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Coloration in New World orioles

1. Tests of predation-related hypotheses

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Summary. Although sexual dichromatism in birds is usually ascribed to sexual selection, some workers argue that avian coloration is better explained by predation-related selection pressures. Supporting evidence for these latter hypotheses comes primarily from broad interspecific comparisons, which can be biased by a variety of factors. This study examines the predation-based hypotheses of Baker and Parker (1979), particularly the Predator Deflection Hypothesis, with reference to two closely-related oriole species: *Icterus parisorum*, which is dichromatic, and *I. gularis*, in which both sexes are brightly coloured. To test the prediction that bright coloration serves to divert the attention of predators away from cryptic young, rates of predation on nests of conspicuous (2 years of age or older) and dull-coloured (first-year). *I. parisorum* males were compared. The results showed equal predation on the young of males in both age/plumage classes. The Predator Deflection Hypothesis also predicts that, once a predator has been detected, brightly-coloured birds should attempt to distract it, whereas cryptic individuals should not. Tests using models of avian predators showed that this was not the case: cryptic *I. parisorum* females responded as aggressively toward the model as did conspicuous conspecific males. The same was true for *I. gularis*. Overall, the results did not support the idea that bright coloration has evolved in response to predation pressure in these species.

Introduction

The evolution of bird coloration

Sexual dimorphism, and specifically, sexual dichromatism, has long been of interest to ornithologists. Following Darwin (1871), most work has suggested that sexual colour and pattern differences in birds are related primarily to sexual selection: that the brightly-coloured sex (usually the male) owes its conspicuous appearance mainly to intrasexual and/or epigamic selection. Cryptic coloration is usually ascribed to a lack or reduction of such sexual selection pressures, which then allows selection for predator avoidance to predominate.

Recently, however, Baker and Parker (1979) (see also Baker and Hounsome 1983; Baker 1985; Baker and Bibby 1987) have advanced the idea that bird coloration – conspicuous as well as cryptic – has "evolved almost entirely in response to predation-based selection pressures ...not... in response to sexual selection pressures" (Baker and Parker 1979, p. 65). Developing this idea, they have proposed several different predation-related hypotheses to account for the evolution of both conspicuous and cryptic plumage and, therefore, for differences among species in the extent of sexual dichromatism. In this paper, I examine the relevance of these hypotheses to an explanation for the bright coloration – and variance in sexual dichromatism – characteristic of species in the avian genus *Icterus* (the New World orioles).

Baker and Parker are careful to describe the conditions or assumptions under which each of their several predation-related hypotheses are likely to apply. Consideration of these limitations reveals that in fact, most of their hypotheses are not relevant to the many passerine species (including orioles), (1) that are not noxious in some way (and whose bright coloration cannot therefore be aposematic), (2) whose conspicuous colors are broadly distributed over the body and always exposed (i.e., do not conform to the pattern Baker and Parker associate with "flash coloration", which is displayed only when predators are nearby, in order to confuse them), and (3) that exhibit biparental care. As Baker and Parker note, their most favoured hypotheses, relating to the idea that a brightly-colored bird is advertising its "unprofitability" as a prey item (i.e., its superior escape abilities relative to dull-coloured individuals of the same species), most likely apply to species in which the conspicuous parent – usually the male – disperses after mating, leaving only the cryptic parent to rear the young. A strategy of advertising unprofitability, "would be unlikely to evolve where, as a result, it throws extra predation risk onto the eggs, mates, and young of a given conspicuous [bird]" (Baker and Parker 1979, p. 71).

However, an idea proposed by Baker and Parker that *is* applicable to species displaying these characteristics is what they termed the "Predator Deflection Hypothesis" (later called the "Decoy" hypothesis [Baker and Bibby 1987]). By this they suggest that the conspicuous appearance of some individuals – usually males – actually serves to attract the attention of predators, and to thereby draw it away from more cryptically coloured birds – usually females and/or young. In this way, they propose, brightly-coloured plumage may have been selected for as a means of defending, and therefore increasing, a colourful individual's reproductive output. These authors feel that the Predator Deflection Hypothesis may be a "particularly plausible" explanation for the evolution of "sexual dimorphism in many monogamous birds, or polygynous birds where the sexes stay together after mating" (Baker and Parker 1979, p. 75).

The supporting evidence Baker and Parker provide for their various hypotheses comes primarily from a review of the literature on 516 species of western palearctic birds. Using multiple regression, they identify associations between the natural history characteristics (reproductive biology, social behaviour, and feeding ecology) of these taxa, and the colour patterns typical of each. Such analyses, while useful for elaborating general trends, are often complicated by a variety of factors, including scarcity or unreliability of the data on some species. In addition, the use of species as statistically independent units can result in substantial bias if similarities among some taxa are due to homology rather than convergence (Ridley 1983). (Baker and Parker did attempt to test for, and control, bias of this type in their analyses.)

An alternative way of testing such hypotheses is to compare closely related species which differ chiefly with respect the amount of sexual dimorphism they exhibit. Here, I report some results of my comparative field studies on the sexually dichromatic Scott's oriole, *Icterus parisorum*, and the monochromatic (both sexes brightly coloured) Altamira oriole, *I. gularis*. Males of both species, as well as female Altamiras, are strikingly coloured in similar patterns of yellow and black (*I. parisorum*) or orange and black (*I. gularis*) – which are exposed all of the time (i.e., do not comprise flash coloration). Neither species is apparently noxious to predators (Sherrod 1978; Hector 1985), and in both, males remain with their mates throughout the breeding season, providing 40–50% of posthatching parental care (Orians 1985). From among Baker and Parker's several hypotheses, therefore, it is the Predator Deflection Hypothesis that pertains to these orioles, and it is this idea that I examine in more detail below. The relevance of sexual selection theory to the evolution of coloration in this genus will be examined elsewhere.

Tests of the Predator Deflection Hypothesis

Predator deflection may occur, and thus may influence the survival of mates, eggs, or young, either before or after conspicuous individuals have seen a predator. If before, the role of the deflecting bird is essentially passive. Predators may search for, or at least see, brightly-coloured birds more often than they do cryptic individuals, whether or not these birds see them (Curio 1976). This would have the result of protecting cryptic individuals simply by default. Alternatively, the primary advantage of association with a brightly-coloured mate or parent may arise from the ability of this conspicuous individual to distract predators once it has seen them. In this case, it is the active efforts of the brightly-coloured bird to attract the predator's attention that may reduce the threat to mates and offspring.

The importance of passive deflection is difficult to assess without some knowledge of the frequency with which predators detect bright- versus dull-coloured birds. Although conspicuous birds are usually assumed to be more subject to predation than cryptically coloured ones, this is difficult to test. The cause of death of a particular bird is not usually known. This reduces the usefulness of data on mortality *per se* for comparing the effect of predation on cryptic versus conspicuous birds. In addition, a number of confounding variables, including differences in size, behaviour, and habitat preference (existing even between sexes of the same species), make determining the effect of appearance alone difficult. These and other factors, such as variance among the perception capabilities of different types of predators, complicate both intra- and interspecific comparisons of the effect of predation on conspicuous versus cryptic birds (Reid 1984; Baker and Bibby 1987). Direct tests of the operation of passive deflection are therefore difficult.

An indirect test of the Predator Deflection Hypothesis can be made, however, by comparing predation on nestlings that have a brightly-coloured parent to predation on conspecific nestlings which are without a similarly conspicuous parent. Such a test applies to deflection occurring either before or after the predator has been sighted (i.e., to both passive and active deflection. A comparison of this nature is possible using Scott's orioles, which exhibit delayed plumage maturation: in their first potential breeding season, males of this species do not posses the brightly-coloured plumage characteristic of older birds of the same sex, but instead, resemble females, and are thus cryptic in appearance. Although many first-year males do not breed, some do. It is therefore possible to compare, intraspecifically, the effect of predation on the offspring of two dull-coloured parents, with that on the young of conspicuous males. A lower rate of predation on young with a brightly-coloured parent would serve to support the Predator Deflection Hypothesis.

In addition to the above indirect test, the active component of predator deflection can also be examined more directly. If this type of deflection is important in explaining the evolution of colour patterns in these species, there should be a difference between the responses of male and female Scott's orioles to a predator. Specifically, the brightly-coloured males should attempt to attract a predator's attention by distraction displays and/or mobbing, while the cryptic females should not. Conversely, there should be no such difference between the sexes of the monochromatic Altamira oriole. Both should engage equally in predator deflection. This prediction was examined by using predator models to test the responses made by birds of each sex in both species.

Methods

Study species and sites

Scott's orioles were studied on the Black Gap Wildlife Management Area in the Big Bend area of west Texas, in 1982 and 1983. During this period, I captured and banded 118 adult birds, and found and monitored 145 nests, observing 63 of them for a cumulative total of approximately 300 h (a median of 4 h per nest).

I quantitatively described the plumage of each Scott's oriole at the time of banding by assigning scores for each of five body areas. The extent of black in the head area was scored from 0–5 (0 indicating no black and 5 representing the plumage typical of adult males), while the brightness (ranging from brown to fully black) of the back, tail, and wings was scored from 1–3, 1–4, and 1–2, respectively. The brightness (i.e., "tint" as defined by Ridgeway [1912]) of the belly colour (from "washed out" or pallid to vivid orange or yellow) was scored from 1–4. These were then summed to that each individual was represented by a single conspicuousness score in the analyses. Adult males (two years of age or older) all attained the maximum total plumage score of 18, while females and young males achieved scores ranging from 4 to 13. Although male coloration is distributed bimodally, female appearance ranges continuously between the minimum and maximum values. It is not possible, therefore, to determine the age of a particular female; females of all brightness levels mate with males in both age classes. These scores represent my view of conspicuousness, incorporating both colour and contrast. While the exact perceptions of a particular predator may be different, I assume (as do Baker and Parker 1979) that this scale is adequate for comparisons of relative conspicuousness.

I studied Altamira orioles near El Encino, in the state of Tamaulipas, Mexico, during 1984 and 1985, as well as briefly in 1986 on the Santa Ana National Wildlife Refuge, in the Rio Grande Valley of Texas. Altamira orioles are more difficult to capture, and thus to band, than are Scott's orioles. (Their nests are higher off the ground and they engage in less overtly aggressive territorial interactions. It is therefore difficult to either place a net so that it is at the level of a nest, and thus in a usual flight path, or to lure birds into nets by setting up conspecific models that mimic intruders). Their nests, however, are much more widely spaced than those of these congeners, and territorial intrusions are very rare. Even without banding, therefore, it was possible to be sure that the birds being observed in the area of a particular nest were in fact the pair associated with that nest. Although *I. gularis* is an essentially monomorphic species, slight differences did exist between the members of most pairs, either in colour or in idiosyncratic features, which in some cases changed daily (disarrayed or missing feathers, for example). With careful and lengthy observation, it was usually possible to determine the sex of any given bird. An assistant and I found and monitored a total of 33 Altamira oriole nests and spent about 320 h observing this species. (A median of 8 h was spent observing each nest.) Only data on birds of known sex are discussed herein.

Both species are diurnally active residents of relatively open country; deserts in the case of Scott's and scattered trees or woodland edges bordering cultivated fields, pastures, or orchards in the case of Altamiras. Both of these habitats contain several different species of common aerial predators, which I observed being mobbed by both male and female orioles on various occasions.

Predation on nestlings

To compare the effect of predation on the young of first-year male Scott's orioles to that on the young of older conspecific males, I performed a *G*-test, using only data on nests: (1) which were not also used in hawk model tests, or experimentally manipulated in some other way, (2) for which the outcome was known, and (3) which, if they had failed, had done so because of predation (rather than desertion or some other cause; various clues make it possible to determine the cause of failure for almost all nests).

Since in some species, younger birds tend to initiate their nests later in the season than do older individuals (Crawford 1977; Flood 1984), and predation rates may vary over the breeding period (Ricklefs 1969), an additional test was conducted to control for these factors. In addition to the abovementioned criteria, only the first nests of each pair (i.e., not replacement or second nests) were included in this second analysis, and the records for both years were combined. The pertinent data were arrayed in a multidimensional contingency table, and the frequencies of nest success (and predation) that would be expected under all possible conditions of interaction among the classifying variables (time of nest initiation, male age, nest outcome) calculated. These expected frequencies were then compared to the observed data using a goodness-of-fit test based on the log-likelihood ratio, and the results used to determine which model(s) of interaction best explained the observed frequencies. The criterion for "best" in such a log-linear analysis is basically "simplest": the least complex model that provides a fit to the data is the most useful one that is likely to account for the observed distribution of the variable of interest (in this case, the frequencies of success and predation). This type of categorical data analysis, based on a log-linear model, is analogous to analyses of continuous data using linear models, such as those employed in analysis of variance and multiple regression. The details of the mathematical procedures used in log-linear analyses were introduced into the biological literature by Fienberg in 1970, and developed more extensively by Bishop et al. 1975. Texts such as those by Zar (1984) and Sokal and Rohlf (1981) provide an introduction to, and description of, the techniques involved.

Model tests

I used models of avian predators to test the response to a potential predator made by both members of the pair at a given nest. A stuffed and mounted Sharp-shinned Hawk (*Accipiter striatus*) was used for tests on Scott's orioles, whereas a Northern Harrier (*Circus cyaneus*) mount (more closely resembling in size and colour the main predatory hawk species found in my Altamira study area) was used in tests on Altamiras. The models were mounted as if perched on the top of an extensible green pole. Each test was immediately preceded by an hour-long period of general behavioural observations, made from a blind located approximately 30 m from the nest. Tests began after I had set the model in place 5–10 m from a nest (5 m in the majority of cases – only for two very high *I. gularis* nests, was this distance closer to 10 m) and returned to the blind. I then timed and recorded in detail the behaviour of the male and female associated with the nest.

Three response periods, which in most cases overlapped to some extent, were considered for analysis: (1) the first 10 min after initial placement of the model; (2) the first 10 min after the arrival of the first member of the pair, regardless of sex; and (3) the first 10 min after both members of the pair had arrived. Thus, individual tests were of variable length; each was concluded after the male and the female attending a particular nest had been present for at least 10 min. For each of these time periods, the number of times the male at each nest mobbed (swooped at and/or hit) the model was compared to the number of times his mate gave a similar response. I tested a total of 29 pairs of Scott's and 11 pairs of Altamira orioles in this way.

Each of the three periods provided a slightly different view of what was happening at a nest. The record of events occurring during the first 10 min after the model was set indicated how rapidly birds could respond to a predation threat. In some cases, however, neither parent had arrived before the end of 10 min. The use of time period 2 thus allowed me to analyse 10 min of data recorded while at least one individual was present to defend the nest. Finally, use of time period 3 minimized the effect of complicating, possibly random, factors (such as the sex of the parent that had fed the young just before I set up the model) on the difference between male and female response; in this last 10 min block, both members of the pair had equal opportunity to respond and had equal potential to be affected by each other's behaviour. The use of these three time periods (rather than an arbitarily determined, single period) has the advantage of accommodating individual or intersexual variation in arrival time.

Results

Predation on nestlings

Although young male Scott's orioles were, on average, brighter in colour than females (only birds captured and scored in the hand included in analysis, n[females] = 33, n[first-year males] = 47; Mann-Whitney U-Test, $U = 346.5$, $P < 0.05$), there was substantial overlap between the range of plumage scores for these two groups (Fig. 1). The median young male score (10) was still closer to the median female score (6) than it was to the invariant adult male plumage value of 18. Most first-year males could, in fact, be described as cryptic and in this respect were quite different from older males.

The behaviour of first-year males toward their mates and young was similar to that of adult males: males in both age groups perched in the vicinity of their nests for a large portion of the time during incubation, and very occasionally fed incubating females. Males in both groups undertook approximately 50% of the post-hatch parental care, feeding nestlings and removing fecal sacs as often as did females, and later assisting in the

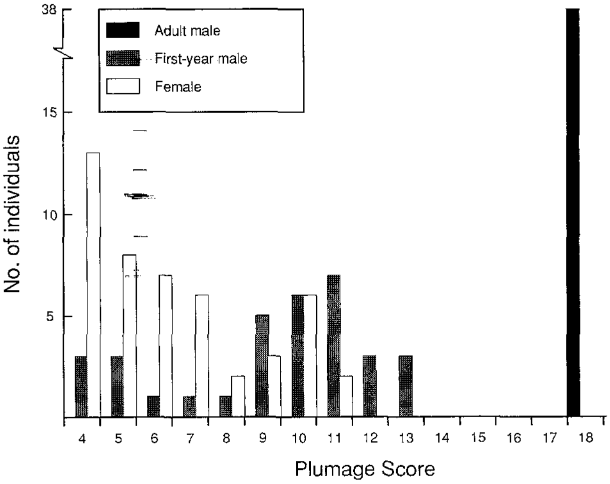

Fig. 1. Total plumage scores for females, adult males, and first-year male Scott's orioles captured and banded in 1982 or 1983

care of fledglings. Thus, any difference between the predation rates of nests of young vs. adult males cannot be ascribed simply to differences in the amount of time they spent near their eggs or young, or in their behaviour at the nest.

Contrary to prediction, there was no significant difference between the predation rates ~~on~~ nests of cryptic vs. conspicuous males in either 1982 or 1983 (Table 1). Analysis of the data arrayed in a three-way contingency table (Table 2) showed that two equally "least complex" models provided a very similar fit to the observed frequencies of success and predation (i.e., the expected frequencies generated by these models were not significantly different from the observed frequencies) (Table 3). The absence of an association between predation rate and male coloration is shown by the lack of an outcome-male age (OM) interaction term in either of these models. Although there was an association between timing of nest initiation and male age (TM), as well as between predation rate and timing (OT), with these factors controlled there was no significant association between the age of a male (i.e., his coloration) and the susceptibility of his nest to predators. This result confirms that of Table 1 and again, contradicts the Predator Deflection Hypothesis.

Table 1. Comparison of the effect of predation on young Scott's orioles with two cryptic parents vs. the effect on those tended by a conspicuous male paired with a cryptic female

Year	Nests of cryptic males		Nests of conspicuous males		G[a]
	No. successful	No. failed due to predation	No. successful	No. failed due to predation	
1982	13	7	16	6	0.290
1983	4	1	21	20	1.610

[a] Test statistic for *G*-test of independence, $G_{\text{crit}(P<0.05)}=3.841$

Table 2. Frequencies of nests belonging to adult and first-year male Scott's orioles that were initiated early or late (i.e., either before or after median nest initiation date) in the breeding season and which either produced fledged young, or failed as a result of predation (Data from 1982 and 1983 combined)

Male age	Timing	Outcome		Total
		Successful	Preyed upon	
Adult	Early	18	4	22
	Late	4	7	11
	Total	22	11	33
First year	Early	5	1	6
	Late	8	5	13
	Total	13	6	19

Table 3. Results of analyses of selected models of interaction among male age (M), outcome of nesting attempt (O), and timing of nest initiation (T). For each tested model, the variables that appear together in parentheses are assumed to be dependent on each other, while their interaction is independent of any other specified interactions or single-factor effects. The log-likelihood ratio provides a goodness-of-fit test comparing the observed frequencies (from Table 2) to the frequencies that would have been expected under each of the listed conditions of interaction. Any *P* values greater than 0.05 signify lack of fit, thus indicating that the proposed model does not explain the observed data. The simplest models (*) that fit the data are those used to explain the observed pattern

Model	*df*	Likelihood ratio (χ^2)	*P*
O, T, M	4	13.78	0.008
(OT)	4	11.42	0.022
(OM)	4	14.07	0.007
(TM)	4	14.07	0.007
O, (TM)*	3	7.71	0.052
T, (OM)	3	13.77	0.003
M, (OT)*	3	7.61	0.055
(OT), (OM)	2	7.59	0.023
(OM), (TM)	2	7.70	0.021
(TM), (OT)	2	1.53	0.464
(OT), (OM), (TM)	1	0.36	0.548

Model tests

Contrary to prediction, males and females of both species were almost always equally aggressive to predator models (Tables 4 and 5). The only significant difference between the sexes was in fact, opposite to what might have been predicted: in time period 3, conspicuously coloured female Altamira orioles responded less aggressively than did their equally-bright mates.

Table 4. Comparison of the responses[a] of male and female Altamira orioles to a hawk model in each of three test periods

Time period	*n*	Mean male response	Mean female response	*Z*[b]	*P*
1	11	9.9	5.6	−1.481	0.139
2	11	10.1	6.1	−1.362	0.173
3	11	14.7	8.8	−2.548	0.011

[a] Number of times subjects swooped at or hit model

[b] Statistic for the Wilcoxon matched-pairs signed-rank test

Table 5. Comparison of the response of male and female Scott's orioles to a hawk model in each of three test periods

Time period	*n*	Mean male response	Mean female response	Z^a	*P*
1	29	4.3	2.8	−0.345	0.730
2	29	5.6	4.4	−0.141	0.888
3	29	5.7	4.8	−0.299	0.765

[a] Statistic for the Wilcoxon matched-pairs signed-rank test

In fact, the response of brightly-coloured Altamira females was consistently weaker, in relation to male response, than that of cryptic Scott's oriole females. This trend was consistent across all time periods: averaging the results, the response of Altamira females was only 59% as strong as that of males, whereas the response of female Scott's orioles was 76% as strong as that of their mates. Comparing the two species with respect to the disparity between male and female responses for each pair (i.e., for each pair, a "disparity score" was obtained by subtracting the female response from that of the male) showed that in at least one time period this difference was significant (Mann-Whitney *U* tests: time period 1, $U=103.5$, $P=0.077$; time period 2, $U=104.5$, $P=0.091$; time period 3, $U=72.0$, $P=0.008$). Within-sex, between-species comparisons showed that this relative difference arose because male Altamira Orioles consistently responded more strongly to the predator models that did male Scott's (Mann-Whitney *U* tests: time period 1, $U=81.5$, $P=0.011$; time period 2, $U=99.0$, $P=0.058$; time period 3, $U=74.5$, $P=0.008$). There was no difference between the two species with respect to the strength of female response (Mann-Whitney *U* tests: time period 1, $U=104.0$, $P=0.073$; time period 2, $U=138.5$, $P=0.514$; time period 3, $U=107.0$, $P=0.104$).

Despite the fact that in a few tests the first bird to appear had been present for over 10 min before his or her mate arrived, there was no substantial waning of response; for neither species was there a relationship between order of arrival and strength of response during any test period (i.e., the member of the pair seen first in the area of the nest and model was not necessarily the most or least aggressive) (Wilcoxon matched-pairs signed-ranks test, $P>0.1$ in all cases). During only four tests did orioles other than the male and female of the pair being tested appear; these "trespassers" stayed only briefly and did not assist in mobbing. When not physically engaged in mobbing the model, males and females of both species alarm called, changed perches frequently, and engaged in behaviour generally indicative of agitation. At no time during several hundred hours of observation did an individual of either species perform any other type of specific "distraction display" (feigning injury in an attempt to lead a predator from the nest, for example), than the mobbing described above.

Discussion

The results of these tests do not support the predictions made on the basis of the Predator Deflection Hypothesis. Firstly, the conspicuous coloration of adult male Scott's orioles does not seem to provide an advantage in terms of deterring or deflecting predators – either actively or passively. The young of conspicuous males paired with cryptic females were taken by predators at least as often as those attended by two dull-coloured parents. It is noteworthy that conspicuous males might have been expected to suffer less from nest predation simply because they are older and therefore more experienced at choosing good territories (i.e., those with reduced susceptibility to predation) or otherwise deterring predators. The fact that the rate of nest predation was the same for males in both age groups is thus perhaps doubly surprising – and provides an even stronger refutation of the Predator Deflection Hypothesis.

That the breeding experience of males appears to have little effect on predation rate may be because, as is true of Northern Orioles (*I. galbula* [Flood 1984]), the territories of first-year males are in fact interspersed among those of older males, and are likely little different in terms of quality. In addition, it may be females that choose the actual nest site, a feature which likely determines susceptibility to predation more than does the territory itself. Since some males of a given age are probably paired with females younger than themselves, while others are mated to older birds, any consistent differences between first-year and older males in this respect are unlikely to occur (only approximately one half of the birds breeding in one year return in subsequent seasons, and individuals change mates between years).

The predator deflection hypothesis is also refuted by the responses birds made to the predator models. Overall, cryptically coloured female Scott's orioles were as aggressive toward the model as were their brightly-coloured mates; they did not attempt to hid, but actively alarm called, approached, and frequently mobbed the hawk mount. Similar responses by both sexes to a predator model have also been shown to occur in a closely related species, the dichromatic Northern Oriole, *I. galbula* (Butcher 1984). Males and females of the monochromatic Altamira oriole also behaved similarly toward the model. If, however, the responses of females are viewed relative to those of their mates, the average reaction of brightly-coloured Altamira females was proportionately weaker than that of cryptic Scott's oriole females. (This was due to a stronger response of Altamira males relative to Scott's males, rather than a between-species difference for females). If conspicuous coloration had evolved as a means of deflecting predators, the opposite result would have been expected.

Another factor considered important by Baker and Parker (1979) is the level of experience characteristic of a species' predators. This makes particular sense in terms of the Unprofitable Prey Hypothesis; for bright coloration to the advantageous as a signal of unprofitability, most predators must be experienced – they must have learned from previous attempts that conspicuous birds are difficult to catch and that chasing them is therefore unprofitable. If bright coloration is to be useful as a mechanism for deflecting predators, on the other hand, a predator must not associate conspicuousness with unprofitability – otherwise its attention will not be held and deflected away from more vulnerable birds. Accordingly, Baker and Parker (1979, p. 75) predict that, "for the evolution of [deflection] coloration, either most predators are naive," and have not learned anything about the relative profitability of conspicuous birds, "or most predators are experienced," and have learned that chasing a brightly coloured bird is sufficiently profitable to be favoured.

This concept is important, since it forms a significant point of contrast between the Predator Deflection and Unprofitable Prey Hypotheses. If a predator becomes "trained" to avoid conspicuous birds because it has had little success capturing them (while, at the same time, it has encountered the more cryptically-coloured mates and/or young of these birds, and found them to be profitable prey items), bright coloration cannot come to serve a deflective function. If on the other hand, the predator has had reasonable success capturing conspicuous prey (and probably finds them easier to see) it will chase brightly-coloured individuals, making it possible for a deflection strategy to evolve. Conspicuous individuals do seem to be taken by various bird-eating raptors (the most important predators on adult, and probably nestling, orioles) at least as often as cryptically-coloured birds (Baker and Bibby 1987; Schnell 1958; Meng 1959). Thus, available evidence suggests that the Predator Deflection Hypothesis is a reasonable one, at least for some species.

A basic assumption of the hypothesis is obviously, therefore, that bright plumage attracts the attention of predators; Baker and Parker (1979) suggest that conspicuousness has in fact been selected for as a means of increasing the chances of attracting this attention. If this so, it is perhaps hard to understand why brightly-coloured birds actually go to their nests, since by doing so, they may increase the chance that a predator will discover their nest site and vulnerable young. To some extent, Baker and Parker do recognize and address this issue. Although it is a condition of their Predator Deflection Hypothesis that "males stay in close association with their families," (as opposed to dispersing after mating) Baker and Parker suggest that these males may remain "vigilant at some distance from the nest site (i.e., guarding rather than rearing)" (Baker and Parker 1979, p. 75).

Such a limitation, however, if absolute, would severely restrict the applicability of the Predator Deflection Hypothesis. In their 1969 survey of North American passerines, Verner and Willson noted that of the 115 species for which data on male parental care was available, males feed nestlings in 113 (98%) of them. This includes 84 of 90 dichromatic species and all 33 monochromatic species, many of which can be considered conspicuously coloured. Similarly, of the 110 Central American passerine species not mentioned in Verner and Willson's survey for which Skutch provided such information (Skutch 1954, 1960, 1969), males regularly feed nestlings in 92 (84%) of them. This total includes 35 dichromatic and 57 monochromatic species, in some of which males and females are conspicuously coloured, while in others both sexes are cryptic. Of the 18 species in which males don't feed, 5 are dichromatic and 13 are monochromatic (some bright, some dull-coloured).

It is difficult to detect a pattern in these data that would support the Predator Deflection Hypothesis. Indeed, the data suggest that if the hypothesis can be applied only to species in which males play no role in feeding young, it's significance as a explanation for the evolution of bright coloration in New World birds may be limited. Moreover, since a general lack of any parental care by brightly-coloured birds is a condition for the application of Baker and Parker's Unprofitable Prey Hypotheses, these data seem to weaken the role of predation-related hypotheses in general; it seems unlikely that many – if any – of these brightly coloured birds are noxious (and thus their appearance aposematic), considering the number eaten by various species of New World hawks (Sherrod 1978; Hector 1985; Palmer 1988).

It is important to note, however, that this summary of the extent of male parental care, unlike Baker and Parker's (1979) extensive multiple regression analysis, does not take into account a range of other ecological and behavioural variables. If because of some other factor(s), the advantages associated with advertising unprofitability or deflecting predators are great enough, even males exhibiting parental care may be selected to be conspicuous. Moreover, Baker and Parker (1979), in fact, showed that when other variables (e.g., diet, level of gregariousness, mating system, etc.) are taken into account, for Western Palearctic birds male parental care is significantly associated with a reduction in male conspicuousness. A similar multivariate analysis needs to be done on New World birds before more conclusive remarks can be made about any relationships they may demonstrate between parental care and the relative brightness of male coloration.

Of all Baker and Parker's predation-related hypotheses, the Predator Deflection Hypothesis remains the one most relevant to orioles, since assisting with the feeding of nestlings does not necessarily preclude vigilance, particularly by males during the incubation period. Male Altamira and Scott's orioles, as well as males of other species in the genus, do in fact spend time perched at some distance from the nest, likely "guarding" it, especially while the female is sitting on eggs (Orians 1985). Such behaviour is consistent with the proposed mechanisms of predator deflection. Nevertheless, my results do not support the idea that bright coloration in the genus *Icterus* has evolved in response to predator-related selection pressures. The effect of such pressures (specifically, selection for concealment) on female appearance in dimorphic species is not examined by these data and remains to be investigated, as does the role of sexual selection in the evolution of oriole plumage colour.

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