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VISUAL DISPLAYS AND THEIR CONTEXT IN THE PAINTED BUNTING

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The 12 species in the bunting genus *Passerina* have proved to be a popular source of material for studies of vocalizations (Rice and Thompson 1968; Thompson 1968, 1970, 1972; Shiovitz and Thompson 1970; Forsythe 1974; Payne 1982), migration (Emlen 1967a, b; Emlen et al. 1976), systematics (Sibley and Short 1959; Emlen et al. 1975), and mating systems (Carey and Nolan 1979, Carey 1982). Despite this interest, few detailed descriptions of the behavior of any member of this genus have been published. In this paper we describe aspects of courtship and territorial behavior of the Painted Bunting (*Passerina ciris*).

STUDY AREA AND METHODS

The study was conducted on St. Catherines Island, a barrier island approximately 50 km south of Savannah, Georgia. The 90-ha study area ("Briar Field" Thomas et al. [1978: Fig. 4]) on the western side of the island borders extensive salt marshes dominated by cordgrasses (*Spartina* spp.). The tract's evergreen oak forest (Braun 1964:303) consists primarily of oaks (*Quercus* spp.) and pines (*Pinus* spp.), with scattered hickories (*Carya* spp.) and palmettos (*Sabal* spp. and *Serenoe repens*) also present. Undergrowth was scanty so that buntings were readily visible when on the ground.

As part of a study of mating systems, more than 1800 h were devoted to watching buntings during daily fieldwork in the 1976–1979 breeding seasons. In 1976 and 1977 observations commenced the third week of May, after breeding had begun, and continued until breeding ended in early August. In 1978 and 1979 observations began in April, several days before the first buntings returned to the study area, and continued until nesting activities ceased in 1978 but only until mid-July in 1979, about 2 weeks before breeding ended.

Adult buntings were mist-netted and banded with a unique combination of aluminum U.S. Fish and Wildlife Service band and three plastic colorbands (two bands/leg). In addition we applied paint (Testor's airplane dope) to either the outer primaries of one wing or the outer rectrices of selected individuals to facilitate identification in the field.

We attempted to visit each part of the study area daily and to observe every resident bunting. Whenever an individual was sighted, its identity, type of activity, location, and the time of day were recorded either on a

TABLE 1
CLASSIFICATION AND DESCRIPTION OF CONTEXTS IN WHICH MALES PERFORMED PARTICULAR BEHAVIORS

Context number	Description of context
I	Unknown; no other bunting present
II	With female that is not its mate
III	With mate
IV	With own mate and neighboring male
V	With neighboring male and its mate
VI	With neighboring male
VII	With fledgling
VIII	Response to playback of species' song
IX	With unidentified greenish yellow-plumaged bunting (unbanded female or yearling male)

tape recorder for later transcription or in field notebooks. Each bunting was followed and its behavior noted until the bird was lost from sight. The location of each sighting was determined with respect to rows of marked stakes placed 20 m apart in a grid covering the study tract. Additional observations were made on buntings attracted to a model of a male bunting placed near a recorder playing tape recordings of the species' song. These responses were filmed with a Super-8 movie camera. Drawings of bunting postures were made from written descriptions and films.

RESULTS

Behavior.—The following descriptions are based on the most frequently observed patterns. The context in which each behavior occurred in males was classified into one of nine categories to simplify presentation and analysis (Table 1). When males were not performing one of the seven displays described in this paper, their behavioral category is classified as "other" in Table 2. This category includes foraging, singing, and maintenance activity. The frequency of "other" behaviors in each of the nine social contexts is used as an estimate of the frequency that buntings experienced these contexts.

(1) Upright: The male hops on fully extended legs with tail raised 45–90° above the body's axis, head extended and slightly raised, and feathers appressed. The wing tips are held below the tail, exposing the red rump (Fig. 1a). This is usually performed on the ground. Fifty-three percent of the uprights were performed in the presence of a female other than the male's mate (context II) or in the presence of a neighboring pair (context

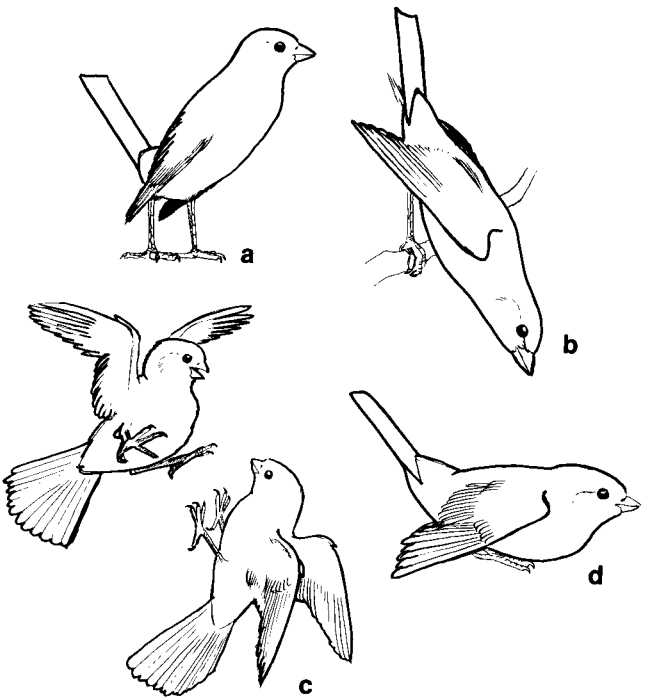

FIG. 1. Painted Bunting displays and postures: (a) Upright, (b) Bow, (c) Flutter-up, (d) Wing Quiver (see text).

V) (Table 2). The number of uprights given in contexts II and V was significantly greater than the number of observations of "other" behaviors in the same contexts ($\chi^2 = 209.9$, df = 1, $P < 0.001$; $\chi^2 = 13.2$, df = 1, $P < 0.001$, respectively). Uprights often occur when two males encounter each other at the perimeters of their territories. In such cases, the males maintain a separation of <1 m as they hop parallel to one another for several meters in the upright posture.

(2) Bow: Bows are performed from perches, at or above the level of the bunting toward which they are directed. The long axis of the body is rotated so that the tail is raised and the head lowered toward the other bird (Fig. 1b). If the bunting is clinging to a vertical perch, such as a cordgrass stem, the long axis of the body and tail is often perpendicular to the ground; if, however, the perch is horizontal, the axis seldom exceeds a 45° angle with the ground. The wing tips are extended from the body and lowered, thereby exposing the rump. Bows occurred significantly more frequently than "other" behaviors in the presence of a female that was

TABLE 2

FREQUENCY OF MALE VISUAL DISPLAYS IN VARIOUS SOCIAL CONTEXTS

Behavior	N	Context[a]									χ^{2b}
		I	II	III	IV	V	VI	VII	VIII	IX	
Bow	104	8.7[c]	13.5	14.4	17.3	29.8	8.7	2.9	1.9	7.7	50.9
Upright	70	11.4	40.0	10.0	8.6	12.9	10.0	1.4	0.0	5.7	236.9
Wing quiver	43	16.3	0.0	2.3	2.3	7.0	37.2	2.3	27.9	4.7	1907.1
Butterfly flight	33	3.0	3.0	6.1	27.3	18.2	39.4	3.0	0.0	0.0	84.8
Moth flight	11	18.2	9.1	18.2	0.0	18.2	0.0	0.0	27.3	9.1	—
Flutter-up	69	—	0.0	0.0	36.2	36.2	26.1	1.4	—	2.9	77.4
Feather pulling	8	0.0	50.0	12.5	12.5	25.0	0.0	0.0	—	0.0	—
Courtship	19	5.3	57.9	26.3	0.0	0.0	0.0	0.0	0.0	10.5	—
Other	4286	51.1	3.9	15.2	4.5	4.1	13.1	3.1	0.2	4.9	—
Total N	4643	2217	226	686	252	252	623	141	24	229	—

[a] See Table 1.

[b] To minimize false positives (Type I errors), the distribution of observations for each behavior (if N > 15) was compared across contexts with that of Other behavior by employing a 2 × 9 contingency χ^2 test. The calculated χ^2 values given in the last column are significant at $P < 0.05$, so χ^2 tests for each behavior (if N > 5) compared with Other behavior in each context were performed and the results reported in the text.

[c] Values are percentages of row totals.

not the male's mate (context II, $\chi^2 = 23.5$, df = 1, $P < 0.001$), with the male's mate and a neighboring male (context IV, $\chi^2 = 36.7$, df = 1, $P < 0.001$), and with a neighboring male and its mate (context V, $\chi^2 = 151.2$, df = 1, $P < 0.001$) (Table 2). Bows are initiated whenever the bunting toward which the bow is directed moves, or when the bowing male itself moves to a new location during an encounter. In the latter case, the bow is given immediately upon landing on the new perch.

(3) Flutter-up: Flutter-ups begin when one male flies toward another approaching male. Both decelerate and extend their feet forward. With an audible beating of wings and with grappling feet, they ascend as high as 5 m (Fig. 1c). Flutter-ups typically end when the still-grappling males drop to the ground, disengage, and fly in opposite directions or sit quietly near each other. Occasionally, one of the males succeeds in gaining the superior position as they ascend, in which case the lower male attempts to disengage itself before they fall to the ground. Usually only one flutter-up occurs during an encounter. Flutter-ups occurred significantly more frequently than "other" behaviors when a pair approached a lone neighboring male (context IV, $\chi^2 = 54.0$, df = 1, $P < 0.001$) or a neighboring male accompanied by its mate (context V, $\chi^2 = 62.2$, df = 1, $P < 0.001$) (Table 2).

(4) Wing quiver: Wing quivers usually occur after a male has landed on the ground or on a perch and is facing another bunting of either sex. The crouching male erects its body feathers, lifts the wings, lowers the wing tips, and raises its tail to about 45° above the body's long axis (Fig. 1d). The lowered wings are rapidly quivered. Occasionally the wings are extended and raised above the back and rapidly quivered (as in Fig. 2c). Wing quivers end with the non-displaying male's flying off alone or being chased by the displaying male. Wing quivers occurred significantly more frequently than "other" behaviors when a male responded to a model of a male and song playback (context VIII, $\chi^2 = 749.9$, df = 1, $P < 0.001$) and when neighboring males encountered each other (context VI, $\chi^2 = 21.5$, df = 1, $P < 0.001$), especially when a male on its own territory was responding to another male's singing nearby (Table 2).

(5) Butterfly flight: Butterfly flights are characterized by slow, deep wing beats and undulating flight. During butterfly flights the body feathers appear to be appressed. Butterfly flights are directed toward a stationary bird or occur when a retreating bunting is being followed. Of 33 butterfly flights, 28 (85%) occurred during interactions between males (contexts IV, V, VI) and for each of these contexts butterfly flights occurred significantly more frequently than "other" behaviors ($\chi^2 = 38.3$, df = 1, $P < 0.001$; $\chi^2 = 16.4$, df = 1, $P < 0.001$; $\chi^2 = 19.7$, df = 1, $P < 0.001$, respectively) (Table 2).

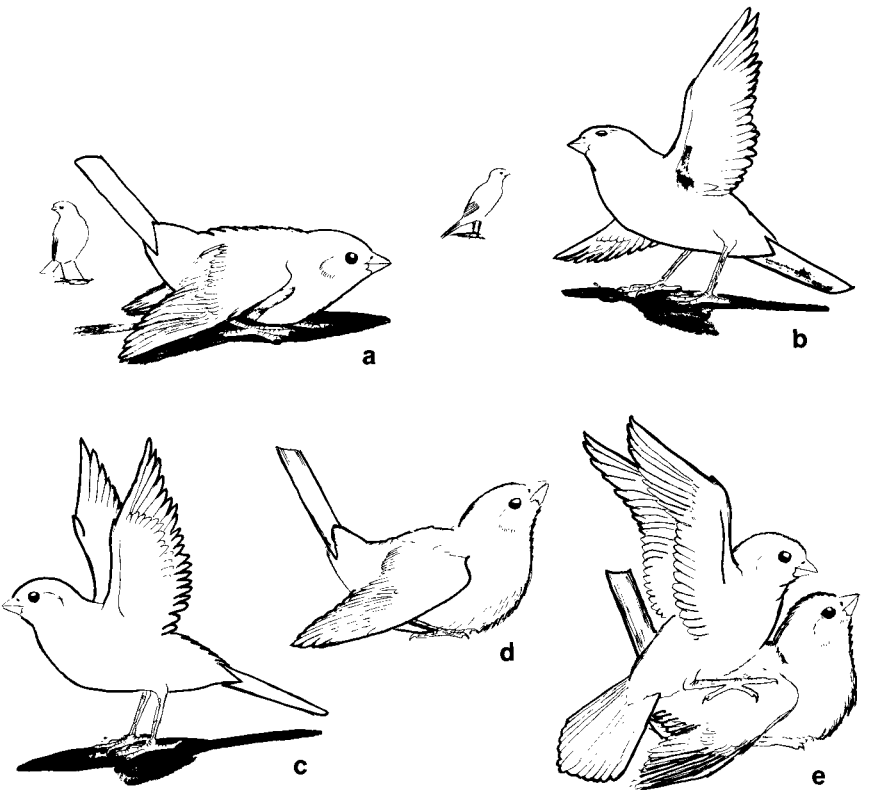

FIG. 2. Courtship sequence (a–c), solicitation (d), and copulation (e) of the Painted Bunting (see text).

(6) Moth flight: In moth flight the body feathers are erected and the extended wings are rapidly fluttered. These shallow wing beats produce a slow, descending flight. Moth flights occur when a male flies during wing quivers.

(7) Feather pulling: Feather pulling occurs after a male dives upon and hits a flying female, driving her to the ground. The male stands upon the crouching female's back, takes one or more of the female's remiges or rectrices in his bill, and appears to pull with a steady pressure for several seconds before flying off. During feather pulling the female remains motionless and sometimes gives soft call notes. Seven of the eight feather pulls involved a female other than the male's mate (Table 2).

Courtship and copulation.—The sequence of displays and postures in-

volved in the establishment or maintenance of a pair-bond are described in this section.

(1) Typical sequence: The male in moth flight glides to an open area of ground 1–2 m from the female. Facing away from the female, the male wing quivers (Fig. 2a). The female hops toward the male, which responds by walking (not hopping) away. The intensity of the male's wing quivers increases at this point and his breast touches the ground. After the female stops, the male turns toward her and straightens his legs. The rate of the wing quivers increases and the wings are gradually and alternately raised to a fully extended position above the back as the male turns toward the female (Fig. 2b). As one wing is raised, the other is extended slightly downward. The male then walks toward the female with both of his wings held rigidly above the back (Fig. 2c). When within 1 m of the female, the male flies to the female and hovers over her using rapid, shallow wing beats, as in moth flight. Either copulation follows (see below) or the female crouches with appressed body feathers and opens her bill while facing the male. If the male tries to mount, either copulation occurs or the female lunges at the male and drives him off. In the latter case, the male often lands nearby and crouches facing away from the female. The male may then begin walking away from the female and repeat the courtship sequence.

(2) Copulation: During copulation the female crouches, erects body feathers, raises tail and head, and lowers her wings (Fig. 2d) as the male hovers, turns in mid-air, and lands on her back (Fig. 2e). The male perches on the female's back, using his wings to maintain balance as his cloaca is brought into contact with the female's cloaca. After 5 sec or less the male dismounts, faces away from the female, and crouches with breast touching the ground, wings drooped, and tail raised. The female remains at the site of copulation and ruffles her feathers vigorously for several seconds. The erection of the contour feathers and the shaking of the body appear more pronounced than are similar movements made during preening.

(3) Contexts: Courtship sequences were observed 19 times, of which 11 (59%) occurred in context II and 5 (26%) in context III. The courtship sequence is not a prerequisite for the occurrence of copulation; females frequently assumed the crouched posture (Fig. 2d) in the presence of males that had not displayed. Copulations not preceded by the courtship sequence occurred in a variety of contexts (Table 3).

Nest-site exploration.—Of 35 observations of nest-site exploration, 32 (91%) involved both members of the pair; the remaining three cases involved only the female. Both birds search the foliage, much as they do when foraging, except that the search is characteristically more rapid and

TABLE 3

CONTEXTS IN WHICH FEMALES CROUCHED IN SOLICITATION POSTURE, 1978 AND 1979 ONLY

	Soliciting female with:					
	Mate	Mate and male	Mate and another pair	Non-mate male	Mate and female	Total
Number	24	11	7	2	1	45
Percent	53.3	24.4	15.6	4.4	2.2	100

no food is taken. The male or female enters clumps of spanish moss (*Tillandsia usneoides*) or other dense vegetation, where it crouches motionlessly. The crouching female, but never the male, frequently arranges foliage around itself. In 12 of 32 cases (37%) involving pairs, the male preceded the female in entering clumps of foliage, thereby appearing to lead the female to potential nest-sites. In one instance, a yearling male perched in a potential nest-site and was mounted several times by its mate (Thompson and Lanyon 1979).

Male parental care.—Males never fed nestlings, but they did defend nests. Males frequently gave loud calls as they followed potential avian predators (Blue Jays [*Cyanocitta cristata*] and grackles [*Quiscalus* spp.]) through the canopy until the predator had left the vicinity of the nest. The only male that entered its own nest did so when Blue Jays were near the nest clump. Several males fed fledglings, but most did not; of 41 broods that produced at least one fledgling, only nine (22%) had fledglings that were fed by the male.

DISCUSSION

The design of this study does not permit detailed discussion of the motivational states underlying the described behaviors. However, some information on the state of displaying individuals is provided by the contextual analysis. In the following discussion we use this contextual information to suggest functions for these displays as well as to compare the form and context of the visual displays of the Painted Bunting with similar displays in related passerines.

Dorsey (1976) reported a display, similar to the Painted Bunting's upright, in Bachman's Sparrow (*Aimophila aestivalis*). In both species the display is performed in a context of potential aggression or danger to the individual. The bunting's upright is similar to the Common Chaffinch's (*Fringilla coelebs*) head-up display, which Marler (1956:62) assigned an intermediate position on a continuum between attack and escape behaviors.

The bow display of the Painted Bunting does not occur in Indigo Buntings (*P. cyanea*) or Lazuli Buntings (*P. amoena*). Instead, in a similar social context, Indigo Buntings rotate the body slowly through an arc from side-to-side and Lazuli Buntings remain motionless; neither lowers the head below the horizontal (Thompson 1965). The head-forward display of many emberizids and fringillids (Hinde 1955, Dilger 1960, Thompson 1960, Andrew 1961, Coutlee 1967, Samson 1977) shares some similarities with the Painted Bunting's bow. The head-forward and bow displays are likely homologous, as they occur in similar social contexts. The bow display probably serves as a low-intensity threat, as has been suggested for the head-forward display (Hinde 1955). A display similar in form to that of the bow of the Painted Bunting has been described in the Hawfinch (*Coccothraustes coccothraustes*) (Hinde 1955); however, although the head is lowered, Hawfinches also erect their contour feathers, which Painted Buntings do not do. Hinde (1955) suggested that the display communicated the submissive status of the displaying bird.

The wing quiver display has been described in Painted Buntings (Parmalee 1959, Thompson 1965, this study) and Indigo Buntings (Thompson 1965, Emlen 1972), but not in Lazuli Buntings (Thompson 1965). A similar display has been reported in Grasshopper Sparrows (*Ammodramus savannarum*) (Bent 1968). The Song Sparrow's (*Melospiza melodia*) puff-sing-wave differs from the wing quivers of the Painted Bunting in that the tail is not raised above the horizontal (Nice 1943). Wing quivers function as high intensity threat displays.

Indigo and Lazuli buntings regularly engage in flutter-ups (Emlen et al. 1975), as do many emberizines (Sabine 1952, Bent 1968). In Painted Buntings flutter-ups usually occurred at the conclusion of a series of encounters between males that were defending space or mates.

Thompson (1965) describes a fluttering flight (our moth flight) in the Painted Bunting as similar to the flight song of the Indigo Bunting (see, also, Thompson 1972), except that in the Painted Bunting no song is given. M. Carey (pers. comm.) frequently observed a fluttering flight in the Indigo Bunting that was often performed without song during territorial encounters between males and during courtship. The fluttering flight associated with courtship in Indigo Buntings is likely homologous with the male flight that precedes copulation in Painted Bunting courtship. The fluttering flight associated with territorial encounters in Indigo Buntings is likely homologous with the Painted Bunting's moth flight. Moth flights performed in similar contexts also occur in fringillids (Condor 1948, Hinde 1955). Wing quivers and moth flights occur in similar contexts and the latter may be a continuation of the wing quiver as the bird changes perches.

The butterfly flight of the Painted Bunting is similar to the undulating flight of the Dark-eyed Junco (*Junco hyemalis*) (Sabine 1952, Balph 1976) and the butterfly flight of the European Goldfinch (*Carduelis carduelis*) (Condor 1948). Communication of the dominance relationship between two birds appears to be the function of the butterfly flight.

The behavior most similar to the feather pull of the Painted Bunting is the pounce of the Song Sparrow (Nice 1943). Pounces in Song Sparrows differ from bunting feather pulls in that pounces also occur during courtship and feathers are not actually pulled. Feather pulls in Painted Buntings were usually directed against females not mated to the attacking males and appear to be a form of defense against trespassing females. Pounces on neighboring females by male Song Sparrows (Nice 1943) and feather pulls by male Painted Buntings never led to solicitations by the females or to copulations.

The courtship displays of Baird's Sparrow (*Ammodramus bairdii*) are similar to the Painted Bunting's, in that the wings are raised and quivered alternately above the back (Bent 1968). Asymetric wing quivering also has been reported in Brown Towhees (*Pipilo fuscus*) (Bent 1968) and Northern Cardinals (*Cardinalis cardinalis*) (Andrew 1961) in unknown contexts and in European Goldfinches in agonistic encounters (Hinde 1955). The general pattern of crouching with raised contour feathers, holding the head level with the body's long axis, and wing quivering occurs in many emberizids (Bent 1968). The differences from the Painted Bunting's courtship pattern that occur in other emberizids include spreading the tail, raising the bill, and vocalizing. Asymetric wing raising is normally absent in the courtship of other emberizids.

The solicitation display of the Painted Bunting is the same as that reported by Andrew (1961) for the emberizines. Female Painted Buntings frequently solicited in the presence of buntings other than their mate and extra-pair copulations occasionally occurred (Lanyon and Thompson, unpubl.).

None of the potential nest-sites examined by Painted Buntings during nest-site exploration was selected as a site for a nest. Many sites are probably examined for each nest that is built, as in the Prairie Warbler (*Dendroica discolor*) (Nolan 1978:102); however, it is possible that the rapid movement and crouching of the female as she is followed by the male play a role in courtship as well as in nest-site selection.

SUMMARY

Descriptions of Painted Bunting (*Passerina ciris*) visual displays and the context in which they occur are based on observations made during four breeding seasons on a barrier island in Georgia. The social context in which the displays occurred was used to infer their function.

Many of these displays are similar to those of closely related species, but the bow display and the form and sequence of courtship displays differ from those of congeners.

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