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## AGGRESSIVE BEHAVIOR IN MIGRANT PECTORAL SANDPIPERS

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The analysis of territorial behavior of migrants and wintering birds may prove to be a particularly fruitful approach to the behavioral analysis of territoriality since some of the complicating elements of nesting territories are lacking. Individuals of some species such as the Mockingbird, *Mimus polyglottos* (Michener and Michener, 1935) and the Anna Hummingbird, *Calypte anna* (Pitelka, 1951) defend somewhat reduced territories in the breeding area throughout the year. Many migratory species maintain territories in the fall and winter but as far as I have been able to determine the only shorebird species which has been reported with a territory at this season is the Lapwing, *Vanellus vanellus* (Lind, 1957). The fact is, however, that individuals of a number of North American shorebirds maintain territories for greater or lesser periods at stops in the course of migration. This account describes territorial behavior of the Pectoral Sandpiper (*Erolia melanotos*) observed on the Delta Marsh of south-central Manitoba, Canada, well south of any known breeding area for this species.

The Delta Marsh is separated from Lake Manitoba to the north by the lake ridge, a low wooded pressure ridge. Near the village of Delta a second similar bar runs parallel 150 meters deeper in the marsh. Recent years of high water flooded the dense stand of *Phragmites* in the intervening marsh, known as the Back Marsh, and at the time of this study it was an open pool choked with submerged vegetation and capped with a mat of duckweed (*Lemna minor*) and algae thick enough in places to support feeding shorebirds. In the shallower parts of the Back Marsh broad spans of debris-littered mud provided favored feeding areas for numbers of Pectorals and other shorebirds. Elsewhere on the marsh Pectorals were widely distributed in areas generally shallower and drier than those situations preferred by most local shorebird species, although some individuals remained with mixed flocks of other species. An occasional individual was seen along the sandy beach of Lake Manitoba and on August 26 two Pectorals were flushed from the edge of a harvested barley field not far from a creek just south of the marsh. Repeated checks of shorebirds frequenting flooded fields at this season failed to detect this species.

### ACKNOWLEDGMENTS

H. Albert Hochbaum, Director of the Delta Waterfowl Research Station, made valuable suggestions which greatly facilitated the assembly of pertinent information in the limited time available for this study. Dr. Frank McKinney took movies which were invaluable in interpreting the behavior described here. Others of the staff at Delta extended numerous courtesies and assistance in the course of the field work. Dr. Peter Marler made helpful suggestions during the preparation of this paper and he carefully read the manuscript. I am indebted to Jerram L. Brown and Dr. Frank A. Pitelka for stimulating discussions of certain aspects of territoriality. Gene M. Christman based the illustrations on movies and photographs taken by Dr. McKinney and the author. At the time these observations were made the author was conducting an experimental study of duck orientation mechanisms supported by the Wildlife Management Institute

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#### METHODS

Most of the field observations were made from a car parked on a dike crossing the Back Marsh. This method of observation was less disturbing to the birds than an unconcealed observer or a blind and the observer could arrive and depart without putting the flock to flight. Moreover, after the birds had become accustomed to the car it could be moved opposite interesting encounters without disrupting them. Most observations were made with binoculars on birds from four to 25 meters from the observer.

Throughout much of the summer of 1956 single Pectoral Sandpipers were noted day after day at certain places at the edge of the marsh and on roads across it. The following summer a careful watch was maintained for the arrival of the Pectorals. The first influx was noted on July 17, and by the morning of July 19, when systematic observations were begun, some Pectorals had already established well-defined territories. No birds were individually marked in the course of this study, but a few birds could be recognized with reasonable certainty by certain morphological and behavioral peculiarities. For example, bird A centered its feeding activities on a small islet and when flushed often flew to a small mud bar at the edge of the marsh. The adjoining territory owners, B and C, were both considerably smaller in body size than A. Bird B was more wary than its neighbors. When it returned to its territory, it almost invariably landed within a foot of a particular spot in its territory and from there fed counterclockwise along the shore until it came opposite a small mat of vegetation a few feet away. Then it would fly across to the mat and feed for a time before returning to its original path around the island. C spent much more time resting and preening than either A or B, usually at the base of a post near the center of its territory. Its feeding routine was as predictable as that of B. Observations of this sort together with a concentration of aggression along well-defined boundaries and the predictability of the outcome of these encounters helped confirm the identities of a few individuals.

#### FLOCK ORGANIZATION AND BEHAVIOR

One flock of about 35 birds occupied the same area of the marsh for 13 days beginning on July 17. Desertion of the area was probably due to repeated human intrusion. A flock of over 50 birds remained at another location from July 21 (and probably a few days before) through August 15, at least 26 days. Probably these birds migrated rather than moved elsewhere on the marsh, since desertion coincided with a general migration of several species of shorebirds in the Delta area and with a sharp decline in the number of Pectorals on the entire marsh. Both of these flocks completely vacated the areas they had occupied. The area of the smaller flock was reoccupied by a smaller number of territorial Pectoral and Semipalmated (*Ereunetes pusillus*) sandpipers a few days later. The area occupied by the larger flock was flooded by heavy rains following the departure and was not utilized again by Pectorals during the summer. None of the flocks under observation contained young of the year; careful vigil failed to reveal these easily recognized birds until August 25.

All of the flocks of the Back Marsh, several hundred birds in all, remained at their chosen locations throughout the day. Shortly after sunset on clear evenings scattered individuals from the many flocks flew up and headed south over the main marsh. The exodus became most pronounced about 20 minutes after sunset, and 15 minutes later the Back Marsh was vacant of Pectorals. On clear evenings the timing was quite precise but on overcast evenings the departure was always earlier, sometimes as much as 25

minutes. Over a mile to the south the Pectorals joined great flocks of other waders: Greater (*Totanus melanoleucus*) and Lesser (*Totanus flavipes*) yellowlegs, Marbled Godwits (*Limosa fedoa*), dowitchers and hordes of smaller shorebirds which had assembled on a long mud bar jutting into the open water of the main marsh. Before sunrise the Pectorals returned to their places on the Back Marsh.

The size of the Pectoral flocks ranged from about 25 to over 150 birds. It soon became evident that flock unity was maintained with little or no exchange of individuals between flocks, for certain individuals were recognizable and repeated counts of individual flocks showed little variation from day to day. Perhaps flock unity was favored in this area by the presence of deeper intervening areas less suited to feeding. Usually when a flock flew up it would not join other flocks circling nearby. Occasionally joining took place but the mixed flocks usually separated before landing. Sometimes a composite flock would land and then, after a brief interval, the foreign flock would fly up and return to its own area.

All flocks included both territorial and non-territorial individuals. The non-territorial birds remained at the core of the flock and territories were established about the periphery. In one flock about 35 birds occupied a central area of about 500 square meters. These were surrounded by from 15 to 17 territorial individuals, some with territories bordering the central area, others farther removed. The percentage of territorial individuals in other flocks was similar.

While any great disturbance flushed the whole flock, any birds remaining behind were usually territorial individuals, although an occasional bird would remain in the central area. If a territorial bird was the first bird to take flight, it usually passed over the central area. Here it might land or pass on, other birds joining the flight as the calling bird passed overhead. If the stimulus initiating flight was not great the flock often flew only 20 or 30 meters before returning. In this situation the territorial birds might return directly to their territories. Usually, however, all the birds landed in the central area. There the territorial birds delayed for two or three minutes, preening and feeding, and then flew out to the territories. The typical creaking call was given continuously during the flight. Often several territorial birds flew up at once and all of them moved out to the territories during a brief span, usually less than a minute once the movement had begun. If the disturbed flock left the vicinity of the Back Marsh, it invariably circled over the ridge to the south in the direction of the evening flight. The flocks were never seen crossing the lake ridge to the north regardless of the wind direction and the approach direction of a disturbance.

#### BEHAVIOR OF INDIVIDUALS

*Displays.*—Only fragmentary notes (Brandt, 1943; Scott, 1951) on the behavior of Pectoral Sandpipers have appeared since Nelson's initial description (1884) of the spectacular balloon display on the breeding grounds in the arctic. Pitelka (MS) reports that this display is used in courtship as well as in male to male territorial encounters. It was not seen during the present study. Some of the fighting postures of the Pectoral are less flexible in their expression than others and all are subject to some variation. For this reason the illustrations which accompany this paper represent only what is considered to be a typical expression of the described postures. The intense sparring and fighting is more likely to be opportunistic than the threats given from greater distance. In fighting particularly the postures often blended imperceptibly one to another.

*Alert.*—An alerted posture (fig. 1a, b, c) with the neck stretched high and the legs straightened is characteristic of many species of shorebirds and other birds as they watch

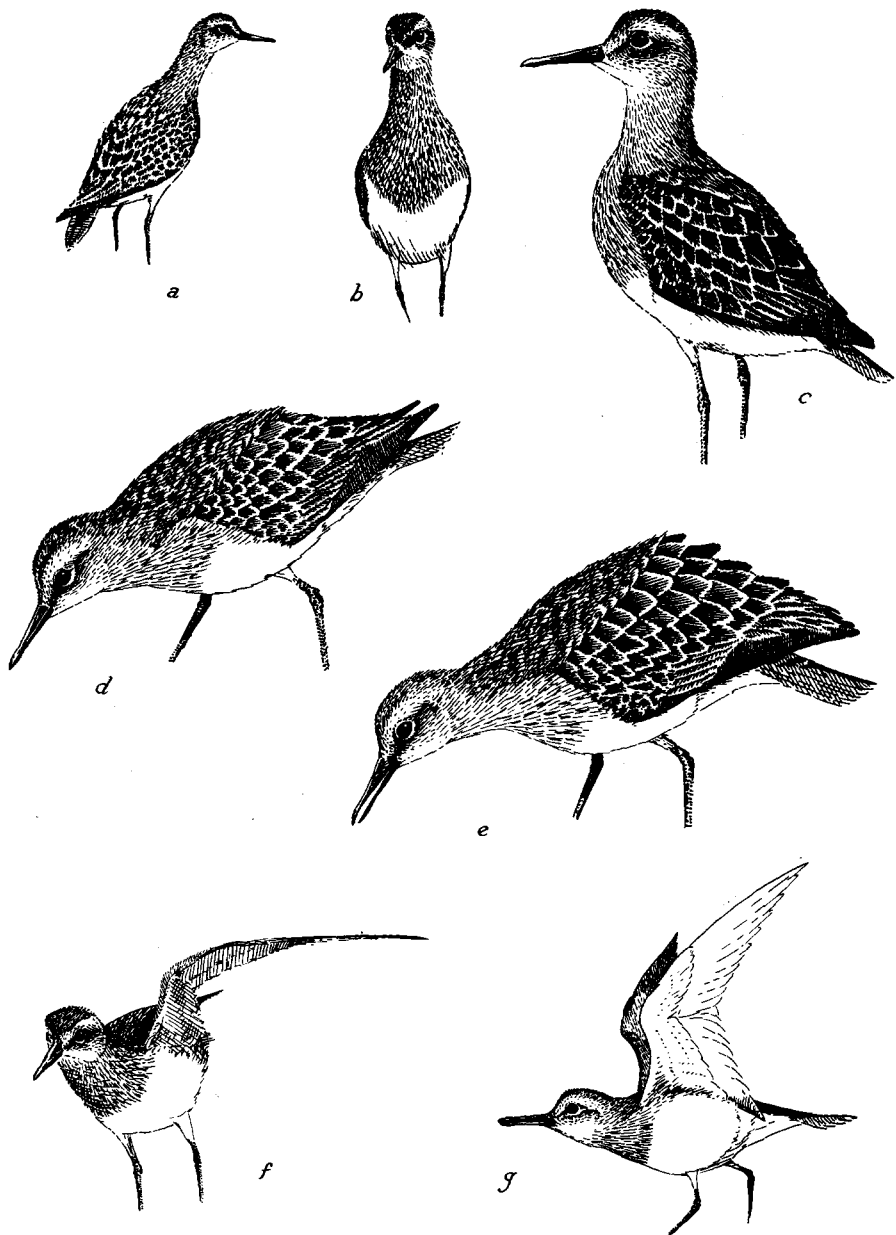


Fig. 1. Typical postures of Pectoral Sandpipers: a-c, alert; d, normal feeding; e, displacement feeding; f, wing-away; g, supplanting. Drawings by Gene M. Christman.

a predator or a potential territorial intruder. In the Pectoral this posture is typically a response to minor disturbances which may or may not precipitate flight. In this situation the head is moved quickly back and forth short distances while the body is held in place. The posture has a range of expression, the intensity of which may be judged by the degree to which the bird stretches the neck and raises the forepart of the body and by the extent and vigor of the backward and forward movements of the head. Often a

hollow sounding *ooot ooot ooot ooot* call accompanies the posture (fig. 1a). Passing flocks of Pectorals, Tree Swallows (*Iridoprocne bicolor*), and even a calling Downy Woodpecker (*Dendrocopos pubescens*) on the nearby ridge elicited this response.

A nearly identical posture but with the head held farther back (fig. 1b, c) preceded almost all supplanting charges and was given anywhere in the territory, often accompanied by a rapidly chattered *id id id id id* call. This behavior seems to convey a considerable element of threat and was often elicited by non-territorial birds which had landed or were about to land nearby. Usually this was sufficient to make an intruder fly up. A similar posture seen in territorial Lapwings (*Vanellus vanellus*), also seems to be threatening (Lind, 1957). At least one observation seems to indicate that neighboring birds did not always distinguish correctly the message conveyed in the two situations in which this posture appeared. Once a slight movement on my part appeared to elicit the alerted posture from a feeding bird less than six meters from me. At once a second territorial bird feeding over three meters from the first assumed the same posture and moved toward it, having apparently interpreted the posture as a threat. The rest of the flock did not react to the movements of these two birds although the alert in response to danger often spread quickly through the flock.

*Crouch.*—In the crouched posture (fig. 3a, b) the head and neck are stretched forward over the ground and the ankles may be bent, lowering the body close to or touching the ground. Sometimes the tail was lowered and occasionally fanned on the side toward the opponent. The back feathers were sometimes erected (fig. 3b) and the carpal joint of the wings held slightly away from the body, but the wing tips remained nearly in place. A harsh, high-pitched continuous squeaking call frequently accompanied this posture. Crouching was a conspicuous feature of territorial encounters and often several pairs of birds throughout the flock were in this posture at once. In territories crouching occurred only at the boundaries, but it was also conspicuous in the non-territorial area. Often an advancing bird would move forward in this posture with minced steps either directly or, more frequently, half-sideways. Crouching frequently stimulated opponents to take up the same posture. Crouching also seemed to inhibit attack. Birds in this posture were rarely attacked regardless of the intensity of the encounters. Most frequently the two crouching birds aligned themselves parallel, facing either toward one another (fig. 4b) or in the same direction (fig. 4a); but sometimes, especially if the birds were facing one another, their alignment formed an angle of over 45 degrees (fig. 4c). No more than two birds were ever seen crouching together.

Some authors (Forbush, 1912; Hudson, 1920) have reported Pectorals "sitting close" in a crouched attitude when approached. Once I saw what appeared to be this posture in a feeding flock of Pectorals as I crawled through a dense stand of *Phragmites* to get a better view. As I neared the edge of the thick vegetation, my presence was detected by several of the nearer birds. At once they crouched in an attitude much deeper than the usual preflight bow (Daanje, 1950), with the head and neck fully extended in the crouched position. Another time, when I chased a bird with a crippled wing down a dirt road it suddenly assumed a posture similar to the crouch and remained motionless. When dogs approached captive caged Pectorals the birds sometimes responded by crouching. On the basis of these observations it seems likely that this posture expresses a considerable element of fear.

*Wing-away.*—A movement of one wing (fig. 1f) raised by a territorial bird as it retreated from a border fight was occasionally seen. Usually the wing raised was the one away from the opponent, thus revealing the upper surface of the wing. Hohn (1957) records what may be a homologous movement in the White-rumped Sandpiper (*Erolia fuscicollis*) and the Baird Sandpiper (*Erolia bairdii*).

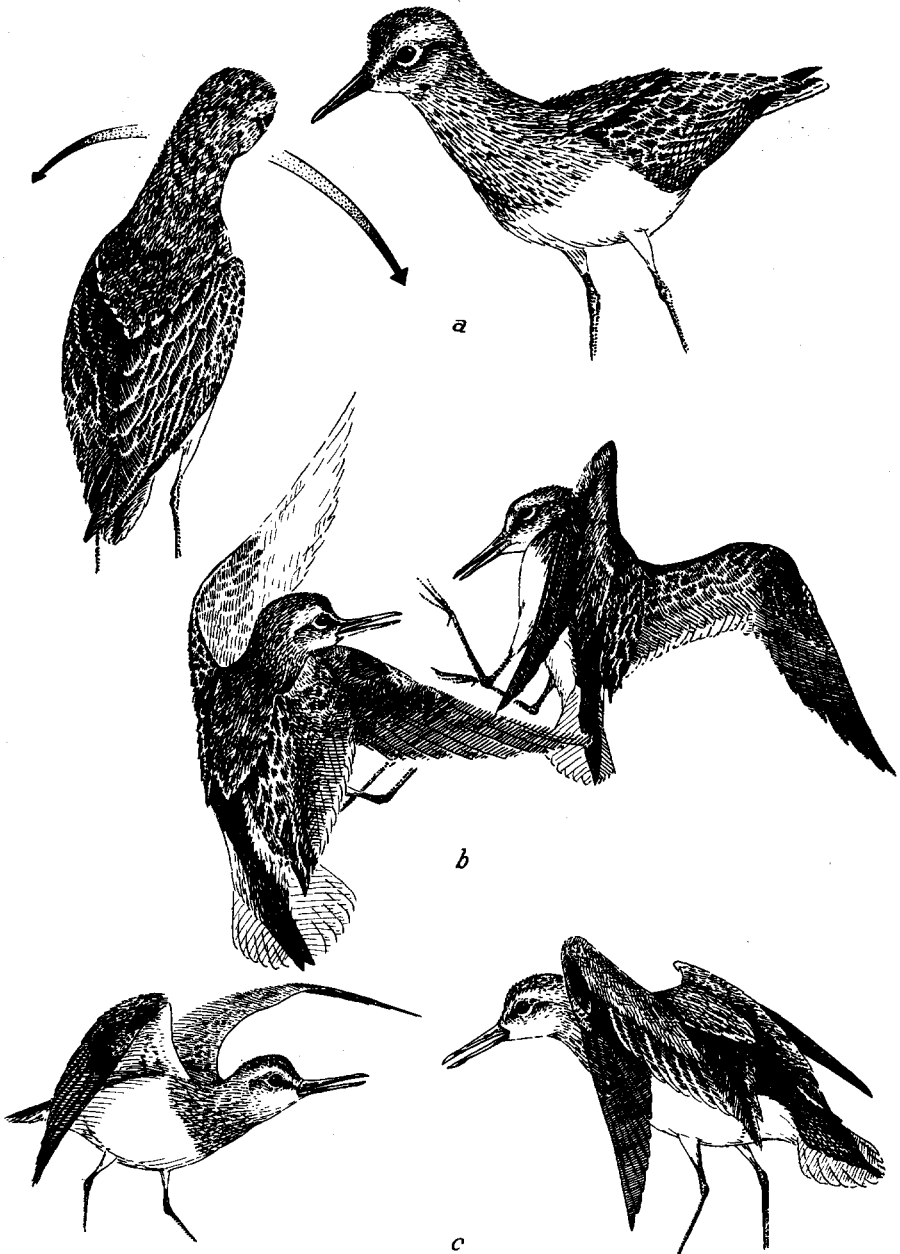


Fig. 2. Aggressive postures of Pectoral Sandpipers: a, sparring, the arrows indicating the direction of head and neck movements; b, fighting; c, sparring in spread posture. Drawings by Gene M. Christman.

*Wing-spread.*—This position (fig. 2c) is similar to the sparring posture but one or both of the wings are held away from the body. The wings are bent sharply at the carpal joint and as the bird stands erect the white undersurface of the wing is exhibited to the opponent. If one wing is held farther away from the body than the other, it is frequently but not invariably the wing toward the opponent, although the two birds

never face more than slightly away from head-on. This position is maintained only during intense encounters and is often interspersed with actual fighting.

*Supplanting.*—Aggressive supplanting is one of the most conspicuous features of the behavior of territorial and central-area birds. In a supplanting charge a bird either rushes across the ground or flies at the opponent or combines the two methods of attack. The choice of the pattern used apparently depends to a large degree on the distance to the territory violator. Flights were more frequent from distances over three meters, but

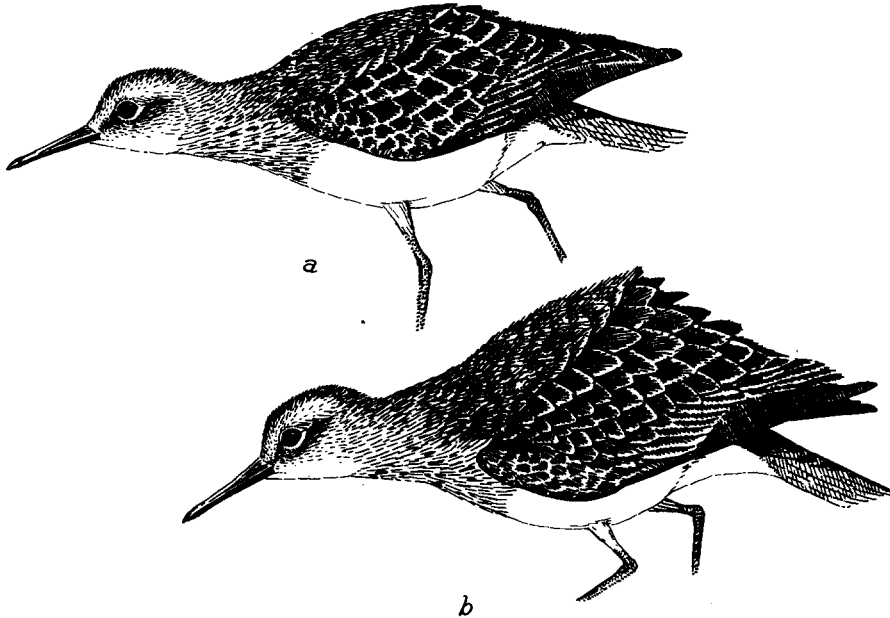


Fig. 3. Two variations of the crouch posture of Pectoral Sandpipers.  
Drawings by Gene M. Christman.

occasional charges on foot were noted from considerably greater distances. The posture of the bird charging on foot is quite variable. Sometimes the head is held low and the body is depressed in a position much like the crouch (fig. 3a). This method of supplanting is more frequent in the central area. Here attacks are usually terminated when the aggressor delivers a jab with its bill or the opponent moves on. During the charge the back feathers are sometimes erected. Less frequently the charge is made in an upright posture similar to the alert or even with the wings held away from the body as in the spread. As a bird flies at an opponent it gives a harsh repeated call. Usually the trespassing bird departs before or as the territory owner lands. Typically the aggressor lands just in front of the bird against which the attack is directed. The study of movies of this action suggests that the attacking bird runs across in front of the opponent with the wings held high overhead (fig. 1g). In one case the trespasser apparently did not see the approaching owner, which landed directly on the back of the feeding bird. Supplanted birds often landed in the territories of other birds only to be quickly supplanted again. Several such encounters might occur before the bird lands in the central area or flies off to another part of the marsh. Often the supplanting charges directed at the intruders draw territorial birds to the edges of their areas, initiating encounters with neighbors.

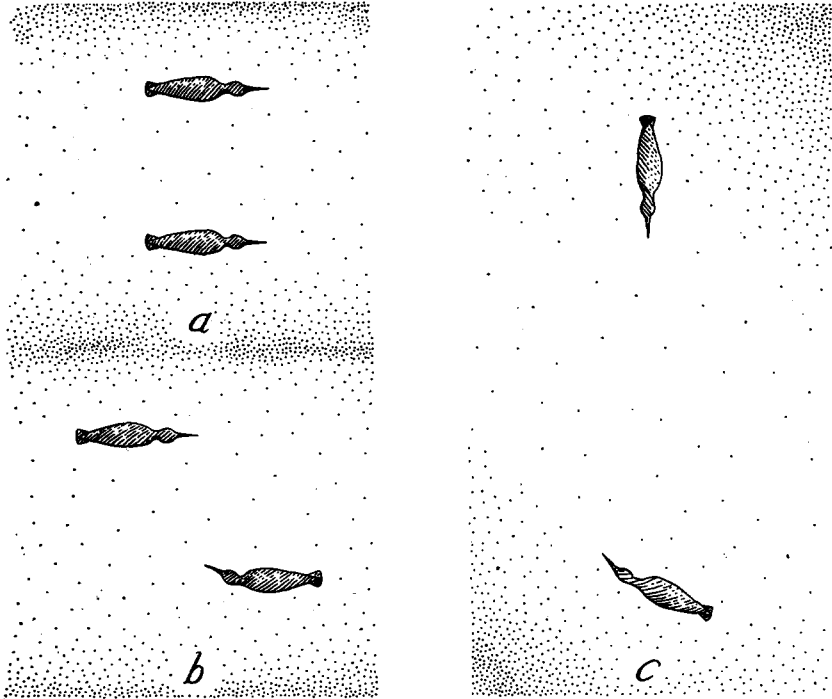


Fig. 4. Orientation of pairs of Pectoral Sandpipers in the crouch posture. The area of light stippling indicates the territorial boundary.

#### INAPPROPRIATE ACTIVITIES

Because of the limited nature of the data presented here a critical review of current ethological concepts and controversies seems inappropriate. Primarily, therefore, the classification of behavior used in describing territorial activities is presented only to facilitate description and to make the information presented more usable to others.

Certain seemingly inappropriate activities typify territorial encounters. Movements of this sort performed under similar circumstances have been termed displacement activities (Tinbergen and van Iersel, 1947) if the expressed behavior is apparently alien to the activated tendency. "Tendency" to behave is used here as a descriptive term more directly related to the observed behavior (Hinde, 1955) than a term such as drive. It implies only that the animal is more likely to behave in one way than in another.

*Displacement feeding.*—Most territorial encounters were preceded by active feeding (fig. 1d) and this usually persisted as a bird approached a neighboring individual. Often, however, long before any signs of posturing had appeared, it became obvious that a boundary dispute was imminent, for the feeding jabs became more intense and the birds moved toward the boundary more rapidly than during undisturbed feeding. As the gap between the two birds closed, the feeding became sporadic and the jabs were sometimes directed at short stubble, a pattern not typical of the usual feeding routine. Now the birds might crouch with the tail lowered and the back feathers erected (fig. 3b) and yet make sporadic jabs into the substrate with the bill. Again, as the birds retreated from the crouch there was first intense feeding but this gradually subsided to the ordinary feeding routine (fig. 1d) as the gap between the antagonists widened. Thus, in this situation, the distinction between normal feeding and displacement feeding could not



be clearly made. Feeding of such an intermediate type may have been functional at times in the sense that particles of food seemed to be swallowed occasionally, but the feeding jabs delivered from the crouched posture seemed to be entirely vicarious. Feeding thrusts unaccompanied by swallowing movements were also interspersed with sparring, either singly or in brief spurts, but always in much more vigorous and halting manner than during normal feeding.

*Displacement sleeping.*—Displacement sleeping is characteristic of fighting in the Avocet, *Recurvirostra avosetta* (Makkink, 1936) and Oystercatcher, *Haematopus ostralegus* (Makkink, 1942). One observation of Pectoral behavior may possibly be referable to this phenomenon. A bird had just supplanted a territorial neighbor that was feeding along a territorial boundary. The attacker immediately crouched and the attacked bird flew to a log several feet away in its own territory and immediately assumed the sleeping position with the head on the back. Before feeding to the territorial boundary this bird had been preening extensively, a characteristic pattern before sleeping. In numerous other similar encounters no such pattern appeared. Thus, if displacement sleeping occurs at all in the Pectoral it is rare at this season.

*Redirection activities.*—Activities appropriate to the activated tendency but with inappropriate orientation have been termed redirection activities (Bastock, Morris, and Moynihan, 1953). Many instances of what appeared to be redirected aggression were noted among the territorial birds. Usually these involved birds at a territory encounter in which one of the participants would suddenly turn and supplant another bird some distance from the original opponent. Typically this second attack was directed at an individual which was exhibiting less aggression at the moment, either a non-territorial individual or a bird of another species. This attack usually supplanted the new opponent and the encounter ended. Typically this behavior pattern was demonstrated by smaller territorial birds when encountering larger individuals and by birds which were being defeated in sparring and fighting maneuvers.

As the territorial boundaries became better known to the observer an alternative explanation of some instances of apparent redirected aggression became possible. Sometimes the object of the new aggression was penetrating the territory of the attacker to a greater depth than the bird that was under current encounter. This situation almost invariably provoked an attack. On the other hand certain of the observations seem beyond doubt to be attributable to a redirection of aggression as the following example demonstrates: Two Pectorals were crouched inches apart at the territorial boundary. Another Pectoral landed less than a meter away in the territory of A. Now bird A left the crouch at once and supplanted the new arrival. In a few moments both A and B were again crouched at the border and again A left to supplant another Pectoral which had landed in its territory, this time passing by two Least Sandpipers (*Erolia minutilla*) which were also feeding in the territory. As A and B again approached one another at the border one of the Least Sandpipers fed to one side of A and slightly deeper in A's territory than A. Suddenly B attacked the Least Sandpiper, moving past A well into A's territory. Now A fell on B, fighting vigorously and B was quickly evicted from A's territory to the border where both birds again crouched. Shortly thereafter both fed away from the boundary.

*Shaking.*—Rapid rotating shakes of the body, closely resembling a similar movement found in most birds, were frequent during preening and after bathing. In this context, interpretation of the function in terms of autochthonous or immediately useful feather rearrangement seems fully adequate. Following territorial encounters shaking was also frequent, usually after the displacement feeding had subsided and the birds had retreated some distance from the boundary. It was also frequent in birds which

had flown off a short distance after having been supplanted regardless of whether or not the supplanted bird had displayed. Shaking appeared here shortly after the birds resumed feeding, more frequently if overt fighting had been a part of the interaction. Shaking rarely or never occurred prior to encounters when normal feeding blended to displacement feeding prior to an aggressive encounter. If, in these contexts, the movement is an autochthonous response to feather misplacement, it might be expected to appear following landing, when the feathers would seemingly be disordered as much as when a supplanting flight without physical contact had occurred.

Andrew (1956) studied a similar movement in several species of *Emberiza*. He found that shaking (feather-settling in his terminology) was prone to occur when the nature of activity changed. His interpretation is that "irrelevant feather-settling movements thus appear to occur when two conflicting tendencies are present, but neither are strong." Armstrong (1952) has suggested that shaking is a displacement activity in similar contexts in the Ringed Plover (*Charadrius hiaticula*) and other birds but Simmons (1955) feels that such movements are more likely to be autochthonous comfort movements in direct response to the misplacement of feathers during display. If shaking results from autochthonous stimulation as Simmons suggests, it still does not explain the latency of its appearance following the encounters just described. This seems to be fully accounted for, however, by Weidmann's (1956) suggestion that in the frightened Mallard the feathers are sleeked and the bird is unable to shake them in order until the retarding influence of the escape drive has been eliminated. The shaking is thus interpreted as an autochthonous response to feather misplacement and sleeking which is probably sympathetically innervated. The latency is explained in terms of the duration of sympathetic response and consequent sleeking. The contexts of Andrew's observations (*op. cit.*) lends support to this hypothesis. It is thus no longer necessary to explain the movement in terms of conflicting tendencies at least not in the sense that the movement is some sort of a behavioral product of the conflict.

*Defecation.*—This is another activity which cannot be categorized simply. It occurred at intervals of several minutes during normal feeding but became increasingly probable in the situations of excitement. It was frequent in the alert posture or the bow (Daanje, 1950) prior to taking flight and also during aggressive encounters, particularly in the crouch, occurring just before and just after the period of posturing and fighting. Simmons (1955) noted defecation as a typical response of frightened waders throughout the year. Careful study of the situations where defecation or defecation movements (spreading the feathers about the vent without producing feces) occur may reveal that a preponderance of such movements occurs when fear rises sharply in any contest.

#### FIGHTING

Fighting and mutual threatening occurred only rarely if one of the participants of a clash was a non-territorial individual. At territorial boundaries, however, clashes involving threatening were numerous and fights were frequent. The most common posture in boundary threatening was the crouch. Often this led to sparring, the birds standing bill to bill swaying the outstretched necks in unison in an arc from side to side (fig. 2a). Sometimes this movement brought one or both of the birds nearly to the position of the crouch again, and indeed a rigid crouch was often assumed at this point. Two birds might begin sparring immediately without crouching first, especially at certain locations where the position of the boundary had become well fixed during numerous previous encounters. Overt fighting might follow crouching or sparring but more frequently it resulted directly from supplanting charges with no preliminary posturing. In

these instances fighting broke out instantly, both birds jumping into the air and kicking and stabbing at the opponent (fig. 2b). The wings seemed to be used only to balance the bird. Sometimes fights lasted several minutes and in these encounters the fighting in flight alternated with fighting on the ground. In the latter the spread posture was used, usually with both wings held away from the sides. Sometimes the spread accompanied the alert posture and at other times it was a part of a lower charging position (fig. 2c, bird on left). These prolonged fights were more frequent when the boundaries were being adjusted during the initial period of territory establishment and at particular points on boundaries which seemed to remain in dispute over a period of several days. Usually fights were brief, with the defeated bird taking flight or retreating slightly and dropping into a crouched posture. In the crouch the defeated bird was usually not further molested. Often the victor also crouched and eventually one or both birds walked away from the boundary, feeding vigorously. But occasionally the victor would press the matter further, leaping atop the crouched opponent and hammering at its head with its bill, finally grasping the feathers of the nape with the bill and tugging at them. In such instances there was no evidence of additional defense by the loser. One such attack resulted in the loser being driven deep into the mud where it remained for some seconds after the victor had relinquished its hold and moved away. The loser slowly rose from the mud but was so wet it was unable to take flight when the flock flushed and it did not fly off until several minutes later. There was no apparent loss of feathers in any of the fights.

#### AREA AND TERRITORY

The outstanding feature of the behavior of the territorial birds was that the tendency to attack or to flee from another bird was dependent on the location of both birds involved. That is, the probabilities of attack or retreat were determined by the location of the territorial individual and its neighbor with respect to certain fixed landmarks. When two birds crouched, they always aligned themselves on their own side of the boundary line. If either bird crossed the line, fighting broke out at once and the positions were quickly corrected.

The boundary was recognized by both parties. When two birds were feeding in adjoining territories, one might appear to be headed directly into the territory of another and a boundary dispute seemed inevitable. Yet just as it arrived at the boundary it would turn to feed along the boundary briefly and then return to a more central location in the territory. This was the characteristic pattern when the neighboring individual was present, even though the owner might make no apparent aggressive move. It seems, therefore, that once the territorial boundary had been established avoidance played a large though less spectacular part in the maintenance of territorial boundaries. When the owner was absent, however, usually visiting the central area, boundary trespass was often flagrant. An example of such behavior and its usual consequences follows: A had been feeding in the central area while B fed in its own territory. Now B fed to the A-B boundary and, slowing its forward progress somewhat, continued into A's territory. B had moved over a meter into A's territory when A returned, calling sharply. B half-ran, half-bounded across the border and dropped into a crouch with back feathers sleeked, less than 10 centimeters behind the line which I had plotted as the fight border. A also dropped into a crouch where it landed, the back feathers erect. From these positions they began feeding, B retreating from the border.

Typically the aggressiveness of territorial animals wanes sharply when they temporarily leave the territory (Nero, 1956; others). Some territorial Pectorals were slightly more aggressive than non-territorial birds when they were flushed to the central

area, although they were considerably less so than during territory occupancy. But differences were slight and often territorial birds were supplanted by residents of the central area. An example follows: A, B, and C had been fighting frequently at their adjoining territorial boundaries. A disturbance flushed them and they flew to the central area, maintaining their relative positions but landing about a foot from one another. In a moment they began feeding in place in a manner in no way distinguishable from normal feeding. At this distance these same birds on their territories would surely have crouched or fought. In a few minutes they returned to their territories.

The territorial boundary between A and B was studied in particular detail. Locations of fights were used to plot the hypothetical border. The plotted location of the border remained constant from day to day, usually varying less than 10 centimeters, but at one point an adjustment of nearly a foot took place over the span of several days. The zone where crouching might normally be anticipated ranged about a foot to either side of this fight line, although occasionally a single bird might crouch more than a meter from the border. Such crouches were never mutual. Anywhere from the border to about two meters from it, agitated feeding might be expected which increased in intensity near the border or the neighbor. Body shaking was most frequent in a wide zone well behind the boundary.

Conflicts were prone to occur in certain positions along a border and fights or mutual crouching were usually confined to these positions. Nevertheless, an entire border existed and some interactions occurred along the whole boundary. Birds D and E sparred many times a day at one point along the border. Here the position of fighting was localized on a small bit of higher ground. But, even on a rather uniform boundary such as that of A-B, interactions were largely localized. About half of all conflicts occurred within six inches of the base of a small clump of debris, the debris being approximately on the boundary. A dead cattail stalk (*Typha*) lying on its side was another point of concentrated boundary interaction. These two objects were the most prominent landmarks along an otherwise quite uniform boundary. Prominent landmarks formed a part of other territorial boundaries. Perhaps the lack of easily recognizable landmarks in a relatively uniform terrain explains in part why fighting was confined to these spots and why boundaries were sometimes less fixed at other positions along the boundary. Von Frisch (1956) found that territorial boundaries of the curlew (*Numenius arquata*) were often drainage ditches which dissected terrain that was flat and unmarked. William J. Maher (personal communication) tells me of watching male Pectorals on May 29 and 30, 1957, giving mutual aerial display on opposite sides of a tributary of the Meade River in Alaska when the narrow channel was the only prominent landmark in an otherwise nearly uniform snow-covered terrain. These observations would seem to indicate that the border is recognized by the surface landmarks in the vicinity of the actual boundary of the occupied area and that the locations of boundaries may be to some degree predetermined by the location of these landmarks.

Throughout the day, territorial defense was continuous regardless of the activity of the territory owner. Daily absence from the territory, largely if not entirely due to disturbances (low-flying aircraft, hawks, human disturbances, and so forth) probably amounted to less than an hour during approximately 16 hours of occupancy. Even in the evening after sunset, with the daily exodus to the main marsh minutes away, disputes and fighting continued seemingly unabated. During prolonged rain the number of aggressive encounters diminished, probably due to the lessened activity, for many birds stood motionless in a resting position or with the head withdrawn. Such occasions emphasized the rarity of inactivity in these birds. The resting posture was not seen at other times. Feeding, fighting, preening, and sleeping consumed the day.

Territorial aggression appeared to wane slightly in August but no general breakdown of the territories was noted. The waning of interspecific aggression was the best indication that the strength of aggression was diminishing.

#### BEHAVIOR IN ESTABLISHMENT OF TERRITORIES

Considerable shifting of boundaries accompanied the establishment of territories. The following account of such an encounter is typical: J, an exceptionally large bird, had repeatedly advanced on K which fed on a small (approximately one by two meters) mud island. As J reached the edge of the flat both birds crouched and suddenly began sparring and fighting. Then both birds dropped back into a crouch and fed in opposite directions from the boundary. J drove off another bird some six meters away on the opposite side of his territory then returned to the boundary shared with K and began sparring, in the course of which K was driven back slightly. A few moments of undisturbed feeding followed but before long J was back fighting and sparring with K again. Most of the encounters were initiated slightly deeper in K's territory than the previous battle and K was always driven back. In less than three hours over 60 such skirmishes occurred and by this time K maintained only a very narrow territory. Finally K was driven from the spot altogether, and it moved a short distance to the nearest area shallow enough for feeding. This was already occupied by another territorial individual and after a brief series of encounters K deserted the entire area. This degree of boundary flexibility was characteristic only of the establishment phase of territoriality and once boundaries were set they remained fixed with day to day shifts amounting to a few inches at most points along the margins.

#### THE SIZE OF TERRITORIES

Most of the territories ranged in size between 10 and 200 square surface meters but one territorial individual confined aggression and active feeding to an area of approximately four square meters and another occupied over 400 square meters. The individuals holding the largest territories were not associated with flocks. Here much of the contained area was deep water or was otherwise unsuited to feeding. In the Little Ringed Plover (*Charadrius dubius*), Simmons (1956) described volumetric territories and noted that territories expanded to include considerably larger areas in the air than on the ground. If the distance to which an individual pursues an intruder is considered the territorial limit, this would greatly enlarge the territories of at least two exceptional Pectorals which repeatedly chased intruders 50 meters or more in the air. However, chasing flights were only initiated toward individuals which passed low over the smaller area on the ground or attempted to land there. Pitelka (MS) reports breeding Pectoral territories in Alaska covering from 25,000 to 60,000 square surface meters. In contrast to the aerial pursuits exceeding terrestrial territorial limits noted above, he reports that aerial chases end at the terrestrial boundaries.

#### INTERSPECIFIC AGGRESSION

Interspecific aggression was noted regularly but was less frequent and intense than intraspecific aggression. Killdeers (*Charadrius vociferus*) were never chased although they remained in the territories for extended periods. Solitary Sandpipers (*Tringa solitaria*) likewise were not evicted. One bird tolerated a Solitary Sandpiper feeding less than two meters away and yet was very aggressive to other Pectorals within a much greater radius. Lesser Yellowlegs were almost constantly associated with the Pectorals in the Back Marsh and interactions were common early in the summer. Either species was likely to supplant the other. No such encounters were seen after July 25. Semi-

palmated Sandpipers were supplanted or tolerated. Least Sandpipers were frequently evicted, the last observed instance being August 4 for this species. On August 11 I noted a Least Sandpiper feeding undisturbed in a Pectoral territory.

On July 21 a young Yellow-headed Blackbird (*Xanthocephalus xanthocephalus*) hopped up to a territorial bird and assumed a begging posture which incited an attack from the Pectoral. A few minutes later the performance was repeated. Normally, Yellow-heads, Robins (*Turdus migratorius*) and other songbirds aroused no noticeable aggression from territorial individuals. Tree Swallows frequently chased single flying Pectorals as they do many other species on the marsh and occasionally Yellow-heads also chased or dove at the feeding Pectorals as they flew low over the marsh.

#### BEHAVIOR OF THE CENTRAL AREA BIRDS

Aggression was also a prominent feature of the birds inhabiting the central area of the flock. The more intense displays were notably less frequent, however, and sparring and overt fighting were rare. Situations inciting aggression differed markedly from those of the territorial birds. In the case of the central area birds, the stimulus most likely to provoke an attack was the proximity of another bird, regardless of its absolute position on the terrain. This form of spacing, depending only on the location of the individual and the proximity of a neighbor regardless of the absolute positions on the terrain has been termed individual distance (Hediger, 1950).

When the birds of the central area were feeding actively, the spacing between individuals usually exceeded a meter. Threatening generally resulted when this distance was reached. During resting, preening, and sleeping periods the aggressive tendency seemed to wane considerably and often several sleeping birds could be seen together in a part of the central area. Protracted periods of resting and sleeping were rare among the territorial birds and there was no indication that the aggressive tendency had diminished.

When the flock gathered in the central area as a response to danger, the spacing was greatly diminished and aggression temporarily ceased. This was also true of spacing immediately on landing. As the alert of the flock lessened, aggression became more prominent and brief encounters, the departure of the territorial birds, and movements away from neighboring individuals, quickly restored the spacing. Just as in the territorial birds, the maintenance of spacing after the flock had become established seemed to depend more on the avoidance of neighbors than on aggression. It is possible, of course, that some slight aggressive threat went unnoticed by the observer in these situations.

In early August a most remarkable behavior appeared. Groups of six or more birds gathered in tight circles, all standing in the alert posture facing the center of the circle. It appeared that the object of the conclave was a bird posturing on its breast with wings outstretched. These writhing birds turned out to be Pectoral Sandpipers, dying apparently from algal poisoning. Unable to stand or fly, they flapped helplessly in place while gathering the audience described above. In this situation the gathered birds seemed to maintain no critical distance whatsoever.

Some of the birds at the periphery of the central area showed a tendency to remain in the same area for some time, driving other birds from a specific area for several consecutive days. One such bird showed a pattern of aggression seemingly intermediate between the usual characteristic territorial behavior and the central area behavior. This bird confined its aggression to a small area of approximately four square meters, but the location of the defended area shifted considerably from day to day.

## DISCUSSION

An interpretation of the adaptive significance of territoriality among transients must first attempt to resolve whether or not the behavior is adaptive in the observed context. It may be argued that in a stable environment the species is maximally adapted and, therefore, any complex behavior pattern may be expected to be fully adaptive at the time when it is observed. But if we renounce the myth of stability this argument retains little validity. Surely variation of pertinent environmental events from year to year may result in the imperfect timing of some behavior, especially if the behavior is timed to less flexible cycles such as changes in day length. We may, therefore, in terms of the observed context of the behavior, feel free to consider both adaptive and inadaptive interpretations.

It is dangerous to examine a single situation in an attempt to determine possible immediate advantages to the population or its individuals. With such an approach one may be misled by exceptional and atypical situations insofar as the population is concerned, especially in a narrow and short-term study. While this approach is pursued in the following discussion, it is with the realization that failure to detect advantage in the population under study does not imply that immediate advantage is not conferred to the species in its spectrum of occupied habitats and localities in this and other seasons. With these reservations, then, territorial behavior in migrant Pectorals will first be analyzed in terms of possible immediate advantage.

It has been suggested (Tinbergen, 1956) particularly for ground-nesting birds that territoriality may serve to reduce losses to predators. In the Pectoral this seems unlikely since the usual predator reaction is not to crouch and remain motionless in the spaced pattern but rather to fly up as a flock. Tinbergen (1951) suggests that the compacting of escaping flocks of birds is a defense mechanism against falcons which will rarely or never stoop directly into a flock. It also seems likely that grouping enables the flock to move more efficiently as a unit (Nichols, 1931), thus preventing vulnerable stragglers. But it is probable that at least some predator reactions are specific to the predator involved, or at least to specific categories of predators. Crouching in place has been reported for Pectorals in response to gunners and dogs along the Atlantic coast when this species was still on the active game list (Forbush, 1912). The nature of certain distraction displays by plovers suggests to Simmons (1955) that these responses were evolved specifically for the predator man!

The prevention of epidemics and disease has been suggested as another selective pressure favoring dispersion (Haldane, 1949). On the Delta Marsh mortality from algal poisoning was heavy. The heaviest waterfowl and shorebird losses were noted in areas where shallow edges were subject to frequent flooding and drying. Losses were localized about the marsh. Semipalmated and Pectoral sandpipers were the hardest hit, accounting for over half of all shorebird deaths. The Semipalmated Sandpiper is sometimes as tenacious to particular sites as the Pectoral, and this tendency combined with preference for shallow edges by these species probably favored repeated poisoning and the consequent heavy losses. On the basis of these observations it seems unlikely that tenacity to site checked losses, although it may possibly have prevented poisoning from becoming more widespread in the population. Such population prophylaxis could not, of course, have been the basis for the selection for spacing.

There has been considerable speculation concerning the advantage of territorial structure in obtaining an adequate or more than adequate food supply. Feeding is the primary activity of territorial birds, occurring with a frequency approached in only a few cases by aggressive encounters. On the Delta Marsh highly aggressive Pectorals may

spend much of the day evicting intruders. In the spectrum of aggressive intensities observed the bulk of the population may have achieved an appropriate balance between despotism and tolerance which allowed maximal utilization of the assured food supply. If this is true, however, it is difficult to understand why other species such as the Stilt Sandpiper (*Micropalama himantopus*) are not pressed to adopt similar measures to satisfy their needs.

The territories were remarkable for the uniformity of the contained habitat, most of it suitable for feeding. The portion used in feeding, however, varied considerably, one bird taking most of its food along the narrow edge of a small island and an adjoining bit of higher ground while driving Pectorals from a considerably larger area. The same was true of A, whose exclusively occupied area contained a large amount of area unsuitable for feeding. No correlation between the intensities of the feeding and the attack tendencies was noted among the territorial birds. They seemed equally ready to attack an intruder whether they were feeding or preening. Of the non-territorial birds, however, there was a tendency to greater spacing during feeding than while sleeping or preening. It should be noted that while the territorial behavior caused feeding Pectorals to be more spaced out than most other shorebird species, the flocks nevertheless remained as discrete entities and on the Delta Marsh Pectorals did not occupy all the habitat which seemed suitable. Scattered highly aggressive birds were exceptional in maintaining themselves in isolation from any flock. Therefore, if the territory is considered to be of feeding utility, it must be assumed that through selection a compromise between the advantages of spacing and the maintenance of flock structure has been achieved.

Active field ornithologists know well that transient individuals of many bird species may delay at stops in migration for periods of from a few days to several weeks. This is especially evident when the rarity of the species confirms individual identity, but it is probably no less true of commoner forms. Furthermore, band records for at least some species show that the same transient individuals may appear in the same precise locality year after year. This suggests that for at least some species the migration may be made in large jumps with protracted resting and feeding interspersed. One thus obtains a picture of a stepwise movement with delays in route sufficient to enhance or replace fat stores, perhaps aided by the elaboration of territorial social structure. This migratory pattern is far less detectable than the comparatively slow day by day advance (Lincoln, 1950) of some species. In developing isochronal lines by mapping identical arrival dates, either for earliest arrivals or estimated peaks, one may mask the extent of individual steps in migration. The movement may be compared to the progress of a feeding flock of blackbirds or starlings. While the forward edge of the flock progresses almost imperceptibly, individual advances must span the flock. Such a saltatory pattern of migration would be difficult to demonstrate directly because of the improbability of immediately consecutive band recoveries. This sort of a migratory pattern is surely to be anticipated in waders and waterfowl (see Cooch, 1955) where jumps must span great expanses of inhospitable terrain.

Having considered the more likely possibilities for immediate advantage, we may now return to the possibility that the observed behavior is not fully adaptive in the context in which it appears. This alternative is satisfied by the suggestion that the observed behavior is a residuum from the breeding grounds, and any advantage to the birds involved must be interpreted on the basis of events which have already taken place. I believe that the evidence at hand favors this interpretation, yet it is surely admitted that the case is far from conclusive.

Since there is no hint of pair relationships in migratory flocks, each individual, in order directly to derive the benefits of territoriality, must maintain its own territory.



But only about a third of the birds adopted fixed territories. The large size of these individuals in comparison with the majority of the birds in the non-territorial central area suggests that they were primarily males. Pitelka (MS) presents the evidence that at least partial separation of the sexes can be made in the field. Unfortunately it was not possible to collect any birds of known behavior.

If this interpretation of the behavior is correct, one might legitimately anticipate the waning of aggressive behavior later in the fall. While there was little breakdown of aggression, the waning of interspecific aggression seems somewhat indicative. Testis size of eight males found dead on August 5 averaged 3.5 mm. (range, 3 to 4.5 mm.). This figure is considerably smaller than that for breeding males but it should be compared with a later fall sample to establish whether testicular regression is complete. Collection and study of the reproductive system of birds of known behavior will be necessary before an adequate judgment of the significance of territory at this season can be made. An analysis of the timing of events of breeding populations (Pitelka, MS) suggests that the Manitoba birds are not thwarted or disrupted breeders but arrivals which have recently completed the breeding cycle to the north.

#### SUMMARY

Flocks of transient Pectoral Sandpipers (*Erolia melanotos*) were studied on a large marsh in southern Canada in July and August. A flock structure was maintained but about a third of the flock also maintained discrete peripheral territories. The central birds also showed considerable aggression but this was independent of local landmarks. One flock remained in the same place on the marsh for 13 days, another for at least 26 days. The birds vacated their occupied areas at night, gathering in large flocks on another part of the marsh.

The usual predator response to hawks and certain mammals is to fly up in a compact flock, territorial birds included. Occasionally, however, crouching in place may appear as a predator reaction.

Several kinds of displays appeared in territorial encounters and some of these postures were used by the central area birds. Fighting with bill and feet was interspersed with intense posturing. The choice of the action employed appeared to be largely an opportunistic response to the position of the antagonist. Interspecific aggression was never pronounced and seemed to be more intense earlier in the season.

Certain seemingly inappropriate activities are described and briefly discussed. Body shaking, a prominent aftermath of territorial encounters, is interpreted in terms of inhibited autochthonous stimuli.

Territory defense was continuous throughout the day, while at night the birds gathered in large flocks with other waders on another part of the marsh. Territory size normally ranged from 10 to 200 square surface meters and most of the included area was suitable for feeding.

On several occasions birds gathered in close groups about dying birds.

The possibilities for the adaptive significance of territoriality at this season are discussed. The limited number of birds holding territories and the gradual waning of aggression suggests that territoriality at this season and location in the Pectoral Sandpiper is an aftermath of breeding-ground behavior.

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