

# MATE CHOICE IN FEMALE NORTHERN ORIOLES WITH A CONSIDERATION OF THE ROLE OF THE BLACK MALE COLORATION IN FEMALE CHOICE<sup>1</sup>

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**Abstract.** In the Northern Oriole (*Icterus galbula bullockii*), many females visited more than one male before forming a pair bond, but pair formation occurred rapidly, with few displays and little aggression. Most pairs were newly formed each year. Only males advertised for mates, and only males displayed at and chased members of the opposite sex that were not their mates. Females apparently did not discriminate against males whose black coloration had been bleached away. Those bleached males that remained on territory successfully paired and raised young. These results suggest that females do not use the black portion of the male coloration to assess male quality or as an arbitrary badge for female choice. If conspicuous male coloration is important to female mate choice in the Northern Oriole, then mate advertising or invitation-to-promiscuous-copulation may be the function of the coloration.

**Key words:** Sexual selection; pair formation; mate choice; plumage coloration; oriole; *Icterus*; behavior; bleach.

## INTRODUCTION

Like many temperate passerines, the Northern Oriole (*Icterus galbula bullockii*) is migratory, breeding seasonally and forming seasonal, monogamous pairbonds. Like some of these species, Northern Orioles are sexually color dimorphic, with conspicuous adult males and cryptic females. Unlike most of these species, female Northern Orioles often nest outside of male advertising territories (Butcher 1984). These features of breeding biology raise the question of the importance of sexual selection, specifically the importance of mate choice, as an evolutionary force. Does sexual selection act differently on the two sexes? Can sexual differences in sexual selection account for the sexual differences in plumage coloration?

In order to address these questions, I observed the behavior of a number of females from the time they arrived on the breeding grounds until they paired with a male for the breeding season. One of the major color differences between the sexes is the black coloration of male orioles; thus, some of the unpaired males were bleached so that most of their black coloration was removed,

making them look completely orange. I was able to see if females would pair with these males when unpaired control males were still available.

## METHODS

I studied the Northern Oriole at three study sites: at a private campground near Monticello Dam at the head of Lake Berryessa, Winters (Yolo County), California (April 1980-1982); at Oak Creek Wildlife Recreation Area headquarters near Naches (Yakima County), Washington (May 1980, May-July 1982); and at Bridgeport State Park near Chief Joseph Dam, Bridgeport (Okanogan County), Washington (June 1980, May-July 1981). At Winters and Naches, I arrived before all but a few orioles. At Winters, I left after most females had begun to build their nests and after some females had laid eggs. At Naches and Bridgeport, I left after most females had fledged young. I observed 115 pairs of orioles, individually color-marked a total of 170 adult orioles (including both members of 59 pairs), and found 91 nests during the three study seasons at these three study sites. Most orioles were individually color-marked on the day of arrival. Because orioles are site faithful after the day of arrival, I was able to determine the date of arrival for many birds that were banded after arrival.

I followed these color-marked individuals during 280 timed focal animal samples during which I often recorded data on a portable tape recorder.

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Focal samples were done between dawn and noon. During focal samples, the focal individual was in sight from 1 to 63 min (Mode = 10 min, Median = 11, Mean = 15.4). Focal birds were in sight for about one-third of the observation time during these focal samples. At Winters and Naches, I recorded the location of color-marked individuals at least once daily between dawn and noon on a detailed map of the study areas.

In addition to these focal animal samples, I removed the mates of four females and three males to observe and time pair re-formation in intensive focal sampling. Removed birds were sacrificed and either made into mounted study skins for studies of aggression or were donated to the Burke Museum at the University of Washington. The mounted study skins have since been destroyed.

My operational definition of pair formation was the time at which I confirmed mutual following of the male and the female. In only two cases did I see pairs break up after mutual following (out of 59 pairs where both sexes were colormarked and 24 pairs where the female was closely watched from the day she first arrived).

I bleached the black areas of eight adult male orioles using a bleach (Roux Rapid Hair Lightener). Most bleached individuals (and three controls) were anesthetized using a 3:7 combination of Vetalar (ketamine hydrochloride in 100 mg/ml) and Rompun (Xylazine hydrochloride in 20 mg/ml) with a dosage of 0.1 mg/g body weight, following the instructions of a local veterinarian (D. Croft, pers. comm.). As a result of the bleaching, adult males were changed from a contrasting orange-and-black coloration to all-orange (with white wing patches). The bleached males were changed dramatically in coloration, but remained quite conspicuous. All bleaching was done to unmated males before the arrival of the females. In Naches in 1980, the male I had bleached disappeared during the ashfall from the eruption of Mt. St. Helens, as did 13 of the 19 colormarked orioles (Butcher 1981). In Naches in 1982, one of the five bleached males disappeared without making any attempt to establish a territory; two of six control males disappeared at Naches in 1982 in a similar fashion. The other six males (two in California and four in Washington) remained on territory for at least a short time (see Results).

I recorded two displays that occurred during pair formation. The *wing quiver* was primarily a

female display and consisted of a stationary female in relatively horizontal posture quivering her wings. The wing quiver was observed in two contexts: when males and females were together during nestbuilding, presumably as part of a solicitation display, and in border disputes (especially when two pairs were disputing potential nesting sites). The *epigamic bow* was the most intense display of *I. g. bullockii* and the one that made the most dramatic showing of the male's coloration. In this display, the male approached a female, raised his bill to a vertical position, lowered and quivered his wings, raised and fanned his tail, and bowed his body forward (with his bill still up). The epigamic bow (exclusively a male display) was sometimes performed when the male's mate was nearby, but was more commonly performed to a female who was not his mate (Butcher 1984).

## RESULTS

(1) At least some females actively chose among the available males.

I saw 24 females on the morning when they first arrived. Thirteen were seen only with their mates. The other 11 females all visited more than one male before choosing a mate or disappearing from the study site. One way to assess the importance of this apparent female choice is to determine how many males were available at the time each female arrived (Tables I and II). In California, each female had more males from which to choose; but in Washington, there were fewer days when more than one female arrived. When more than one female arrives on a given day, they must compete among themselves for the available males, thus they must rush their decision in order to maximize their chance of mating with the best available male.

(2) Pair formation occurred rapidly, with few displays and little aggression.

Although almost half the females were seen with more than one male, it is not clear what criteria they used for mate choice. Since females frequently nested outside the male's mate advertising territory, territory quality should not be a primary component of female choice. However, few male behaviors were consistently observed that could have been used for mate choice. I saw 24 females on the morning they first arrived. First sightings for 15 of these females ranged in time from 05:40 to 09:40. Twenty-one

TABLE 1. The timing of male and female arrivals in Naches, Washington, early in 1982, and the number of males available from which each female could choose, assuming no females had been removed (Mean = 2; Median = 2).

Arrival	Male	Female	No. of unpaired males
7 May	1 <sup>a</sup>		
11 May	2		
12 May	3, (4) <sup>c</sup>	[1] a, b, c	3
16 May	4	[1]	3
17 May		[1]	2
18 May		(1)	
20 May	5, 6, (7)	1, 2, 3, 4, 5, (6)	3, 2, 1
26 May	7		
28 May		6	1
30 May	8	7	1
31 May	9, 10, 11		
2 June		8	3
3 June		9	2
4 June		10	1
10 June		11	

<sup>a</sup> Each number refers to the arrival of a breeding individual. Resident males and females are numbered in the order of their arrival. A total of 11 pairs were on site on June 10, 1982.

<sup>b</sup> Each of the first three arriving females (in square brackets) was removed prior to the arrival of the next-arriving female.

<sup>c</sup> Parentheses and square brackets denote individuals that appeared for a while, then disappeared. The first three females (in square brackets) were experimentally removed, the female arriving on 18 May (in parentheses) disappeared after being seen for a few hours before she could be removed, and one of the females arriving on 20 May disappeared after being seen for a few hours. The two males (in parentheses) defended a mate advertising space for a few days, then disappeared. (A number of males were banded or seen that did not breed here.)

of the 24 females were paired by 11:00 on the morning they were first seen. Two of the three females that were not paired by 11:00 were seen at the breeding colony for about two hours on one morning, then disappeared; the third split her time between two neighboring males on two consecutive mornings. Thus, natural pair formation is very rapid in this species.

I removed the mate of four females in the morning to observe pair re-formation. Two females had re-paired by the morning after their mates were removed, and one female re-paired on the afternoon of the day after her mate was removed. The fourth female had not re-paired 48 hours after removal, when I left the study site. Thus, pair formation was very rapid for three out of four females whose mate was removed.

I studied the number of displays and the amount of aggression during pair formation in three ways: (a) I recorded all displays performed during the formation of 17 of the 24 pairs seen on their first morning, (b) I looked at the behavior of four females whose mates had been ex-

TABLE 2. The timing of arrival of male and female breeders in Winters, California, 1982, and the number of males available from which each female could choose (Mean = 4.65; Median = 5).

Arrival	Male	Female	No. of unpaired males
24 Mar	1 <sup>a</sup>		
25 Mar	2		
29 Mar	3		
4 Apr		1 <sup>a</sup>	3
5 Apr	4, 5		
6 Apr	6		
7 Apr	7		
8 Apr	8		
9 Apr	9	2	8 <sup>b</sup>
		3	7
		4	6
10 Apr		5	5
12 Apr	10-13	6	8
13 Apr		7	7
		8	6
14 Apr	14-16	9	8
		10	7
15 Apr	17	11	7
16 Apr		12	6
		13	5
		14	4
19 Apr	18-21	15	7
		16	6
		17	5
		18	4
		19	3
		20	2
		21	1
20 Apr	22	22	1
21 Apr	22, 24	23	2
		24	1
22 Apr	25	25	1
26 Apr	26	26	1

<sup>a</sup> Each number refers to the arrival of a breeding individual. Resident males and females are numbered in the order of their arrival. There were a total of 26 pairs on site when we left in 1982.

<sup>b</sup> When more than one female arrived on a particular day, one female was assumed to choose among all the available males; the next, among all but one, etc.

perimentally removed, and (c) I presented mounted, stuffed skins of female orioles to unpaired males and recorded the behavior of the males to the mounts.

Four of the 17 females who were watched during pair formation did wing quiver (usually interpreted as a solicitation display, as described in the Methods) in the presence of their new mate; two of the 17 males performed an epigamic bow (usually a display from a male to a female not his mate, as described in the Methods) in the presence of their new mate.

Nine of the 17 males chased their mates on

the morning they met. Most of this aggression occurred (a) on the days when many birds arrived, and (b) when females visited neighboring males. Male chases of mates may be selectively advantageous because (a) females chased towards the center of the territory might have fewer encounters with neighboring males that could lead to aggression against the female or courtship of the female, (b) females might be selected to remain only with males that chase because chasing might correlate with high interest or good health relative to other males, or (c) chasing might be a quick way of separating females with a low likelihood of pairing from females with a high likelihood of pairing. Neighboring males also chased females on the morning of arrival; males often chased neighboring females during the nestbuilding period as well (see below).

Mutual following, foraging, and quiet sitting were by far the most common behaviors even early on the mornings of female arrival. Males were frequently aggressive to neighboring males. Females frequently wandered outside their mate's territory, thereby inducing male-male aggression and occasionally chases of the female by the neighboring male. Thus, most of the aggression that accompanied pair formation did *not* occur *between* the individuals of the newly-forming pair.

Of the four females whose mate was removed, I was only able to observe the pair formation behavior of one. Two of the females paired with males that had not previously been seen to defend space in the nesting colony; both of these newly-formed pairs were first noticed when they jointly arrived at the colony to carve out a nesting space. Thus, I observed their efforts to obtain a nest site, but only after the pair had formed. The third female remained at her nest, and an unpaired male moved from a nearby territory to her nest site. The only overt intersexual behavior observed on the day this pair formed was a copulation. The fourth female had not re-paired 48 hours after removal, when I left the study site. The rapidity of pair formation of the two pairs that formed out of sight suggests that there could not have been much display or aggression.

I presented a mounted skin of a female oriole to eight unpaired males, all of which were defending a territory and advertising for mates. Only three males responded to these presentations, despite the fact that the five nonresponding males were on their territories for 5–20 min of the 30 min the mounts were up and despite the fact that

the mounts were placed in open and central locations on the male's territory. All three males that responded to the mount did an epigamic bow, two of the three attempted to copulate with the mount, and two of the three displayed aggressively at the mount. My interpretation of the lack of response of the five males is that males apparently do not need to display at females to initiate pair formation. Apparently, females initiate pair formation by approaching and following territorial males.

Thus, I was able to confirm in three ways that pair formation occurs rapidly, with a few epigamic displays and a few aggressive chases.

(3) Most pairs were newly formed each breeding season.

The apparent rapidity of pair formation might be due to pairs from the previous year getting back together. However, like most passerines, Northern Orioles are short-lived. Fifty-four percent (50 of 93) of the adult birds banded in one year returned the next year, pooling all sites and years (range 31%–79%). During the three years of the study, both individuals of 11 colorbanded pairs (out of 26 colorbanded pairs) returned the following year. Of these, three pairs re-formed. Thus, about half the birds failed to return each year; and of those that did return, only about one-third paired with their previous mate. If these figures are representative, then about 84% of returning orioles choose new mates each year and about 91% of all pairs are new each year.

(4) Only males advertised for mates.

On average, adult males arrived ahead of females (Tables I and II). Soon after arrival, adult males began to chatter and sing frequently in a limited area. When females arrived, they paired with males the same morning. When males paired, their song and chatter rates declined immediately (see also Beletsky 1982a re *I. g. galbula*). Females sang and chattered, but never at the rates observed in unpaired males (see also Beletsky 1982b re *I. g. galbula*).

I removed four paired males during the nestbuilding period (three at Winters, California, in 1982 and one at Bridgeport, Washington, in 1981). None of the four females whose mate had been removed advertised for a new mate by increasing song or chatter rates or otherwise behaving conspicuously on territory. However, three of the four females re-paired with a new male within 36 hours of the first mate's removal.

The fourth female remained by her nest and tried to defend it against a pair that built within 2 m. I left California before determining her fate.

(5) Only males chased and displayed at members of the opposite sex that were not their mate.

I recorded 30 chases between females and one or more neighboring or intruding males. Thirteen of the chases occurred during pair formation (1.63 chases per hour of observation) and 14 occurred during nestbuilding (1.09 per hour). Three occurred between the time of pairing and nestbuilding (0.37 per hour). Most of these chases ended out of sight, but some of them ended in a potentially dangerous fight between the male and the female. Chases during the nestbuilding period appeared to be attempts at forced extra-pair copulations.

In 16 cases, I observed a male perform an epigamic bow to a female that was not his mate; in nine of the 16, the female's mate was present during the bow. Two of 18 males performed this display to their newly-arriving mate, and three of eight unpaired males performed this display to a mounted female oriole on their mate advertising territory. Thus, this display is most often performed by a male to a female that is not his mate. It seems to be an invitation to a promiscuous copulation, even though copulation was not seen following the display.

(6) Females do not prefer to pair with black and orange males over bleached orange males.

Four bleached males were defending territories when females arrived in 1982, one in Winters, California, and three in Naches, Washington; all four successfully obtained mates.

One male disappeared until five days after bleaching, when he reappeared in the center of the most densely occupied habitat and immediately attracted a mate. They remained together and built a nest there.

Another male held the largest pre-breeding territory of all Washington males even after he was bleached. A female arriving on 16 May chose this male for a mate; she had three bleached and two unbleached males among which to choose (one of the unbleached males was a new arrival). She was consistently chased by the established unbleached male and this bleached male before choosing the bleached male. This female was removed the same evening. A female arriving on 17 May chose an unbleached male out of the five

males. She was also removed. On 20 May, six females arrived; they had seven males (three bleached and four unbleached) among which to choose. Two of the unbleached males were new arrivals that day, including one male in subadult plumage. All adult males (including three bleached males and three unbleached males) obtained mates; the subadult male did not. This bleached male and the mate he obtained on 20 May nested together and successfully raised young.

A second bleached male in Washington attracted a female on 20 May, the day that the six females arrived together. However, three days later this female deserted him and paired with an unbleached male whose mate disappeared. This bleached male was seen off-and-on with other females. On 2 June, 17 days after arriving on territory, this male finally formed a long-term bond, and the pair successfully raised young.

A third bleached male in Washington attracted a female on 20 May, the day that six females arrived simultaneously. They nested and successfully raised young.

## DISCUSSION

A number of female orioles visited more than one territory before choosing a mate. However, I have no information concerning the criteria females used to decide upon a mate. Territory quality should be unimportant, since females often nested outside the male's mate advertising territory. There were no consistent behaviors that males performed during courtship. All four bleached males that remained on territory eventually attracted a mate; three of the four attracted a mate early in the breeding season, on the same day as the controls. Thus, a fairly dramatic change in coloration did not interfere with the males' ability to attract mates.

The results of the bleaching experiment are consistent with those reported for Common Yellowthroats (*Geothlypis trichas*) (Lewis 1972). In that species, males whose black masks were obscured by yellow paint attracted females on the same schedule as did controls. The results of epaulet-dyeing experiments on male Red-winged Blackbirds (*Agelaius phoeniceus*) were equivocal: Peek (1972) found that males were unable to attract mates until the black epaulet covering was removed; Smith (1972) reported that males that were able to maintain their territories were able

to attract females, although he did not compare harem sizes of the experimental and control males.

When the head feathers of 150 penguins were cut off, these individuals showed impaired pairing success relative to controls (Jouventin 1982). Unfortunately, no behavioral observations were reported, so four possible causes of the impaired pairing success cannot be distinguished: (1) lack of pairing effort by manipulated birds, (2) lack of success in intrasexual aggression over mates, or rejection by prospective mates because of (3) uncertain species identity or (4) insufficient intersexual attraction.

Two major hypotheses might account for female preferences for conspicuous male coloration (Butcher and Rohwer 1989): the mate choice hypothesis (Fisher 1930, 1958; Zahavi 1975; Borgia 1979; Ridley 1981; Hamilton and Zuk 1982; Kirkpatrick 1982) or the mate attraction hypothesis (Parker 1982, 1983). Mate choice implies active comparison of males by females, whereas mate attraction might be a passive phenomenon, with no costs or benefits to females. This study demonstrates active female behavior to allow male comparisons, but suggests that a major color change did not cause females to reject potential mates.

Bleaching the black areas of the male orioles caused a dramatic change in appearance of the experimental birds, but had no measurable effect on mating success. This result casts considerable doubt on the idea that females use the black coloration of male Northern Orioles to glean information concerning genetic quality. If the altered coloration had been natural, it would have been the result of a mutation. Since most mutations are harmful, females, at the very least, should have been suspicious of the experimental males. However, there is no evidence that females treated bleached males any differently from controls. The time of pair formation was identical for the two groups. However, it is possible that a larger sample size would have demonstrated subtle differences in the pairing success of bleached and control males.

Neither the black coloration nor the black and orange contrast could have served as an arbitrary badge for female choice (Kirkpatrick 1982), since males were acceptable as mates even without this badge.

The manipulated orioles were nearly as con-

spicuous after bleaching as before, because the orange colors of the individuals remained. Thus, I have yet to test whether lowered conspicuousness will cause lowered mating success in orioles, as predicted by the mate advertising hypothesis (Parker 1982, 1983). In a future manipulation, the male orioles should be made more cryptic and more female-like, perhaps by the use of a gray, green, or brown hair dye.

Only the black areas of the orioles were manipulated. A future study might concentrate on manipulating the orange coloration. In House Finches, females prefer redder males, and males can be made redder by adding carotene to the diet (G. Hill, pers. comm.). The amount and intensity of orange in adult male Northern Orioles is variable; perhaps this variability has an environmental component like the red of House Finches and/or is subject to female choice.

This study did not consider the ability of bleached males to obtain extra-pair copulations, even though there was evidence that extra-pair copulations may be important in this species. Conspicuous coloration may be especially important to the epigamic bow, which I interpret as an invitation to extra-pair copulation. Coloration may function in the display: (1) to dazzle the female, attracting and holding her attention (Ridley 1981), or (2) to impress the female that (a) the male has the right to display on his territory, or (b) the male is fearless enough to display in front of the female's mate (Borgia 1979). Any future color manipulation should test the relative ability of experimental birds to achieve extra-pair copulations.

In conclusion, the results reported above suggest that at least some female Northern Orioles compare neighboring males and choose among them. However, the criteria of choice are not clear. Apparently, the black coloration of male Northern Orioles does not function as a signal of genetic quality to females since bleached males were acceptable as mates. If coloration is important in the mating behavior of Northern Orioles, then mate advertising or invitation-to-promiscuous-copulation may be the function of the coloration. Further studies will be required to establish either of these functions.

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