SOLITARY SANDPIPER EARLY REPRODUCTIVE BEHAVIOR[1]

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THE Solitary Sandpiper (*Tringa solitaria*) is among the least known of Nearctic birds, primarily because of its inaccessibility during the breeding season. The species nests about muskeg and woodland pools using old nests of such passeriform species as the Rusty Blackbird (*Euphagus carolinus*), Robin (*Turdus migratorius*), Common Grackle (*Quiscalus quiscula*), Cedar Waxwing (*Bombycilla cedrorum*), Bohemian Waxwing (*B. garrulus*), Eastern Kingbird (*Tyrannus tyrannus*), and Gray Jay (*Perisoreus canadensis*). It is not known if they ever preempt nests, but at least occasionally they use freshly made nests (D. F. Parmelee, pers. comm.). Eggs have been found from 1.2–12 m above the ground and from the shoreline to 200 m away, usually in conifers but sometimes in deciduous trees (Henderson 1923, Street 1923, Bent, 1929, Sutton *in* Bannerman 1958) and rarely (perhaps) in cattail (Todd 1963). *T. solitaria* is also known to be solitary and, perhaps, territorial year-round; and does not migrate in flocks as do most waders (Hudson 1920, Todd and Carriker 1922, Wetmore 1926, Sutton *in* Bannerman 1958). This unique combination of solitary and arboreal habits makes *solitaria* of special interest, and the paucity of information concerning Solitary Sandpiper behavior leads me to present my data despite their preliminary nature. I published data on acoustical behavior separately (Oring, 1968).

STUDY AREA AND METHODS

I studied Solitary Sandpipers from 15–26 May 1968 at Crimson Lake Provincial Park, 12 km northwest of Rocky Mountain House, Alberta, Canada. The area was characterized by fens of black spruce (*Picea mariana*) separated longitudinally by sandy ridges covered with quaking aspen (*Populus tremuloides*) and ponderosa pine (*Pinus ponderosa*). Many of the muskegs or fens contained one or more deep ponds about which Solitary Sandpipers bred in the stunted spruce trees.

Birds were filmed with a Bolex H16 movie camera and 150 mm lens. Films were subsequently analyzed with a Bell and Howell time and motion analysis projector (Model 173) and a Craig-Projecto-Editor (Model KE-16). Sexes were differentiated only before and after sexual encounters and the laying of eggs.

I spent a total of 95 hours and 35 minutes observing Solitary Sandpipers on the breeding ground. Of this 79 hours and 30 minutes were spent watching members of one pair (pair A) and occasionally the pair in an adjacent territory. I studied three other pairs and lumped the data from all five pairs, as sample sizes are too

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[1] Dedicated to Lennart Raner of Vänersborg, Sweden, a lifelong student of *Tringa* behavior, who taught me how to study arboreal sandpipers.

TABLE 1
TIME SPENT WATCHING SOLITARY SANDPIPERS

Hours	Pair A Muskeg	Pair A beaver pond	Pair A puddle	Pair A totals	Other birds elsewhere	Grand totals
04:00–10:00	33:55	8:25	:15	42:35	4:00	46:35
10:00–16:00	5:55	11:05	4:25	21:25	5:35	27:00
16:00–22:00	—	6:00	9:30	15:30	6:30	22:00
TOTALS	39:50	25:30	14:10	79:30	16:05	95:35

small to allow comparisons of individuals. The pair studied most intensively I watched at three places: the muskeg where it bred, a beaver pond 1 km away, and a small puddle about 1 km from both the muskeg and beaver pond. Time spent at these three observation points is summarized in Table 1.

HOSTILE BEHAVIOR

As pairs were already formed and territories established when I arrived, I was unable to study these aspects of behavior. I determined the territory of one pair, which was kept under more or less constant observation. The male vigorously defended the muskeg pond where he nested, as well as the beaver pond and puddle where he fed. Whenever he flew between these spots, each about 1 km from the other two, he sang and chased any Solitary Sandpipers encountered. The territory of this male thus consisted of approximately 0.5 sq km roughly in the shape of an equilateral triangle. The pair's home range was considerably larger if one takes into account that once or twice a day, one or both birds usually flew some distance out of the regularly defended area to various temporary feeding places. In 10 of 17 observed aggressive encounters the sex of the attacking bird was known, and in each case it was a male.

Aggressive encounters were initiated when a resident bird saw or heard an intruder. At times intruders were intercepted high in the air; at other times they were not challenged until they landed or wandered close to a resident. It was not uncommon for a resident male to chase off an intruder high over and far from a breeding or feeding spot with the chaser's mate trailing behind. In *solitaria*, the sex of a stranger was identified by the way it responded to male threats—rival males fled or attacked; females indicated submission or remained passive.

Figure 1 summarizes the sequence of events in hostile encounters. Postures involved in such encounters are described below and illustrated in Figure 2. All were assumed in silence.

Upright.—This posture functions as a low intensity threat and may precede or follow the wing-up posture, as it commonly does in post-copulatory situations. At other times it is alternated with the head-

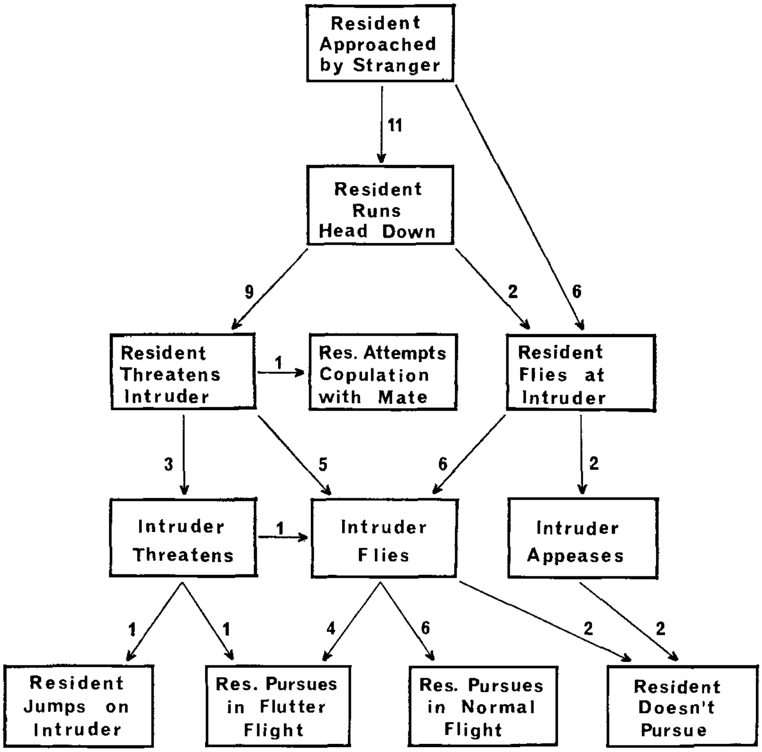

Figure 1. Diagram of behavioral sequences typical of hostile encounters.

down posture. It is characterized by the head being forward, beak horizontal, neck stretched vertically, chest out, tail horizontal, legs stretched, and feathers of crown erect (Figure 2A). A bird in this posture is usually facing a nearby bird. Both may be in this posture simultaneously. A similar posture has been reported for a variety of shorebirds including at least three tringine species: *T. totanus* (Grosskopf 1959), *Limosa limosa* (Lind 1961), and *Numenius arquatus* (von Frisch 1956).

Head-down.—This posture occurs during the early attack phase of an aggressive encounter. As the attacking bird approaches an intruder, tendencies to attack and flee come more closely into balance, and the attacking bird tends to assume a posture described below as wing-up. The head-down posture is characterized by the head being lower than the partly spread and slightly raised tail, the beak pointing forward, and the neck being shortened (Figure 2B). Sutton (*in* Bannerman 1958) described a series of aggressive encounters among fall migrants in Okla-

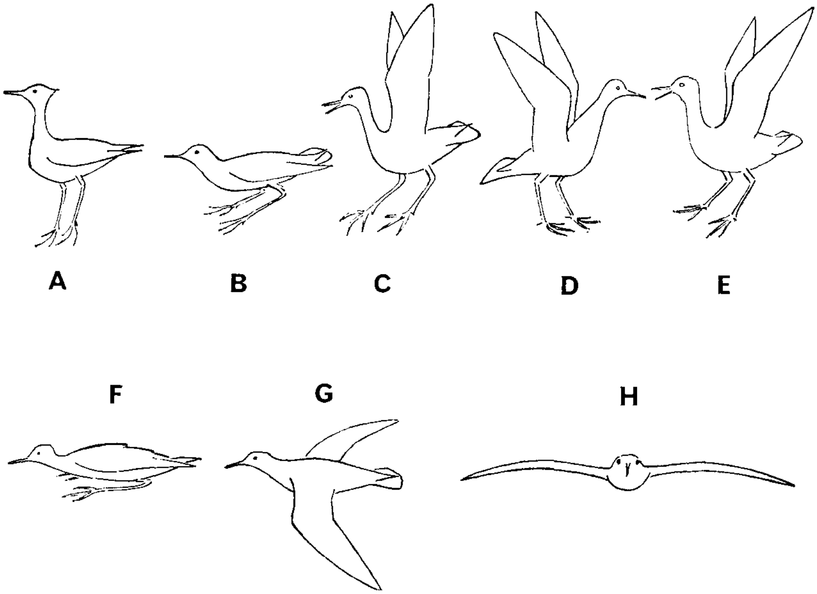

Figure 2. Male postures employed during hostile encounters: A, upright; B, head-down; C, wing-up; D, E, overt fight; F, crouch; G, flutter flight—lateral view; and H, flutter flight—frontal view.

homa in which both the head-down and wing-up postures were alternately assumed. This posture is similar to one found in many scolopacid species including *T. totanus* (Grosskopf 1959), *L. limosa* (Lind 1961), and *Tryngites subruficollis* (Oring 1964).

Wing-up.—This posture is assumed when tendencies to attack and escape are in equilibrium or when the tendency to escape dominates. In this posture head is up, neck outstretched, beak pointed downward at about 30°, wings straight overhead, and tail fanned and raised about 30° (Figure 2C). This posture is sometimes assumed by both the attacking and fleeing bird and, in addition, occurs when two equally dominant birds face each other. In the latter case this threat posture is usually a prelude to a fight. This same posture is employed in sexual situations. Postures very similar to this have been reported in sexual situations in *L. limosa* (Lind 1961) and *Arenaria interpres* (Bergman 1946), and from aggressive situations in *T. subruficollis* (Oring 1964).

Overt fights.—Postures during overt fights are highly variable because the tactics of each individual change according to those of his opponent and in conjunction with his immediate environment (Figure 2D, 2E). As only two fights were observed and no films taken, no detailed description will be made. The two fights occurred when a resident ran at an intruder first in head-down, then in wing-up posture. The intruder, instead of fleeing, turned and stood still in wing-up posture. Each bird then tried to position himself so he could peck downward at his opponent. This positioning was accompanied by wing thrashing. The fights ended after one bird got behind and above the other and pecked down on him.

Crouch.—This display functions in appeasement. The appeasing bird sits on its tarsi, head low, tail down, concealing the white maximized during threat (Figure 2F). In both cases where appeasement postures were seen, they were successful in reducing the aggression of an attacking or pursuing bird (Figure 1). Similar crouching postures have been reported in *Actitis hypoleucos* (Poulsen 1950), *A. macularia* (Oring MS), *L. limosa* (Lind 1961), and *N. arquata* (Gewalt 1955).

Flutter flight.—In addition to the power flight typical of the species, *solitaria* has a ritualized flight similar to that of *Actitis*. Lind (1961) reported a similar "quiver-flight display" in *L. limosa*. In *solitaria* this flight is employed both in aggressive situations and in short flights—either as a distraction from the nest (and probably also young) or when flying from one prospective nest site to another. Clement (quoted by Todd 1963) mentioned it in a distraction context. In this flight the wings are held nearly straight out from the body and beat through only 15° vertically. The tail is fanned and slightly depressed, the head slightly raised, and chest extended (Figure 2G, 2H). In 4 of 10 aerial chases, the chaser employed this ritualized flight. In all four cases, the flight was 3–4 m high, and was employed by both the bird chasing and the one being chased as they circled the contested area. This flight was seen on two other occasions as a single bird arrived at its territory. In the latter two cases, another bird may have been present but no aggressive encounters occurred.

SEXUAL BEHAVIOR

In tringines, copulations are restricted largely to the period from about 5 days before the first egg is laid to the day the second (occasionally the third) egg is laid. When I arrived on the breeding ground 16 May, pair A was already copulating and continued to do so until 23 May—the day their second egg was laid. All told I counted 10 copulations and 11 attempts, including 7 copulations and 9 attempts by pair A.

In all cases the male uttered epigamic calls (Oring 1968) while approaching the female from the rear, or side and then rear. In most cases, the female stood still or walked very slowly as her mate performed the wing-up (= precopulatory) display. If the female remained still,

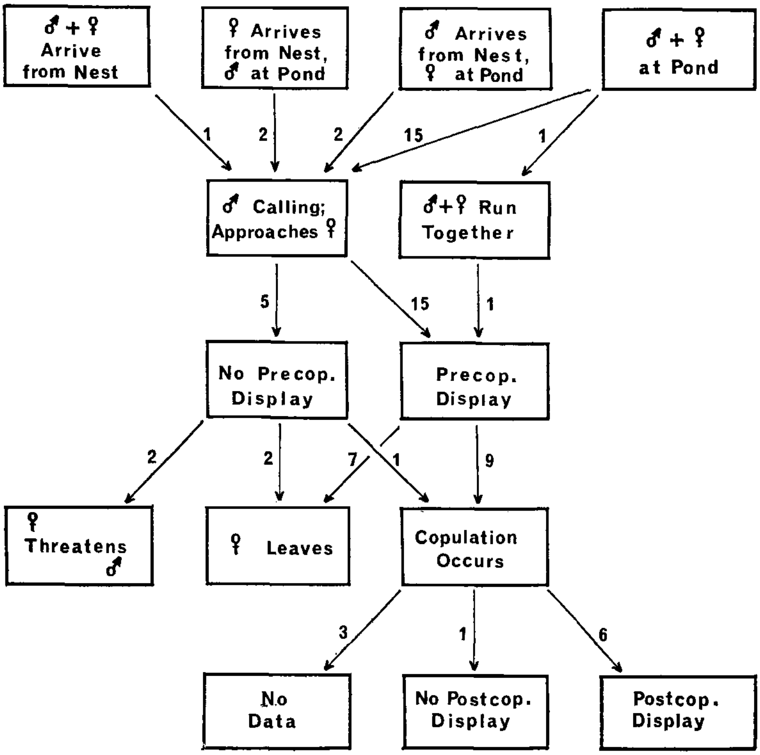

Figure 3. Diagram of behavioral sequences typical of copulatory situations.

the male began wing fluttering and mounted. Copulation was terminated when the female ran out from under the male. It was followed virtually always by a brief wing-up (= postcopulatory) display and then an upright posture. In situations where the female did not remain still in response to the precopulatory wing-up, this display was maintained for up to 8 seconds as the male walked after the female. The sequence described above is summarized in Figure 3. Postures are described below and illustrated in Figure 4; and three copulations that were analyzed frame by frame are summarized in Table 2. Similar copulation sequences were described in *Tringa nebularia* (Nethersole-Thompson 1951: 102–106).

Pair A was watched for 79 hours and 30 minutes (Table 1). Although this pair was studied nearly twice as long at its nesting muskeg as at the pond where it often fed (39:50 vs. 25:30 hours), all sexual encounters took place at the pond. Copulations and attempts appeared equally likely to occur at any time the pair was feeding at the pond;

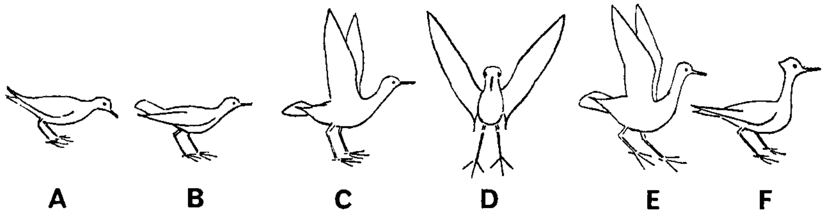

Figure 4. Postures typical of copulatory sequences: A, male approaches female in initial approach posture after uttering epigamic calls; B, tail is partly raised and fanned in transition to; C, precopulatory wing-up display as female is closely approached; D, just prior to mounting, male begins wing flutter which continues during copulation followed by; E, postcopulatory wing-up as female runs away from male; and F, upright if female turns toward male. See Table 2 for durations of above postures during three copulation sequences.

however birds were usually in the nest vicinity in the muskeg between 05:00 and 08:00. Not a single copulation or attempt was seen between 05:30 and 08:00 though I was in the field at this time each day. Numbers of copulations and attempts observed are summarized in Table 3. During the week from 5 days before the first egg through the day the second egg was laid, pair A performed 0.27 copulations and 0.35 attempts/hour of feeding for a total of 0.62 sexual encounters/hour. Pair A were probably feeding two to three times as many hours as I watched them and thus were involved in approximately 40 to 60

TABLE 2

DURATION IN SECONDS OF EVENTS IN THREE FILMED COPULATIONS ANALYZED FRAME BY FRAME

Behavioral sequence	Copulation 1	Copulation 2	Copulation 3
♂ initial approach (A+B)[1]	Walking slowly	Walking slowly	Walking fast
♂ precop. display (C)[1]	1.38	—	6.92[2]
♀ reaction to precop.	0.71	0.42	1.38[2]
♂ wing flutter (D)[1]	Moves slowly	Stops	♂ pauses 0.63 ♀ stops
♂ mount/copulate (D)[1]	3.38	3.13	2.13
Copulation ended	12.42	7.92	9.33
♂ hangs on	♀ runs out	♀ runs out	♀ runs out
♀ alert posture	0.17	—	1.25
♂ postcop. display (E)[1]	+	+	+
♂ upright alert (F)[1]	0.67	0.63	0.63
♀ walks to ♂	0.67	1.92	1.46
♂ still upright alert,	6.97	6.50	—
♀ walks away	+	+	+
TOTALS	26.37 seconds	20.52 seconds	23.73 seconds

[1] Letters correspond to specific reproductive postures identified in Figure 4.

[2] Duration of initial approach posture and precopulatory display more typical of unsuccessful attempts because female walked away rapidly.

TABLE 3
NUMBERS OF COPULATIONS (LEFT) AND ATTEMPTS (RIGHT)
RELATIVE TO TIME OF DAY

Time	Pair A	All pairs
04:00–10:00	1–4	1–4
10:00–16:00	4–0	6–0
16:00–22:00	2–5	3–7
TOTALS	7–9	10–11

encounters during this week. Certainly this number of encounters is sufficient to allow each member of the pair to learn thoroughly the individual behavioral characteristics of its mate, assuming that even minor differences occur. Such familiarity would provide considerable advantage to renesting pairs as it would enable them to breed in minimal time.

Initial approach.—Similar to head-down posture except that the head is slightly raised, the beak is pointed downward at 45°, the back slopes slightly downward, and the tail position varies from 30° up to 30° down (Figure 4).

Precopulatory wing-up.—Identical to wing-up shown in hostile situations (see above).

Wing flutter.—Wings flutter 10–45° above the horizontal, head is lowered and beak is pointed downward 30°. The wing flap rate is 2–3/second.

Copulation.—The male positions his head so as to enable pecking on the back of the female's head. The male's treading feet seemingly provide stimulation for eversion of the female's cloaca. The male's wings continue to flutter 10–45° above the horizontal until the cloacae come into contact at which time he turns the rear of his body under the female.

Postcopulatory wing-up.—Identical to wing-up shown in hostile situations (see above).

Display flight.—*T. solitaria* has a weakly undulating display flight that is accompanied by a high pitched, repetitive song (Oring 1968). During the flight, arcs are only 1–2 m in height and often the bird employs silent direct flight for 100 m or more before arching upward and singing. As the displaying bird arcs upward, the wingbeat becomes much more rapid and shallow. I never saw this flight performed repeatedly over the nesting area but usually as a male flew by the nesting area when coming to or leaving the muskeg. Display flights were more common during the day on which the first egg of the clutch was laid than at any other time. The repeated circuitous flights mentioned by

Grinnell (1900) were probably performed during the territorial establishment and/or pair formation phase of the season. This display flight is somewhat similar to that of the Wood Sandpiper, *Tringa glareola* (Kirchner 1963; Oring MS) and markedly less ritualized than that of the Green Sandpiper, *T. ochropus* (Oring 1968).

NESTING BEHAVIOR PRIOR TO INCUBATION

Pair A was seen nest-site prospecting on 16 May between 06:00 and 07:30, and nest visiting on 19, 20, 21, and 22 May between 05:10 and 09:40. Prospecting was accomplished when the male flew to a spruce, landed from 1.5–10 m high, and alternately walked down branches, stopped and looked around, or uttered contact calls (Oring 1968). Occasionally, especially in association with flying to another tree, he sang or gave epigamic calls (Oring 1968). The female perched silently, high in a nearby spruce, while the male searched.

Pair A found and revisited at least three old nests. It was impossible for me to observe nest visits closely without the risk of scaring the birds. I do know that on each of four mornings both birds visited the vicinity of at least two old nests, and that one member of the pair spent considerable periods of time actually on a nest. I presume that nest building was going on at this time as it is in *T. ochropus* (Oring MS) and other tringines. Bits of paper I placed in the nests were rearranged.

In contrast to the situation during prospecting, where the active or searching bird was much more vocal than its partner, during visiting the bird at the nest was far less vocal than its mate, which flew back and forth between the pond and nest. This same situation occurs in *ochropus* where I found that the male is the chief prospector, the female the nest-builder (Oring MS). I have not been able to prove that this is the case in *solitaria* though I believe it to be so.

The only nights prior to egg laying that pair A spent at the muskeg pond were 19–20 and 20–21 May. Before 19 May both members of the pair spent the night at the beaver pond 1 km from the muskeg. The first egg was laid about 07:15 on the 22nd, the second sometime on the 23rd, the third between 11:25 and 18:30 the 24th, and the fourth before 06:30 on the 26th.

During the egg-laying period at the one nest I watched, the sitting bird frequently engaged in typical shore bird nest-building behavior, i.e. scraping, pulling, throwing, and relief. All of the nest lining material thus manipulated was gathered while the bird was sitting or standing on the nest itself. Much of it was obtained by pulling material out of the rim of the nest proper. I made no attempt to describe this action in detail.

After three eggs were laid I replaced them with Killdeer (*Charadrius vociferus*) eggs. When the fourth was laid, I took it and the Killdeer eggs. Prior to this time when approaching the nest, I deliberately made myself obvious some distance from the nest. Both times the bird flushed and flew silently to a nearby tree with neither flutter-flying nor tail-spreading. When taking the final egg, I surprised the sitting bird at close range. It flutter-flew with tail spread to a nearby tree and sat uttering alarm calls (Oring 1968) for 20 minutes. This was between 06:40 and 07:00. I returned to the nest at 08:00 and 08:45 and observed the same behavior, which I interpreted as a combination of distraction and alarm-flee behavior. Both members of the pair were present at 08:00 and 08:45 when one took the active role in distraction and alarm, while the other remained 100 m away giving only a few alarm calls. The collected eggs were incubated in Minneapolis, Minnesota at 38° C and 90 percent relative humidity. Three of the four hatched: after 23 days, 15 hours; 23 days, 18 hours; and 24 days, 3 hours.

INTERSPECIFIC INTERACTIONS

I saw male Solitary Sandpipers in close proximity to other tringines on six occasions. Of the two Greater Yellowlegs (*T. melanoleucos*) encountered, one was ignored and the other was chased off with a head-down attack. Lesser Yellowlegs (*T. flavipes*) were encountered three times and each time *solitaria* in wing-up threat drove off *flavipes*. A Spotted Sandpiper was approached with a head-down posture and pounced upon.

On only two occasions were birds of prey seen in the vicinity of *solitaria*. A Sparrow Hawk (*Falco sparverius*) was ignored, and a Marsh Hawk (*Circus cyaneus*) elicited an upright posture accompanied by alarm calls (Oring 1968) and subsequent flight.

DISCUSSION

Solitary Sandpipers vigorously defend large, all-purpose territories around muskeg ponds. Old Rusty Blackbird nests are nearly always available beside such ponds as the range and ecological preferences of this species are virtually identical to those of *solitaria*. The availability of such nests throughout *solitaria*'s range has undoubtedly influenced its success. Were it not for Rusty Blackbird nests, *solitaria* often would have had to nest far from ponds; that in turn may have led to the evolution of larger territories and a communication system designed for efficiency over longer distances. Such a situation, where available nests are widely spaced and often long distances from feeding spots, has influenced the evolution of *ochropus*, leading to larger body size, larger tail with a greater contrasting pattern, a more visibly obvious display flight involving deep undulations and dives, and vocalizations that are lower in frequency, louder, more frequent, and more specialized (Oring 1968).

The reproductive behavior of *solitaria* is similar to that of its ground-nesting relatives. Solitary Sandpipers search for and find several nest sites that they modify with building methods typical of ground-nesting scolopacids. They show no evidence of morphological adaptations for arboreal living, and only the location of nest-site prospecting and subsequent nesting can be considered an arboreal, behavioral adaptation. The head, body, tail and wing positions assumed by *solitaria* are very similar to those found in other tringines, these postures seemingly having a common origin in preflight intention movements. Though these postures vary on a continuum, indicating slight changes in motivation, it is possible to describe typical display intensities. In doing this, the similarity of postures employed in agonistic and reproductive situations is obvious, i.e. head-down and initial approach postures are quite similar; wing-up, upright, and flutter-flight displays occur in both agonistic and reproductive situations; and the copulation posture of females is much like the crouch posture of submissive males. It appears that *solitaria* males employ their simple repertoire of visible displays in both reproductive and agonistic encounters, possibly indicating similar physiological regulation of behavior.

ACKNOWLEDGMENTS

D. Parmelee critically reviewed the manuscript and prepared the drawings. R. Lister and D. Parmelee kindly advised me about study areas and field problems. The entire staff of the Bell Museum of Natural History was immensely helpful. The Chapman Fund of the American Museum of Natural History loaned me photographic equipment. Financial aid was provided by PHS training grant No. 1 TO1 GM01779.

SUMMARY

Solitary Sandpipers were observed for more than 95 hours at Crimson Lake Provincial Park, Alberta. Large, all-purpose territories were defended by males who identified the sex of an intruder by its behavior. The one territory measured was approximately 0.5 sq km. Frequent copulations and attempts allowed ample opportunity for the learning of individual behavioral characteristics. All copulations occurred at feeding ponds some distance from nesting areas. Postures involved in hostile encounters were similar to those used in reproductive situations, and both varied in a continuous way depending on the bird's motivation. *T. solitaria* shows no noticeable arboreal adaptations other than the stereotyped habits of prospecting and nesting in trees.

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