PLUMAGE COLORATION AND CONSPICUOUSNESS IN BIRDS: EXPERIMENTS WITH THE PIED FLYCATCHER

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ABSTRACT.—Hypotheses concerning predation, sexual selection, and communication in birds often assume that individuals differ in conspicuousness. However, few studies have tested this by measuring the response of individuals that receive the signals. We investigated the effect of plumage coloration on conspicuousness by presenting caged Pied Flycatchers (*Ficedula hypoleuca*) to unmated territorial males and measuring the time until a response (either courtship or aggression) from the territorial male was observed. In the first experiment, we presented caged males and females at various distances and degrees of habitat openness. Caged birds elicited responses more rapidly in open than in closed habitats, and response time increased with distance. Black-and-white-colored males seemed to trigger a response more rapidly than brown-colored females, at least in open habitats. In the second experiment, we presented bright-colored males, dull males, and bright-painted dull males. All trials were made at the same distance. Caged birds again elicited more rapid responses in open than in closed habitats. Bright-colored males seemed to trigger a response more quickly than dull-colored males, but only in closed habitats. Painted birds elicited response times intermediate to those of bright and dull males. The difference in interaction between color and habitat in the two experiments is difficult to explain but may have been caused by differences in background related to seasonal development of vegetation. One possible problem with experiments on conspicuousness is that the response may be delayed after the receiver has detected the signal. Field observations of the behavior of territorial birds suggested that this probably did not confound the results of our study. Thus, the results support the intuitive but previously untested hypothesis that a bright and contrasting coloration makes birds more conspicuous to conspecifics. *Received 30 December 1995, accepted 10 April 1996.*

GREAT VARIATION exists in animal coloration both among and within species. This may have evolved in response to predation (Cott 1940; Baker and Parker 1979; Harvey and Paxton 1981; Guilford 1990; Endler 1991; Dumbacher et al. 1992; Götmark 1992, 1993, 1995), sexual selection (Hamilton and Zuk 1982, Parker 1983, Hill 1991, Sætre et al. 1994; review in Andersson 1994), intraspecific communication (Rohwer 1975, 1982; Whitfield 1986; Slagsvold and Lifjeld 1988; Butcher and Rohwer 1989), or for species recognition (Rowland 1979, Endler 1983, Andersson 1994). Several of these hypotheses assume that an individual with bright or contrasting coloration is conspicuous (i.e. more easily discovered) than one with a dull and cryptic coloration (Cott 1940, Parker 1983, Slagsvold and Lifjeld 1988, Butcher and Rohwer 1989, Endler 1991).

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Testing whether various plumage colors and patterns differ in conspicuousness is a difficult task. Birds of different color may differ in detectability to humans (Götmark and Unger 1994, Götmark and Hohlfält 1995), but bird vision is different from and perhaps better than that of humans (Goldsmith 1990). Ideally, response by receivers of the signal (e.g. color), such as a conspecific or a predator, should be measured (Bennett et al. 1994). Experiments also must be designed to ensure that a response can be observed once the subject has received the signal.

Pied Flycatchers (*Ficedula hypoleuca*) vary in plumage color. Males range from black-and-white (i.e. "bright") to brown (i.e. "dull"), whereas all females are brown (Drost 1936). Males benefit from a bright plumage because they are preferred by females as mates (Sætre et al. 1994), but bright males seem to pay a cost in terms of a higher predation risk (Slagsvold et al. 1995; but see Götmark 1992, 1993, 1995). The benefit of bright plumage may increase if bright individuals are more easily discovered by intruding males and prospecting females (Slagsvold and Lifjeld 1988). However, the cost

of bright plumage may increase at the same time if bright males also are discovered more easily by predators. An unresolved issue is whether plumage color actually influences conspicuousness to other birds.

The purpose of this study was to test whether bright and dull Pied Flycatchers differ in conspicuousness to conspecifics. We tested this by measuring the elapsed time before wild males responded to caged birds of different colors. In addition, we varied distance between sender and receiver of signals and habitat openness to see whether these factors affected the time to response.

An important question is whether response time really reflects the time it takes the receiver to detect the signal. A receiver could delay a response after detecting a signal. In order to address this question we also examined the behavior of the receivers after they had responded to caged birds. We predicted that if a signal is responded to immediately, then intensity of the response should not vary with habitat or distance. However, if response intensity decreases with decreasing habitat openness or longer distances, this could indicate that the receiver of the signal also may have delayed the response time.

STUDY AREA AND METHODS

Study area.—The study was done in two woodland areas (Sinober and Brenna plots) near Oslo in southeastern Norway during the breeding seasons of 1991 and 1993. The study areas consisted of a mixture of deciduous and coniferous forest of varying degrees of openness. Only males were tested, and they were unmated and defended one or more nest boxes. If a male defended more than one nest box, the trial was done at the preferred nest box of that male as judged by daily observations.

Caged birds.—To test the influence of plumage color, we presented Pied Flycatchers in a wire netting cage (24 × 33 × 35 cm; netting diameter 1.6 mm, spacing 1.3 cm) at varying distances from a nest box and recorded the time elapsing until response by the resident male. In 1991, two different males, both of color score 3 (Drost 1936), and two different females were used in the cage. The Drost color score classifies male plumage color on a scale from 1 (bright) to 7 (dull). Males with scores of 1–3 can be described as bright with contrasting black-and-white plumage, whereas males with scores 5–7 are dull brownish and female-like. In 1993, two bright males (both of color score 1.5) and two dull males (color scores 5 and 7) were presented. In addition, we presented two males that

originally had a dull plumage (color scores 5 and 6.5) but were dyed black with Nyanzol dissolved in 10% hydrogen peroxide in order to resemble bright males. The painting made brown parts of the plumage black, but because the whitish patches of dull males are not as large and pure white as those of bright males, the black-painted males had less contrasting plumage than naturally bright males.

The 10 caged birds were captured shortly after arrival on the breeding areas. They were held in captivity during the period of presentations and released afterwards. During most of the time in captivity, the birds were kept in wooden cages with a front of wire netting, and they were given unlimited access to mealworms and water. The birds were put in the wire netting cages during presentations and were provided with mealworms. During presentations they behaved calmly and gave no calls but moved around in the cage. As far as we could judge, all birds behaved similarly in the cage.

Presentations.—The cage was fixed to the trunk of a tree about 1.5 m above the ground and was covered with a blanket connected to a string. The observer was positioned at a distance of about 20 m from both the cage and the nest box of the male to be tested. After fixing the cage in place, the observer waited at least 3 min before starting the experiment by pulling the string and exposing the cage. We required that the test male was in normal song activity and close to the nest box (less than about 10 m away) for the experiment to start. The time elapsing until the male responded to the caged bird was recorded. Unmated male Pied Flycatchers respond to caged birds with bright plumage (bright males or black-painted birds) with aggressive behaviors that include flying to the cage, whereas they respond to dull birds (females or dull males) with courtship behaviors that include flying to the nest box opening and giving enticing calls (Slagsvold and Sætre 1991, Sætre and Slagsvold 1992). We used either of these two responses as evidence that the male had discovered the caged bird. The duration of each trial was 30 min. If the male had not responded within that time, then we assumed that the caged bird had not been discovered. We excluded trials where other Pied Flycatchers appeared.

In the first experiment (1991), the cage was placed at four different distances from the nest boxes of males (i.e. 5, 10, 20 and 40 m). We used three kinds of habitats that differed in vegetation density in the area between the cage and the nest box: (1) open (cage was fully visible from the nest box with no interfering vegetation); (2) partly open (cage was visible from the nest box but some bushes or trees obstructed the view); and (3) closed (cage was difficult to see from the nest box due to many trees and bushes but could be seen more easily from other directions). In the second experiment (1993), all trials were done at a distance of 10 m from the nest box, and in only two habitats (open or closed). Trials were conducted from 18 May to 17

June 1991, from 0710–1500, and from 1 to 10 June 1993, from 0625–1315. Trials were conducted both in sunshine and in cloudy weather, but not during rain.

Experiment 1 consisted of 85 trials at the nest boxes of 30 different males in the Sinober and Brenna plots. Individual males were tested 1–6 times (median of 3). Resident males tested more than once always were exposed to different combinations of the color (sex) of the caged bird, distance, and habitat, and they were not tested more than once per day. Experiment 2 consisted of 90 trials at the nest boxes of 15 different males in the Brenna plot (all males present). Each male was tested with each of the six different combinations of color (bright, dull, and black-painted) and habitat (open and closed). This design permitted pairwise comparisons of the response of males to each type of presentation. The order of presentations differed among males so that one-third of them were first presented with a bright bird, one-third with a dull bird, and one-third with a black-painted bird. Half of the trials of each color type were first done in open habitat, the other half in closed habitat. Trials alternated between open and closed habitat for each male. Twelve different orders of presentation were used for the 15 males; thus, three orders were used on two males each. The design ensured that all types of presentations would have about an equal probability of being done first, second, and so on in the sequence of six trials for each male. Finally, as in experiment 1, no males were tested more than once per day. Analyses revealed that study area, date, time of day of the trial, order of trial, and the identity of the caged bird had no significant effects in either experiment ($P > 0.11$ in all tests; data not shown).

Response intensity.—To test whether the response time was likely to reflect time to detect the caged bird, we measured the intensity of the response during a 1-min period immediately after the time of response. This was done in 1991 on all trials in the Brenna plot and in trials after 21 May in the Sinober plot. We recorded the time spent on or inside the nest box and the time spent on the cage. The total of these times was used as a measure of response intensity.

Statistical analyses.—We used one-tailed tests because all existing theory predicts that the caged bird should be discovered sooner if it is bright, in open habitat, or at a short distance than if it is dull, in closed habitat, or at a long distance. In tests where the value of the z-statistic is given, negative z-values (and thus low P-values) indicate that the trend was in the predicted direction, and positive z-values (and thus high P-values) indicate that the trend was opposite the predicted direction. All other tests were two-tailed, and this is stated explicitly in every case.

In the 1991 experiment, some males were tested more than once (see above). To avoid pseudoreplication, we also performed the correlation analyses with a reduced sample size, including each male only once for each sex of the caged bird (the first trial).

The use of only a limited number of caged birds in presentations also could be a source of pseudoreplication. We restricted the number of caged birds for ethical reasons, because keeping them in captivity sometimes prevented them from breeding during that year. Using different caged birds in every trial would have required 175 caged birds, whereas we used a total of 10 birds. However, as stated above, there was no evidence that the resident males reacted differently to individual caged birds. Therefore, this kind of pseudoreplication probably did not bias our results.

In the 1991 experiment, we controlled for the effect of habitat when analyzing the effect of distance (and vice versa) by using Kendall partial rank-order correlation (Siegel and Castellan 1988). Although we wished to control for the effect of distance and habitat simultaneously to assess the independent effect of plumage color, no nonparametric test is available for such tests. Instead, we performed a three-factor ANOVA to obtain an idea of the relative effects of plumage color, distance, and habitat on the time to response. Because of unequal sample sizes and differences in distribution of variables, the data violate the assumptions of ANOVA, but they may nonetheless provide some useful insight. To avoid missing cells, the distance variable was grouped into two levels, short (5 and 10 m) and long (20 and 40 m) distance. If the resident male did not respond to the caged bird during the trial (30 min), the time to response was assigned an arbitrary value of 31 min. The time to response was log-transformed to approach a normal distribution. We also performed ANOVAs with arbitrary values of 60 min instead of 31 min for trials with no response, but the results were similar. ANOVAs using each male only once (to avoid pseudoreplication) against caged males and females, respectively, produced results similar to the total data set.

RESULTS

RESPONSE INTENSITY

In the 1991 experiment, the response intensity of resident males to caged males was unaffected by both habitat (Kendall partial rank-order correlation, $T_p = -0.05$, $n = 21$, $P > 0.25$; distance held constant) and distance ($T_p = 0.07$, $n = 21$, $P > 0.25$; habitat held constant). When the caged bird was a female, habitat again had no effect on response intensity ($T_p = -0.02$, $n = 35$, $P > 0.25$; distance held constant), whereas response intensity decreased with distance ($T_p = -0.27$, $n = 35$, $P = 0.01$; habitat held constant). This suggests that response time reflects detection time.
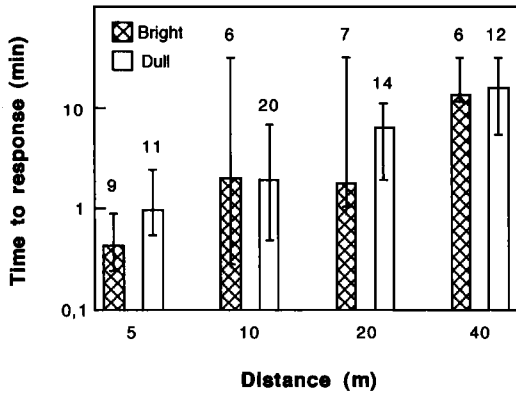
FIG. 1. Time (logarithmic scale) elapsing until response to the caged bird by resident male Pied Flycatchers in relation to distance between the caged bird and the nest box of the male, and the plumage color of the caged bird (bright male or dull female). Bars indicate median values, lines the 25–75% interval. Trials in which there was no response to the caged bird were assigned a value of 31 min. The upper 75% value for caged males at 10, 20 and 40 m distance, and for females at 40 m, was 31 min (i.e. no response). Numbers at top indicate sample sizes. Data from the 1991 experiment.
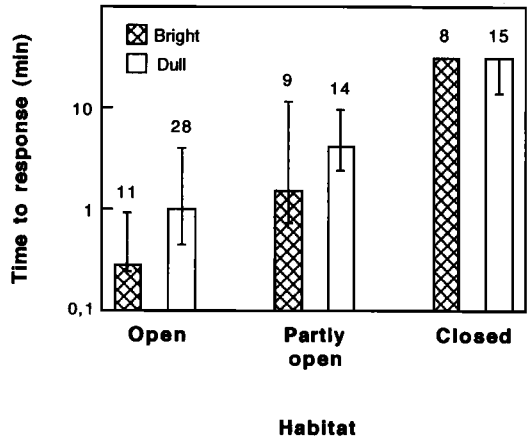
FIG. 2. Time (logarithmic scale) elapsing until response to the caged bird by resident male Pied Flycatchers in relation to habitat and the plumage color of the caged bird (bright male or dull female). Bars indicate median values, lines the 25–75% interval. Trials in which there was no response to the caged bird were assigned a value of 31 min. The median time was 31 min (i.e. no response) for both colors in the closed habitat. Numbers at top indicate sample sizes. Data from the 1991 experiment.

EFFECT OF DISTANCE AND HABITAT

Experiment 1.—Both distance and habitat had significant effects on response times in 1991 trials with male and female caged birds. Response times were quicker when the caged bird was presented closer to the nest box than when farther away (Kendall rank-order correlation, $T = 0.42$, $n = 85$, $P < 0.0001$; Fig. 1), and when it was in open versus closed habitats ($T = 0.59$, $n = 85$, $P < 0.0001$; Fig. 2). Distance was still significant when controlling for habitat openness (Kendall partial rank-order correlation, $T_p = 0.24$, $n = 85$, $P < 0.001$), and the effect of habitat openness was still very strong when controlling for distance ($T_p = 0.51$, $n = 85$, $P < 0.001$). Furthermore, we analyzed the trials with male and female caged birds separately to control for the effect of color in addition to habitat or distance. The effects of distance (caged males: $T_p = 0.22$, $n = 28$, $P < 0.05$; caged females: $T_p = 0.24$, $n = 57$, $P < 0.01$) and habitat (caged males: $T_p = 0.65$, $n = 28$, $P < 0.001$; caged females: $T_p = 0.47$, $n = 57$, $P < 0.001$) were significant for each sex.

Because some males were tested more than once, we analyzed the data in two additional ways to avoid pseudoreplication. First, we performed the correlation analyses with a reduced sample size, including each male only once for each sex of the caged bird. The results were similar to those with full sample size (data not shown). Second, we compared the responses of males that were tested at least twice in one kind of habitat or at one distance, and with the same sex of the caged bird in both trials. Response times were fastest for the shortest distance in 12 of 12 males (trials in the same kind of habitat; Wilcoxon matched-pairs signed-ranks test, $z = -3.06$, $P = 0.001$). Response times also were more rapid in the most open habitat in five of six males (trials at the same distance; $z = -1.57$, $P = 0.058$, same test). In conclusion, analyses showed that both habitat and distance had independent effects on the time elapsing until resident males responded to a caged bird.

Experiment 2.—Response time to a caged bird was again more rapid in open than closed habitats in 1993 trials with only males (bright, dull, and black-painted; Fig. 3). Response times were faster in open than in closed habitat for 12 of 15 males tested on bright males (Wilcoxon matched-pairs signed-ranks test, $z = -2.33$, $P = 0.010$), 13 of 15 males tested on dull males ($z = -2.39$, $P = 0.008$), and 13 of 15 males tested on black-painted dull males ($z = -2.56$, $P = 0.005$). Distance did not vary in this experiment.

EFFECT OF PLUMAGE COLOR

Experiment 1.—We compared response times when the caged bird was a bright male versus a dull female. The color of the caged bird had no effect (Mann-Whitney U-test, $z = -0.99$, $n = 85$, $P = 0.16$). Color still had no significant effect when we analyzed the data separately for each distance (5 m: $z = -1.64$, $n = 20$, $P = 0.051$; 10 m: $z = 0.03$, $n = 26$, $P = 0.51$; 20 m: $z = -0.15$, $n = 21$, $P = 0.44$; 40 m: $z = -0.10$, $n = 18$, $P = 0.46$; Fig. 1). However, an interaction between habitat openness and the color of the caged bird seemed apparent (Fig. 2). Bright-colored males elicited more rapid responses than did dull-colored females in open habitat ($z = -2.58$, $n = 39$, $P = 0.005$) but not in partly open habitat ($z = -1.04$, $n = 23$, $P = 0.15$) or in closed habitats ($z = 1.44$, $n = 23$, $P = 0.93$). Splitting of data to perform tests of each combination of distance and habitat was not possible because sample sizes became too small.

The data were further analyzed by using each male tested only once for each sex of the caged bird in order to avoid pseudoreplication. The results were similar to those with full sample size (data not shown). Only four cases were available where trials were made with both male and female caged birds at the same distance in the same habitat with the same test male. Test males responded quicker to caged males in two cases and to caged females in the other two cases.

An ANOVA (see Methods) showed that the time elapsing until the resident male responded to the caged bird was most strongly influenced by the kind of habitat ($F = 35.9$, df = 2 and 73, $P < 0.0001$). Bright males elicited faster responses than dull females ($F = 5.02$, df = 1 and 73, $P = 0.014$), indicating an independent effect of the color of the caged bird. Distance also had a significant independent effect ($F = 3.75$, df = 1 and 73, $P = 0.029$). The ANOVA also suggested that there was an interaction between habitat and plumage color ($F = 3.59$, df = 2 and 73, $P = 0.017$). Thus, the ANOVA supported the conclusions from the nonparametric analyses.

Experiment 2.—In this experiment, the effect of plumage color on response time was investigated by pairwise comparisons. Bright males elicited quicker responses than dull males by 13 of 15 males tested in the closed habitat (Wilcoxon matched-pairs signed-ranks test, $z = -2.61$, $P = 0.005$), but this was not the case in
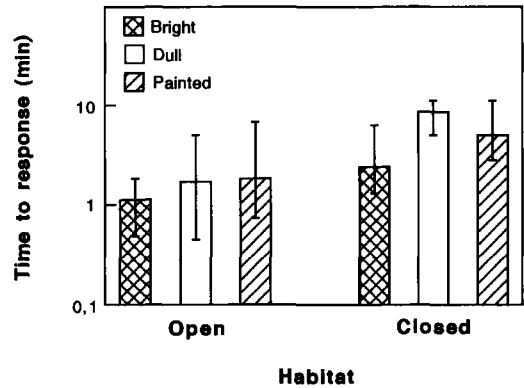

FIG. 3. Time (logarithmic scale) elapsing until response to the caged bird by resident male Pied Flycatchers ($n = 15$ for each type of presentation) in relation to habitat and the plumage color of the caged bird (bright male, dull male, or black-painted dull male). Bars indicate median values, lines the 25–75% interval. Data from the 1993 experiment.

the open habitat (only 8 of 15 males responded to the bright male sooner; $z = -0.80$, $P = 0.21$; Fig. 3).

Black-painted dull males were expected to be discovered more rapidly than dull males. This was the case in 10 of 15 comparisons in the closed habitat (Wilcoxon matched-pairs signed-ranks test, $z = -1.42$, $P = 0.078$) but in only 6 of 15 comparisons in the open habitat ($z = 0.23$, $P = 0.59$; Fig. 3). We expected that painted males would take somewhat longer than bright males to be discovered because painted males had less contrast in their plumage. Response time to bright males was faster for 10 of 15 males in closed habitat ($z = -2.33$, $P = 0.010$) and for 11 of 15 males in open habitat ($z = -2.22$, $P = 0.013$; Fig. 3).

DISCUSSION

Animal senses differ markedly between different systematic groups. For example, mammals and birds exhibit clear differences in vision (Goldsmith 1990). In order to assess the effect of distance, habitat, and other factors on conspicuousness, responses of the actual receivers of the signal must be measured, and tests must reflect the range of variation that is relevant to the receiver (Bennett et al. 1994).

Conspicuousness or motivation?—We attempted to study how distance, habitat, and plumage color influenced conspicuousness of Pied Fly-

catchers to conspecifics. To assess conspicuous-ness we recorded how quickly the caged birds were detected. We used the first observable response (courtship or aggression) as evidence that the caged bird had been discovered, but such responses do not necessarily correspond to the actual time that the resident male detected the caged bird. A receiver of a signal could delay the response for a variety of reasons. However, there are two lines of evidence that lead us to believe that using the time of response as a measure of the time of detection is reasonable.

First, field observations of resident males during trials suggested that they often first responded after having moved to a position where the caged bird was easier to see, and then the response followed almost immediately. It was quite rare that a resident male responded after having perched in one place for some time. However, we did not record and quantify this systematically, which should be done in future studies.

Second, the results showed that the response intensity toward caged males was not related to distance or habitat, which might have been expected if motivation differed. The results concerning response intensity toward caged females showed that habitat had no effect, whereas response intensity decreased with distance. Thus, the effect of distance on time to response with caged females may have been caused by a low motivation to respond to females at long distances.

It is more difficult to assess whether the receiver's motivation to respond varied with plumage color of the caged bird. Resident males respond to bright birds with aggression, even if they are black-painted females, whereas dull birds are treated as females and, hence, are courted, even when they are males (Slagsvold and Sætre 1991, Sætre and Slagsvold 1992). Thus, differences in response in relation to color could be caused by differences in motivation to respond to a bird that is perceived as a male versus a bird that is perceived as a female. We cannot completely rule out the possibility that it is important to respond more quickly to an intruder of one sex than the other. However, field observations suggested that responses to all types of caged birds were rapid and strong once the test male was in a position to discover the caged bird. Furthermore, it is difficult to understand why a territorial, unmated male

should delay a response to either sex. Birds perceived as females should be courted immediately, whereas birds perceived as intruding males should be chased away as soon as possible. If anything, a prospecting female might be more important for male fitness than a male intruder. The female may become the mate of the male, whereas intruding males are rarely able to displace a resident male. If males are more motivated to respond to caged females and therefore delay responses to caged males, then females should be "discovered" sooner than males. The opposite was found in the present study, however. In conclusion, we think it is unlikely that the results of the present study were biased by variation in motivation to respond.

Effect of distance and habitat.—The results appeared to confirm the prediction that distance and habitat affected conspicuousness to conspecifics; birds responded faster in more open habitat and when caged birds were placed at closer distances. These may seem to be obvious results, but such effects nevertheless need to be verified experimentally. The results indicated that the absolute values of differences were rather large and may have important consequences for several aspects of avian ecology and behavior (see below). Furthermore, the demonstration of predicted effects of distance and habitat suggests that the experimental design worked and should be appropriate for testing the hypothesis that plumage color affects conspicuousness.

Effect of plumage color.—In 1991, bright individuals were discovered sooner than dull individuals, at least in open habitat. Presentation of a bright male and a dull female to test the effect of plumage color might be considered ambiguous because differences in responses could be an effect of sex rather than color. However, previous studies have shown that plumage color functions as a cue for sex determination (Slagsvold and Sætre 1991, Sætre and Slagsvold 1992). Territorial males respond to both females and dull males with courtship, whereas bright males, painted females, and painted dull males are responded to with aggression. Thus, differences in response probably are an effect of color, not of the real sex of the caged bird.

Even so, we used only caged males in the 1993 experiment to avoid possible sex differences in

the behavior of the caged bird. We used both bright and dull males, and in addition used a black-painted dull male to control for any behavioral differences between bright and dull males. The results showed that bright males elicited faster responses than dull ones. However, in this experiment this difference was evident only in the closed habitat, in contrast to the first experiment where the difference was found only in the open habitat.

The surprising difference in interaction between plumage color and habitat in the two experiments is difficult to explain. One possibility is that there was an interaction between plumage color and the color pattern of the background that had different effects in open and closed habitats. The only obvious difference between the two experiments was in time of season; trials were done on average 10 days earlier in 1991 than in 1993. In addition, the seasonal development of the vegetation was at least one week later in 1991 than in 1993 because of very low temperatures in the end of April and in May. Therefore, trials done in 1991 were more against a background of dead leaves on the ground and naked branches and tree trunks, at least in the early trials. In contrast, most trials done in 1993 were against a predominantly green background; the leaves of the trees were well developed and the ground vegetation had emerged. The color pattern of the background is expected to affect the conspicuousness of an individual (Endler 1984, Marchetti 1993, Götmark and Unger 1994, Götmark and Hohlfält 1995) and may have played a role in our experiments, though we did not quantify the background coloration.

Nevertheless, in both experiments individuals with a bright plumage color had an increased conspicuousness relative to dull individuals. Another study of detectability of Pied Flycatchers with humans as observers (Götmark and Hohlfält 1995) showed that humans detected mounts of male Pied Flycatchers more rapidly than mounts of females when mounts were placed on the ground, but not when they were placed in trees. Götmark and Hohlfält (1995) suggested that the black-and-white plumage of males are an example of disruptive coloration that makes males difficult to see against a background of contrasting patches of light and shadow in trees. Further studies are needed to test whether conspicuousness to Pied

Flycatchers themselves depends on whether an individual is on the ground or in a tree.

Implications of differential conspicuousness in relation to color.—In birds, brightly colored males seem to be at an advantage relative to dull males because they are preferred by females as mates (Hill 1991, Sætre et al. 1994). However, females only visit a restricted subset of males in an area (Bensch and Hasselquist 1992, Dale et al. 1992). Males will therefore benefit from any character that increases their chances of being discovered by females (Parker 1983). Song is known to attract females (Eriksson and Wallin 1986) and may be the most important means for males of signaling their presence to females. However, a bright plumage color also may help to increase detectability as shown by the present study, though the relative importance may be small compared with song. This provides a mechanism for the evolution of bright coloration through intersexual selection even in species where females do not prefer bright males (Parker 1983).

Males also may benefit from a bright plumage color in the context of territory defense because the bright plumage may signal the presence of territory owners. This would be advantageous if intruders often retreat once they discover that a territory is already occupied (Slagsvold and Lifjeld 1988). In contests over territory ownership, residents often will have an advantage (Maynard Smith and Parker 1976), and owners may therefore often avoid conflicts simply by signaling their presence to intruders.

The results also may have implications for the relation between plumage coloration and predation. Slagsvold et al. (1995) found that among Pied Flycatchers, predation risk from Eurasian Sparrowhawks (*Accipiter nisus*) is highest on bright males. This makes sense if a bright plumage increases conspicuousness to the sparrowhawk as well as to conspecifics. Bright males may suffer more predation simply because they are more easily detected. A rigorous test of this hypothesis should measure how quickly the sparrowhawk itself discovers bright and dull males. However, studies with stuffed Pied Flycatchers showed that sparrowhawks and other predators attack dull mounts more often than bright ones (Götmark 1992, 1993, 1995), as suggested by the unprofitable prey hypothesis (Baker and Parker 1979). In these experiments, the bright and dull models were placed on exposed

sites and/or near each other so that the predator may have discovered both models very easily and almost simultaneously (see Götmark 1995 for alternative interpretations of his experiments). Thus, it is still possible that live bright males are more conspicuous to sparrowhawks than are dull males under natural conditions, but this requires further study.

In conclusion, the results of our study suggest that a bright and contrasting coloration increases conspicuousness to conspecifics. This conclusion has implications for the evolution of bright plumage and/or sexual dichromatism in relation to mate attraction, territory defense, and perhaps predation. However, we need more detailed studies to be able to explain the difference in interaction between color and habitat observed in the two experiments. There also is a need for similar studies using a predator such as the Eurasian Sparrowhawk as the receiver of the signal.

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