

COURTSHIP OF THE AMERICAN REDSTART

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COURTSHIP has been described by Morris (1956b: 261) as "the heterosexual reproductive communication system leading up to the consummatory sexual act," and thus encompasses activities from pair formation through copulation.

Courtship in the American Redstart, *Setophaga ruticilla*, is roughly divided into three periods: pair formation, pre-nest building, and nest building. The behavior during each is described. The causation, function, and derivation of some of the displays are postulated. Definitions of some terms and methods used in analyzing displays are described elsewhere (Ficken, 1962) and generally follow the methods of Tinbergen (1959).

Approximately 12 pairs were studied intensively during the courtship period in the course of three seasons (1957-1959) in Renwick Bird Sanctuary, Ithaca, New York. Individuals were distinguished by differences in color and/or pattern. Many other pairs were studied more casually and a hand-raised male and female were observed in captivity.

AGONISTIC DISPLAYS

Agonistic behavior of the species is discussed in detail elsewhere (Ficken, 1962), but since some intra-pair agonistic displays occur during the courtship period, they are mentioned briefly here.

Song. There are two principal song types, the Accented Ending Song predominating during territory establishment and pair formation and then declining, while the Unaccented Ending Song increases in relative frequency later in the season. Some songs uttered near the female are muted.

Harsh Chip. This is frequently given by the female. When it is uttered slowly the male often approaches; when it is uttered rapidly he retreats.

Zeeep. This flight call is more frequently given by the female and may function in keeping the male informed of her location.

Snarl. This is a threat often given by the female when the male approaches very closely, and frequently precedes her attacks.

Bill Snaps. These sometimes occur as the female lunges at the male.

Circling. A Circling flight with ritualized wing movements is common in encounters between males at boundaries. The male occasionally performs Circlings toward the female (probably indicating a hesitancy to approach) but these lack the ritualized wing movements.

Fights. As in male-male encounters, the male and female strike at each other without contact. Fights occur when the male approaches too closely and are apparently initiated by the female.

Glides. These are performed by the male above or below the female, usually as he flies away from her.

Head Forward Gape. This display is performed more commonly by the female, when the male approaches very closely. Attacks follow if the male does not retreat.

Neck Withdrawn Gape. This display is given only by the male and occurs when he approaches and perches below the female. Unlike the preceding display it rarely leads to attack and is a weaker threat.

Tail Spread. This is a component of many displays but also occurs alone in many different situations, but typically when the birds are somewhat fearful.

DESCRIPTION OF COURTSHIP DISPLAYS

Only those displays which probably express a sexual tendency, i.e., which sometimes precede copulation, are discussed here.

Male displays. There are many variations of male courtship displays, and there are many different display components involved making these the most complex of all the displays of this species.

Some displays show little change in form as the motivation of the animal shifts. These displays tend to evolve a "typical intensity" (Morris, 1957). On the other hand, some displays do not have this all-or-nothing characteristic but are more variable and graded, with many possible combinations of components. Graded displays can convey more subtle motivational shifts than displays with a typical intensity, and in general are more common in aggressive situations (Marler, 1961). However, the courtship displays of the male redstart are graded, probably as a result of the very

TABLE 1
MALE COURTSHIP DISPLAYS

Display number	Fluff	Bow	Tail spread	Wings				Vocalizations		Number of observations
				Out	Up	Alternate wave	Simultaneous wave	Song	Eeeee	
1	X									10
2	X								X	6
3	X							X		1
4	X			X						1
5	X		X			X				2
6	X ¹	X	X							3
7			X			X				1
8			X		X ²					1
9		X	X				X			1
10		X	X							6
11		X	X	X						3
12		X	X			X				1

¹ Only breast feathers fluffed.

² Body tilted.

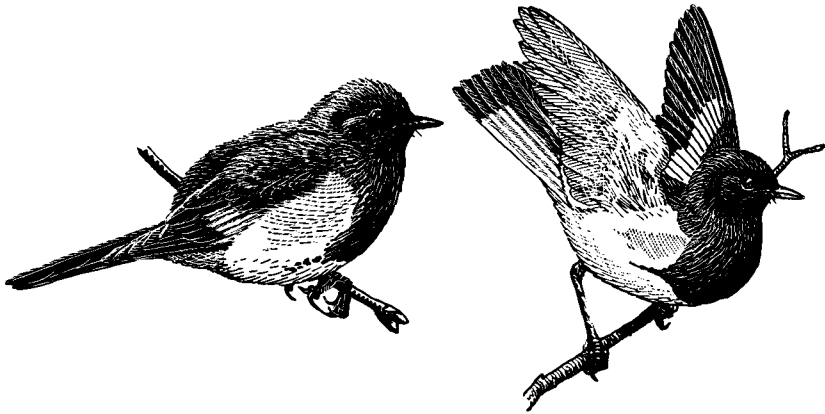


Figure 1. Left. Fluffed posture of male (Display number 1, Table 1). Right. Sleeked posture of male, including bow, tail spread, and wing waving (Display number 9, Table 1). Drawings by William C. Dilger.

complicated shifts of the attack, escape, and sexual tendencies. Agonistic displays of the redstart, on the other hand, are much more simple, possibly because they are reflecting only the attack and escape tendencies.

Table 1 indicates the various combinations of display components and the number of times they were observed.

(1) Feather postures. There are at least two discernible intensities of fluffing of the plumage (for explanation of terms used in the description of feather postures, see Morris, 1956a: 79). The lowest intensity (i.e., least exaggerated) consists of a slight fluffing of the breast and back feathers. The higher intensity includes, in addition, fluffing of the scapulars and head, and the rump feathers are ruffled (Figure 1, left). The head is held in the normal position.

Fluffed displays are sometimes accompanied by tail spreading, wing movements, and bowing (Table 1) and grade into the other, more complex displays. For the sake of convenience in the discussion, the displays are divided into two groups: those involving Fluffing (Nos. 1-6 in Table 1) and those with Sleeked plumage (Nos. 7-12).

(2) Positions of the body. In displays 6, and 9 through 12, the neck is raised above the normal position. In addition, the breast is often lowered in a bow (Figure 1, right). On the one occasion that a male displayed on the ground, his body was markedly tilted sideways.

(3) Tail spread. The tail is always maximally spread and held cocked above the body when tail spreading occurs as a component of courtship displays.

(4) Wing positions. In the wings-out position (Table 1), the wings are

held out from the body slightly but are not shivered or extended. In the wings-up position, the wings are held motionless above the back and may be waved either alternately or simultaneously.

(5) Vocalization. A subdued vocalization resembling the *Eeeee* given during female Soliciting sometimes accompanied Fluffed postures. However, it sometimes occurs in the absence of other display components. On one occasion song accompanied a Fluff.

Many courtship display components are apparently derived from flight intention movements. The tail spread is probably indicative of conflict between a strong sexual tendency and a strong escape tendency (see Ficken, 1962). The bow is probably derived from an upward flight intention movement and resembles the lowering of the breast in preparing to take off to a higher perch. Since it occurs only as a component of courtship displays it probably expresses a strong sexual tendency, indicating a readiness to fly up and mount the female. Wing waving, also confined to courtship displays, probably indicates a strong sexual tendency and may be derived from the balancing movements of copulation.

The male courtship displays, particularly the Fluff, are similar to those of various members of the genus *Dendroica*, as are other behavior patterns (Ficken and Ficken, 1962), indicating, as is suggested by Parkes (1961), that the redstart is probably closely related to this group of warblers.

Mutual display. Bill touching was observed only three times. The male and female touched bills briefly following approach by the male. The tails of both birds were spread.

Female displays. The form of the female precopulatory display, generally referred to as Soliciting, is similar to that described by Andrew (1956: 262) for emberzine finches. It involves a horizontal, crouched body, wing shivering, and often elevation of the tail. A low volume *Eeeee* often accompanies this posture. Rarely, there is a slight tail spread.

PAIR FORMATION

Pair formation is the period from the initial meeting of male and female until the time that a lasting bond is formed. A female never left a male after she once remained for as long as an hour. Apparently the female does not approach many males before acquiring a mate.

Females arrive during the night and usually secure mates by the following morning. Observations were made of several probably initial contacts between males and females. Once a female flew from a distance of about 75 meters into the area of a male's territory where he had just been singing, but he had moved off to a distant end of the territory. The female foraged for about 10 minutes and then left, never to return. Later that day she was with a male on an adjacent territory and became his mate.

This female apparently was attracted by the male's song, since he was probably not visible to her initially.

In perhaps more typical cases the female approaches the male by moving in gradually, often until she reaches the tree where he is singing. The male usually chases her as she flies in circles but the female does not leave the area. She usually Tail Spreads and Harsh Chips after being chased, but soon approaches the male again and is again chased. In one case, as the male was chasing the female, she turned on him and a midair Fight ensued. Fighting, however, is rare during the first day.

In two out of four initial meetings the female remained for the breeding season with the first male met; in two other cases she left. In one of the latter instances, described above, the male and female had no contact, and in the other there were few chases and the male largely ignored the female. This suggests that an aggressive reaction of the male may be necessary to induce the female to remain.

Redstarts are sexually dichromatic, but first-year males (most of which do not breed; Ficken, 1962) resemble the female except for a few black feathers in the region of the head. There are also several behavioral differences between the sexes, which may function in sexual recognition. A male intruder, when chased, usually returns to his own territory immediately, but the female does not go far and often circles back with the male still in pursuit. When a male chases another male, both birds usually stay on a horizontal plane, but a chased female keeps descending until she reaches the ground. Females typically forage at lower elevations than do males.

Males initially react aggressively toward females entering their territories, much as they would to intruding males. Thus there are no special displays associated with pair formation, all of the displays being agonistic and occurring in other situations. This is also true of pair formation in the thrushes studied by Dilger (1956).

Although males react toward females in the same manner as they would toward intruding males, this does not indicate that they do not possess the ability of "sexual recognition." In fact, males later in the season react less aggressively to female than to male intruders, indicating that they do differentiate between the two, at least sometimes.

In some species which show marked sexual dichromatism, the reactions of a male in breeding condition to males and females are different from the beginning of the season on (see Nice, 1943: 200 for examples). In species where the dichromatism is less marked or absent, the same first reaction is often shown to both male and female intruders (Nice, 1943: 200; Dilger, 1956: 344). The strikingly dichromatic redstart, however, acts as do most non-dichromatic species upon initial contact of the sexes.

PRE-NEST BUILDING PERIOD

This period begins when the pair bond is formed and continues until the inception of nest building. The pre-nest building period varies in length among individual females, depending upon their time of arrival. The period may be as long as 60 hours in early-arriving females, and as short as 12 hours in later arrivals.

During this period, the female frequently approaches her mate by flying directly toward him. He usually flees when she is still about a meter away, ending his flight with a Glide. Gliding only occurs during this period and ceases abruptly once nest building commences. The male generally flees when the female approaches. However, the male sometimes flies out at her when she is some distance away. She then flees and he chases her. Initially the female flees when the male is quite far away, but later in the season, only when he is about a meter away.

Occasionally a male swoops at his mate and chases her. She flies progressively lower until she is on the ground. Next, the male lands on her back or pulls at her tail. She struggles and the male always leaves first. Swoops are probably aggressive, but when the female is on the ground in a horizontal posture, he evidently reacts sexually and tries to mount. However, copulation apparently never occurs at this time and the male does not perform the copulatory motor patterns (bringing the tail down or wing fluttering) while on her back. Once a female Solicited after such an encounter, but only after the male had left.

At first the female explores the entire territory. This is the period when the female learns the territorial boundaries and becomes acquainted with all parts of the territory before finally selecting a nest site. She gradually restricts her activities to certain areas. At this time the male starts following her, instead of *vice versa*.

There is individual variation in behavior during pre-nest building. Some males frequently swoop at their mates while others do so very rarely. Some females Chip constantly during their first day on the territory while others are silent except after male attacks. Some females threaten or even Fight with their males; most do not. Despite this variation, the motivation of both birds during this period is generally as follows: the sexual tendencies of both sexes are weak (no courtship displays or copulation attempts), the attack tendency of the male has decreased slightly compared with the pair formation period, and the female's escape tendency is lower than it was initially.

NEST BUILDING PERIOD

Females generally begin nest-site selection shortly after restricting their movements within the territory. Males usually follow their mates closely

TABLE 2
COURTSHIP DISPLAYS AND THEIR ASSOCIATION WITH THE STAGE IN THE NESTING CYCLE

Stage	Type of male display		Female Soliciting
	Fluff	Sleeked	
Site selection	3	0	3
Early nest building	9	2	2
Late nest building	8	8	14

and occasionally some males (three out of eight) tried out sites while their mates were also doing so. The female always approached the site after the male left and performed site "trying" behavior (sitting in the crotch, turning) in the same crotch. However, no female built in a crotch that a male had thus "directed" her to, and the ultimate site is determined solely by the female.

Females often Harsh Chip or Zeep when approaching or sitting in a site, particularly if the male is not close by, and these vocalizations usually result in the male coming closer. Males show little aggression while following the female around during nest-site inspections, and sometimes follow but a few centimeters away from her. However, males still swoop at females engaged in activities away from the nest-site area. Such females then react more aggressively toward their mates than they did during previous stages, by giving Head Forward Gapes, often accompanied by Snarls and Bill Snaps (see Ficken, 1962: 628-629 for a discussion of female territorialism). Fights between the two now become common.

Sexual displays occur for the first time during nest-site selection but are infrequent. Females occasionally Solicit after the male approaches. Males sometimes assume the Fluff and give *Eees*. However, neither copulation nor attempted copulation occurs (unless one considers swooping and grabbing of females as attempted copulation).

Once a site is selected, the female immediately begins building the nest, a process which requires about three days. Displays and copulations are frequent during the last part of nest building and for a day after the nest is completed. Even during this period males only approach their females about every 40 minutes during the morning, rarely during the afternoon, and there is a slight resumption of sexual activity in the early evening. All sexual activity ceases rather abruptly the day before the first egg is laid.

Table 2 indicates the period during the nesting cycle when the two main types of male displays were observed. The various displays are combined into two types: (1) Fluff and (2) all others, most of which involve Sleeking of the plumage. The birds were observed for approximately equal periods during all phases of the nesting cycle, but since sufficient quantitative data were not obtained, the figures in Table 2 should only

TABLE 3
PRECOPIULATORY ACTIVITIES AS RELATED TO COPULATIONS

<i>Male initiates</i>		
<i>Male</i>	<i>Female</i>	<i>Copulation</i>
Courtship display number 1 (Table 1)	Resting posture	Incomplete
Courtship display number 6	Resting posture	Incomplete
Courtship display number 10	Resting posture	Incomplete
Courtship display number 11	Resting posture	Incomplete
Courtship display number 5	Solicits	Complete
<i>Female initiates</i>		
<i>Female</i>	<i>Male</i>	<i>Copulation</i>
Solicits (2 cases)	No display, mounts	Incomplete
Solicits (1 case)	No display, mounts	Complete

be used as an indication of the types of displays during different periods.

Fluffed postures occur earlier in the season than the other displays (Table 2). The male is stationary and does not show the agitated movements seen in other courtship displays. Fluffing may be continued for several minutes while the other displays are usually of very short duration.

The Fluff seems primarily to express a conflict between weak escape and sexual tendencies. Evidence for this includes the fact that males never threaten or attack the female following this display and usually leave after ceasing the display, indicating a weak escape tendency; also, performance of the Fluff early in the nesting cycle and the rarity of copulation attempts following it (two attempts at mounting seen) indicate that it expresses a weak sexual tendency.

In response to 15 Fluffs, females in 8 cases gave no overt reaction, 5 bouts of Harsh Chips, and 2 Solicits. Fluffed postures commonly function as signals of submissiveness in many passerines and are often "reverse movements" (e.g., Marler, 1956: 10), that is, the opposite in form from the posture of a bird which is ready to attack. Females only allow such close approaches when males are in this display and only when males Fluff does the pair remain close together for periods as long as a few minutes without overt aggression.

The Sleeked displays are generally performed from about 0.5 to 1 meter away from the female. Their orientation often shifts while the bird is displaying; the male often faces the female, and then quickly moves to either side of her. These displays are generally of very short duration and the male flees quickly if the female is not receptive. These displays sometimes precede copulation attempts (Table 3).

The response of the female to these displays is varied. Recorded responses (16) were as follows: Harsh Chips, 10; Head Forward Gape, 3;

TABLE 4
CONTEXT OF SOLICITING POSTURE

<i>Context</i>	<i>Number of observations</i>
In response to male approach	19
While male present	10
Immediately after male leaves	9
"Spontaneous"	9

lunges at male, 1; leaves, 1; and Solicits, 1. Although the female usually does not react sexually, these displays probably act, in time, to decrease her attack tendency and to increase her sexual tendency.

Soliciting is more frequent during late nest building than at earlier stages (Table 2). It is frequently preceded by Harsh Chips, and infrequently by Zeeps; both bring the male closer. The subdued *Eeeee*, which is associated with Soliciting, may also attract the male if he is nearby, but does not seem to have great carrying power and therefore probably functions as a short-range communication.

Soliciting is frequently given "spontaneously" (i.e., the male is not nearby and has not approached the female recently—see Table 4), often after the female leaves the nest following a bout of building. In some cases, the female Solicits immediately after the male leaves, or ceases Soliciting when the male approaches. This may be due to a conflict between the attack and sexual tendencies when the male is near, so that the sexual tendency is not expressed. Soliciting certainly indicates a strong sexual tendency. The response of the male to Soliciting is often mounting, although he may sometimes flee.

Apparently only one or two copulations per season occur in any pair, unless the nest is destroyed or deserted. All observed copulations took place on a horizontal tree limb about 6 meters up, and usually about 6 or 10 meters from the nest. Copulations are very short in duration. Table 3 summarizes the data on the behavior of both birds immediately preceding copulation. Copulations were designated as incomplete if the male obviously did not make cloacal contact with the female (did not bring his tail down under hers).

Incomplete copulations are a result of inadequate sexual responses by either the male or female. In cases where the male displays and the female remains in a resting position and the male mounts, the female does not threaten him, but neither does she crouch or give any other sexual response, and the male quickly leaves. Apparently females must assume the proper posture before copulation can take place; cloacal contact is seemingly impossible if the female does not elevate her tail. In the cases where

the female initiates copulation by Soliciting, the male flies straight to her, landing nearby, performs no displays, but immediately mounts.

ATYPICAL SEXUAL ACTIVITIES

Redirected copulation by a captive male was reported and discussed in Ficken and Dilger (1960). This male performed incomplete copulatory movements on a mound of droppings after courting the overtly unresponsive female for several months. Displays were never performed to the substitute object but only to the female.

"Pseudomale" behavior of females (Morris, 1955) was observed three times in the wild. In two instances a male was sitting in the crotch of a tree in a rather crouched posture. The female flew in, landed on his back and fluttered her wings, but did not bring her tail down. The male then flew off. It appears that "pseudomale" behavior is stimulated by the crouched posture of the male, which resembles the posture assumed by a sexually motivated female (see Morris, 1955, for discussion of causal factors). In another instance this behavior followed an incomplete copulation. The male approached the female again, she crouched slightly, they Bill Touched, and then the female briefly mounted the male. A Fight followed and the male left.

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SUMMARY

The pair formation period is marked by aggressive approaches to the female by the male, the latter fleeing when repulsed, but not leaving the territory. The attack tendency of the male decreases, and his sexual tendency increases by the time of nest-site selection. On the other hand, the attack tendency of the female apparently increases as does her sexual tendency.

Courtship displays occur during nest building. Male displays are divided into two main types: Fluffed and Sleeked. There are intermediates and this is apparently a "graded" display. Fluffed displays first occur during nest-site selection and apparently reflect a weak sexual tendency. They reduce female threats and attacks. Sleeked displays occur during nest building and apparently reflect a somewhat stronger sexual tendency. These displays only infrequently lead to copulations and probably function in long-range stimulation of the female. If the female Solicits the male usually approaches and mounts without preliminary displays. All sexual activity ceases the day before the first egg is laid.

Atypical sexual activities include redirected copulations and "pseudo-male" behavior.

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