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Display Behavior of Male Sprague's Pipits

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ABSTRACT.—Male aerial territorial displays of Sprague's Pipits (*Anthus spragueii*) are described in detail for the first time. Aerial displays were performed primarily in the morning, with four males' average display rates ranging from 11.8–34.8 min. One male displayed continuously for 3 hrs; no other passerine has been documented to have such prolonged aerial displays. Display flight energetics were estimated with implications explored. *Received 6 March 1997, accepted 17 March 1998.*

Among the least known resident North American passerines is the Sprague's Pipit (*Anthus spragueii*). The dearth of information on this species is not surprising given its highly cryptic plumage and habits. In fact, even territorial males' persistent and relatively conspicuous flight display have never been described in detail. Here, I present the first information on male display rates and energetics of Sprague's Pipit.

STUDY AREA AND METHODS

Territorial males were studied during 15–20 June 1995 and 20–23 May 1996, just north of Thompson Lake, Lostwood National Wildlife Refuge, Burke County, North Dakota. This location is precisely where Green (1992) censused annually breeding grassland passerine species, including Sprague's Pipits, during 1987–1990. The study site is rolling, mixed grass prairie (*Stipa* spp., *Agropyron* spp.), interspersed with small seasonal wetlands, in the Missouri Coteau physiographic region (Green 1992). The study area was prescribe-burned on 14 August 1980, 8 August 1982, 9 July 1985, and 15 May 1992. More than 90% of above ground plant growth and litter was eliminated in the burns (Green 1992; K. Smith, pers. comm.).

Territorial males were not marked in 1995; however, the sex of birds studied was confirmed by collection at the end of the observation period. In 1996, three territorial males were captured with mist-nets using a study skin as a lure. A recording of flight display calls was played from the grass beneath the lure. Captured males were color-marked on the lower abdomen with a non-toxic, permanent ink marker ("Magic Marker" by Binney & Smith Inc., Easton, PA). This ink wears off within a week or two, leaving the bird unharmed (pers. obs.). In this paper, "T" followed by a number is used to designate 1995 territorial males, and initials refer to 1996 color marked territorial males. Total number of observation hours were: May (24.75 morning, 6.5 afternoon), June (24.5 morning, 10.0 afternoon). Contiguous territorial male display rates were simultaneously quantified on several occasions, hence the hourly totals of individual males under Display Rate section exceed the above totals.

Observations of displaying males were made from the periphery of each display area. The following parameters were recorded: number of display calls, number of wing beats between display calls, duration of display, wind speed and direction, and temperature. A stopwatch was used to quantify aspects of the display flight. Limited tape recordings were made of displaying males with Sony TCM- 5000EV and Sony TC-D5Pro II cassette recorders, and Sennheiser ME 80 and ME 66 microphones.

Estimates of display flight energetics were calculated using Pennycuick's (1989) computer software program (Program # 1). Flight speed used in predicting energy expenditure of flight by Program # 1 was zero. Mass ($\bar{x}$ = 23.5 g) and wing span ($\bar{x}$ = 255 mm) were measured from two territorial males (KU 87231-2) before preparation. Hourly windspeed data were obtained from Lostwood N.W.R. headquarters (681 m in elevation), about 2 km from the study area.

RESULTS

Males were not uniformly distributed through the study area; all territorities were located in elevated areas with short grass and relatively low sedge and forb (mainly Asteraceae) densities. Highest male densities were along a north–south oriented ridge that separated two seasonal, shallow wetlands. Along this ridge's steepest section (ca 710 m in length), five males held territories in 1995; at least three were present in 1996. All three 1996 territorial display arenas were in sites where males had been removed in 1995. In 1995, five other territorial males were present along ridgetops with similar vegetation characteristics of a broad rolling area to the south. Because of low display rates, it was unclear how many territorial males occupied the southern area in 1996.

Displays were simple but often prolonged. Males took advantage of the almost ever-present wind by flying from the ground into the wind until they were from 50 to over 100 m

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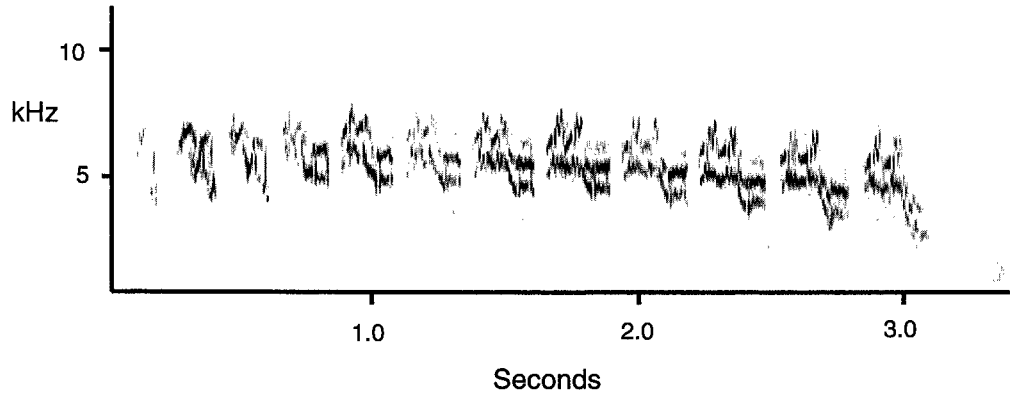

FIG. 1. Spectrogram of flight display song of a territorial male Sprague's Pipit (*Anthus spragueii*).

above the ground. Displays were limited to a relatively small area ($\bar{x}$ = 61.3 × 55 m; n = 3). The males invariably flew into the wind, while constantly flapping their wings until they gave the 7–12 syllable display song. This song is a thin, relatively high pitched "tzsee-tzsee-tzsee-tzsee-tzsee-tzeee-tzeee", of 2.5–3.0 sec duration (Fig. 1). As can be seen in the spectrogram (Fig. 1), the syllables are complex in structure, appearing as harmonics that modulate in frequency. Simultaneously with beginning the display song, the wings were extended parallel to the body, and the bird entered a glide for the duration of the song. When in the glide, males were displaced backward by wind; however, they did not appear to drop much in altitude. Terminating the song, males resumed flapping until the next song. Wing beats between songs varied considerably, ranging from 7-27 beats. Wind speed did not appear to affect wing-beat interval (# of wing beats between display songs). For example, during one of the windiest observation periods ($\bar{x}$ = 29.4 km/h), T1 averaged 14.5 wing beats between songs, whereas the same individual averaged 17.5 wingbeats in a 20.3 km/h wind, and 10.9 wing beats in a 24.6 km/h wind.

At the end of each display bout (defined as uninterrupted display) males either folded their wings and dropped directly to the ground within the display area, or they chased other pipits that had entered the display area. On one occasion, male T1 interrupted its display to chase an adult male Chestnut-collared Longspur (*Calcarius ornatus*) that flew across his territory. Males were never observed singing on or near the ground.

The frequency and duration of display bouts and the frequency of songs per bout varied considerably within and among males and between years, with displays concentrated in the morning. Territorial males displayed less in May 1996 than in June 1995. In May, male BK's longest display bout was 32 min (7.3 songs/min), and RD's was 41 min (7.0 songs/min). These display rates were the highest per bout. However, although highest display rates/min were recorded in May, duration of bouts was greater in June. In May males BK and RD averaged morning display bouts of 12.3 min (13.75 h; n = 3 mornings) and 11.8 min (15.25 h; n = 4 mornings) respectively, whereas in June T1 and T2 averaged 16.9 min (11.2 h; n = 3 mornings) and 34.8 min (8.75 h of obs. on 3 mornings) respectively. On 19 June, T2 displayed continuously for 2 hr 59 min (5.7 songs/min). A nearby male, T1, displayed for as much as 1 h 13 min (6.01 calls/min) in a single bout.

Afternoon displays were generally rare. No displays were recorded during 6.5 h of afternoon observation in May 1996. Only one male displayed during a total of 10.0 h of June afternoon observation. On 15 June, T1 displayed from at least 17:00 C.S.T. until 20:00, with only two breaks of 8 and 3 min each. During this period, he called 806 times (4.5 songs/min). During an additional 8 h of observation over the next two afternoons (15: 50–19:45), he was heard singing only a few times during one 15 min period. Based on

minimal display rates, males do not appear to take advantage of thermal activity which increases in the afternoon with temperature.

Display in male pipits is presumed to involve high energy expenditures because of the high costs of flight (Pennycuick 1989). Average headwinds during 17:00–20:00 on 15 June while male T1 displayed was 20.3 km/h (5.67 m/sec). Pennycuick's (1989) model predicted that the minimum power speed (V_{mp}) for displaying males was 5.9 m/sec, and that maximum range speed (V_{mr}) was 10.4 m/sec. V_{mp} was the air speed at which the least amount of work was done (or fuel consumed) per unit time. V_{mr} was the air speed at which the least amount of energy was expended per unit distance. Estimated fat consumption for flight display at V_{mp} [1.7 W for chemical power, 3.9×10^7 J/kg for energy density of fat (Pennycuick 1989)] was 0.157 g/h. Thus, a male at this site displaying under the above climatic conditions for three consecutive hours (n = 2.63 h of constant flapping; an average of 2.3 sec were subtracted for each song/glide) would expend an estimated 0.41 grams of fat, or 1.8% of its body mass ($\bar{x}$ = 22.8 g ± 0.2 SE; n = 4). Although all four territorial males that were collected had only light amounts of fat, I did not quantify what percent fat reserves comprised the total body mass. In small nonmigrating birds, 3–5% of the body mass is fat (Gill 1990), thus the above estimate for fat expenditure for a three hour display would result in consumption of about 40% to nearly 60% of a male pipit's fat reserve.

DISCUSSION

No other passerine has been documented to have such prolonged aerial displays. Maximum continuous male display of the renowned Skylark (*Alauda arvensis*) is 68 min (Rollin 1943), and unpaired males of the Woodlark (*Lullula arborea*) have been recorded performing displays of 70–90 min (Mackowicz 1970). Skylark display bouts average 2.0–2.5 min (Cramp 1988) to about 4 min (Hedenström 1995), and Woodlark song bouts usually last about 2 min (Mackowicz 1970). No Old World *Anthus* is known to have extended aerial displays (Cramp 1988), and the only species that comes close is the Short-billed Pipit (*Anthus furcatus*) of southern South America. One male *A. furcatus* was recorded singing continuously for 55 min before it dove to the ground after tape playback (Belton 1985). Interestingly, this pipit has been suggested as the closest relative of Sprague's Pipit (Hall 1961, Ridgely and Tudor 1989).

Although Sprague's Pipit display bouts are prolonged, display behavior appears to be limited to a few weeks (Coues 1874; R. Murphy and K. Smith, pers. comm.). Murphy and Smith (pers. comm.) have noted persistent male display from the time of arrival (third week of April) through the third week of May at Lostwood NWR, followed by a period of two to three weeks where display rates are reduced, followed by another period of elevated display rates. I would hypothesize that this bimodal display regime is related to the breeding cycle, with display rates decreasing once a first clutch of eggs is laid and copulation opportunities decrease. A similar cycle has been widely documented in the Motacillidae and many other passerines (Cramp 1988). The second period of elevated display rates may coincide with onset of replacement broods or initiation of second broods. Because of differential nesting success, male display rates should become less synchronized as the season progresses.

The available data seem to support this hypothesis. The median date of clutch initiation near Kyle, Saskatchewan, Canada, about 500 km northwest of Lostwood, was 8 June (Mahr 1973); however, this figure is based on pooling all nests. This undoubtedly included failed first attempts as well as second broods. Seventeen nests located during the last 20 days of May (no nests were located during the first 10 day period) probably best exemplify first-clutch initiation dates in southwestern Saskatchewan; mean incubation and nestling periods were 14 days and 11 days, respectively, with 50% of pipits fledgling between late June and mid-July (Mahr 1973). Mahr (1973), working with unmarked birds, estimated an average of 1.5 broods yearly for this species at Kyle, Saskatchewan. At the same locality, Sutter et al. (1996), using radio telemetry, documented at least one example of a second brood: a female that initiated a second nest 21 days after her first clutch fledged.

My observations of display rates coincide with these periods. Perhaps lower display

rates recorded in May 1996 compared with June 1995 resulted from birds having just completed egg laying in May. I located a nest with 5 eggs (a complete clutch) on 22 May in RD's territory. During the third week of June, birds may have been in the final stage of the first brood, and preparing for second broods. I flushed one presumed female carrying food during this period.

Given that flight is energetically very costly (Pennycuick 1989), males should be minimizing energy expediture and maximizing vocal transmission by displaying when wind conditions are optimal. From an energetic standpoint males should display at or near the minimum power speed V_{mp}, the speed with minimum energy cost (Pennycuick 1989). Indeed, during male T1's marathon display period, 17:00–20:00 on 15 June, the wind was an average of 5.6 m/sec and the estimated V_{mp} was 5.9 m/sec. Hedenström and Alerstam (1996) demonstrated that a Skylark's (*Alauda arvensis*) average airspeed during horizontal song flight displays did not differ significantly from the predicted V_{mp}.

Theoretically, maximal sound transmission in grassland environments should be at dawn when daylight wind perturbance is least (Morton 1975, Henwood and Fabrick 1979). Unlike all the other grassland passerines at Lostwood, male Sprague's Pipits rarely displayed at first light; they typically were not heard until after 04:30, over 30 min after dawn. Males may need to obtain some food resources and for the wind to approach V_{mp} before they begin extended displays. Detailed analyses of the energetics of this pipit's display will need to incorporate a number of biotic and abiotic factors to determine more precisely what parameters best explain temporal occurrence and duration of pipit displays.

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