Aspects of the Breeding Biology of the Eastern Willet

Catoptrophorus semipalmatus

A report submitted to the Director General of the Canadian Wildlife Service with respect to Contract Number KL229-7-5288

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March, 1978

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Introduction

Little is known of the adaptive significance of the territorial system of the Eastern Willet *Catoptrophorus semipalmatus* with respect to the breeding ecology of this species.

During May through July 1976, changes were noted in territorial size and the intensity and nature of territorial defence both on and off the feeding and nesting territories in relation to the phase of the breeding cycle. Unfortunately, I was unable to gain quantitative data for the critical period of territorial establishment during early May.

With reference to Canadian Wildlife Service Contract No. KL229-~~K~~-5288 the specific aims of the 1977 study were to gather information on the initial period of territorial establishment. This period must be considered very important to subsequent territorial behavior. Field work was planned for the last two weeks of April and the month of May, 1977.

Study Area

The study area was on the estuary of the Gaspereau River at Horton Landing, 2.5km from Avonport (45°07'N, 64°17'W), Kings County, Nova Scotia (~~Figure~~ Figure 1). It consisted primarily of a salt marsh, 50 to 135 and 700 m. in width and length, respectively (Figure 2). This marsh was bounded on one side by a dyke wall, approximately 4 m. in height and, on the other, by mud banks which descended some 20 m. to the river bed. The

area was almost completely covered by Spartina alternaflora and a narrow band of S. patens along the base of the dyke. A strip of gravel occurred at one end of the marsh, next to the dyke. Tides covered the marsh twice daily.

Hayland and pastures comprised the flat, reclaimed terrain behind the dyke.

Arrival and Establishment of Territory, 1977

The first Willets appeared at Horton Landing on 1 May. One pair fed briefly on the saltmarsh but did not remain in the study area. An unpaired male (Pair 1), occupied an area of saltmarsh at the southeast end of the study area. No territorial behavior was exhibited by this bird until joined by a female on 3 May. They remained in the study area until 4 May when they moved West of the wharf.

A second pair (Pair 2) arrived on the study area on 4 May. Territorial defence was observed within 50 minutes of arrival on the saltmarsh. The male of this pair had been colormarked the previous summer. This male and his mate occupied the same area of saltmarsh held the previous summer.

On 5 May, a second pair of Willets (Pair 5) were present and exhibiting territorial behavior on the saltmarsh. This pair, both colormarked the previous summer, occupied the same saltmarsh territory they held in 1976.

On 9 May, both birds of Pair 3 were observed across the Gaspereau River from Horton Landing. The male of this pair had been colormarked the

previous summer. This male was involved in territorial disputes indicating that the shore territory of this pair was across the river. This pair was observed in the study area on 12 May.

Tomkins (1965) found that Willets in South Carolina and Georgia arrived on their breeding grounds in small groups of mixed sexes. Some had already formed pair bonds while others were actively seeking mates. Data from the present study seem to indicate that the arrival of paired birds is preceeded by the arrival of a few individual males. The lack of territorial behavior in the unpaired male Willet, despite the presence of Willets in the vicinity, is interesting. Nothing directly pertaining to this could be found in the literature. Tomkins (1965) states that during the pre-nesting time, the territory of the male willet is the area around the female. However, he apparently never considered the fact that a relatively stable shore territory may also be maintained by both members of the pair.

Unfortunately, because of cold weather, high winds and heavy rainfall during mid-May 1977, the Willets did not remain to nest at Horton Landing. Heavy wind and high waves often drove the Willets from the saltmarsh to the pastures and plowed fields behind the dyke where they fed on such occasions. After 12 May, Willets were seldom seen in the study area and by 30 May only Pair 2 remained at Horton Landing. This situation is in marked contrast to that of 1976. This is reflected in the chronology of events for each of the pairs during 1976 and in May 1977 which is summarized in Tables 1 and 2, respectively.

As the willets failed to establish adjacently held territories as they had in 1976 the aim of the proposed research programme for 1977 could not be achieved.

This report emphasizes the final analysis of the territorial system established in 1976 and includes pertinent information gained during May, 1977.

Materials and Methods

Daily checks for the presence of Willets were made on the saltmarsh during the last two weeks of April. A grid system was established on the saltmarsh during the third week of April. Observations were carried out from 1 May until 30 May, 1977.

The Marsh was marked off in a 25 x 50 m grid with color coded wooden stakes. This enabled accurate plotting of the locations of birds on gridded field maps.

All observations were conducted from a car situated on top of the dyke. This provided an excellent vantage point and caused little disturbance.

Observation periods ranged from one to six hours in length. Two observers conducted observations simultaneously, each looking at one member of a pair. Every 5 minutes the location of each observed bird was plotted on the grid-map. All activities and movement of the birds within the consecutive five-minute periods were recorded. The birds were

observed with 7 x 35 binoculars and X15 to X60 zoom telescopes.

At low tide the willets often left the marsh to feed in the river bed on the mudflats beyond. For this reason, most observations were conducted three hours before and after high tide when the high water forced the Willets onto the saltmarsh.

Individual birds were recognized by colored leg bands that had been placed on them the previous summer.

Five methods of illustrating territory size and shape were applied to the territory data gathered during 1976 - 1977. The first three were conventional methods, often used in accessing avian territory. The final two were designed specifically to analyze the territory data gathered in the present study.

The five methods of analyzing territory that were applied and criticized in this study are briefly listed as follows:

a) The Mapping Method: described and criticized by Best (1975)

b) A modification of the Mapping Method: described by Stefanski (1967)

c) The Observation-Area Curve Method: described by Odum and Kerenzlon (1955)

d) Comparison of "Home Range" and "Defended Area" of individual willets during 3 phases of the breeding season. These phases are: Phase I - Before Incubation (1 - 29 May); Phase II - Incubation (30 May - 17 June); Phase III - Young on the Marsh (18 June - 29 July). This method was used to compare the absolute areas of Home Range and Defended area occupied by males and females and the changes that occurred during the breeding season.

e) A method utilizing the grid columns on the saltmarsh was devised to illustrate the shape and location of the territories of individual pairs. This method illustrates the proportion of time each pair spent in each area of the territory. The changes that occurred during each phase are also indicated by this method.

The areas of the willet territories as determined by each of the five methods used were calculated with a planimiter.

A. Territorial Description

During the summer of 1976 and May 1977, willets had separate shore, nesting and feeding areas.

a) The shore territories consisted of a tidal saltmarsh which was used by the adults for feeding, loafing and later for rearing the young. A dyke wall and mash edge bordered these territories on two sides (Figure 2). Both members of the pair defended this territory. The actual lateral boundaries of these territories were transient, often only with stable borders for one or two days at a time. Lateral boundaries sometimes changed by as much as 150 m.

b) The nesting territories were separate from the shore territories and showed some spatial relationship to them. The area around the nest-search areas and later, the nest, was vigorously defended by both sexes during the pre-nesting, egg laying and incubation stages. The actual size of this area was not determined but appeared to have a radius of at least 3 m.

c) During low tide, the willets often fed on the mudflats or river bottom. The male of each pair defended an area around the female and, later, around the fledged young. Although the same pairs often returned to feed in the same general area, an actual feeding territory was not regularly defended. During incubation, individual members of a pair were

often noted feeding in these areas.

B. Territorial Behaviour.

1. Intraspecific behavior. With respect to conspecifics, territory was maintained by three types of behavior. (a) Vocalization. Vocalization pertains to the "pill-willet" and "pill-will-willet" call. The bird faces the intruder, assumes an erect ~~pastime~~ posture with the tail depressed and neck extended, and repeats the call loudly until intruding willets have left. Both sexes emit this vocalization. The call of the female is flatter in tone and is thus readily distinguished from that of the male. During Phase I and II, the female vocalizes less frequently and often only in response to the call of her mate. In phases I and II, 1976, 109 and 54 "pill-willet" calls were recorded for the males and females, respectively. Of the female calls, 13 or 24% were in responce to the call of the male. A more equal ratio of female to male "pill-willet" calls of 68 to 72 occurred during Phase III, 1976. (b) Chase. Frequently a chase follows the "pill-willet" call if an intruder does not respond appropriately to the vocalization. The resident willet flies after the conspecific and chases it out of the area. During Phases I and II males were involved in this activity more than females. During 1976, 21 chases were initiated by males and only 6 by females. Until the onset of incubation the male, returning from a chase, sometimes gains altitude and decends over his territory while performing the territorial "wing-wave" display (Tomkins, 1965; Vogt, 1938). At least 3 of 6 wing-wave displays observed in 1976 followed a chase. (c) Physical encounter. Two types of encounters were

observed. Type I encounters occurred primarily between territorial and intruding males during the pre-nest period. An encounter is initiated by the presence of an intruder. The resident male gives the "pill-willet" call and subsequently either "struts" in erect posture or flies towards the conspecific. When facing and immediately adjacent to one another the birds "bite" each other on the neck, bill, wings and legs with their mandibles. They often attempt to get on the other's back. These encounters frequently terminate in the water with one bird standing on top of the other and alternately biting and bobbing him under. These encounters occur when another male threatens to annex a part of the resident male's territory. The resident was successful in driving off the intruder in all but one of 19 encounters observed. In June, 1976, the male of Pair 2 was displaced by the male of Pair 3 when the latter's brood was brought to the marsh.

Females do not usually participate in Type I encounters. In 1976, the female of Pair 3 was briefly involved in a Type I encounter with male Pair 2. Females may feed, stand alert, stand on one leg with head under wing or adopt a crouching position typical of that exhibited by the female during copulation. On one occasion the resident male violently attacked his mate after successfully repulsing an intruding male. The female quickly adopted the sexual crouch and her mate ceased the attack.

Once nesting commenced, Type II encounters occurred along the temperory territorial boundaries held in common by adjacent pairs. In erect posture, the two birds strut parallel to one another back and forth along

the boundry. Frequently one will crouch and run at the other who, in turn, jumps away; parallel strutting is then resumed. Usually, the encounters end with both birds moving away a few m and preening or feeding. Male versus male encounters were most frequent. One female versus female and one mixed-sex encounter were observed in 1976.

Intraspecific territoriality exhibited by both sexes during each Phase of the 1976 season was analyzed to detect changes in the frequency of interactions. Four types of intraspecific territorial behaviors were counted: Vocalization, Chase, and Type I and II Encounters. The number of territorial events per hour was computed. The collection of data on individual pairs was discontinuous and cumulative observations of individual willets sometimes totalled less than 5 hours in each phase. For this reason, data on each of all males and all females were combined to obtain an adequate sample. Table 3 summarizes the number of territorial events per hour for each sex and phase. Males were most territorial during Phase I with 2.45 territorial events per hour. Although females were never as territorial as males, interactions between females increased in frequency with each phase attaining 1.9 per hour when young were on the marsh.

Interspecific behavior.

2. Interspecific behavior. Willets responded interspecifically as well. This occurred in four forms.

a) Vocalization. This is a repetitious "kluk-kluk" call which increases in frequency as an interspecific intruder approaches. During Phase III,

the "pill-willet" call was also used interspecifically.

b) Ground chase. This was frequently directed towards another species of shorebird. The willet would adopt a crouching position and run at the intruder until it moved off. This is similar to Type II physical encounters.

c) Aerial chase. This consisted of a silent flight after an interspecific intruder.

d) Mobbing. The first mobbing occurred 24 hours before the young appeared on the marsh. Willets fly to the intruder, chasing and harassing it while emitting the "kluk-kluk" call. Often the alarm call "pwh-e-e-e" or the less intense "pwhe-who" is given as willets start to mob. Any creature that poses a threat to the brood is mobbed. This incorporates a rather large and varied group including gulls, hawks, owls, ravens, crows, dogs, humans, deer, and even the occasional boat and aircraft. The female of the pair invariably initiates mobbing and does so more intensely than the male. Pairs with young mob most frequently but they may be joined by conspecifics.

The frequency of interspecific territorial encounters occurring in 1976 was examined. Four types of behaviors were tallied: vocalization, ground and aerial chase, and mobbing. As with the intraspecific territorial events, data on individual willets were combined by sex and phase. The number of territorial events per hour was determined and is in Table 4.

Interspecific territorial events by males and females occurred infrequently during phases I and II averaging 1.5 and 1.4, and 0.07 and 0.08 per hour, respectively. During Phase III, however, interspecific territoriality increased to 2.56 and 3.07 events per hour for males and females, respectively.

Interspecific territorial events were also analyzed with respect to the type of animal that evoked the response. All animals stimulating ground chase, aerial chase, or mobbing reactions of willets were divided into one of two groups: potential predators and non-predators. The potential predators included all animals posing a possible threat to willets or their young. These included Red Tailed Hawk Buteo jamaicensis; Marsh Hawk Circus cyancus; Great Black Backed Gull Larus marinus; Herring Gull Larus argentatus; Common Crow Corvus brachyrhynchos; Common Raven Corvus corax; Great Blue Heron Ardea herodias; Short-Eared Owl Asio flammeus; Great Horned Owl Bubo virginianus ~~(Gmelin)~~; domestic dogs and humans. The non-predators included all animals that evoked ground or aerial chasing (no mobbing) but appeared to pose no direct threat to willets. They were Red-Winged Blackbird Agelaius phoeniceus; Starling Sturnus vulgaris; Barn Swallow Hirundo rustica; Belted Kingfisher Megaceryle alcyon; Short-Billed Dowitcher Limnodromus griseus; Greater Yellowlegs Totanus melanoleucus; Lesser Yellowlegs T. flauipes; Spotted Sandpiper Actitis macularia; Black-bellied Plover Squatarola squatarola; and Semipalmated Sandpiper Ereunetes pusillus.

Eighty-nine percent or 139 of 156 of the interspecific territorial reactions of females were predator-oriented compared with 65 percent or 93 of 142 of the male reactions. These data are summarized in Table 5.

C. Analysis of Shore Territory.

I concentrated my observations on the shore territories at Horton Landing because they were the largest, most readily observable and were utilized most frequently throughout the season. Changes of the lateral sides of the territories posed problems in analysis. The usual methods of determining territory size and configuration were meaningless when applied to willets.

The "Mapping Method" (Best, 1975), the common practice of constructing a polygon or curved shape around all points where a given individual or pair of birds was recorded during the breeding season seemed inappropriate at best. When applied to the data of the present study it resulted in polygons encompassing central portions of the saltmarsh as shown in Figure 3. Although this method did surround all paints where a given pair had been observed during the season, it would lead the reader to believe that the shore territories stopped a few m. from the marsh edge and dyke wall and possessed irregular, jagged lateral borders. This method does not take into account the fact that these shore territories are tidal and that many of the observations were carried out at a time when the willets were limited to the upper shore by the encroaching tide.

It is not valid to assume that a particular point where a willet has been plotted represents the corner of a polygonal territory. The upper and lower boundaries are fixed and only the lateral borders need be determined. This point would be better interpreted as representing a line that crosses the shore territory at right angles from its upper to lower natural boundary.

To a certain extent, the polygons depicting territory increased in size as the number of observations increased. This indicates a danger of bias from unequal time spent in observing individual pairs.

Finally and perhaps most importantly with respect to willets, no indication of fluctuation in territorial boundaries is given if only one polygon is constructed for the entire breeding season. The size and location of territories cannot be analyzed with respect to each phase of the breeding cycle. Changes throughout the breeding cycle cannot be monitored. The result is a static and meaningless representation of dynamic territorial boundaries.

This method is only slightly improved by analyzing the territories by phase of the breeding season as Stefanski (1967) did in his study with Black-capped Chickadees Parus atricapillus. Figures 4, 5 and 6 show the willet territories as determined by the "mapping method" for Phases I, II, and III of 1976. The resultant polygons show changes in location from phase to phase but still illustrate angular territories in the middle of the marsh. This method gives no indication of which parts of these areas

were actually defended and to what extent the boundaries reflect occasional forays outside the usual territory. Table 6 gives the areas of each territory during different phases as determined by the Mapping Method.

Idom and Kuenzler (1955) devised a technique of determining territory in passerines. A polygon was constructed around each series of 10 consecutive points depicting the location of a bird. Each series of 10 observations adds a new area to the territory. Each addition decreases in size in proportion to the total area until a cut-off point is reached. This point of "diminishing returns" occurs when a series of 10 points yields less than a 10 percent increase in total area or, 1 point yields less than a 1 percent increase in area. At this time, the size and configuration of the territory have been determined. Any stray points outside of this area represent territorial infractions. Figure 7a presents this method.

Problems arose when this was applied to the mobile willet territories. In 9 of 13 cases, the cut-off point was never attained. Each additional point caused an increase in total area that exceeded 1 percent. The longer a pair was observed, the larger the resultant polygon became. Figure 7 b illustrates this.

A more serious problem arose. In 4 of 13 cases, the cut-off point was attained a number of times. Because a pair often remained in a relatively constant area for several consecutive days, the 1 percent cut-off point was attained often within a day or two of observations. If mapping had ceased at any of these points, the next shift in territorial boundaries

would not have been recorded and very inaccurate territorial maps would have ensued. Figure 7 c illustrates this problem. Thus, this technique would preclude recording any shift in territory as the breeding season progressed. Finally, the polygons constructed by this method have the same problems as those of the Mapping Method technique. They indicate that the shore territory exists in the middle of the marsh and not that it extends from upper to lower natural borders. Furthermore, it does not distinguish between the "home range" and "defended area" of the birds. These polygons encompass only the central portions of the saltmarsh, possess jagged and irregular lateral borders, are biased by unequal observation time for each pair, and present a relatively static representation of shore territory.

Willets commonly fed and loafed well into a neighbour's territory if the residents were not present or were at the far side of that area. If the residents were absent, the adjacent pair would often temporarily defend large sections of the area of the former pair. A salient feature of willet shore territories is the great overlap in area utilized by adjacent pairs. This made the mapping of these territories difficult unless they were presented on a daily basis. This was too lengthy a procedure.

Wilson (1975) discribes territory as a combination of home range with a central defended core area. This core area is the area of greatest use and within which the bird is presumably invincible. In an attempt to reduce the amount of overlap and to better express the territories oc-

cupied by pairs of willets another method using polygons was applied. I thought that "defended area" might be a better approximation of territory than the entire area of utilization as examined previously. In this method two polygons for each phase of the breeding season were constructed for each individual willet. One, representing "defended area", encompassed only those points where intraspecific territorial interactions took place. The outermost points of vocalization, chases and lines where Type I and II physical encounters occurred formed the perimeter of the polygons. The second, representing "home range", surrounded all points of presence rather than interactions. "Defended area" and "Home range" were determined for each willet during Phase I, II and III of the 1976 season. Figures 8, 10 and 12 show "defended area" for each willet and Figures 9, 11 and 13 show the limits of "home range" for each bird in each of the three phases. The area of each polygon is presented in Table 7.

The defended area was often found to extend beyond the limits of the home range polygon. Furthermore, defended areas were found to overlap although not to the extent of those for home range.

While possessing many of the same problems as the previous polygon methods, this technique does have certain advantages. Although it was not suitable for illustrating the locations and limits of territories, it was a useful measure of absolute area of defended area and home range. The defended area and home range were combined to determine the average area of defended area and home range for males and females (Table 8).

The areas of defended area and home range of females were less than those of males throughout the season. Males and females possessed the largest defended areas and home ranges during the period when the young were on the marsh. In particular, the defended areas of both sexes increased markedly during this third phase.

A new method of defining territory was devised using the percent of time spent in each area of the gridded saltmarsh. Territories occupied during each of the 3 phases of the season were analyzed. Since both males and females defend shore territory against conspecifics, data from both sexes were used to determine the territory of each pair. The proportion of time each pair spent in each 25 m column of marsh was calculated and plotted as a histogram. Subsequently, maps were constructed showing the territories of each pair. Figures 14, 15, 16 present the territories during the 1976 season and Figure 17, the 1977 season as determined by this method. The area of each is presented in Tables 9 and 10.

A salient feature of these maps is the expression of"Exclusive" and "Non-Exclusive" areas. Exclusive Area refers to any column occupied exclusively by one pair during that particular phase. Non-Exclusive Areas are columns where two or more pairs occurred - the areas of overlap of territories. Exclusive areas are indicated by columns of solid shading on the marsh maps. Non-Exclusive areas are illustrated by cross-hatching.

The horizontal axis of each corresponding histogram is spatial in nature. Each column of the histogram represents the percent of time each

pair occupied the 25 m wide column of marsh directly above.

This method circumvents several problems encountered with the polygons. Most importantly, the "no-man's land" which existed between the edge of each polygon and the marsh edge or dyke wall is eliminated. Territories are expressed as sections of the saltmarsh rather than areas within it. The jagged lateral boundaries are eliminated. The percentage of time expressed for each pair is derived from the proportion of the total time that a particular pair was observed during a particular phase. Because of this, the amount of time pairs spent in various areas of the marsh is comparable, even though there was variation in the total time different pairs were observed in a phase.

The histogram illustrates the amount of time a pair spent in various areas of the territory. This is felt to be a good expression of the actual use of the Exclusive and Non-Exclusive areas.

In summary, the transient nature of the lateral boundaries of the shore territories of willets necessitates the use of several new methods of describing territory. By utilizing two types of polygons, the first encompassing all points of territorial defence and the second, all points of presence, the locations and areas of defended area and home range may be determined for each individual willet. This is useful for comparison of absolute areas of defended area and home range between individuals, between sexes, and between phases of the breeding season.

However, there are limitations, previously described, with this method that are inherent in the use of polygons.

The grid-column method circumvents the shortcomings of the polygons by expressing the shore territories as sections of marsh naturally bounded on two sides by the river bank and dyke wall. The combination of map and histogram illustrates the most frequently used areas of each territory and makes expression of areas of overlap between adjacent territories more meaningful. This method does not reflect the actual observed areas of the individual territories. Instead, it presents what must be considered maximum territory size.

A combination of both methods are necessary to adequately analyze the shore territories of the willet.

Nesting territory.

Limited information was gathered on nesting territories. Their size and shape were not determined but each pair appeared to defind a radius of about 3 m. from the nest.

During 1976, six nests were located in dykeland pastures at Horton Landing. These fields were separated from the shore territories by the dyke wall and road adjacent to it. The locations of the nests show some relationship to the sequence of shore territories (see Figure 18). Nests were 75 to 262 m. from the respective shore territories of the adults. Distances between nests averaged 118 m. and ranged from 71 to 202m.(Table 11).

A density of 1 nest per 1.37 ha was determined for the main nesting field. Nests found in dykeland pastures were not completely visually isolated from each other. The pastures are relatively flat and vegetated by grasses less than 1 m in height.

No nests were found at Horton Landing in 1977. Willets were observed to search for prospective nest-sites in the same areas where they had nested the previous year (Figure 19). Pair 2 was believed to nest in the nest-search area but abandoned the nest before it was located.

Cold weather, strong winds and heavy precipitation during mid-May are believed to be responsible for the scarcity of nests at Horton Landing in 1977. Grass tufts in the pastures were not sufficiently developed to conceal a willet and nest until late in May. Heavy precipitation left the main nesting field wet in most areas and flooded in others.

Acknowledgements

Grateful thanks are extended to the Canadian Wildlife Service for the financial assistance provided for this study. L. Hansen gave valuable field assistance.

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TABLES

TABLE 1. Chronology of Events for each pair of willets during the breeding season of 1976.

Event	Pair 2	Pair 3	Pair 4	Pair 5
Arrival	(1 May)*	(1 May)	(1 May)	(1 May)
Copulation	(15 May)	(15 May)	(15 May)	(15 May)
Nest search	17 May		18 May	
First egg	20 May	(15 May)	(21 May)	(20 May)
Incubation	29 May	(24 May)	(30 May)	(29 May)
Nest deserted	7 June		8 June	
Copulation resumed	16 June		13 June	
Renest and incubation	(20 June)			
Young on marsh	15 July	17 June		22 June
Young fledged		14 July		
Female departs	16 July	16 July		
Male & young leave marsh		20 July		
Male & young separate		27 July		
Leave breeding grounds		29 July		

* Dates in parentheses are estimates.

Table 2. Chronology of events for each pair of willets during the breeding season of 1977.

Event	Pair 1	Pair 2	Pair 3	Pair 4
Arrival M	1 May	4 May	9 May	5 May
F	3 May			
Copulation		7 May	12 May	17 May
Nest Search		12 May	12 May	12 May
Incubation		26 May		26 May
Desert Nest		20 June		(30 May)*
Leave Study Area		21 June	27 May	30 May

* Dates in parentheses are estimates

Table 3. Number of intraspecific territorial events per hour for males and females in each phase of the breeding season in 1976.

Phase	Male (N=4)	Female (N=4)
Phase I	$\frac{77}{31.48}$ 2.45 e/h	$\frac{21}{28.28}$ = 0.74 e/h
Phase II	$\frac{61}{28.28}$ 2.16	$\frac{40}{24.88}$ = 1.61
Phase III	$\frac{162}{74.52}$ 2.17	$\frac{151}{79.54}$ = 1.90

Table 4. Number of interspecific territorial events per hour for males and females in each phase of the breeding season of 1976.

Phase	Male N = 4	Female N = 4
Phase I	$\frac{5}{31.48}$ = 0.15 e/h	$\frac{2}{28.28}$ = 0.07 e/h
Phase II	$\frac{4}{28.28}$ = 0.14	$\frac{2}{24.88}$ = 0.08
Phase III	$\frac{191}{74.52}$ = 2.56	$\frac{244}{79.54}$ = 3.07

Table 5. Potential predator and non-predator oriented interspecific territorial events in 1976 and 1977.

Cause of Interspecific Event	Male	Female
Potential Predator	93	139
Non-Predator	49	17
Total Number of Events	142	156

TABLE 6. Area (m^2) of willet territories in 1976, as determined by the Mapping Method

Pair	Summer 1976	Phase I	Phase II	Phase III
Pair 2	19,806	17,825	16,281	*
Pair 3	22,588	7,688	12,844	21,312
Pair 4	21,175	9,288	16,144	*
Pair 5	24,950	13,406	17,269	15,375
Refer to Figure	3	4	5	6

* Pairs 2 and 4 abandoned their nests and were not present in the study area during Phase III.

TABLE 7. Area (m^2) of Defended Area and Home Range for each willet during different phases at the breeding season in 1976.

		Area of Defended Area			Area of Home Range		
PAIR	SEX	PHASE I	PHASE II	PHASE III	PHASE I	PHASE II	PHASE III
Pair 2	M	13,081	7,562	*	16,194	12,188	*
	F	694	0	*	12,844	7,862	*
Pair 3	M	919	2,069	17,069	7,406	1,662	19,500
	F	0	1,038	17,606	7,875	8,900	17,569
Pair 4	M	8,306	1,312	*	11,300	16,425	*
	F	1,462	225	*	11,625	13,044	*
Pair 5	M	11,225	12,331	9,069	7,238	14,869	15,356
	F	6,050	6,400	6,719	8,588	9,625	11,656
Refer to Figure		8	10	12	9	11	13

* Pairs 2 and 4 abandoned their nests and were not present in the study area during Phase III.

TABLE 8. Average area (m^2) of Defended Area and Home Range for Willets in 1976.

Sex	Phase I	Phase II	Phase III	Phase I	Phase II	Phase III
Male	8,383	5,818	13,069*	10,534	11,286	17,428*
Female	2,052	1,916	12,162*	10,233	9,858	14,612*

* N = 2; in all other cases, N = 4.

TABLE 9. Area (m^2) of Exclusive and Non-Exclusive areas of Willet pairs for each phase of the breeding season in 1976.

Pair	Phase	Exclusive Area	Non-Exclusive Area	Total Area
Pair 2	Phase I	10,875	11,450	22,325
	Phase II	5,575	12,450	18,025
	Phase III	*	*	*
Pair 3	Phase I	0	14,725	14,725
	Phase II	0	19,075	19,075
	Phase III	10,525	13,025	23,550
Pair 4	Phase I	8,775	9,100	17,875
	Phase II	12,200	6,325	18,525
	Phase III	*	*	*
Pair 5	Phase I	1,525	14,275	15,800
	Phase II	6,225	14,900	21,125
	Phase III	5,725	13,025	18,750

* Pairs 2 and 4 abandoned their nests and were not present on the study area during Phase III.

TABLE 10. Area (m^2) of Exclusive and Non-Exclusive Areas of Willet pairs during Phase I, 1977.

Pair	Exclusive Area	Non-Exclusive Area	Total Area
Pair 1	0	14,525	14,525
Pair 2	10,150	14,525	24,675
Pair 3	0	3,450	3,450
Pair 5	10,925	3,450	14,375

TABLE 11. Data of nest locations in 1976.

Pair	Nest to Shore Distance	Nearest Neighbour	Distance from Mean High Water Mark
Pair 2	94 m.	202 m.	112 m.
Pair 2*	262	116	281
Pair 3	75	101	75
Pair 4	300	75	300
Pair 5	112	101	112

* denotes a second nesting attempt.

FIGURES

FIGURE 1. Location of the study area.

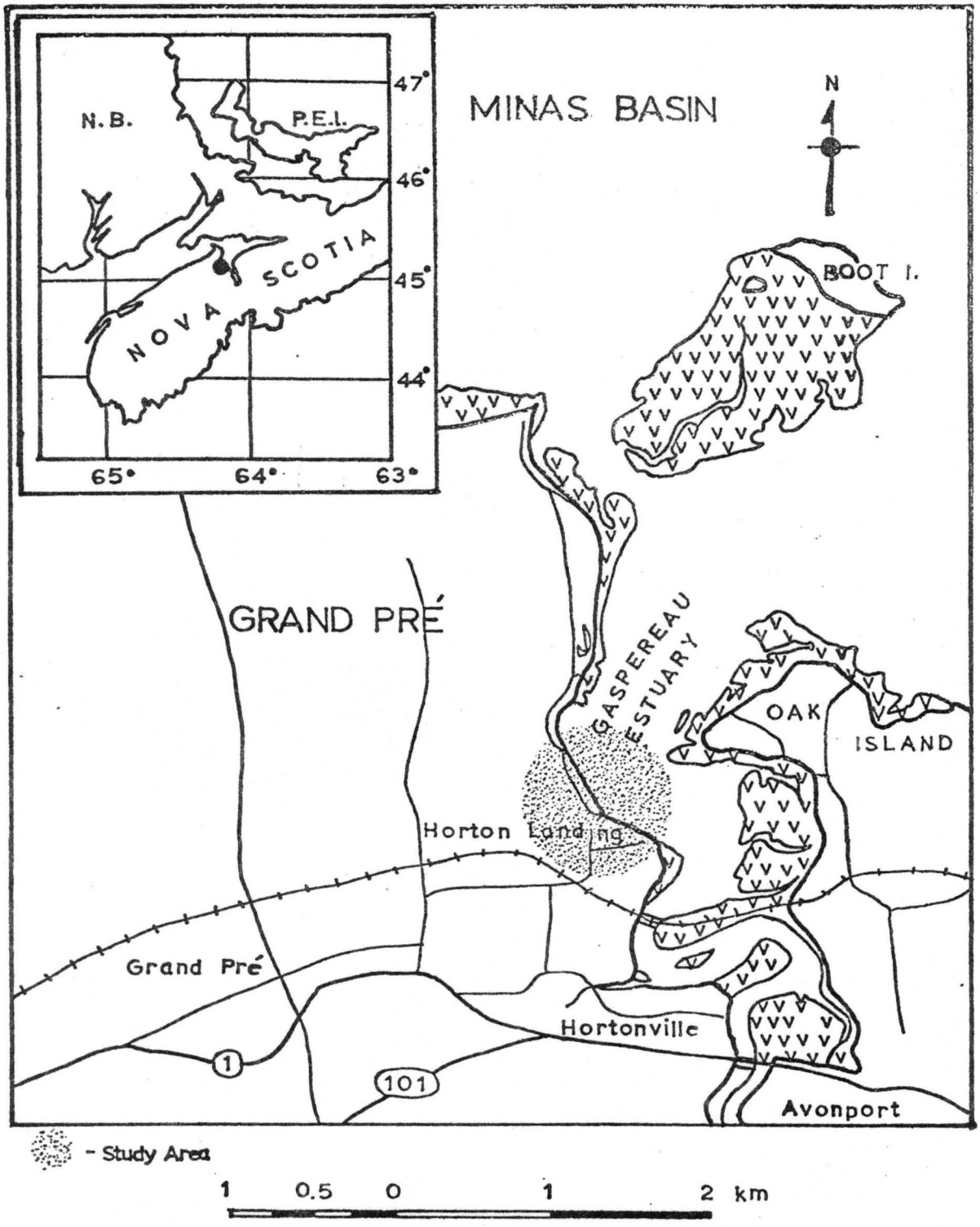

N.B.
P.E.I.
NOVA SCOTIA
47°
46°
45°
44°
65°
64°
63°
MINAS BASIN
N
BOOT I.
GRAND PRÉ
GASPEREAU ESTUARY
OAK ISLAND
Horton Landing
Grand Pré
Hortonville
Avonport
1
101
- Study Area
1 0.5 0 1 2 km

FIGURE 2

FIGURE 2. The study area on the Gaspereau estuary.

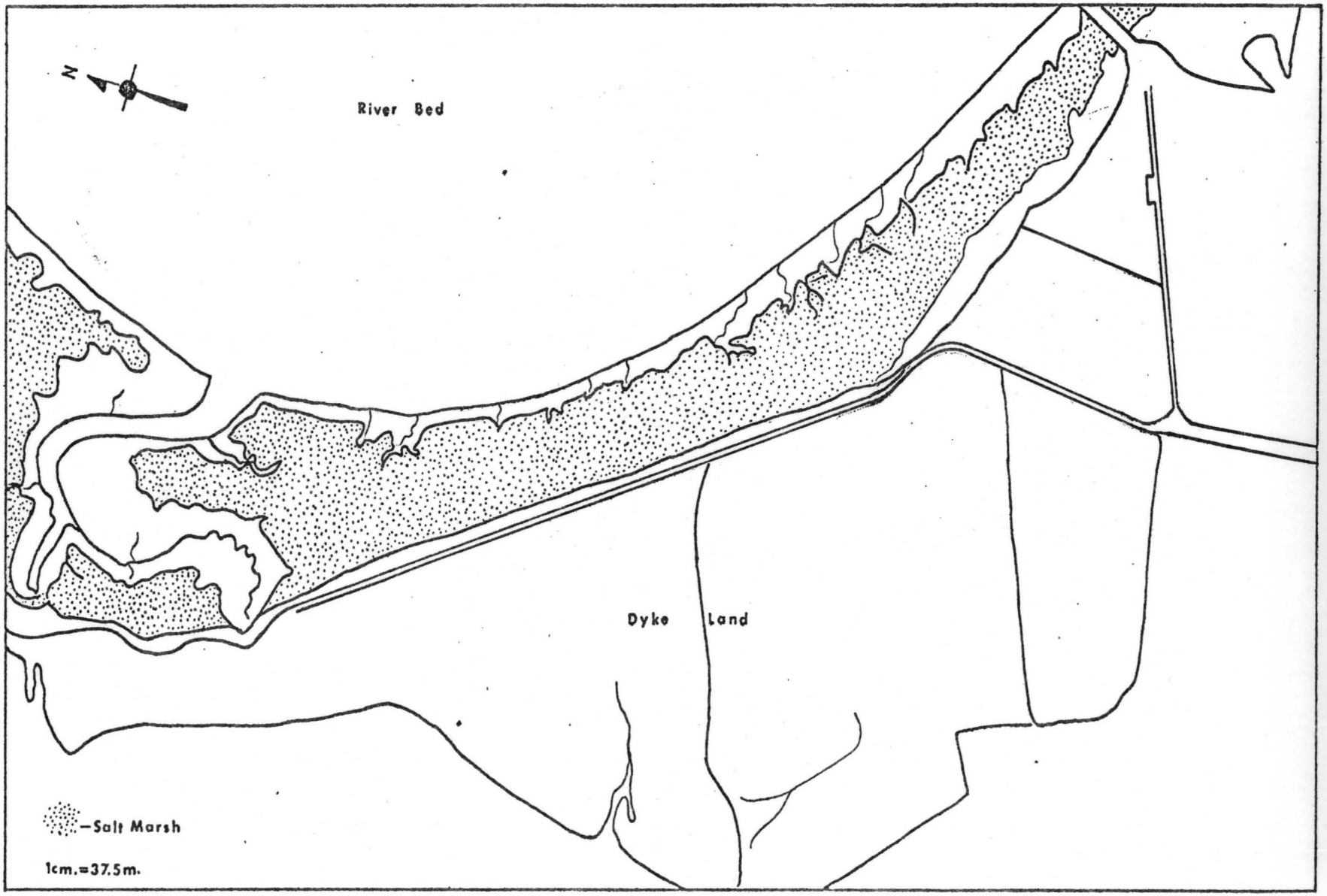

N
River Bed
Dyke
Land
—Salt Marsh
1cm.=37.5m.

FIGURE 3

FIGURE 3. Territory of each pair of Willets during the breeding season of 1976 as determined by the Mapping Method.

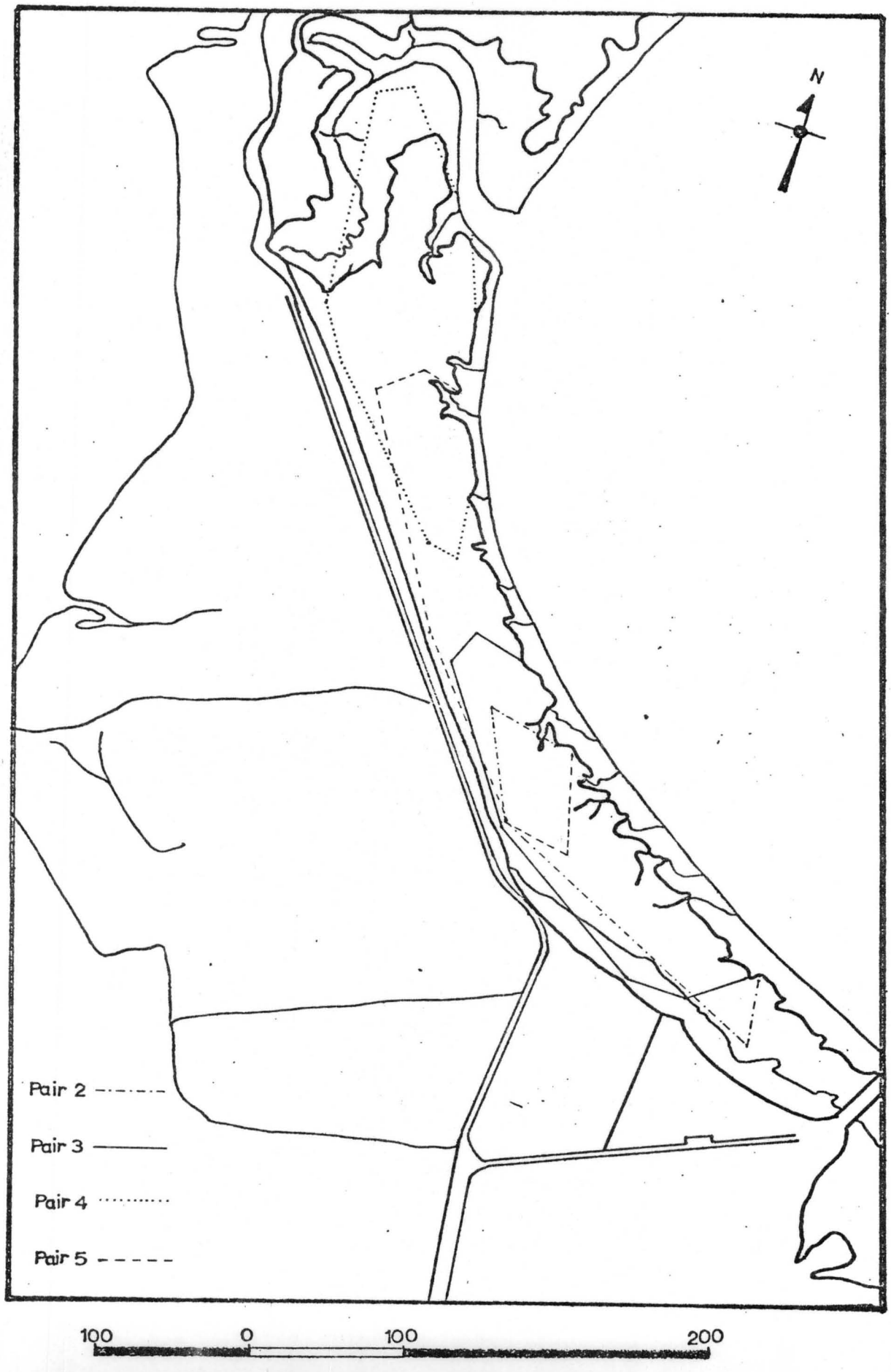

N
Pair 2
Pair 3
Pair 4
Pair 5
100
0
100
200

FIGURE 4

FIGURE 4. Territory of each pair of Willets during Phase I of the breeding season of 1976 as determined by the Mapping Method.

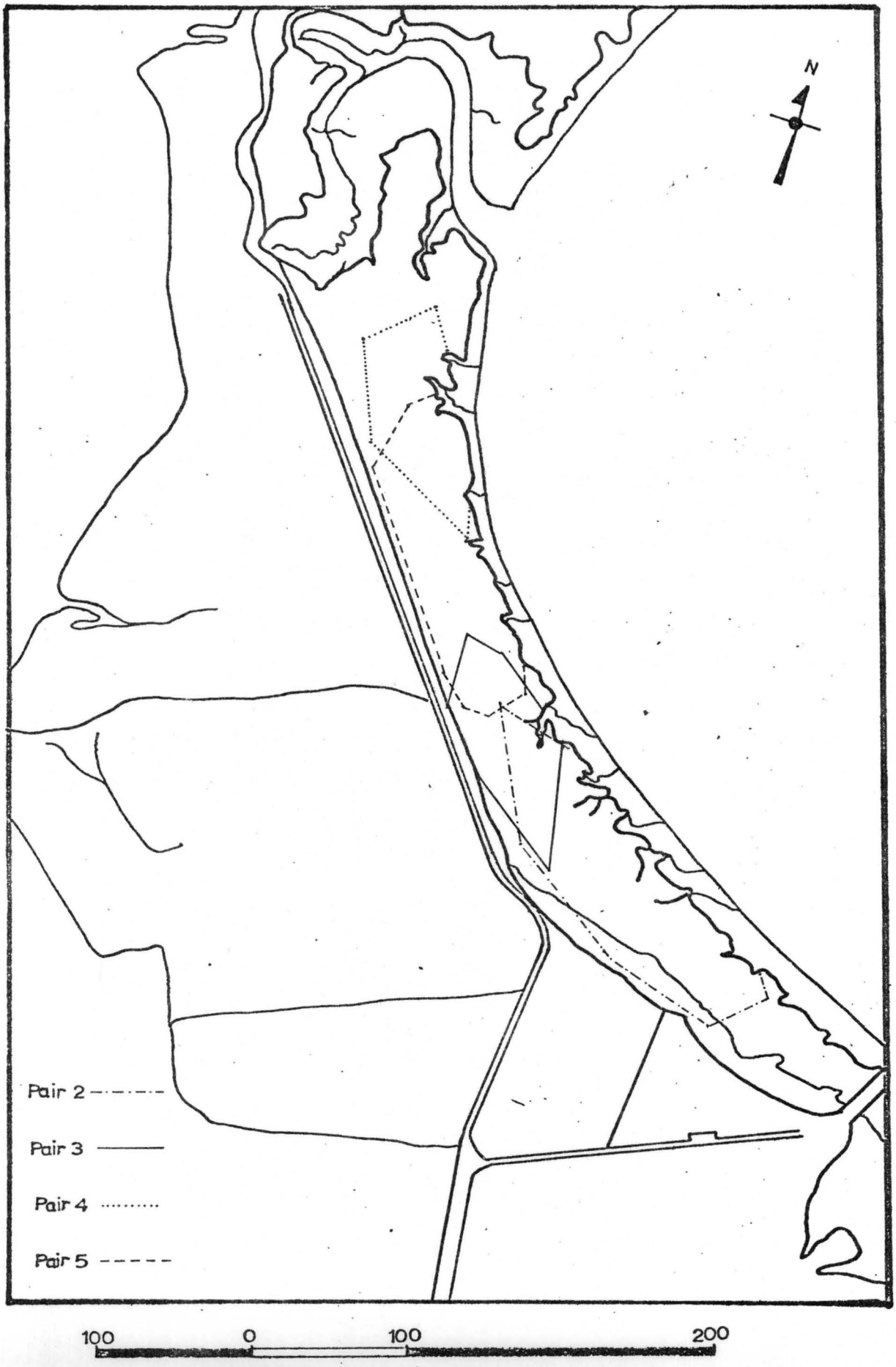

N
Pair 2
Pair 3
Pair 4
Pair 5
100
0
100
200

FIGURE 5

FIGURE 5. Territory of each pair of Willets during Phase II of the breeding season of 1976 as determined by the Mapping Method.

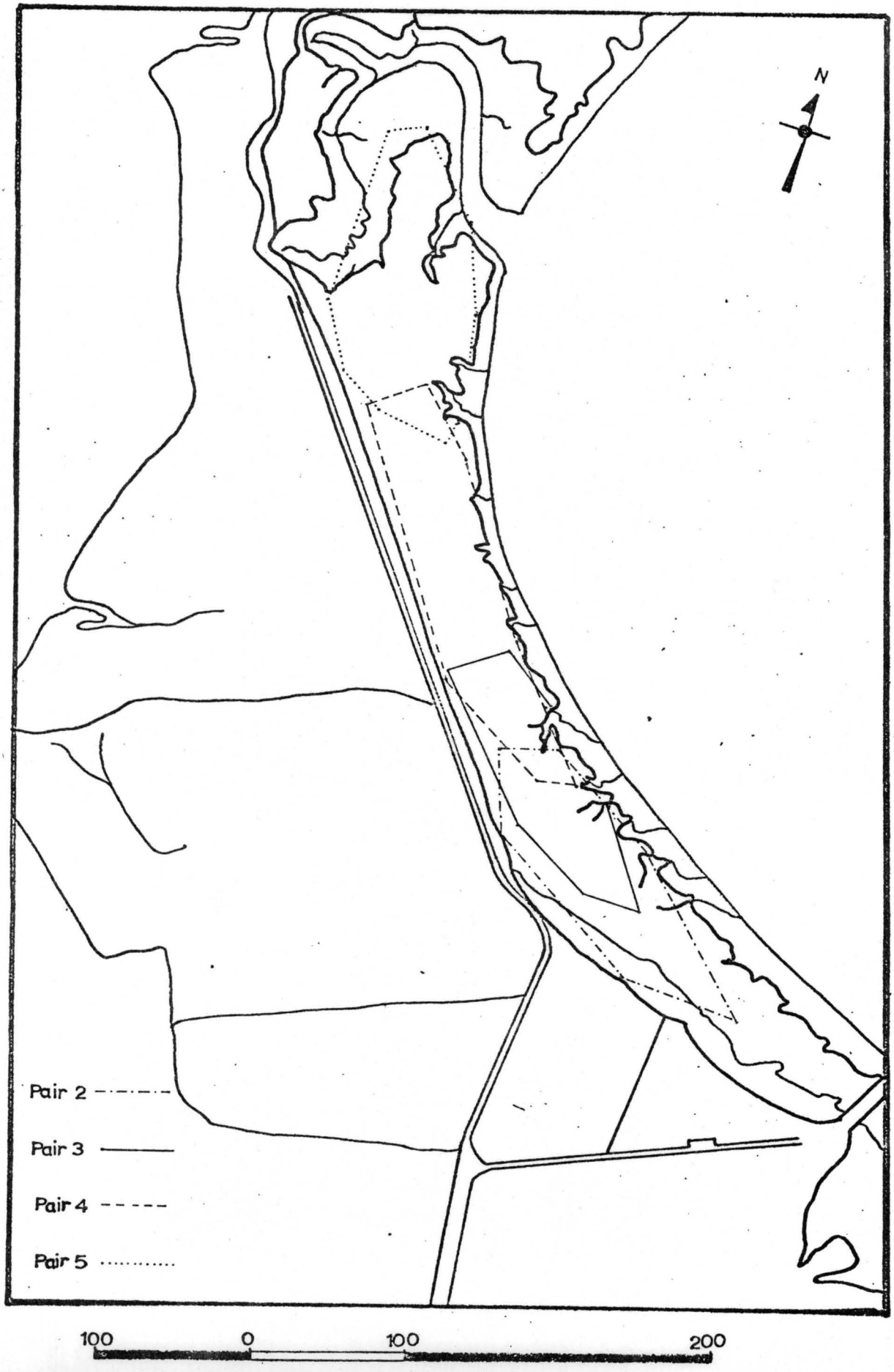

N
Pair 2
Pair 3
Pair 4
Pair 5
100
0
100
200

FIGURE 6

FIGURE 6. Territory of each pair of Willets during Phase III of the breeding season of 1976 as determined by the Mapping Method.

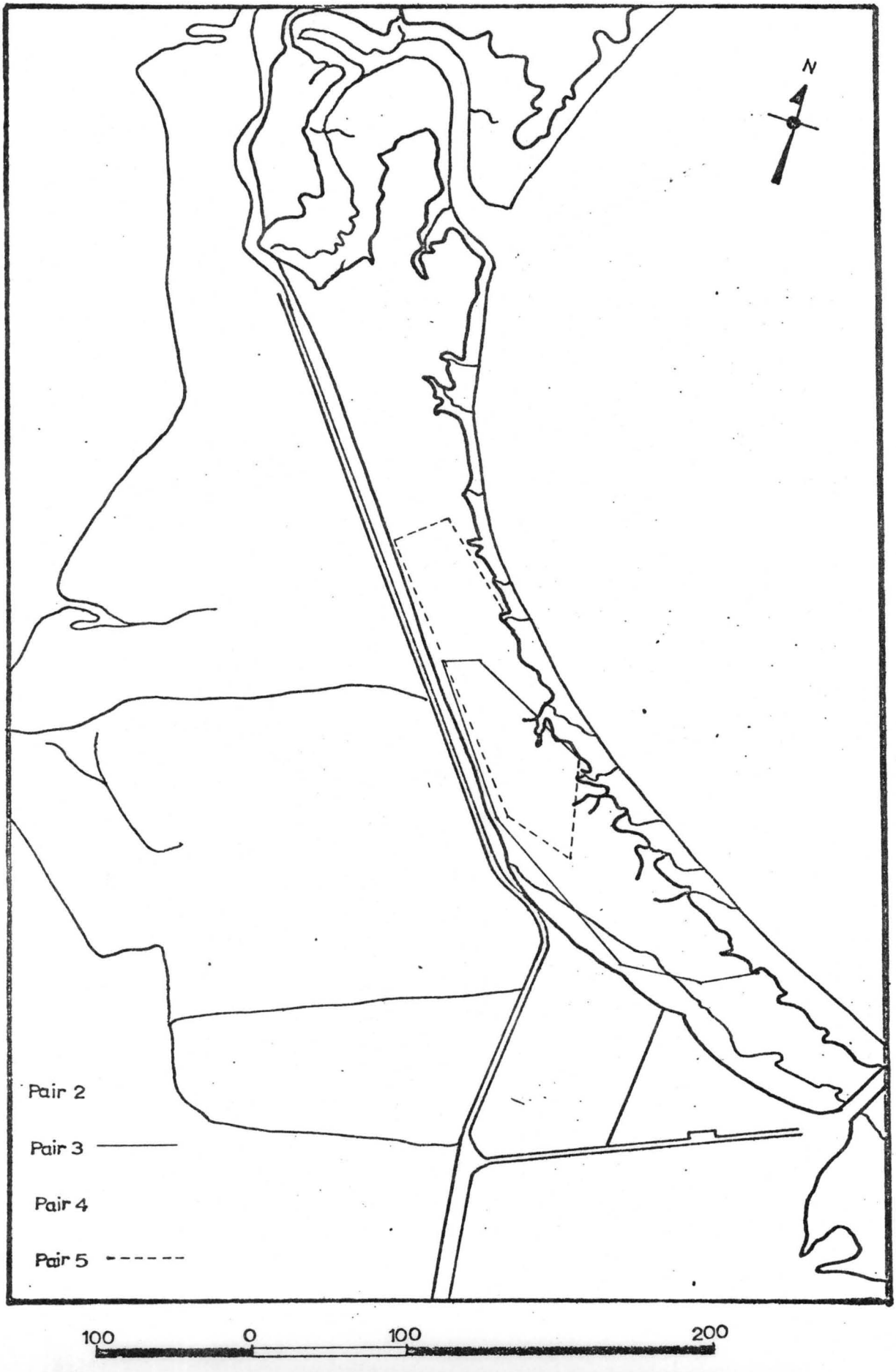
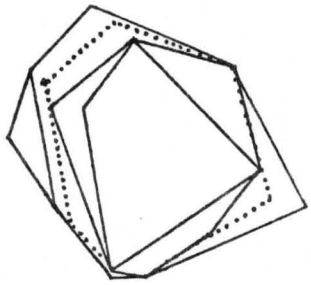
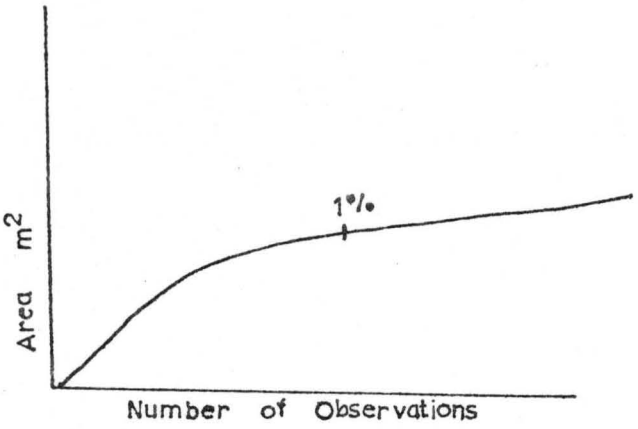

N
Pair 2
Pair 3
Pair 4
Pair 5
100
0
100
200

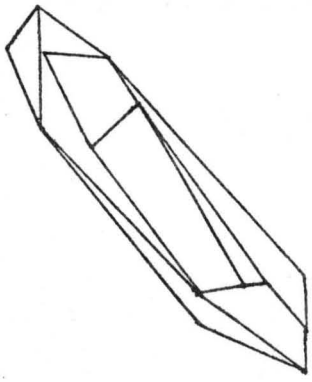
FIGURE 7

FIGURE 7. Application of the Observation Area Curve Method of determining territory size (based upon Odum and Kuenzler (1955).

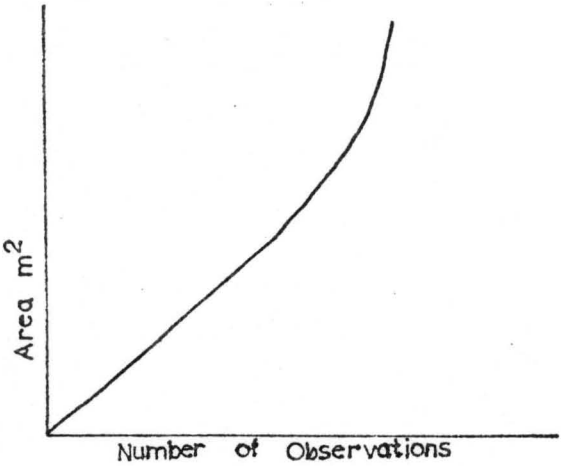


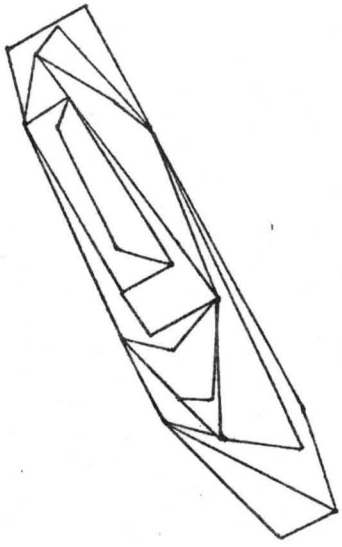
a*


Area m²
1%
Number of Observations



b


Area m²
Number of Observations



c

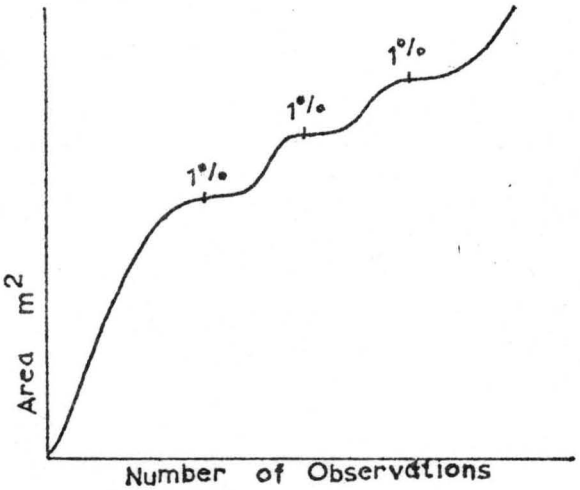

1%
1%
1%
Area m²
Number of Observations

FIGURE 8

FIGURE 8. Defended Area of each individual willet during Phase I of the breeding season of 1976.

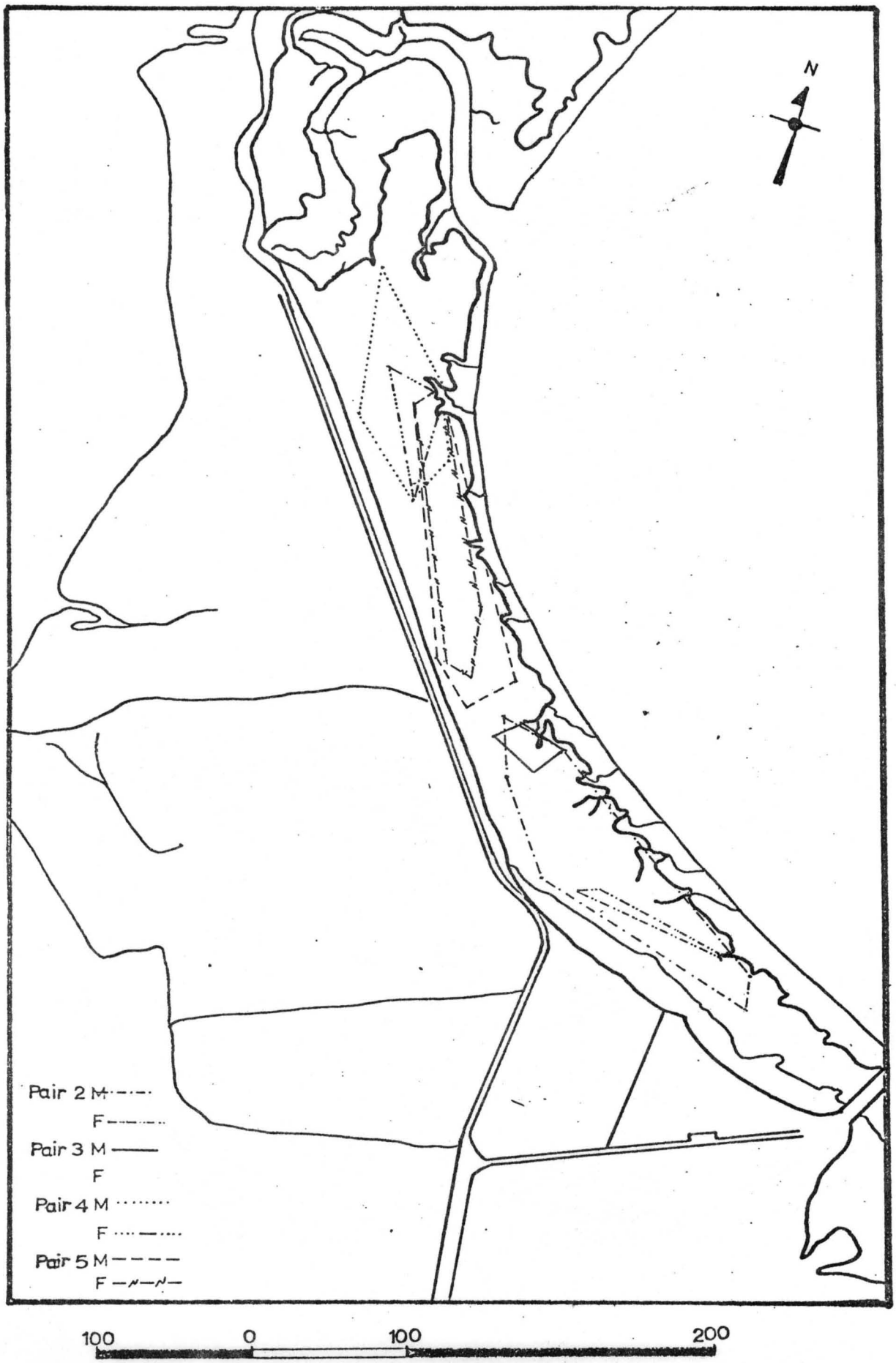

N
Pair 2 M
F
Pair 3 M
F
Pair 4 M
F
Pair 5 M
F
100
0
100
200

FIGURE 9

FIGURE 9. Home Range of each individual willet during Phase I of the breeding season of 1976.

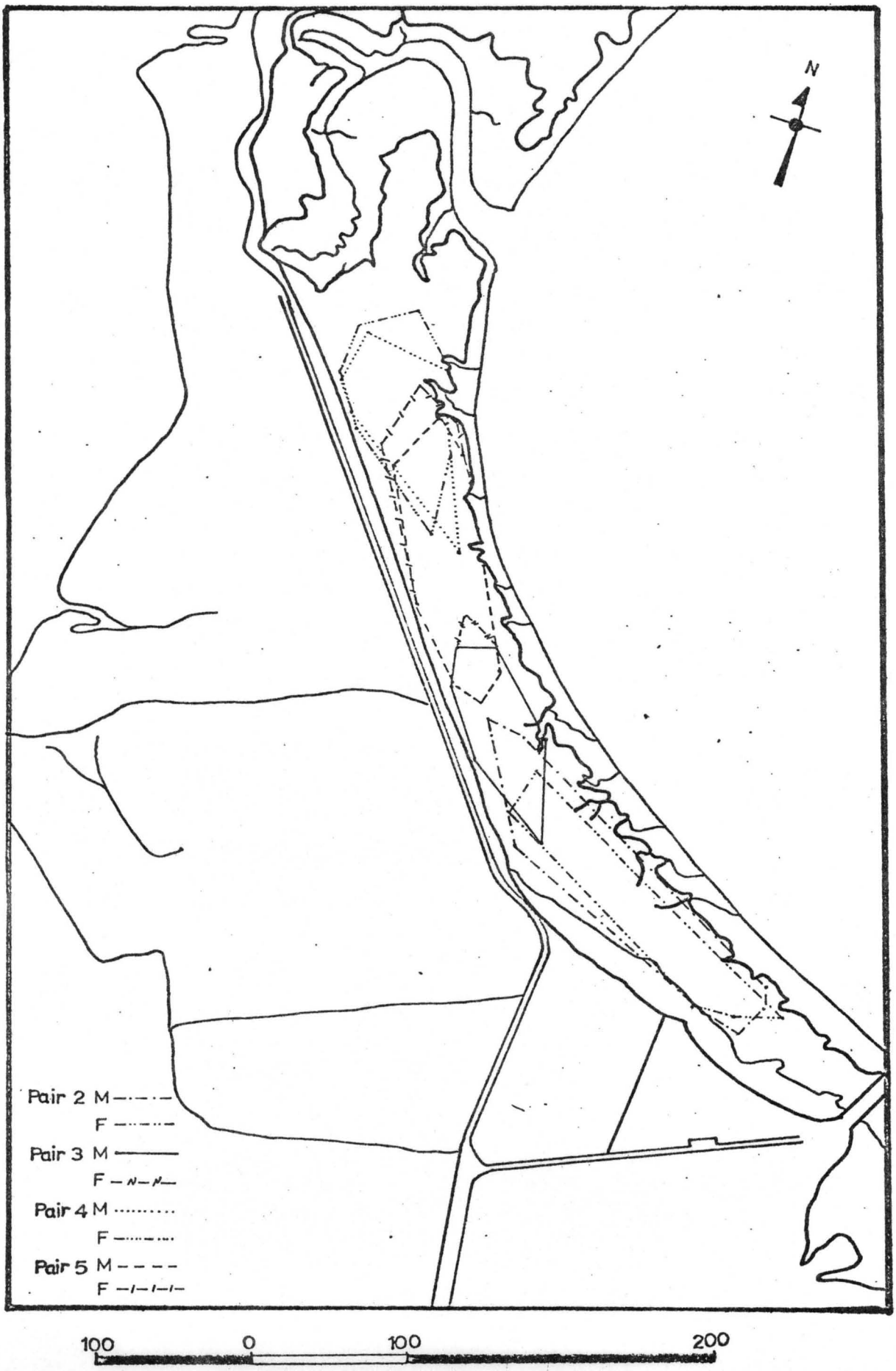

N
Pair 2 M
F
Pair 3 M
F
Pair 4 M
F
Pair 5 M
F
100
0
100
200

FIGURE 10

FIGURE 10. Defended Area for each individual willet during Phase II of the breeding season of 1976.

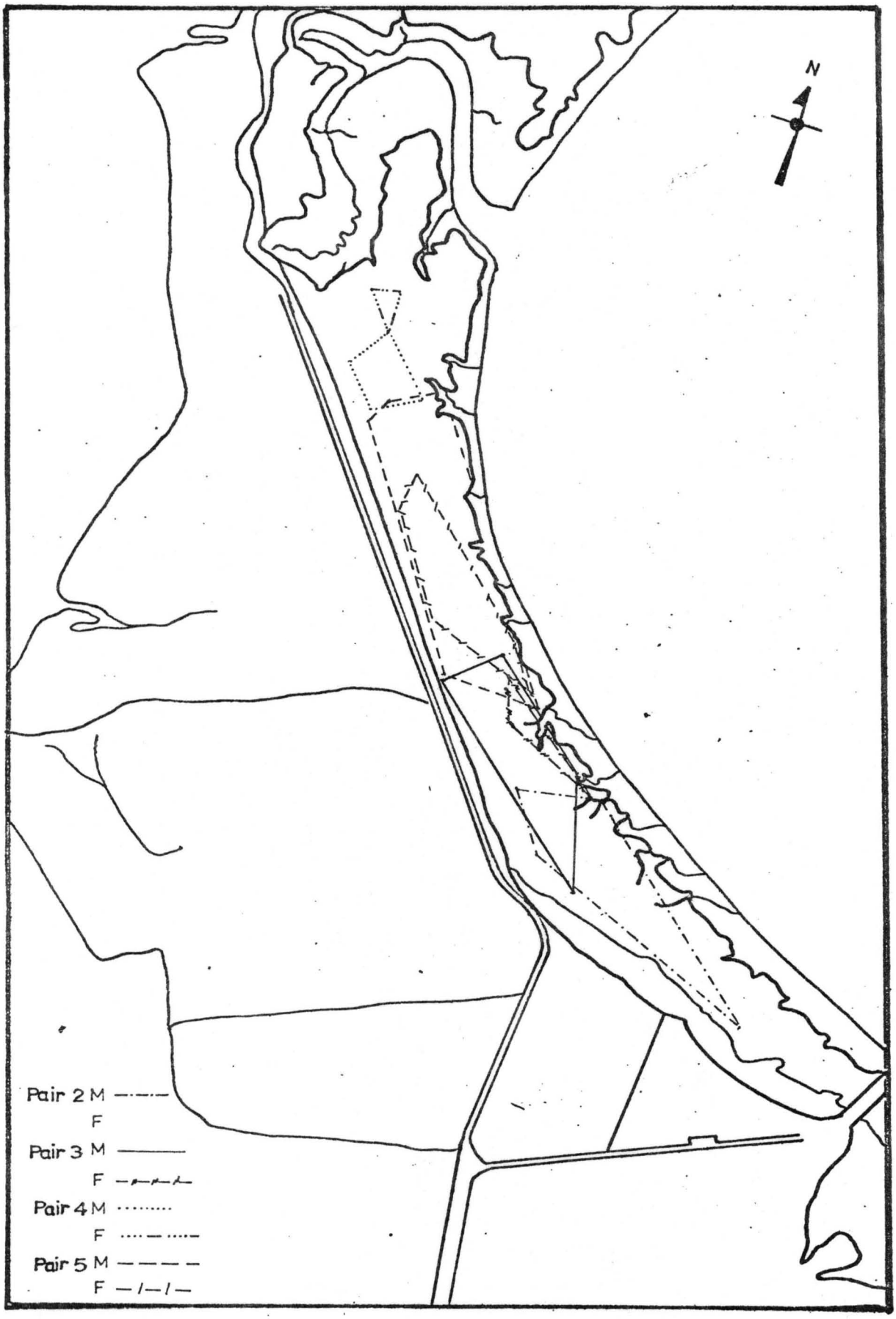

N
Pair 2 M
F
Pair 3 M
F
Pair 4 M
F
Pair 5 M
F
100
0
100
200

FIGURE 11

FIGURE 11. Home Range of each individual willet during Phase II of the breeding season of 1976.

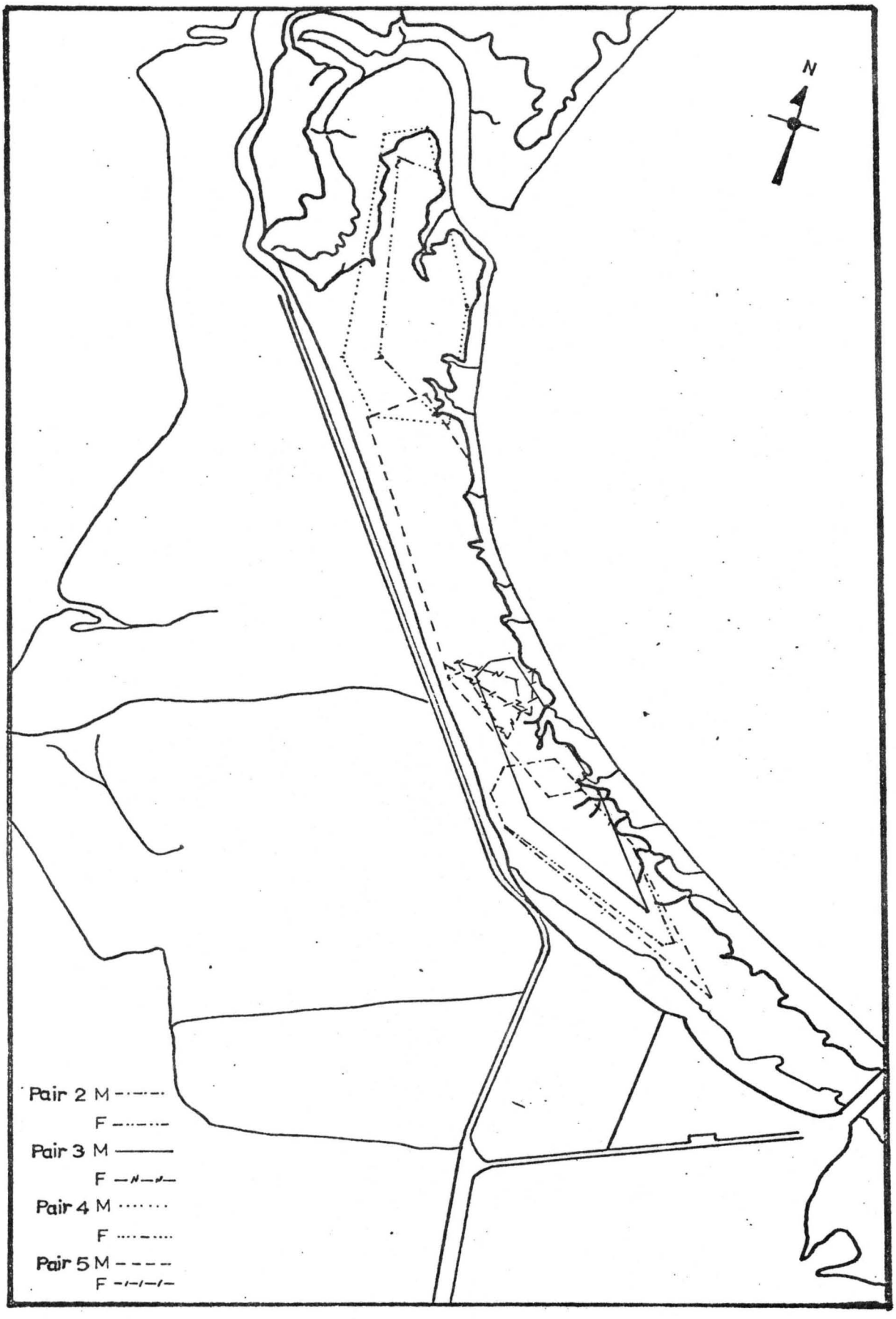

N
Pair 2 M
F
Pair 3 M
F
Pair 4 M
F
Pair 5 M
F
100
0
100
200

FIGURE 12

FIGURE 12. Defended Area of each individual willet during Phase III of the breeding season of 1976.

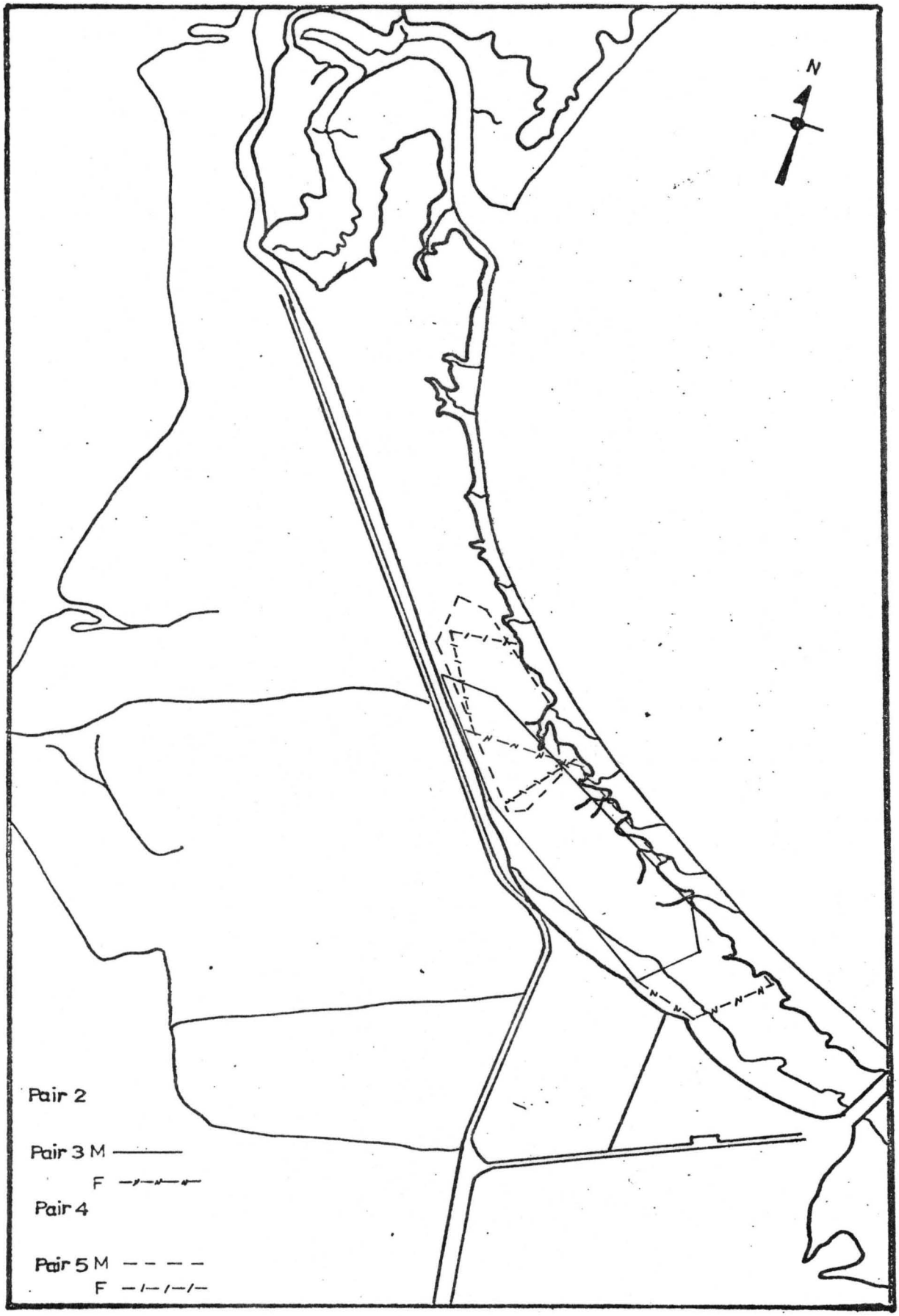

N
Pair 2
Pair 3 M
F
Pair 4
Pair 5 M
F
100
0
100
200

FIGURE 13

FIGURE 13. Home Range of each individual willet during Phase III of the breeding season of 1976.

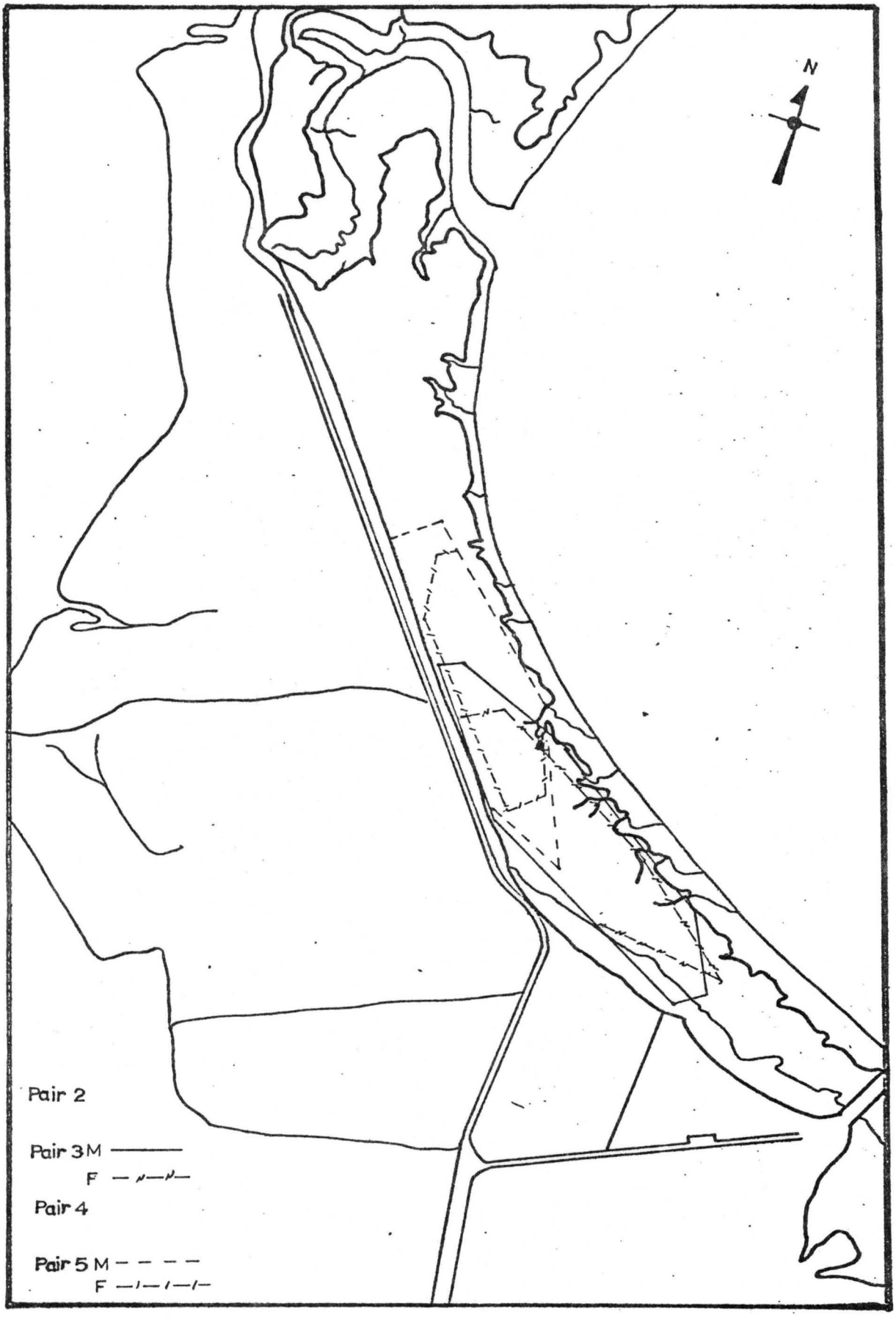

N
Pair 2
Pair 3 M
F
Pair 4
Pair 5 M
F
100
0
100
200

FIGURE 14

FIGURE 14. Territory of each pair of willets during Phase I of the 1976 breeding season as determined by the grid-column method.

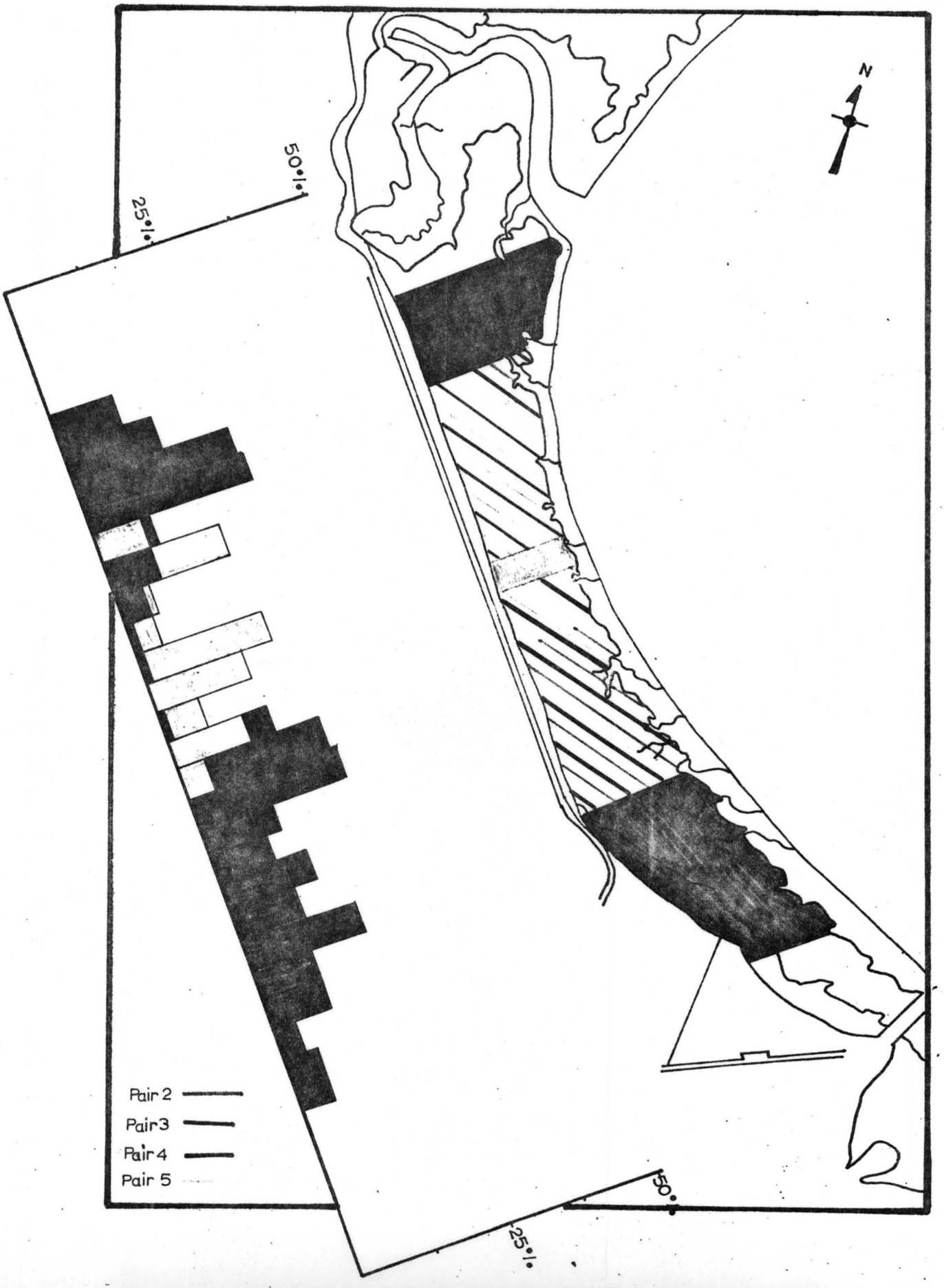

N
50°10'
25°10'
Pair 2
Pair3
Pair4
Pair 5
50°
25°10'

FIGURE 15

FIGURE 15. Territory of each pair of willets during Phase II of the 1976 breeding season as determined by the grid-column method.

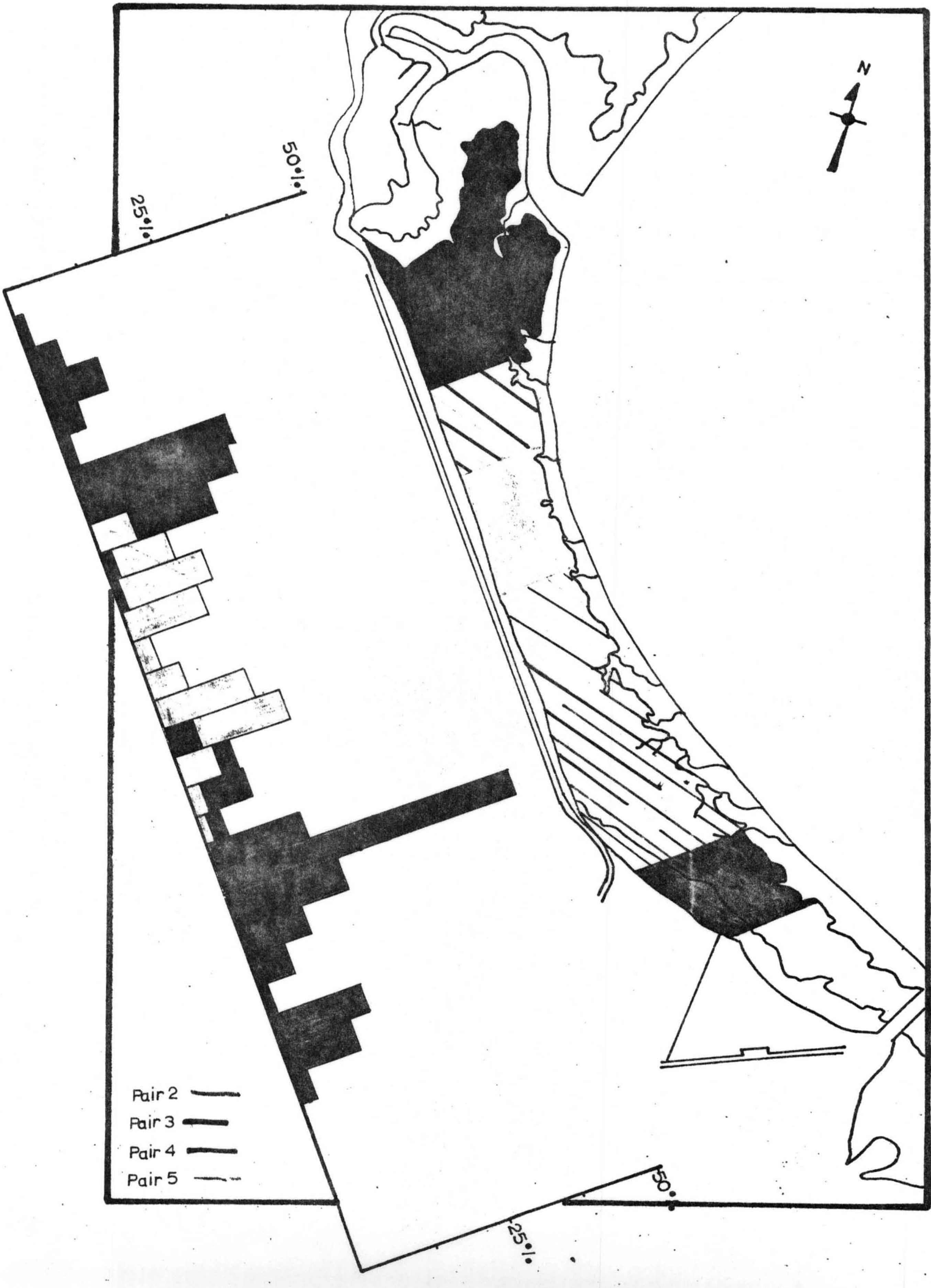

N
Pair 2
Pair 3
Pair 4
Pair 5

FIGURE 16

FIGURE 16. Territory of each pair of willets during Phase III of the 1976 breeding season as determined by the grid-column method.

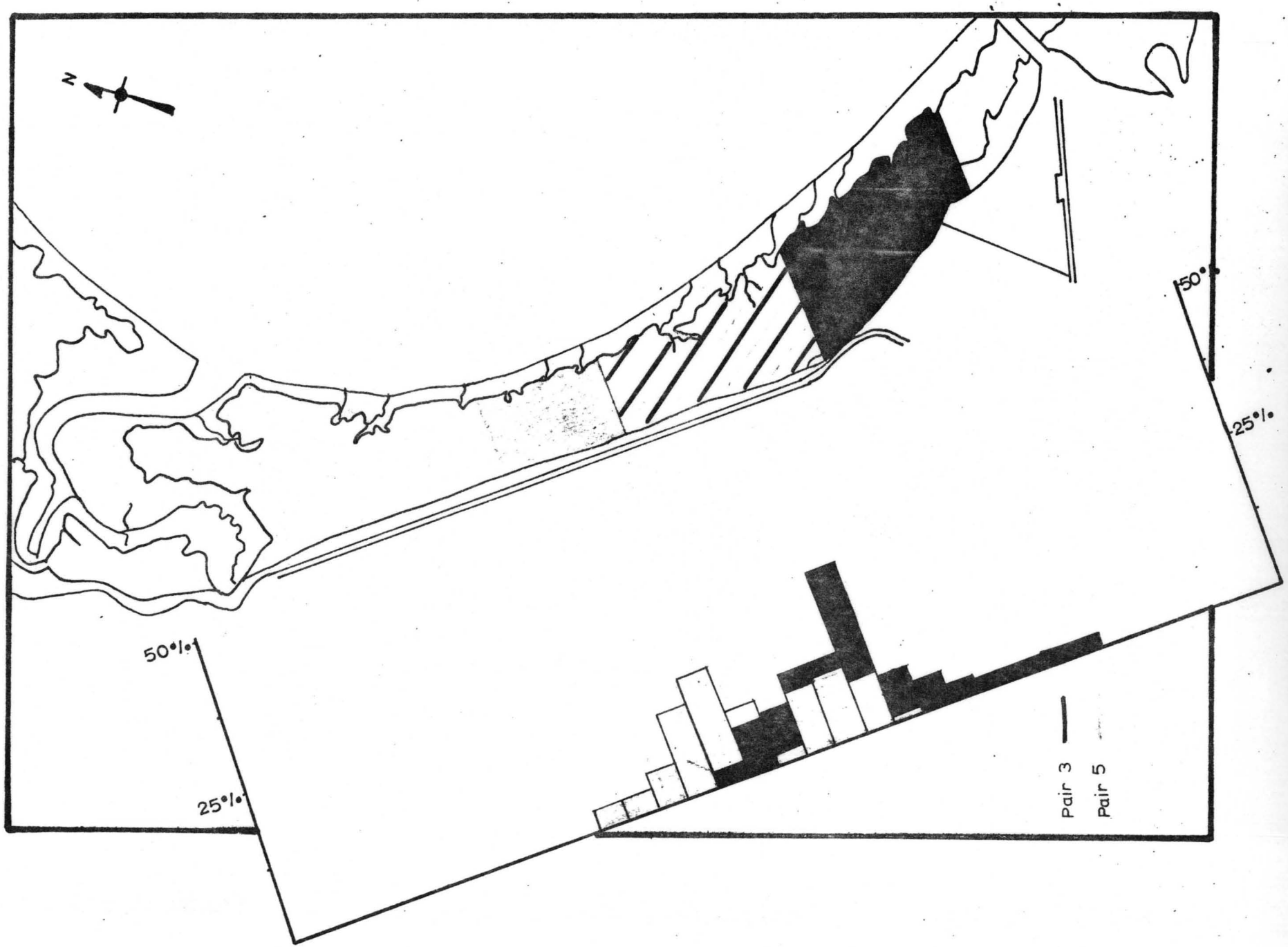

N
50%
25%
50%
25%
Pair 3
Pair 5

FIGURE 17

FIGURE 17. Territory of each pair of willets during Phase I of the 1977 breeding season as determined by the grid-column method.

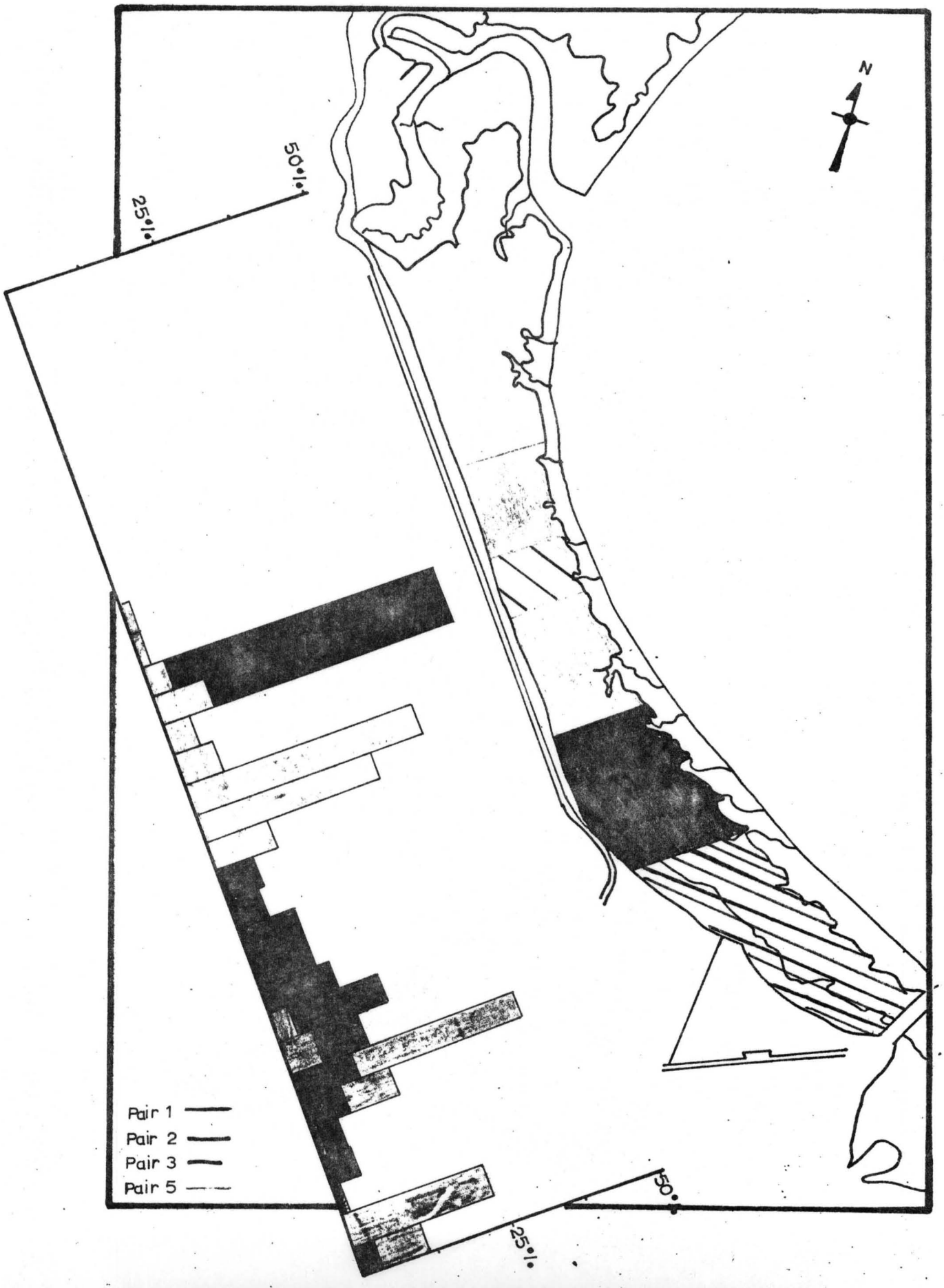

N
50'
25'
Pair 1
Pair 2
Pair 3
Pair 5
50'
25'

FIGURE 18

FIGURE 18. Nest locations and flight routes of willets to their shore territories during the breeding season of 1976.

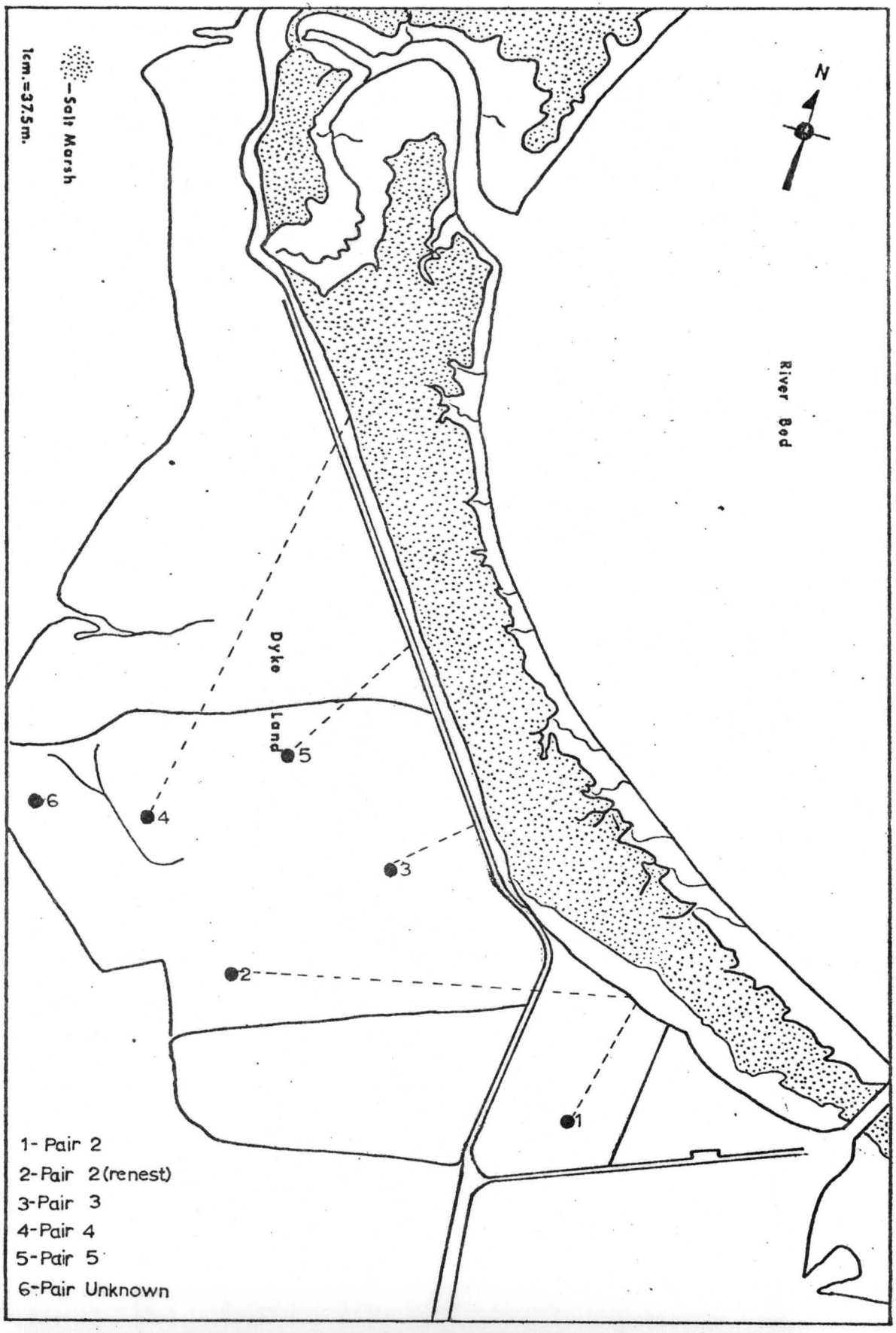
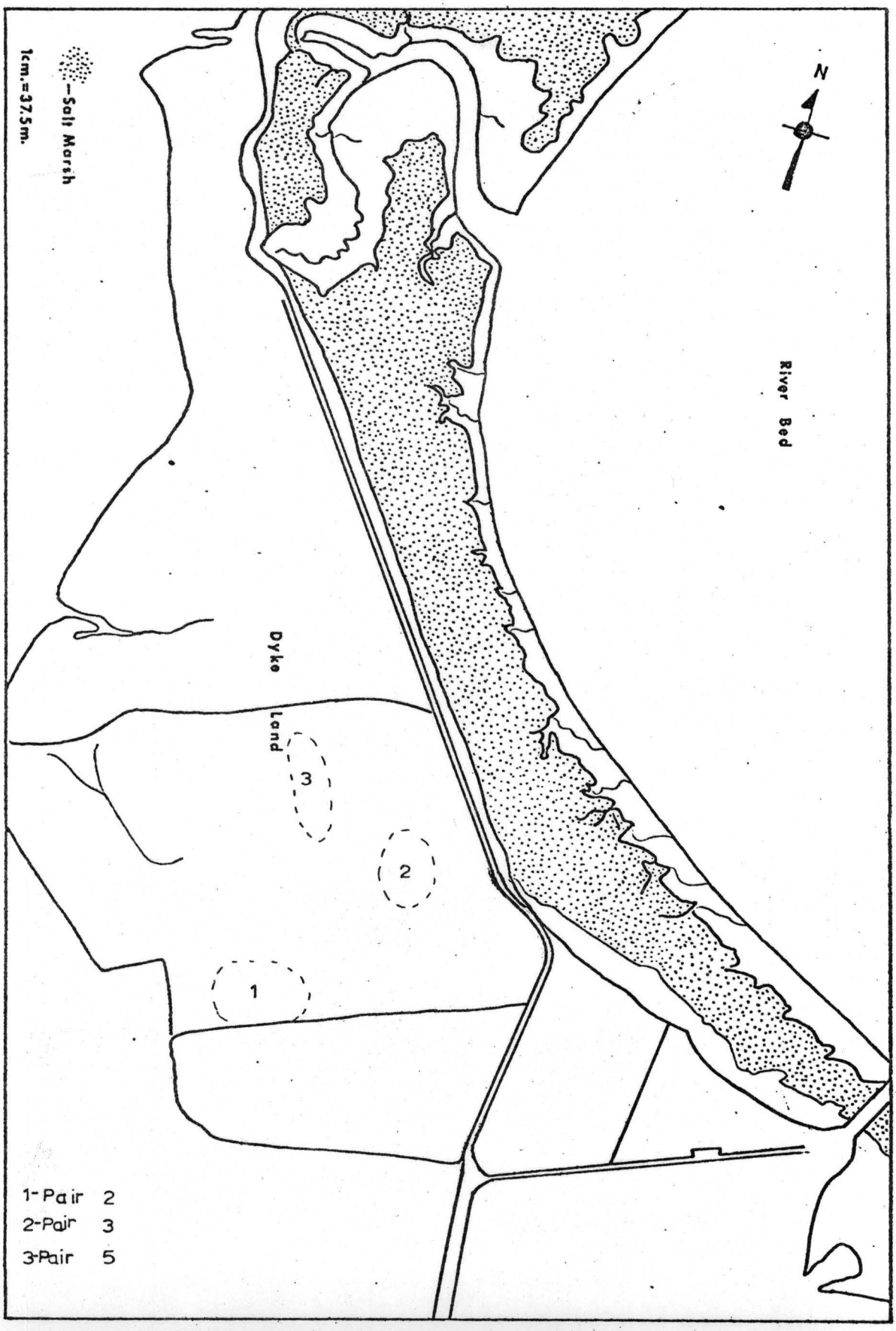

N
Salt Marsh
1cm.=37.5m.
River Bed
Dyke
Land
1
2
3
4
5
6
1- Pair 2
2- Pair 2 (renest)
3- Pair 3
4- Pair 4
5- Pair 5
6- Pair Unknown

FIGURE 19

FIGURE 19. Nest search areas of willets in 1977.


N
River Bed
Dyke
Land
Salt Marsh
1cm.=37.5m.
1
2
3
1-Pair 2
2-Pair 3
3-Pair 5