspicuous at close quarters by Baker and Parker (1979) and our panel of ornithologists, but it is possible that marks on the underparts, such as the black breast of White Wagtails, are used mainly for signalling to conspecifics. On upper parts, the wagtail is mostly gray. Because the wagtail occurs mainly on the ground, aerial predators would see mostly the upper body parts.

Do the results of the detectability test apply to the species outside of the experimental situation? We suggest they do, but additional tests are needed. The pipit occurs in green, brown, and yellow grassland, the wagtail at shores or close to water, and at intensively grazed or disturbed areas (Cramp 1988). With the exception of some human-modified habitats, the background colors of these habitats are among the ones tested ("rock" is common at shores used by wagtails). The Blackbird occurs in woodland, often foraging on green or brown forest floor. The woodpecker mostly climbs trees, surrounded by brown-gray trunks and green foliage (Cramp 1985). It usually should be more conspicuous than female Blackbirds; a cryptic plumage in tree-climbing birds would be expected to be similar to that of treecreepers (Certhiidae and Climacteriidae), woodcreepers (Dendrocolaptidae), some ovenbirds (Furnariidae), and some apparently cryptic woodpeckers (Short 1982).

Why should birds of prey avoid the Great Spotted Woodpecker?—There are at least five reasons for why the diurnal birds of prey (especially Goshawks) avoided the Great Spotted Woodpecker. First, predators may avoid prey that they have not earlier seen or caught (Curio 1976, Smith 1980, Schlenoff 1984, Götmark 1994b). It seems unlikely that the woodpecker was a novelty for hawks. Both woodpeckers and Blackbirds are relatively common, highly vocal birds, nesting in densities of at least 1 pair/km^2 in woodland (Cramp 1985, 1988). Both species are preyed upon by Goshawks (Höglund 1964, Opdam et al. 1977, Cramp and Simmons 1980), as well as Sparrowhawks (Opdam 1978). Most attacking Goshawks were juveniles that should have seen woodpeckers and Blackbirds during the approximately three months that they had been hunting for themselves.

Second, woodpeckers might be distasteful and avoided through learned or innate responses in predators (Cott 1947, Smith 1975, Guilford 1990b). However, the feeding test with falcons did not support this explanation. As palatability of birds may vary seasonally (Cott 1947), additional tests are needed to evaluate seasonal change in palatability (the specimens we used were from different seasons).

Third, woodpeckers might be aggressive and able to defend themselves with their strong bill. Fourth, woodpeckers might often escape predators by being vigilant and jumping to the other side of trunks (Cramp 1988, Lima 1992), or by being agile in flight (the Great Spotted Woodpecker had lower wing loading than the Blackbird). Birds foraging on the ground, such as thrushes, may also be easier to catch than tree-climbing birds (Selås 1993). Finally, the Blackbird is about four or five times as common as the woodpecker in southern Sweden (Ulfstrand and Högstedt 1976). If predation is frequency dependent and higher on more common prey (Murdoch and Oaten 1975, Allen 1988), hawks are expected to prefer attacking Blackbirds.

Future studies.—One possibility is that *Accipiter* hawks tend to avoid all woodpecker species due to, for instance, the woodpeckers' strong bill, or their behavior. As there also are cryptically colored woodpeckers (Short 1982), the shape of the species, and not their coloration, might deter predators (J. A. Endler pers. comm.). In the autumn of 1992, we examined this by exposing normal and dull Great Spotted Woodpecker mounts in the study area (the later ones made brown on upper parts by bleaching and painting). We recorded about as many attacks on dull mounts (25; at least 10 by hawks) as on normal mounts (23; at least 10 by hawks), suggesting that shape per se might deter predators. However, the result is inconclusive; there are no brown-colored woodpeckers in Europe, and the dull mounts may be attacked infrequently due to a novelty effect (Schlenoff 1984, and references therein). In future studies, one should compare predation risk for conspicuous and (real) cryptic woodpecker species that occur in the same area.

The European woodpeckers are all black-and-white or black, except for two green and presumably cryptic *Picus* species, which differ from the other species in several respects (for instance, by foraging mostly on the ground). Further studies of these and other conspicuous and cryptic woodpeckers are needed to establish whether contrastingly colored woodpeckers are unprofitable prey for predators, as suggested by our results.

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COLOR PLATE

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