Wilson Bull., 100(1), 1988, pp. 36–49

BREEDING DISPLAYS AND VOCALIZATIONS OF WILSON'S PLOVERS

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ABSTRACT.—Breeding season displays and vocalizations are described for Wilson's Plovers (*Charadrius wilsonia*) from Texas and Virginia. Aerial displays appeared to be absent, but horizontal and upright territorial displays and Parallel Runs (with horizontal posture) occurred. The female approached the side of the male in the Scrape-ceremony. Precopulatory postures include a posture (Forward-tilt) and a behavior during Marking time (tail flicking) not reported for other plovers. Mounting lasted 15–66 sec (N = 4), was confined to the nesting territory, and included the male grabbing the nape of the female and toppling by the pair. Alarm and distraction displays included Head-up, Squatting, Mock-brooding, Crouch-run, and Broken-wing displays. The Broken-wing display was rare before hatching in Texas, but not in Virginia. Ten vocalizations are described, including nine with sonagrams, several of which have never been described for this species. The displays and vocalizations of this species are compared to those of several other plovers. *Received 8 Mar. 1987, accepted 24 Aug. 1987.*

The lesser plovers (*Charadrius*) are a worldwide group of about 30 species, similar in anatomy, ecology, and behavior (Cramp and Simmons 1983). Relationships within the genus are unclear; similarities in displays (Phillips 1980) do not match similarities in plumage and anatomy (Bock 1958), although the displays are poorly known for many species. This paper describes a number of breeding displays and vocalizations of Wilson's Plover (*Charadrius wilsonia*), few of which have been described previously (Bent 1929, Tomkins 1944). These descriptions, together with recent descriptions (Phillips 1980, Cairns 1982) and compilations (Johnsgard 1981, Cramp and Simmons 1983) of some of the displays and vocalizations of other lesser plovers, enable a more thorough comparative analysis than was possible previously.

STUDY AREAS AND METHODS

I studied Wilson's Plovers in 1979 at Laguna Atascosa National Wildlife Refuge, Cameron County, Texas, and in 1980 at Matagorda Island, Aransas National Wildlife Refuge, Calhoun County, Texas. I made observations during April to July 1979, April to June 1980, and at both sites in June 1981. I also observed breeding Wilson's Plovers at Metompkin Island, Accomack County, Virginia, in June 1984, but all the figures are from displays and calls of Texas birds. The study areas are described in greater detail elsewhere (Bergstrom 1988). I watched plovers from a truck or a blind with 7 × 56 binoculars or a 55 × spotting scope, and used the spotting scope as a 1000-mm telephoto lens for photography. I recorded vocalizations at a tape speed of 19 cm/sec with a Uher 4000 tape recorder, Uher microphone,

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and Sony 48-cm parabola (1979), or with a Nagra E tape recorder and Sennheiser shotgun microphone (1980). I analyzed recordings with Kay Elemetrics 7029 or 7800 Sonagraphs on the 8 kHz scale with a wide band filter. All drawings of birds were made from photographs. Names of displays and vocalizations follow Cramp and Simmons (1983) where possible.

TERRITORIAL BEHAVIOR

Males were already establishing territories when I arrived in Texas on 11 April 1979 and 17 April 1980. Males chased males, and few females were seen. The following postures and displays were used in territorial contexts.

Standing.—In this posture, the back was held at an angle of about 30° above horizontal, and the bill was held just slightly below horizontal (about 5°, Fig. 1A). The neck was withdrawn and the breast band appeared narrow.

Horizontal-hunched.—This posture (Fig. 1B) was used during rushes toward or chases of other birds. The back was parallel to the ground, the neck shortened, and the tail was not fanned or lowered. Sometimes there was a hump created by back feathers (as in the upper male in Fig. 1F). Often a "Song-rattle" (see below) was given when the bird chased in this posture; at the same time the breast band bulged down, forming a variation, the Horizontal bulged-breast posture (Fig. 1C). This posture had a hump in the back, as if the feathers were compressed laterally, and it was held only briefly by the chasing bird. During rapid chases on the ground I saw a third form of this display, the Horizontal spread run (Fig. 1D), in which the breast feathers were spread out past the wings with neither the back nor the breast band feathers bulged.

Upright-hunched.—This stationary posture was used by males as a threat either before or after a run using the Horizontal-hunched or Horizontal spread run posture. The back was more vertical than in the Standing posture (70° above horizontal), the neck and breast band were expanded, and the white breast feathers were fluffed out and spread over the forward edges of the folded wings. Chasing males often gave this posture both before and after a chase, but the chased male used only the Horizontal-hunched posture. Fig. 1E shows the same pair of males as Fig. 1D, when the chasing male had paused in the Upright-hunched posture, and the chasing male had paused looking back at him.

Parallel Run.—In territorial encounters, two males (or in one case a defending female and an intruding male) sometimes ran parallel to each other, both using the Horizontal-hunched posture, occasionally with bulged breast (2 cases) but not a spread run. The two usually followed a straight line that appeared to mark a territory boundary, then each would turn outward 180°, and repeat the run along the same line in the opposite

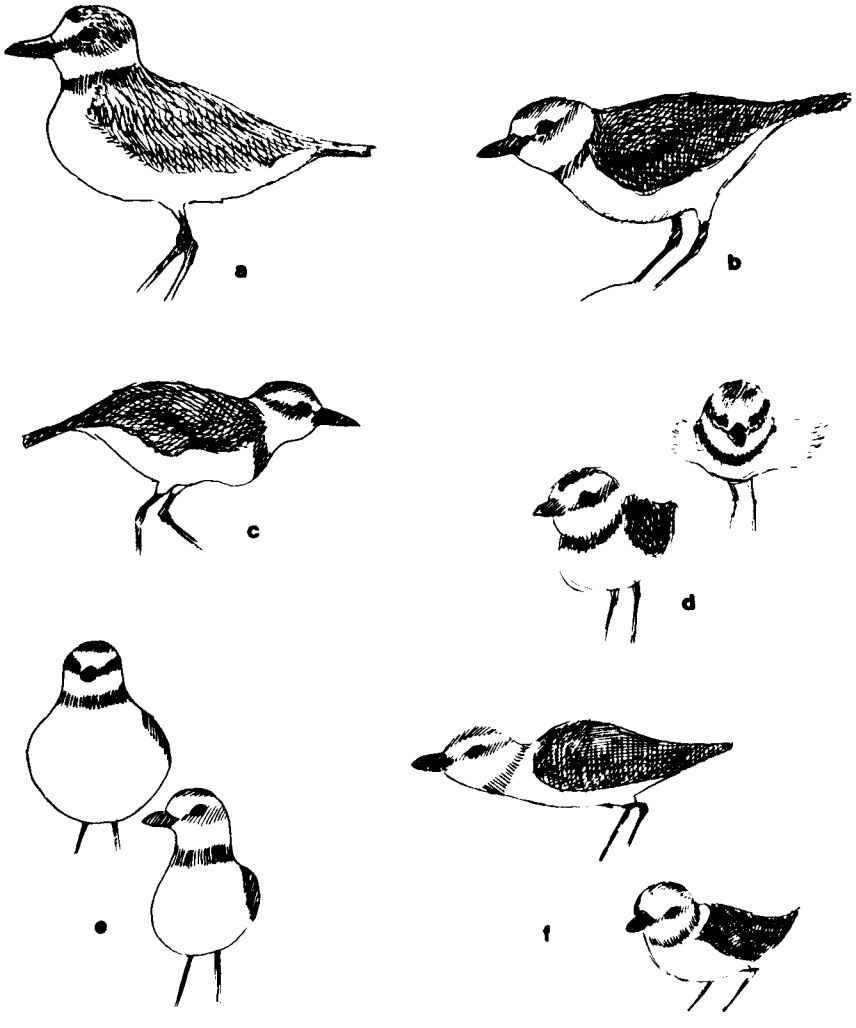

FIG. 1. Territorial postures of Wilson's Plovers: (A) Standing, (B) Horizontal-hunched, (C) Horizontal bulged-breast, (D) Horizontal spread run by chasing male in back, male in front doing Horizontal-hunched, (E) Upright-hunched by chasing male in back, male in front doing Horizontal-hunched with head up, (F) Parallel Run; birds were farther apart than shown, but in this orientation.

direction. This display was seen during territory establishment (two males on 17 and 18 April 1980 at Matagorda), when a pair with chicks was near a pair with eggs (14 June 1979 at Laguna Atascosa, with the female with eggs involved as well), and between two males tending chicks near a puddle

(19 July 1979 at Laguna Atascosa). The latter pair are shown in Fig. 1F; the males were actually farther apart than shown. It was also seen on 13 May 1980 at Matagorda between a nesting male on his territory and another male that had adopted one of his chicks, which was being tended nearby (Bergstrom 1988). No vocalizations were heard during this display.

COURTSHIP AND COPULATION

I arrived in Texas too late to see pair formation. I also did not see the aerial displays used by other male plovers (Cramp and Simmons 1983), but I suspect that Wilson's Plovers lack this display (at least in Texas and Georgia), as it continues during scraping (Cramp and Simmons 1983), and Tomkins (1944) did not see it either. The first time I saw pairs together was at scraping (see below). I saw precopulatory displays (only up to marking time) 10 times, and complete copulation 6 times. These sequences always took place in the territory near a scrape, never after clutch completion, and usually (but not always) immediately after a Scrape-ceremony. All complete copulations seen followed a Scrape-ceremony. I saw the following displays and behavior by pairs.

Scraping.—The male made several scrapes in his territory. Males did most of the scraping, but females sometimes scraped in a depression started by their mate. Both sexes engaged in ground-pecks and then side-throws (Cramp and Simmons 1983), when they tossed bits of stone or twigs back toward the scrape as they left it. Then, while they were on the scrape, these bits were arranged in a circle around the nest cup, or occasionally as a crude lining. The nest cup was made by kicking back with the breast down and tail up, rotating the body to make a round depression. I could not see the details of the foot movements. The cup was about 8 cm across. Similar scraping occurred on concrete or asphalt pavement, but it only cleared a bare spot.

Scrape-ceremony.—If a female came near a scraping male, he would step sideways out of the scrape away from the female, with his side toward her. If she approached, he pointed in the direction of the scrape with his bill ("bow," Phillips 1980), lowered his wing near the scrape and raised his wing away from the scrape, and fanned his tail down. Once a faint "Mooing" call was heard, presumably by the male (see below). The female then entered the scrape, passing the male's head (Fig. 2A). I saw this ceremony five times, as early as 20 April (1980) and as late as 2 June (1981). Once it included only the male stepping out of the scrape sideways, just before the female laid the first egg in the nest.

Horizontal bulged-breast.—This was used only by males in approaches to females prior to and after scraping. A similar posture was used in territorial chases (Fig. 1C), but during courtship it was held for longer periods, was silent, and was used with an exaggerated "prancing" gait.

Forward-tilt.—This precopulatory display often followed the Horizontal bulged-breast. The male lowered his head but kept his bill almost horizontal, with his back about 45° above the horizontal (Fig. 2B and 2C). Males also "pranced" after females in this posture.

Upright-hunched.—If the female stood still in the posture shown in Fig. 2C and 2D, the male switched to the Upright-hunched posture directly behind her, as shown in Fig. 2D. The female posture was tipped forward slightly from Standing. The male's Upright-hunched posture was less extreme than the version used in chases, with less puffing of the breast feathers.

Marking time.—If the female continued to stand in front of him, the male (while in the Upright-hunched posture) began kicking his feet up (approx. 2 kicks/sec) until they almost touched his breast, as shown in Fig. 2D with the male on the left. He flicked his tail from side to side with each kick, and often continued kicking and tail flicking for 30 sec or more. The 10 incomplete sequences I saw (including the one shown in Fig. 2) usually ended at this point, when the female walked away while the male was Marking time.

Mounting and copulation.—I saw plovers copulate 6 times, always in the pair's territory. The male hopped on the female's back and continued the foot movements in a reduced form, but with no tail flicking, for timed intervals of 15, 25, 44, and 66 sec (called "trampling" by Tomkins 1944), In 1 instance mounting was not preceded by Marking time. In all cases the male then grabbed the back of her neck with his beak, thrust his pelvis down, passed his tail around hers, and maintained cloacal contact for only a few seconds. The pair then fell back together in 5 of the 6 cases. Both birds preened after copulation; no vocalizations were heard before, during, or after it.

ALARM AND DISTRACTION DISPLAYS

The displays described below were given in response to my presence (usually outside the truck or blind, but see below) unless otherwise noted.

Head-up.—In alarm, Wilson's Plovers raised their heads, extended their necks, and tilted their bodies back to about 60° above horizontal (Fig. 3A). Birds also used this posture when they occasionally approached me in the truck or blind and stood about 3 m away giving *Tweet* calls (see below). Less extreme, silent versions (with less neck extension) were given by groups by adult plovers to a dog that came near a pond where they were drinking and bathing, to a thirteen-lined ground squirrel (*Citellus tridecemlineatus*) near nests in 1979 at Laguna Atascosa, to a western diamondback rattlesnake (*Crotalus atrox*) near nests in 1980 at Mata-

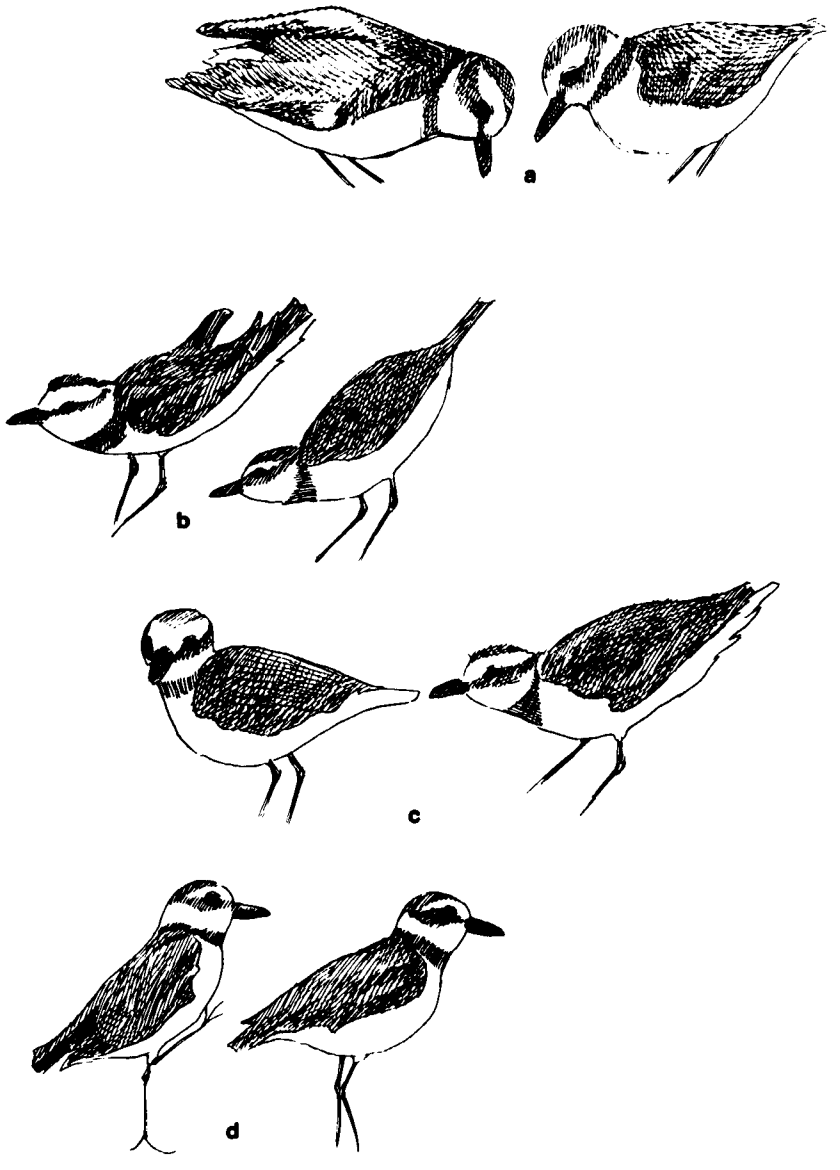

FIG. 2. Courtship postures of Wilson's Plovers: (A) male on left bowing as female on right enters scrape, (B) two different males doing Forward-tilt, (C) male on right doing Forward-tilt toward female on left, before Marking time, (D) same pair as in C, male on left in Upright-hunched posture and Marking time, female on right.

gorda, and in 1980 at Matagorda by a single male in response to a coyote (*Canis latrans*) and a perched Great Horned Owl (*Bubo virginianus*) near its nest.

Squatting.—Squatting appeared to be a more extreme alarm display (Fig. 3B). In addition to responding to me in this manner, I also saw Wilson's Plovers use this in response to Willets (*Catoptrophorus semipalmatus*) that were walking near their nest. It differed from Mock-brooding (see below) in that the head was low and the body was flattened during Squatting.

Mock-brooding.—Plovers often responded with Mock-brooding when I approached their nests during incubation. Groups of 10–20 plovers would gather near me, giving *Tweet* and *Peet* calls (see below), standing in Head-up postures. Birds at the edge of the group, usually females, would run silently 10 m or more from me in a Horizontal-hunched posture. They then settled behind a clump of vegetation or in a hollow for 6–17 sec (N = 3), as if settling on a nest, and then jumped up to repeat the display elsewhere.

Distraction-lures.—The "Crouch-run" had the tail fanned down and wing tips held out and quivering (Fig. 3C). No call was heard, and the wing movements were minor, so it was probably not a true rodent-run display (Cramp and Simmons 1983). Although less common than either of the following, it often occurred along with them. The "Broken-wing" display, which occurred in both stationary and moving birds, was accompanied by a buzzy "Distraction" call (see below). The stationary display (Fig. 3D) included birds beating their wings up and down together (Cramp and Simmons 1983:160) with the wingtips moving in a circle, and the tail fanned down. In some instances (Fig. 3E), birds drooped one wing toward me, reminiscent of the Scrape-ceremony. This display was often given next to an object, such as the cow manure in Fig. 3E. Sometimes both wings were held in the air briefly (Fig. 3F). Stationary Broken-wing displays were also given to Willets, once to a Willet near a plover nest and once to a Willet trying unsuccessfully to steal a fiddler crab (*Uca* sp.) from a plover. Mobile Broken-wing displays were performed farther from me; the bird dragged its wings on the ground while moving away from me. The mobile form was more common, unless chicks were visible nearby, in which case the stationary display was more common.

Broken-wing displays were normally performed 10 m or more away from me. Wilson's Plover parents came no closer than 5 to 8 m while I was banding their 1- to 3-day-old chicks, and most often gave Head-up postures and *Tweet* calls (see below) during the banding rather than distraction displays. Broken-wing displays were rare in Texas unless chicks

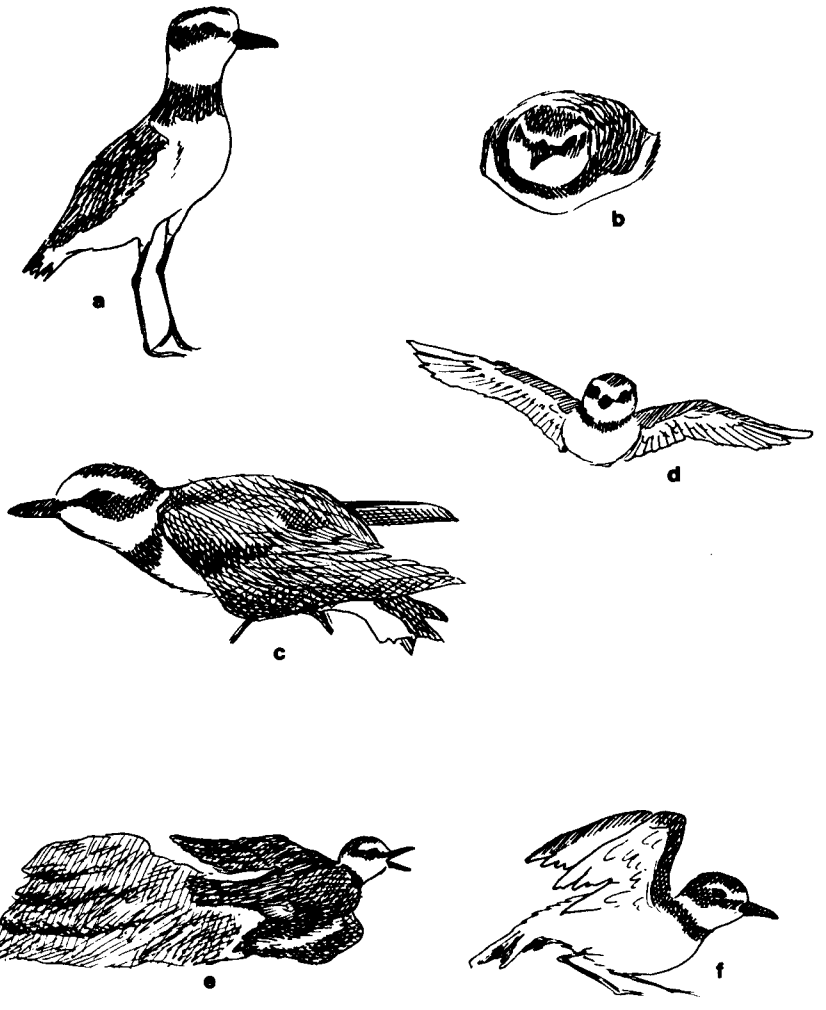

FIG. 3. Alarm and distraction postures of Wilson's Plovers: (A) Head-up, (B) Squatting, (C) Crouch-run, (D) Stationary Broken-wing, (E) Stationary Broken-wing next to cow manure, wing drooped, (F) Stationary Broken-wing with wings up.

were present (usually after mid-May). During incubation, a Head-up posture with *Tweet* calls (see below) and Mock-brooding were the most common responses to me. In contrast, Wilson's Plovers in Virginia used the Broken-wing display frequently in response to humans both during incubation and the chick period (K. Terwilliger, pers. comm.).

VOCALIZATIONS

Tweet call.—This was the most common call given to me when I was near the nest, and seemed to be mainly an alarm call. It was a clear whistle slurred up, ranging in frequency from 1.5–5 kHz (Fig. 4A). It was usually given by a bird in the Head-up posture, and birds always bobbed their bodies slightly as they gave the call; it seemed to be used most often by males. It was always separated from other calls, and was always given singly. I heard it less often in other contexts: territorial fights between males, and when one parent tending chicks was replaced by the other parent (see Bergstrom 1988).

Peet call.—This short whistle occurred singly or, more commonly, in pairs or triplets, often following a *Tweet* call (Fig. 4B). *Peet* calls were more common when I was moving, while *Tweet* calls were more common when I stood still. When I moved near a group of birds that were using Mock-brooding, they often gave a chorus of *Peet* calls (Fig. 4C), which varied in frequency. A sound spectrogram I made from a record of Wilson's Plover calls from Puerto Rico or the Virgin Islands (Reynard 1969) is virtually identical to the *Tweet* and triplet *Peet* calls shown here.

Pip call.—This sounded like and looks like a low-intensity *Peet* call. It was given when one bird left the nest, but never at nest relief. *Pip* calls given by a female leaving the nest are shown in Fig. 4D. *Pip* calls were heard at 9% of 81 male departures from the nest at six nests watched from a blind in 1980 for 108 h. Females gave *Pip* calls during 9% of 102 departures from the same nests; one female gave the call twice just before her mate went to the nest (not at nest relief). Both sexes of three pairs used the calls, only the male in one pair, and neither sex in two pairs. As it was usually given when the mate was not present, and not at nest relief, its function is unclear; it could have been in response to me in the blind.

Fweep call.—This call was louder than the *Pip* call, and it was used mainly by the arriving bird during nest relief. It was often given in series (Fig. 4E). It was used most often when the sitting bird was slow to leave the nest, and it was followed by nest relief. I heard this call during 32% of 38 nest reliefs seen in the same 6 pairs in 1980; 67% of the 12 birds giving those calls were females. The structure of this call is similar to parts of the "Song-rattle" (see below) but the *Fweep* call was lower in volume and much shorter.

"*Song-rattle.*"—This was given by both sexes during territorial displays and by males during chases, both on the ground and in the air (Fig. 4F and G, by the same male). It appeared to be given by chasing birds only. It was sometimes given to me by birds giving alarm displays. It often was accompanied by puffing out the neck band.

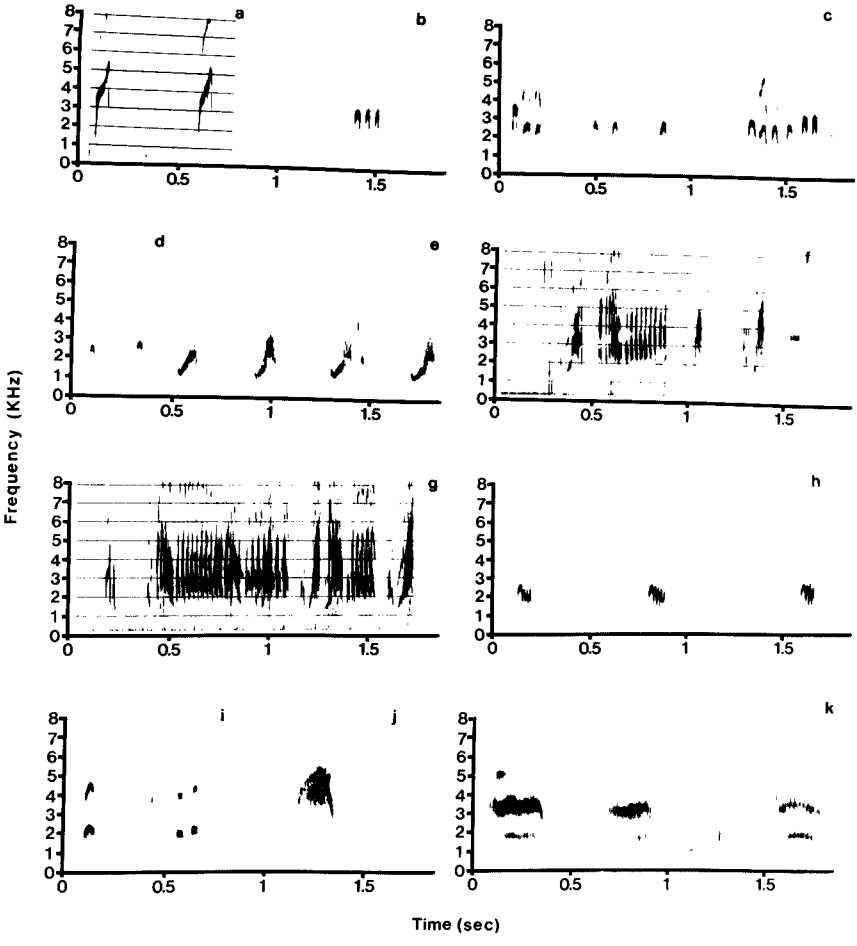

FIG. 4. Sound spectrograms (wide band filter) of vocalizations of Wilson's Plovers. (A) *Tweet* calls, (B) triplet *Peet* calls, (C) chorus of *Peet* calls by several adults, (D) *Pip* calls, (E) *Fweep* calls, (F) "Song-rattle," (G) longer "Song-rattle" by the same male, (H) *Chup* calls, (I) *Peep* calls, (J) *Cheep* calls, (K) "Distraction" calls.

"Brood" call.—A call was used by parents to lead or brood their chicks; in both Texas and Virginia I could see the parent's throat move (about once per second) and the chicks following or brooding, but I could not hear the call. A probable variant of the "Song-rattle," the *Chup* call (Fig. 4H), was given by a male leading his chicks along a road near my truck at Laguna Atascosa in 1979. Although this was the only call I heard given

by parents to chicks, its similarity to the "Song-rattle" and the bird's proximity to my truck make me suspect that the call was given in response to me, and it was probably not the normal call to the chicks.

Peep call.—This was a soft call made by a young chick while I was holding it, and it resembled the *Pip* call of adults (Fig. 4I).

Cheep call.—This was a louder, higher-pitched distress call given by the chick mentioned above while I was banding it (Fig. 4J). This usually caused the parent(s) to come closer to me and give *Tweet* calls.

"Distraction" call.—This was a buzzy call given only during Broken-wing displays. It was given in series, and usually descended in pitch (Fig. 4K). This female gave three bursts of 4, 3, and 7 calls each, with a mean pause between bursts of 1.0 sec and within bursts of 0.63 sec.

"Mooing" call.—I heard this call during the Scrape-ceremony, but did not record it. It sounded like the distant mooing of a cow.

DISCUSSION

The displays and vocalizations of Wilson's Plovers in Texas and Virginia were similar to those described by Tomkins (1944) for the same species in Georgia (Table 1), with a few exceptions. The only territorial posture he mentioned was squatting, which I saw in alarm contexts only (see above). Tomkins (1944) saw Broken-wing displays during incubation, when they also occurred in Virginia but not in Texas (see above). Copulation in Texas appeared to be more limited to the nesting territory than it was in Georgia (Tomkins 1944:262). I did not see or hear a male display and call given from the scrape preceding the Scrape-ceremony, with bill and tail up (Tomkins 1944:265).

An increase in the intensity of distraction displays during the breeding cycle, similar to that in Wilson's Plovers in Texas, also occurs in other shorebirds, including several plovers (Gochfeld 1984, Bomford 1986). Geographic variation in the timing and occurrence of distraction displays (such as that found in the use of the Broken-wing display) is less common, but also occurs in several other shorebirds (Gochfeld 1984:336).

Many behavioral patterns of Wilson's Plovers resemble those of other plovers. Similarities with the behavioral patterns of three other plovers, Snowy Plovers (*Charadrius alexandrinus*), Mountain Plovers (*C. montanus*), and Double-banded Dotterels (*C. bicinctus*) were determined subjectively, based on similarity of structure and context with published descriptions and sonagrams (Table 1). Alarm and distraction displays are not listed because they are quite similar in many plover species (Cramp and Simmons 1983). The name used by other authors for a similar behavior or "same" (if they used the same name) is listed.

TABLE 1
SIMILAR DISPLAYS AND VOCALIZATIONS IN OTHER PLOVERS

	Wilson's Plover[a]	Snowy Plover[b]	Mountain Plover[c]	Double-banded Dotterel[d]
Territorial displays				
Horizontal-hunched		Same		
Horizontal bulged-breast			Head-down threat	Same
Horizontal spread run		Horizontal threat	Horizontal threat	Horizontal spread
Upright-hunched		Same	Upright threat	Erect puffed breast
Parallel Run		Same	Same	Same
Courtship displays				
Scrape-ceremony	Nest-location	Same	Scrape exchange	Scrape exchange
Horizontal bulged-breast	Running crouch?	Horizontal dance[e]	Head-low	Same
Upright-hunched	Stands erect?	Same	Upright precopulatory	Upright posture
Marking time	Same	Same	Same	Parade march
Vocalizations				
Tweet	*Peet*	Same	*Tu-lup*	Same
Peet	*Tut-tut*	*Prrr*		*Tic*
Fweep		"Song-rattle"		
"Song-rattle"		Same		"Cheedle"
"Distraction" call	Harsh guttural	Same		
"Mooing"	Dove note	Same	Same	Same

[a] *C. wilsonia*, Tomkins (1944), except Bent (1929) for *Tut-tut*.
[b] *C. alexandrinus*, Cramp and Simmons (1983).
[c] *C. montanus*, Graul (1973a) for displays, Graul (1974) for calls.
[d] *C. bicinctus*, Phillips (1980), except Bomford (1986) for upright posture.
[e] Boyd (1972); similar context, but posture lacks bulged breast.

The plovers listed all use a horizontal posture in the Parallel Run, but some other plovers (e.g., Killdeers [*C. vociferus*], Phillips 1972, and Piping Plovers [*C. melodus*], Cairns 1982) use an upright posture in a similar display. Tail flicking during Marking time has not been reported in other plovers. The only posture in other plovers resembling the Forward-tilt of Wilson's Plovers is the Forward-oblique display of Ringed Plovers ([*C. hiaticula*], Cramp and Simmons 1983:135, fig. A right), which is used by females but not males before copulation. Many of the other postures of

TABLE 2
CHARADRIUS PLOVERS WITH PLUMAGE OR DISPLAYS SIMILAR TO WILSON'S PLOVER

Plumage group (Graul 1973b)	Display group (Phillips 1980)
Wilson's Plover	Wilson's Plover
Collared Plover (*C. collaris*)	Collared Plover
Madagascan Sandplover (*C. thoracicus*)	Madagascan Sandplover
Ringed Plover	Snowy Plover
Little Ringed Plover (*C. dubius*)	Three-banded Plover (*C. falklandicus*)
Semipalmated Plover (*C. semipalmatus*)	Kittlitz Sandplover (*C. pecuarius*)
Long-billed Plover (*C. placidus*)	Malaysian Sandplover (*C. peronii*)
	Chestnut-banded Sandplover (*C. pallidus* = *venustus*)

Ringed Plovers are different from those of Wilson's Plovers. The greatest number of similarities in the table occur with Snowy Plovers; they lack only the bulged breast in the horizontal posture in territorial and courtship contexts.

The Scrape-ceremony and copulation behavior of Wilson's Plovers resemble those of seven other *Charadrius* in which the female also approaches the side of the male, the male grabs the nape of the female during Mounting, and the pair topples (Phillips 1980) (Table 2). Mountain Plovers lack the nape-grabbing, and Double-banded Dotterels have a choking display not found in Wilson's Plover (Phillips 1980). This display group has some anatomical similarities (Phillips 1980) but it has a variety of plumage patterns, while six other *Charadrius* with head plumage patterns similar to those of Wilson's Plover (Graul 1973b) (Table 2) have a variety of Scrape-ceremonies and copulation behaviors (Phillips 1980, Cramp and Simmons 1983).

Bock (1958) grouped Wilson's Plover with the ringed plovers, similar to the plumage group in Table 2. In basing his groupings within this genus mainly on plumage, he assumed that plumage was a primitive characteristic. However, plumage could be subjected to considerable selection pressure (Graul 1973b), so similarities in plumage could be derived, just as similarities in behavior could be either primitive or derived. In the absence of firm knowledge about either set of characteristics, it is useful to use both in a taxonomic analysis (Bock 1958:71). Further analysis, possibly using different characteristics, is needed to determine the phylogenetic relationships within this genus.

ACKNOWLEDGMENTS

Research in Texas was supported by the Henry Hinds Fund, the Eli A. Nierman Foundation, the Frank M. Chapman Fund, the E. A. Bergstrom Fund, and the Alexander Bache

Fund. Research in Virginia was supported by a Glenn Grant from Washington and Lee University. I thank A. R. Kiester, K. Terwilliger, and the staffs of Laguna Atascosa National Wildlife Refuge and Aransas National Wildlife Refuge for assistance in the field; the Nature Conservancy for permission to work on Metompkin Island; L. Bergstrom for drawing the figures; S. J. Arnold and S. A. Altmann for the use of their sound recording equipment; and C. S. Adkisson and J. Mehner for letting me use their sonagraphs. I thank W. Graul, A. R. Kiester, E. H. Miller, G. W. Page, R. E. Phillips, T. Sordahl, and reviewers G. W. Page and J. R. Walters for helpful comments on earlier versions of the manuscript, and I thank my wife, S. Still, for support and encouragement.

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Voucher photographs (accession nos. V06/3/001–V06/3/010) illustrating postures and displays described in the above article have been deposited with VIREO, Academy of Natural Sciences, 19th and The Parkway, Philadelphia, PA 19103.