BIONOMICS OF THE PIED STILT (<u>HIMANTOPUS LEUCOCEPHALUS</u>) IN NEW ZEALAND : WITH SPECIAL REFERENCE TO BREEDING BEHAVIOUR.

A thesis presented in partial
fulfilment of the requirements for the degree
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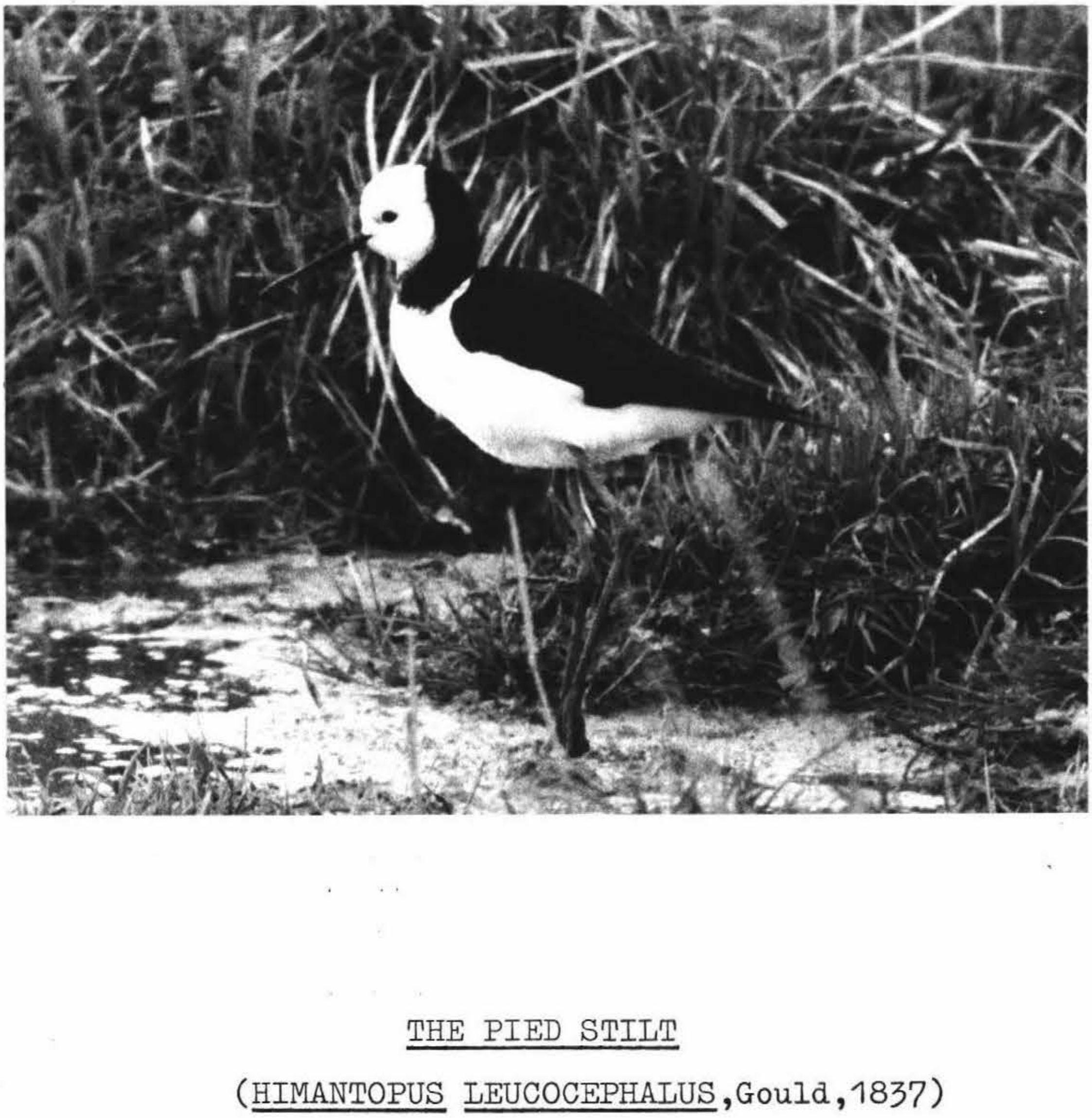

<u>THE PIED STILT</u>

(<u>HIMANTOPUS</u> <u>LEUCOCEPHALUS</u>,Gould,1837)

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CHAPTER I

INTRODUCTION

A. INTRODUCTION.

i) Aims of the Study.

Although the Pied Stilt, Himantopus h.leucocephalus, Gould,1837 * is one of New Zealand's most common wading birds there has been very little published work on it. The purpose of this study therefore was to gain knowledge of the general biology of the Pied Stilt with special reference to breeding behaviour. It has been suggested (L.Gurr, pers.comm.) that the large numbers of Pied Stilt may be responsible for genetic swamping, through interbreeding, of the Black Stilt Himantopus novaezealandiae Gould,1841 which is now quite rare and its breeding range restricted to a very small area of New Zealand - the Waitaki River system. The intention was that this study should provide information as a background to further investigation of the problem.

This study is based on field observations made between February 1969 and December 1970 in the Manawatu district around Palmerston North, where Pied Stilts are found in large enough numbers to permit relatively easy observation, except during the winter months when their numbers drop considerably.

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* Nomenclature for New Zealand birds follows that laid down in the Annotated Checklist of the Birds of New Zealand (Kinsky,1970). Other bird species are as prescribed in the Handbook of British Birds (Witherby et al,1943) or in the specific reference works quoted.

It should be noted that data was collected over only two years and breeding data over only one season. In addition there were innumerable difficulties in the mechanics of data collection. In such a study therefore it should be recognised that some statements are made with the realisation that there is little evidence or data in support of the opinion.

ii) Previous Work.

Little work had been done on the Pied Stilt until mid 1960's. Since then an increasing amount of work has been done, mostly in the South Island, but little of this is published. For instance J.Hamel's (pers.comm.) work in Otago on seasonal and individual variation in Pied Stilt plumages. Most of the previous published work on stilts consists of brief observational notes in Notornis and occasionally a more detailed note of some particular aspect (Stokes et al 1959, Pullen 1967). In the better known New Zealand bird books of Oliver (1955), Stead (1932) and Turbott (1967) the coverage is anecdotal and sparse and includes no quantitative work. Similarly there is little available on the only other member of this family of waders - the Avocet (Recurvirostra sp.). Makkink (1936) published a sixty page ethogram on the European Avocet (R.avosetta) which was useful, if largely descriptive and non-quantitative. Thus recourse has been made to what material is available on less closely related birds of the suborder Charadrii which includes plovers, dotterals, oystercatchers, sandpipers and godwits. These at best give a rough guide to methodology.

iii) Affinities.

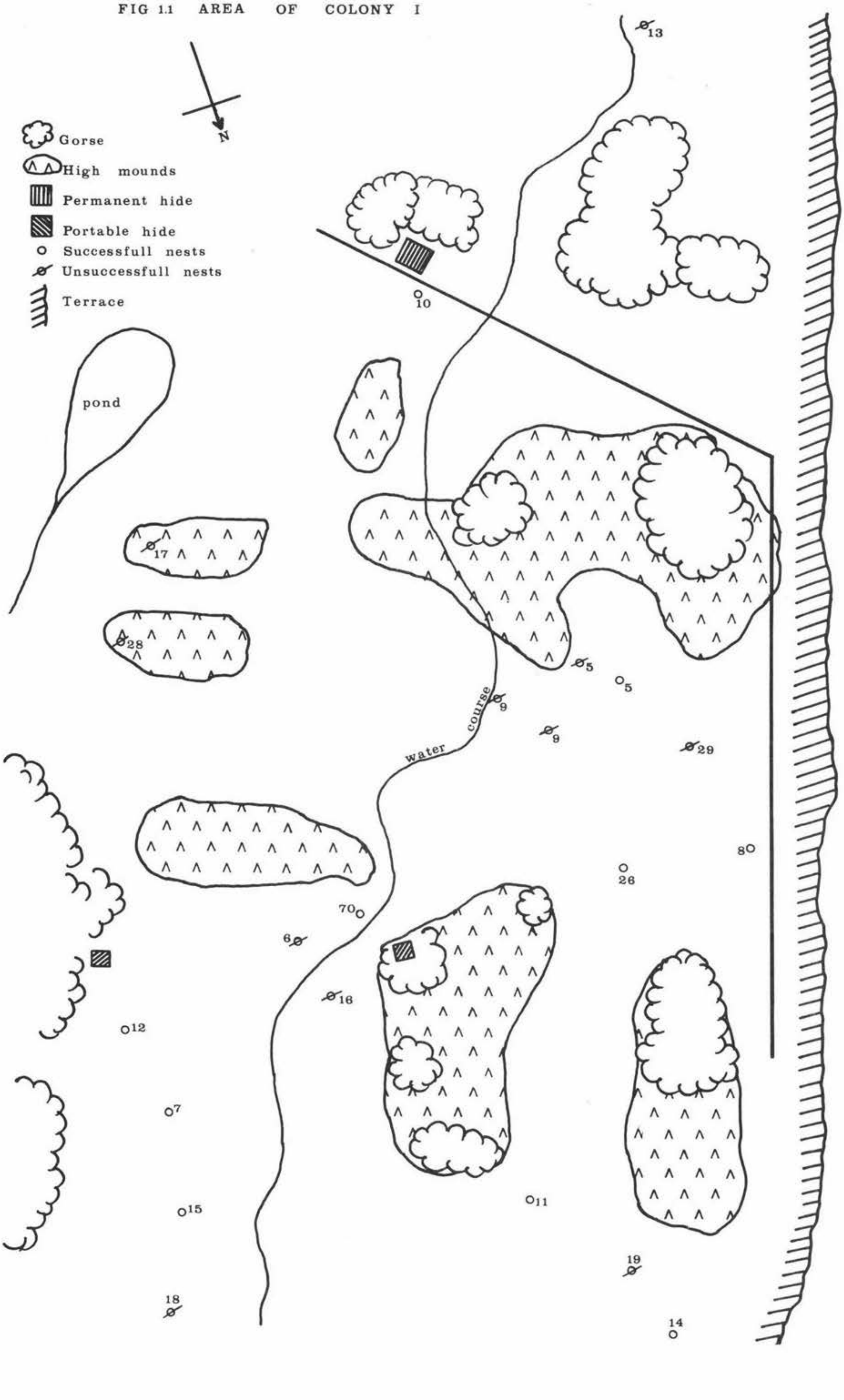
The Pied Stilt belongs to the family Recurvirostridae, Sub-family Recurvirostrinae which includes stilts and avocets. Apart from New Zealand it is found on some New Zealand offshore islands and in Australia though there is no evidence of movement between Australia and New Zealand (Kinsky, 1970). The closest relative of the Pied Stilt in New Zealand is the Black Stilt which, I believe, on the basis of evidence (p.40) should be included in the same species, i.e. they are morphs of the same species. It is not known how the Pied Stilt came to Australia and New Zealand, but it has three widely distributed close relatives; the Black-winged Stilt *Himantopus himantopus* in Europe, Asia, southern Africa and Australia; the Blacknecked Stilt *H.mexicanus* and the Hawaiian Stilt *H. knudesni* in southern and western United States to Peru and Brazil. The latter two have been suggested as races of the Black-winged Stilt (Hanzak, 1967). Possibly the Pied Stilt has also arisen from the Black-winged Stilt as there are few significant differences in either plumage patterns or bodily measurements.

B. HABITAT DESCRIPTION.

Pied Stilts spend much of the non-breeding season along rivers and at river estuaries where they feed along the edges of open shingle banks and in shallow, slow-flowing water. Seldom are they found feeding close to any sort of dense cover.

During the breeding season the stilts move onto breeding colonies. Records from the Ornithological

FIG 1.1 AREA OF COLONY I



Society of New Zealand (O.S.N.Z.) nest record cards have been analysed for nesting habitat preferences and the results summarised in Table 4.1 (p.85). As in the non-breeding season, birds tend to prefer an open situation such as river or swampland.

During this study three colonies were under observation eight miles west of Palmerston North at Awahuri near the Oroua river. The two major ones were close together; one on a swampy paddock (Colony I) and the other (Colony II) on the river beside it. These two may have been parts of the same group of birds as there was considerable movement between them. However, because the habitats were distinct they were separated for recording purposes. The third colony (Colony III) was a small one on a swamp about a mile from the others and was used for comparison.

Colony I was used for most of the observations on breeding behaviour and it was here that nest building and laying first took place. This colony consisted of an area of 2-3 acres in a paddock of some 10-12 acres. Water lay over this area for most of the year and over the central part throughout the year. A narrow channel ran through the area and water flowed through this all year from a pond at one end to the river at the other. Another small pond lay along the eastern edge of the colony area (Fig. 1.1).

Thus it can be seen that this was an extremely wet area (Plate I) which carried an abundance of fresh water insect life as a food source for the stilts. As a result of the continual wetness swamp plants were found

PLATE I

Close up of part of Colony I showing the extreme wetness of the area.

PLATE 2

Mounds of coarse grass and weeds in which some nests were built.

in abundance. Large clumps of gorse were found around the edge of the colony and throughout the area there were 12-18 inch high mounds of coarse grass and weeds (Plate 2). Table 1.1 gives a list of the major species of plants found in the area.

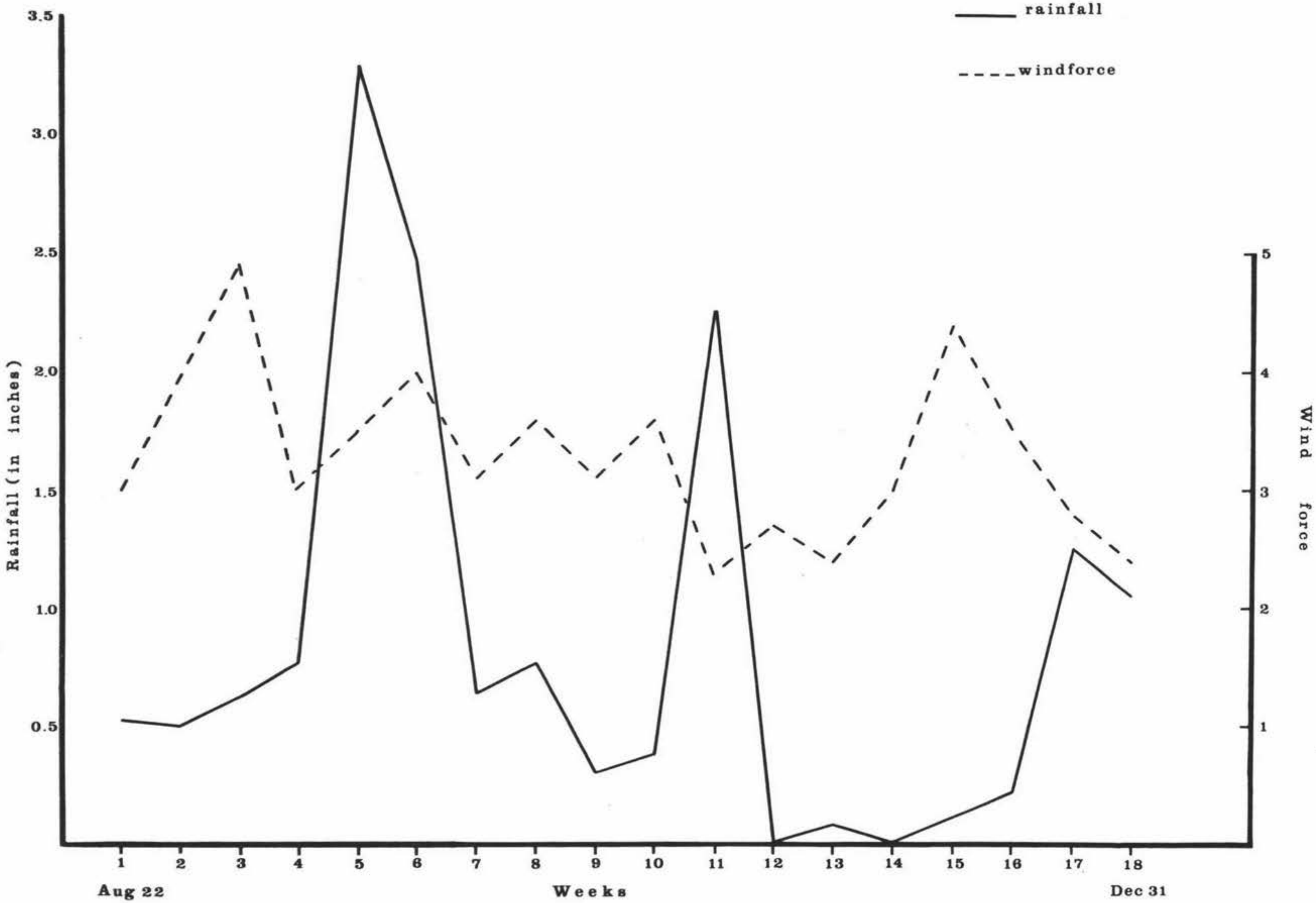
TABLE 1.1 MAJOR PLANT SPECIES FOUND ON COLONY I

Specific name	Common name
Rumex crispus	Curled dock
Ulex europeaus	Gorse
Polygonum decipens	Wireweed
Nasturtium officinale	Watercress
Mimulus guttatus	Monkey flower
Ranunculus repens	Creeping buttercup
Juncus autiflorus	Rush
J.effusus	Rush
Lotus uliginosus	Greater Birds-foot Trefoil
Mariscus ustellatus	Sedge

The habitat of Colony III was basically similar to that of Colony I and comprised a hollow with a creek running down one side. There was no gorse, however, and less vegetation on the whole. Most of the vegetation consisted of clumps of rushes with some swamp plants present around the edges and along the creek.

Colony II was spread along $\frac{1}{4}$ mile of river bed and consisted almost entirely of sand, shingle and stones. Large amounts of driftwood were also present and some pairs nested amongst this. Most, however, nested amongst the shingle and stones close to the edge of the river. This appeared to be the preferred habitat. There

FIG 1.2 TOTAL WEEKLY RAINFALL AND MEAN WIND FORCE FROM BEGINNING OF LAYING



was a large island in the middle of the shingle bed and the main vegetation on this was lupin (Lupinus arboreus) with the addition of a few trees, but no stilts were found nesting near this.

C. CLIMATIC CONDITIONS.

All rainfall and temperature records were taken from R.N.Z.A.F. Base, Ohakea and wind records from Grasslands Division, D.S.I.R., Palmerston North. Both of these stations are approximately eight miles from the study colony and so only reflect the climatic conditions on the colony in a broad way. They do, however, give a reasonably accurate measure of precipitation.

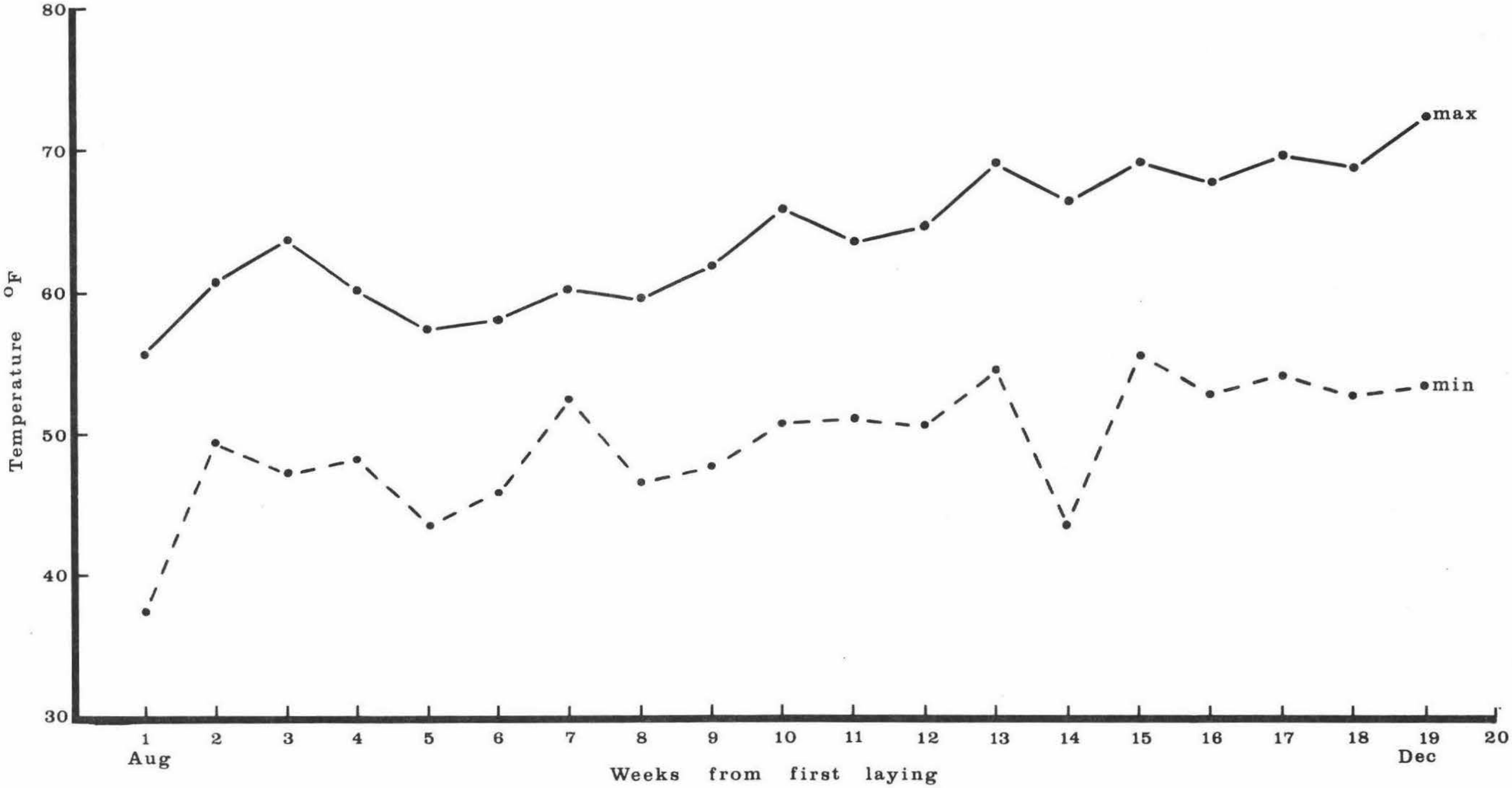
i) Rainfall.

Total precipitation in the area over the breeding period, i.e. during the last six months of 1970 was 21.65 inches. This gave a monthly average of 3.6 inches (range 1.71-6.65 inches (Table 1.2). Rain fell on 123 days out of 184 during this period though there was only a trace on 39 of these days. For these 123 days the range was 0.01 inches to 1.5 inches of rain per day, the average being 0.26 inches per rain day. Figure 1.2 shows total weekly precipitation from time of laying and indicates three peaks of rain during this period. It was the latter two peaks in particular which account for the loss of eggs due to flooding and, I believe, for the loss of some chicks hatched during these periods (see p. 145).

ii) Temperature.

The lowest temperature recorded during the breeding period was 31.9°F and the highest was 75.2°F. However, as the colony was in a relatively sheltered situation I believe the temperatures reached could have been more

FIG 1.3 MEAN WEEKLY TEMPERATURE FROM START OF LAYING PERIOD



extreme than these. Evidence from the thermometer, used to calibrate the thermistor apparatus (p. 19), which read 80.5°F at one time, substantiates this claim. Mean monthly maximum temperature was 61.6°F and mean minimum was 47.35°F (range 55.8°F - 69.2°F maximum and 42.0°F - 53.6°F minimum) (Table 1.2). Figure 1.3 shows mean weekly temperatures throughout the laying period. It shows a general increase in temperature throughout the period apart from two marked decreases; in maximum and minimum temperatures in week five, corresponding to an increase in rainfall and in minimum temperature in week fourteen, for which no reason was found. In addition there was a slight decrease in temperature in week two again corresponding to an increase in rainfall.

iii) Wind.

Prevailing wind was from the west to northwest and occurred on 67% of the windy days during the laying period, which was 62.2% of the total laying period. There was some wind on 93% of this period. For the last six months of the year there was wind on 84% of the days and of these 62.5% was from the west to northwest. This period would have covered most of the courtship and nesting activities prior to laying, although most of the calm days (77%) were during July and August.

Wind strength ranged from Force 1 to Force 7 with a mean force of 3.1. The mean number of miles run per day (as an indication of wind speed) was 186.5 miles. Mean monthly wind force and miles run per day is shown in Table 1.2. The mean weekly wind force from beginning of laying is shown in Figure 1.2 and, except in general trend, appears to bear only slight relationship to rainfall and temperature.

For the most part the colony was protected from strong winds by the terrace down the west side and patches of high gorse on most of the other three sides (Fig.1.1). However wind did tend to funnel through some of the clumps of gorse, particularly from the south and southeast. Wind only occurred from this direction; however, on 11.4% of days during the six month period. The most important effect which the wind had on the stilts was the prevention of successful copulation (p.83). During periods of relatively strong wind incubating stilts appeared to sit more tightly on the nest, leaving it for shorter periods of time and less frequently. Non-incubating birds sought shelter behind clumps of rushes or gorse or stood hunched, in the open, facing into the wind.

D. METHODS.

i) Observation.

Two hides were constructed for observation purposes; one close to where stilts nested the previous season, and a portable one close to the centre of the colony where stilts nested in the 1970 breeding season (Fig. 1.1). The majority of records were obtained by direct observation either from one of the hides or in the open. Observations were recorded on a Philips Memo Taperecorder and later transcribed in full into a notebook. A pair of 7x35 binoculars was used for observation. Before breeding activities began visits were made to Colonies I and II at least once a week for three months and once a day thereafter. After laying began two daily rounds were made to check nests. Visits were made only once daily to Colony III. In patrolling the areas new nests were marked with a numbered peg and subsequently plotted on a map of the area when they contained an egg (Fig.1.1). Photographic records were taken with a 35mm Asahi Pentax camera using 300x and 500x lenses. Also a movie record of some behavioural sequences was taken with a Canon Zoom 518 Super 8 camera.

ii) Measurements.

As each egg was laid or a new nest found, eggs were numbered with a vivid marker pen and measured with vernier calipers accurate to 0.01 cm. Volumes were calculated from these measurements by the method recommended by Stonehouse (1966). Although the ink tended to wear off the eggs the numbers were still clearly visible at the end of the incubation period. A small plastic bag with a 100 gm spring balance was used to weigh eggs soon after laying and chicks within one or two days of hatching.

A sample of birds was collected under special permit, throughout the study period by shooting with a .410 shotgun. The method of measurement of these followed that suggested by Gurr (1947) using vernier calipers accurate to 0.10 mm. Measurements were placed on a separate card for each bird (Appendix I) and duplicated in a notebook. Timing of various behavioural sequences was made with an Ilona cumulative stopwatch calibrated in 1/10th second intervals.

iii) Trapping and Banding.

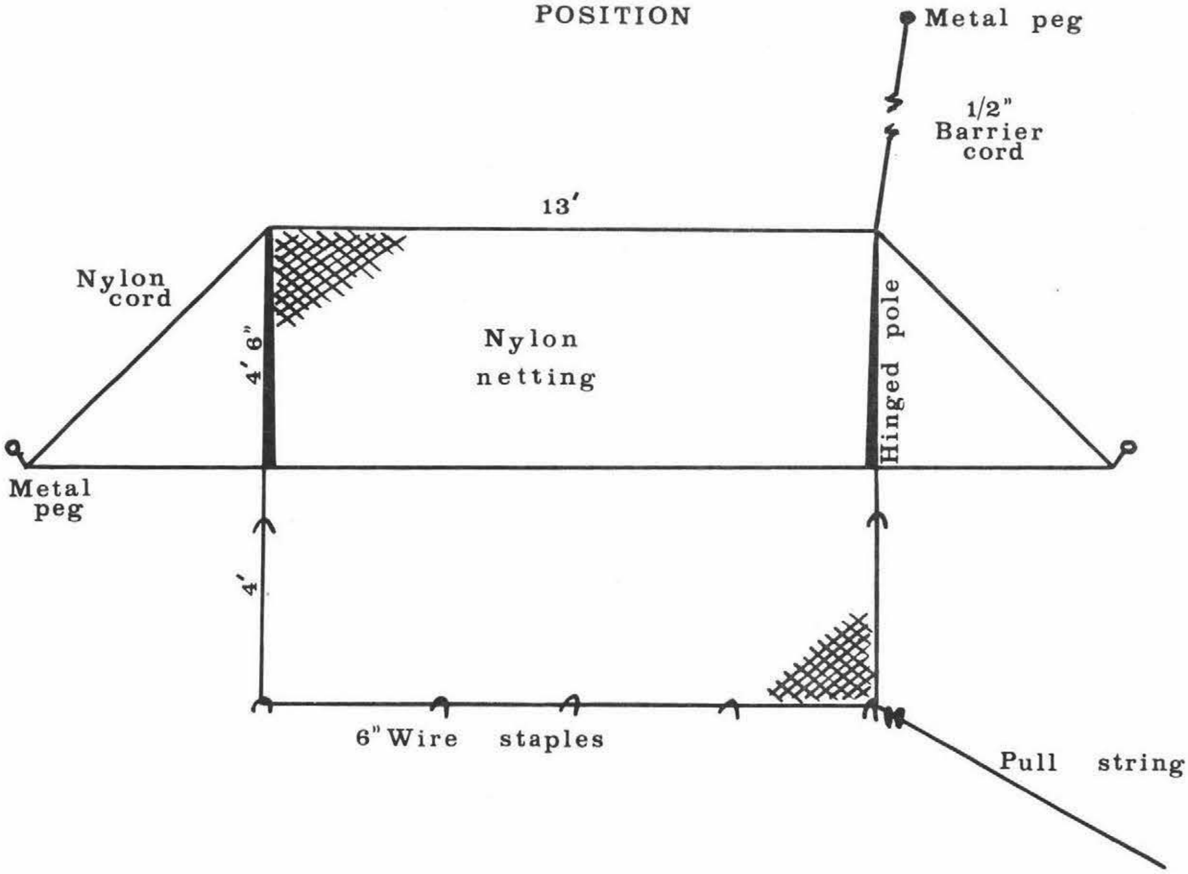
The birds were trapped in order to band and mark them individually so they could be recognised as individuals and in this study especially during laying and incubation. A Rhodamine B solution was used for marking as suggested by Gullion (1965). In addition it was hoped to put a colour on one bird and attach a small radioactive source to it for automatic detection on the nest, similar to the method used by Barbour (1963). Three methods of trapping were tried to trap adult stilts.

(a) During the non-breeding season a mist net 40ft long and 9ft high was set up on the river at a favourite feeding site of the stilts. The stilts, however, are extremely wary birds and have excellent eyesight. Thus this method failed, even at night. A mist net was also set up on Colony I during the breeding season, again with no success.

(b) A second method, that of clap-trapping was tried on Colony I during the breeding season. The clap-trap (Plate 3, Fig.1.4) was left on the colony in the set position for a week to allow the stilts time to habituate to it. Twice the stilts came close to the trap but faults in the trap setting caused by problems with the terrain, prevented it springing properly. Thereafter the stilts never came within range of the trap, such was their wariness even though a period of days was allowed between attempts.

c) The third method tried was that of using a drop trap. Again this was tried during the breeding season on Colony I. The trap was constructed of extra strength

FIG 1.4 PLAN OF CLAP TRAP IN SPRUNG POSITION



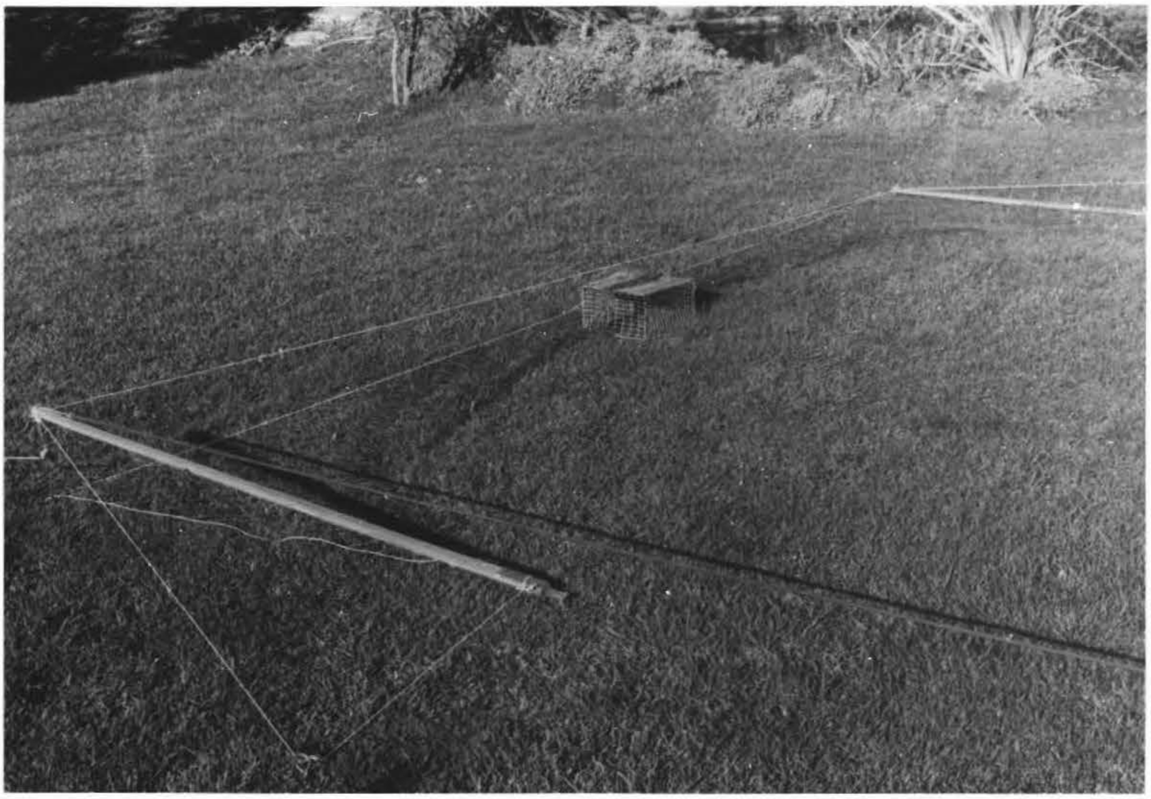


PLATE 3

Clap trap in set position. (Photo by R.R.SUTTON)

PLATE 4

Tambour chart recorder used to determine attentiveness.

Number 8 wire, making a frame six feet by four feet by one foot nigh which was covered with mist netting. The trap was initially set up at a 45° - 50° angle on an established territory. This gave no success as the pair on the territory kept well away from it. Setting the trap over a nest site on which the pair were actively building was next tried. Again there was no success as the pair moved to another site. Even placing a stuffed mounted bird inside the trap failed to lure the pair in, although they appeared agitated by the model's presence. On one occasion when the mounted bird was placed just outside the trap it was attacked by a Harrier Hawk, Circus approximans. Finally the trap was set up over a nest containing eggs. After about an hour a parent finally returned to the nest, first for only a few minutes at a time before finally settling. The trap was sprung and the bird trapped, marked and banded, then released. It never returned to the nest, however, and its mate, after incubating all the following day, finally deserted the nest also. As there were so few nests on the colony it was decided to discontinue these trapping attempts for fear of further nest desertions.

While attempts at banding adults met with no great success, some chicks were banded, both with colour bands and aluminium numbered bands supplied by the Wildlife Service, Department of Internal Affairs. Aluminium bands were put on only when the chicks were at least a week old, as prior to this the legs were too small to hold the bands properly. Difficulty in finding chicks after this age resulted in only eight being banded.

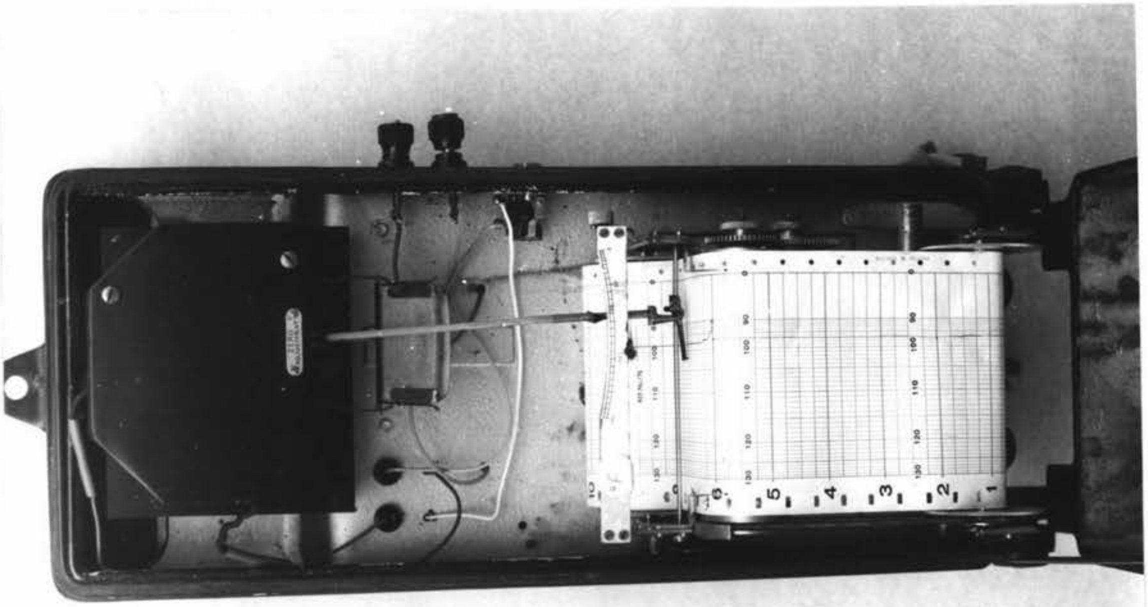

1
2
3
4
5
6
90
100
110
120
130

PLATE 5

Transistor radio receiver for temperature impulses.

PLATE 6

Temperature chart recorder.

iv) Automatic recording.

Automatic recording devices were used in two phases of incubation.

(a) Attentiveness was recorded by a copper pressure-tambour and a modified Evershed-Vignole chart recorder similar to the method suggested by Gurr (1949). The tambour, covered with stretched rubber dam, was placed under the nest and covered with only a thin layer of nest material so the eggs were as close to the tambour as possible. Periodically, material needed removing from between the eggs and the tambour due to the continued building activity of the incubating stilts, especially in wet weather. In the damp conditions the rubber dam perished quickly and required replacing every four or five days. A 40ft length of $\frac{1}{4}$ inch rubber tubing connected the tambour to the chart recorder (Plate 4).

(b) Temperature of incubation was measured by a radio-telemetric thermistor device placed in a stilt's egg after the cap and contents of the egg had been removed. The cap was fixed in place with araldite and the egg filled with stilt egg albumin through a small hole in the cap using a syringe. A loop antenna was placed in the nest around the eggs under the nest material and connected to a transistor radio receiver (Plate 5) 50ft away. This passed the signals received from the egg to an Evershed-Vignole voltmeter which transferred the impulses onto the chart (Plate 6). (For technical description and circuitory see Appendix II).

The recorder was run off two 12 volt batteries and the thermistor circuit run off two 1½ volt mercury batteries connected in parallel. Due to continual interference from stock the area around the equipment was fenced off. This, however, did not protect the equipment from the weather. On one occasion on Colony III a flash flood covered all equipment ruining the receiver and requiring the rebuilding of the recorder circuit.

TABLE 1.2 MEAN MONTHLY MEASUREMENTS OF CLIMATIC FACTORS OVER THE BREEDING SEASON.

	July	Aug.	Sept.	Oct.	Nov.	Dec.	Mean
Rainfall	3.84	3.34	6.65	3.46	1.71	2.65	3.60
Temperature							
Maximum	55.8	56.7	59.4	62.4	66.0	69.2	61.60
Minimum	42.7	42.0	45.9	42.3	50.4	53.6	47.35
Wind Force	3.0	2.91	3.69	3.26	2.76	3.09	3.1
Miles Run	135.2	132.9	208.9	228.0	183.1	231.1	186.5

CHAPTER II

GENERAL BIOLOGY

A. BODILY CHARACTERS.

i) Measurements of Adult birds.

A total of 29 females and 34 males from monthly samples were measured according to the methods recommended by Gurr (1947), except that the depth of beak was taken at the proximal end of the exposed culmen and the length of lower mandible from the corner of the mouth to the tip. Table 2.1 gives the measurements obtained, damaged characters being omitted. All measurements, apart from beak length, are smaller than those given by Oliver (1955). However since he did not state his sample size or method of measurement, comparison of the two groups is difficult. Except in bill measurement the Pied Stilt appears to be smaller than its European relative, the Black-winged Stilt, (Witherby et al,1943).

Of the characters measured, only the following showed a significant difference ($p < 0.05$) between male and female measurements : total length of beak, wing length at first primary, tarsus, toe and tail. Only wing length and tarsal length showed a significant difference of $p < 0.01$ using an unpaired t test. Figures 2.1 and 2.2 show the spread of these characters respectively, comparing male and female, and the means are indicated. In addition Figure 2.3 shows wing length and tarsal length plotted against each other. Although there is some considerable degree of overlap

TABLE 2.1 MEASUREMENT OF ADULTS (IN CMS)

Character	FEMALES				MALES			
	No. in Sample	Mean	Range	Standard Deviation	No. in Sample	Mean	Range	Standard Deviation
Beak Length	25	6.75	6.01-7.22	0.30	32	6.94	6.17-7.74	0.38
Exposed Culmen	25	6.08	5.31-6.57	0.31	33	6.20	5.61-6.93	0.28
Lower Mandible	26	6.69	5.97-7.27	0.36	32	6.79	5.92-7.46	0.33
Width	29	0.62	0.53-0.74	0.05	34	0.63	0.56-0.76	0.04
Depth	29	0.67	0.58-0.75	0.04	34	0.68	0.50-0.80	0.06
1st Primary	29	21.95	18.18-23.85	1.32	34	22.87	19.81-24.36	1.16
Tarsus	27	9.22	7.89-10.26	0.45	32	10.03	9.03-11.58	0.67
Toe	29	3.38	3.16-3.76	0.15	34	3.27	3.04-3.81	0.18
Toe-nail	29	0.47	0.33-0.59	0.06	34	0.49	0.36-0.65	0.06
Tail	29	7.57	6.64-8.11	0.36	34	7.76	7.11-8.36	0.34

FIG 2.1 LENGTH OF WING AT FIRST PRIMARY

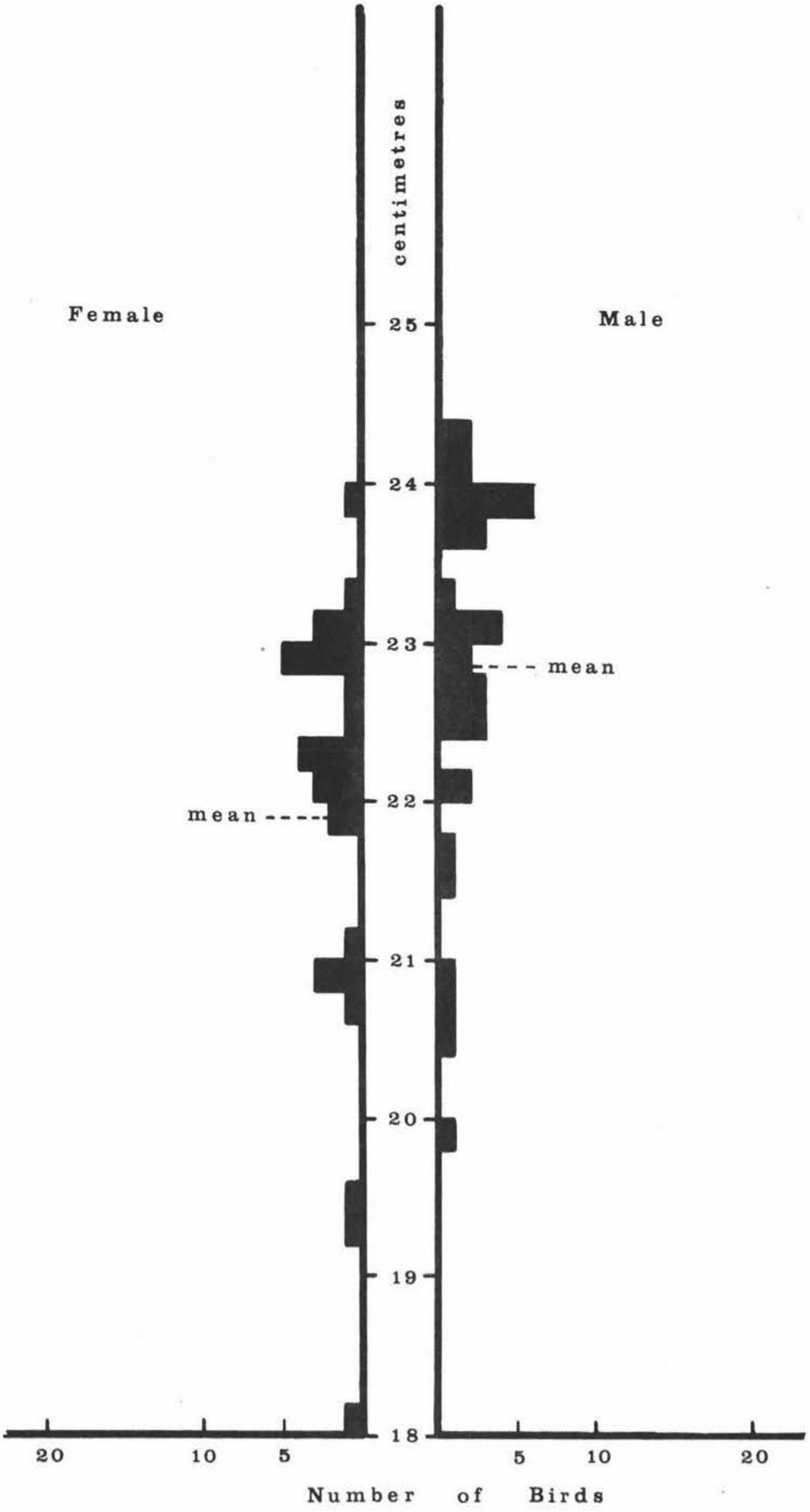


FIG 2.2 LENGTH OF TARSUS

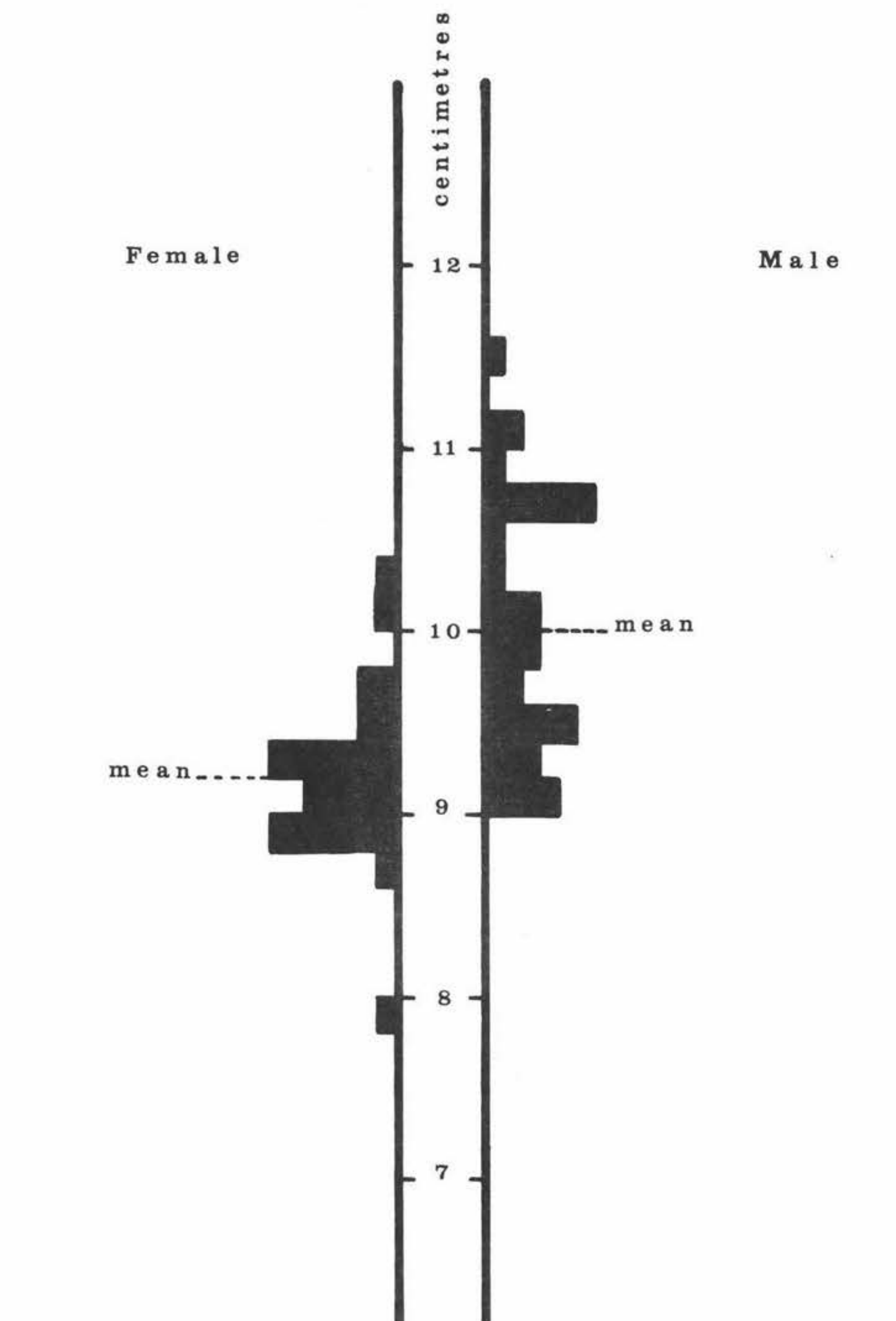


FIG 2.3 RELATION BETWEEN WING LENGTH AND TARSAL LENGTH

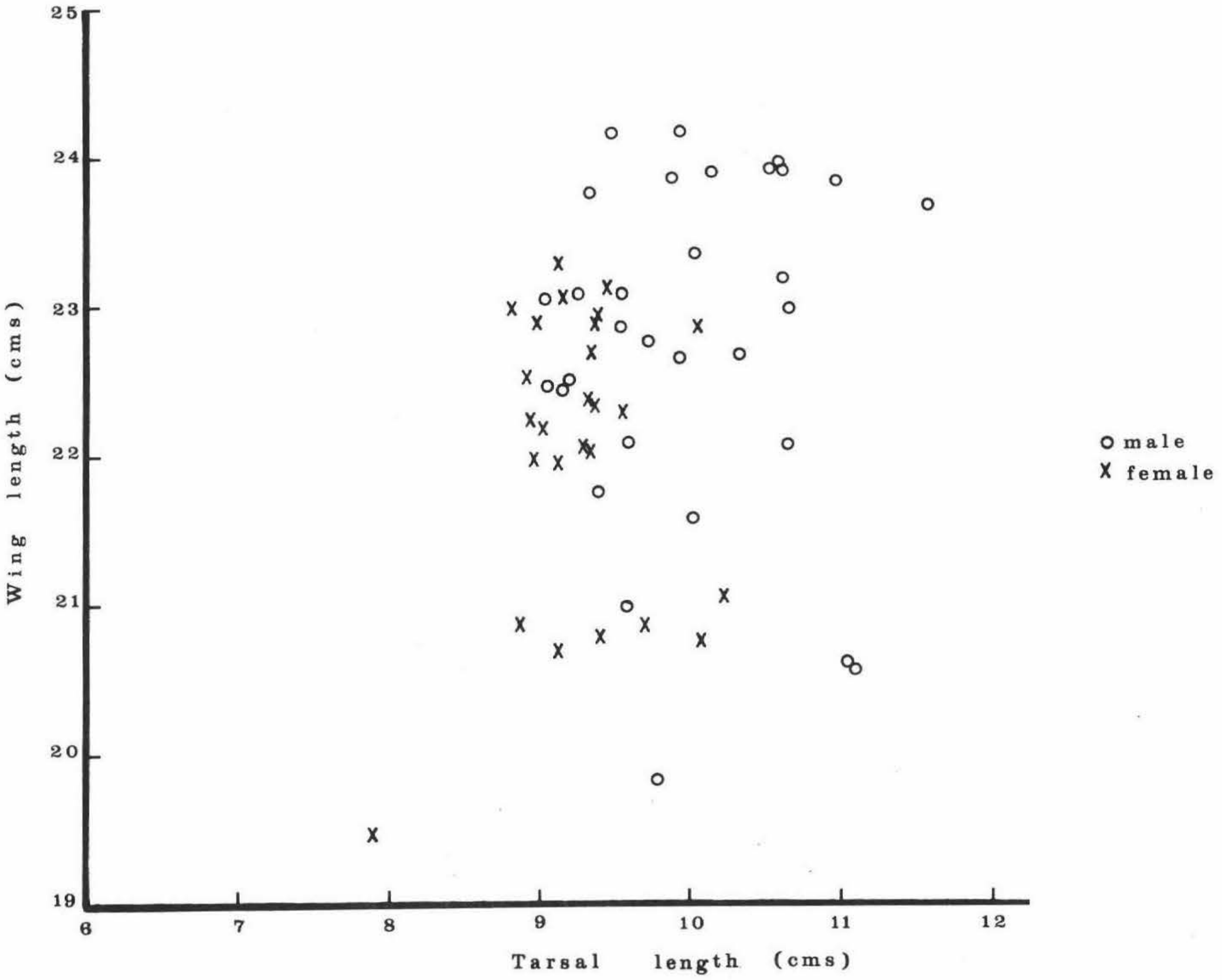
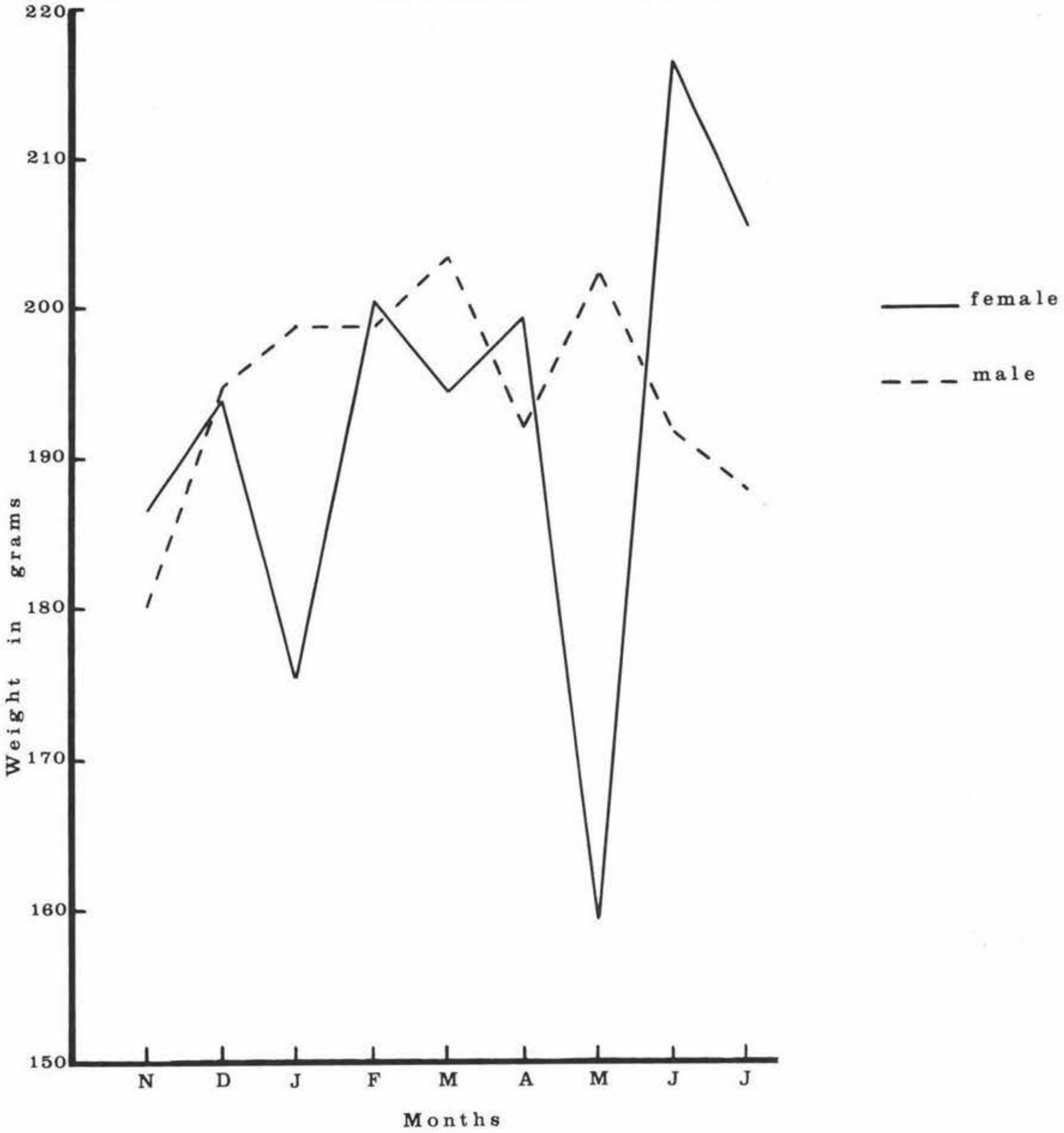


FIG 2.4 SEASONAL VARIATION IN BODY WEIGHT



it does indicate a tendency of the sexes to separate on the basis of these characters.

ii) Seasonal Variation in Body Weights.

Because of considerably difficulty in obtaining monthly samples, the sample size was variable and at times very small. This fact has been considered in discussion.

Specimens were weighed as soon as possible after death on a beam balance accurate to 0.1 gm. Table 2.2 shows mean monthly body weights and range, with 1969-70 monthly totals being combined for males in June and July. These figures are plotted in Figure 2.4 and indicate considerable variation both within and between the sex. In general, however, male body weights appeared to be higher and were relatively stable throughout the year, except for a drop in winter and a rise in spring. The drop in female body weights in January may be a result of the post-nuptial moult; the examination of skins taken at this period indicate new plumages being grown. Discrepancies between male and female weights in the winter months are probably due to variable or small sample size.

Baldwin and Kendeigh (1938) show for 85 species of birds that almost without exception body weights are highest during the winter months. Assuming that stilts follow a similar pattern this may explain the high body weights of males and females in May and June respectively. Indications are, in both July and November, that females weigh slightly more than males during the breeding season. In all probability this may be attributed to two factors; firstly female gonads are on average

TABLE 2.2 SEASONAL BODY WEIGHT OF ADULTS (gm)

MONTH (1970)	FEMALES			MALES		
	No.in Sample	Mean	Range	No.in Sample	Mean	Range
August						
September						
October						
November	3	186.66	180.0-190.0	2	180.00	173.0-187.0
December	3	194.00	190.0-197.0	6	194.80	180.0-218.0
January	7	175.21	118.5-202.0	3	198.93	187.4-212.4
February	1	200.50		1	198.90	
March	3	194.50	184.9-209.5	4	203.40	186.4-218.2
April	2	199.45	177.8-221.1	6	192.20	185.8-201.3
May	2	159.45	143.5-175.4	2	202.30	190.3-214.3
June	3	216.5	183.8-239.2	4 *	191.90	158.3-215.0
July	1	205.3		5 *	187.80	142.1-214.7

* Includes samples from 1969-70.
Samples could not be taken in August, September and October. Assumptions are made for these months based on trends in the periods before and after.

three or four times as heavy as male gonads at this time (Table 2.3) though this difference is by no means near the total weight difference, and secondly females appear to spend much more time feeding during the early breeding period (see p. 89), while males search for a suitable nest site and does the bulk of the nest building. Just prior to laying the female joins in nest building activities (see Chapter IV). It has been suggested for some passerines, e.g. the Blackbird <u>Turdus</u> <u>merula</u> (Gurr, 1954) and Song Sparrow <u>Passer</u> <u>domesticus</u> (Nice,1937), that the higher female body weight may be due to her decreased activity at this time as she alone does the incubating and the brooding. In the Pied Stilt, however, both sexes incubate and brood the young so such a suggestion would not account for the differences in body weight at breeding in this case.

iii) <u>Seasonal Variation in Gonad Weights</u>.

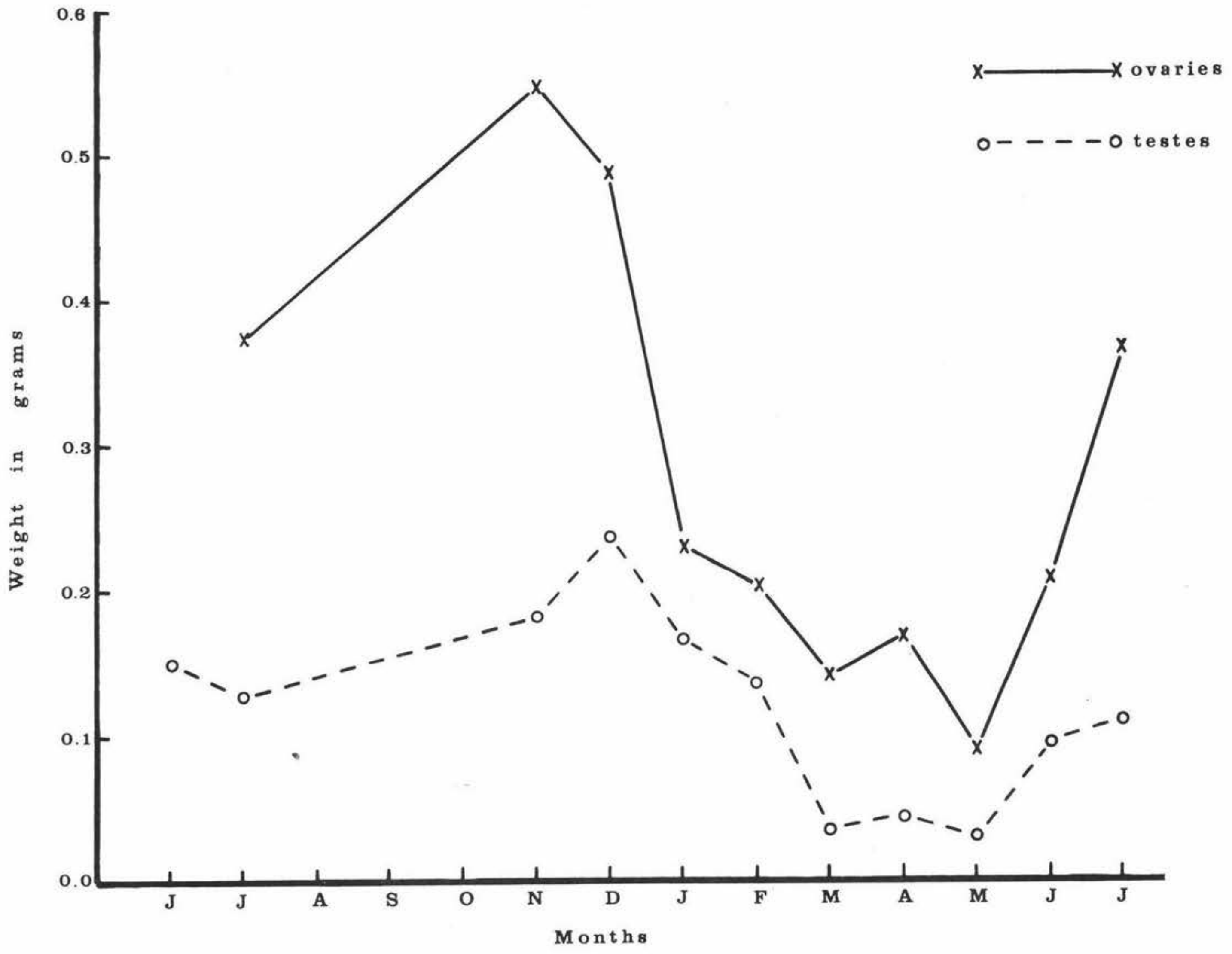
The gonads of 28 females and 33 males were examined and weighed on a Mettler balance accurate to 0.0001 gm. Table 2.3 shows the monthly means and ranges of these weights from November through July with samples taken in 1969-70 combined in June and July. It will be seen from Figure 2.5 that the curves for ovaries and testes closely approximate each other in their tendency to drop from a high peak in November to reach their lowest level through March to May and rising again sharply prior to breeding in June and July. A larger sample would probably show a continued increase in weight throughout the breeding season or at least a steadily maintained high weight. While following the same trend, the testes

TABLE 2.3 SEASONAL GONAD WEIGHTS (gms)

MONTH (1970)	OVARIES			TESTES		
	No.in Sample	Mean	Range	No.in Sample	Mean	Range
August						
September						
October						
November	3	0.545	0.504-0.567	2	0.175	0.124-0.227
December	3	0.485	0.289-0.596	6	0.233	0.050-0.478
January	7	0.1882	0.067-0.298	3	0.160	0.110-0.205
February	4	0.201	0.025-0.463	2	0.134	0.066-0.202
March	2	0.140	0.138-0.143	4	0.032	0.017-0.05
April	2	0.169	0.137-0.244	6	0.040	0.025-0.070
May	2	0.089	0.072-0.108	1	0.028	
June	3	0.2078	0.179-0.244	4 *	0.094	0.019-0.148
July	2 *	0.3681	0.3622-0.374	5 *	0.109	0.072-0.177

* Includes samples from 1969-70.

FIG 2.5 SEASONAL VARIATION IN GONAD WEIGHT



weights are lower than the ovary weights throughout the year. The first eggs were found in the last week of August, but territorial behaviour and nest site activities had been much in evidence since early June when the records show an increase in gonad weights.

Stilts breed in loose colonies (Lack, 1968), their nest territories being relatively large compared with those of any other colonial breeders (e.g.Red-billed Gulls Larus novaehollandiae defend only the nest and its immediate surrounds), the nests being some 40 yards from the nearest neighbour on average. However it is probable as Darling (1938) suggests that the association with other members of the species engaging in breeding activities acts as an exteroceptive stimulus to gonad development. The overall stimulus to breeding activities is in all probability under photoperiodic and climatic control (Farner, 1964), but the finer subtleties of synchronisation are dependent on the interplay between all the various stimuli. According to Armstrong (1965) pairing-up marks the initiation of the process of synchronisation of male and female development. Carpenter (1933) states "It seems evident that the biological function of the secondary sex activities is that of establishing the essential in-phase synchronised relationship of excitation and readiness necessary for the occurrence of primary sex activity and other reproductive behaviour." Armstrong (1965) indicates that while the male reacts more to other males in the initial stages the female is stimulated more by the male. This indicates some sort of feedback mechanism by which behaviour stimulates gonad development in the opposite sex which in turn stimulates further courtship behaviour. The first territory observed, i.e. the area from which other stilts were driven off, was toward the end of June, although subsequently there was no nesting on this territory. It was therefore nearly a month from the time breeding activities began at the beginning of June, to the formation of the first territory, which indicates that development of gonads coincides with the formation of territories and nesting. It also indicates the necessity of linkage between internal and external stimuli.

iv) Plumage and Plumage Changes.

Oliver (1955) has described the plumage characters of the Pied Stilt in four stages : nestling, juvenile, immature and adult. My observations generally confirm Oliver's, but supplement them in at least two respects. Firstly,the undersurface of the wings of the skins studied were a dark brown-black rather than a pure black. Secondly, by no means all adults have a white band across the mantle. To the contrary the majority have a black and white band, while more have pure black right down the neck to the upper back than have a white band across the mantle. From observations of 140 birds (including sample skins) the neck and mantle were each classified into three groups; black, white and mottled (i.e. intermediate) colouration. Table 2.4 shows the percentage distribution of these categories.

Oliver (1955) gives a general description of the Pied Stilt. He adds, however, that "practically every

TABLE 2.4 PERCENTAGE DISTRIBUTION OF ADULT NECK AND MANTLE PLUMAGE COLOURATION (n = 140)*

	WHITE	MOTTLED	BLACK
COLLAR	51.43	38.57	10.00
MANTLE	12.86	51.43	37.71

* Twenty immature and juvenile birds and four fledglings were also observed. These were not classified as ages and therefore stage in plumage succession were not known.

bird is different in its pattern of colouration". The figures in Table 2.4 also indicate considerable variability between adult birds. It must be stated that these divisions are quite arbitrary, and if each bird is examined individually small variations are found especially in width of collar and mantle, and in tail plumage, even within a group. Tail feathers especially vary almost individually. However it is not possible to distinguish individuals in the field as the variations are too small and the tail feathers too difficult to see clearly. Individuals may be recognised within small groups if the pattern of head, neck or mantle plumage is sufficiently different. This method was used to distinguish between male and female of pairs at any time after they had been observed copulating (Plate 7). With the majority of pairs, however, the plumage was not sufficiently different to be able to distinguish male and female when they were apart.

As mentioned previously, it appears from the birds collected that the Pied Stilt goes through a post-nuptial moult which begins in December and is completed by late March. Further evidence for this was gained by observing large numbers of feathers appearing along the edge of the river of Colony II in late December. By noting the feather types occurring and from the skins available it appears that the body feathers are the first to be replaced, and that the moult then works outward to the back, scapulars, secondaries and finally the neck, head and tail. Primaries are among the last to be replaced. From the middle of February onwards

PLATE 7

Pair showing individual markings around head and neck areas. (Female is sitting incubating and the male standing).

birds with black-tipped white feathers on the head occurred with increasing frequency until all but one of those collected in May, June and July showed them. They occasionally occurred at other times also and of the total sample taken 42.9% (33) showed this flecking on the head and 50% of these occurred from May through to July. J.Hamel (pers.comm.) considers this to be indicative of a pattern of gradual change from juvenile to adult plumage which lasts two to three years. If this is so it is surprising that all of the birds collected in these three months show this tendency. On the other hand this may be due to the fact that at this time adults may be on the breeding colonies and are not available for sampling. The fact that those sampled did have developed gonads may support Hamel's view (pers. comm.) that these are young birds about to breed for the first time and may breed late in the season. If the black flecking on the head and neck is evidence of a pre-nuptial moult then this is the only evidence available, as the rest of the plumage at this time was slightly worn. The only way to be sure of these points is for larger monthly samples to be taken.

I have noted from observations through the year of family parties containing two to four juveniles, that sibling juveniles vary considerably in plumage patterns. (I have assumed that the family parties observed actually comprised true siblings). These findings agree with those of Hamel (in press) who suggests that such variability between juveniles of the same age may swamp seasonal variability, making it difficult to effectively separate one and two-year-plus birds on the basis of plumage. However at least 20 young birds in immature plumage were seen on the breeding colony during breeding and these could only have been the previous seasons chicks, unless there are more than two broods per year, but there is no evidence to suspect this. From general observation I believe that these birds attain their adult plumage in the post-nuptial moult following their first year, and that fledglings attain their juvenile plumage at the same time.

v) Status.

A number of birds were also observed with black or black-tipped white feathers on other parts of their body. These areas were mainly on the underside of the body, especially around the base of the legs and under the tail, but they were also seen occasionally on the upper back under the wings. Oliver (1955) regards the adult Pied Stilt in his general description "as the normal and presumably genetically stable form of the species"(p.301) and considers those with more black in the plumage to be hybrids between the Pied and Black Stilts. The latter is considered by Turbott (1967) to be a mutant of the Pied. This would make almost all the birds collected and seen in this study "hybrids", and only 8.5% of the pure Pied strain. This appears to be an unusually low percentage if the Pied is a pure subspecies. In his discussion on the Black Stilt, Oliver (1955) finally takes the view that it is the Pied Stilt which is the mutant and that "the ancestral form of the species was black" (p.305). As evidence he states that "the area of brownish black on the Black Stilt corresponds to that of white in the Pied Stilt" (p.305). I maintain that this is no evidence at all, as the brown area may still survive if the Black was to arise from the Pied. Apart from this observation no evidence or reason is given for the view of either Turbott or Oliver.

Fleming (1962) considers that evidence suggests that the Pied Stilt is a young colonist from Australia and that the Black is probably a mutant of the Pied Stilt and has arisen since its arrival in New Zealand. Another possibility based on plumage similarities is that these two species have arisen from different parent stock; the Pied Stilt from the European Black-winged Stilt via Australia, and the Black Stilt from the Black-necked Stilt of North America. Were this the case one would expect they would have difficulty interbreeding. Although Soper (1967) notes their "apparent reluctance" to do so, the presence of relatively large numbers of apparent "hybrids" (as noted frequently in Notornis) would indicate otherwise.

The Black Stilt has in all probability arisen due to its better adaptability to some factor in the environment. Possibly this is intrinsic as the black colour does not appear as cryptic as the Pied. Black Stilts in general have retreated to the open rivers and plains of South Canterbury and North Otago (Turbott, 1967), and although they are often seen in the north during the summer and autumn reportedly only breed within the Waitaki River system (Kinsky,1970), so it might be reasonable to assume that it is adapted to this environment. Despite this Black Stilts are slowly decreasing in number, partly as a result of their preference for nesting on rivers which are subject to flooding and of the tendency to interbreed with Pied Stilts.

It appears that at the present time the problem of which is the mutant is not able to be solved from available evidence. However there are no grounds such as marked differences in body measurements or habitat preferences for keeping the two species separate. It may be seen from Table 2.5 that the mean measurements of adult birds in this study are, in the case of the bill and tarsal measurements, intermediate between Oliver's measurements for Pied and Black Stilts. These measurements have been used in the past to separate the two species. The variability in the measurements in Table 2.5 would appear to indicate no grounds for division into species on this basis.

Habitat as a selection process during the breeding season clearly does play some part in the extremely local concentration of the black form (or species). The subtleties of this selection pressure may be elusive but obviously works in favour of the black form in this rather circumscribed locality at this period in the life cycle, but is not efficient in preventing interbreeding elsewhere. It is the view of this author, therefore, that they should not be considered as separate species but polymorphic members of the same subspecies, and the "hybrids" as intermediate forms between the two extreme morphs. Fleming (1949) appears to be of the same view.

TABLE 2.5 COMPARISON OF ADULT MEASUREMENTS WITH THOSE OF OLIVER (1955) FOR BLACK AND PIED STILTS.

	Pied Stilt (This Study)		Pied Stilt (Oliver)		Black Stilt (Oliver)	
	Range	Mean	Range	Mean*	Range	Mean*
BILL	60-77	68.5	61-66	63	69-76	72
WING	182-243	224	230-250	240	240-255	247
TAIL	66.4-83.6	76	76-80	78	83-90	86
TARSUS	79-102	96.2	108-110	109	85-95	90
MID TOE	31.6-37.6	34.2	38-43	40	38-40	39

* The mean here is taken as being the middle of the range.

Other New Zealand species with polymorphic members which earlier were considered different species or sub-species include the South Island Fantail (*Rhipidura fuliginosa fuliginosa*), Variable Oystercatcher (*Haematopus unicolor*) and the Stewart Island Shag (*Leucocarbo carunculatus chalconotus*). These species have recently had their morphs included in the same species or sub-species (Kinsky, 1970).

B. FOOD ANALYSIS.

The gizzard contents of each stilt collected was analysed and a record kept of recognisable food remains. As soon as possible after shooting 2cc of 70% alcohol was placed in the gizzard of each corpse using a syringe and plastic tube. This immediately halted digestion. In some cases, however, this was not possible until half an hour or longer after death, by which time the soft organisms in particular were decomposed and hardly recognisable. Moreover some birds were shot at a period of the day when they were not feeding and therefore contained only remnants of food in the gizzard. The frequency of occurrence of food types appears in Table 2.6 and gives some indication of the trend in food selection. It will be noted that the diet is varied throughout the year, but most varied in summer. Some species were taken in almost every month sampled, for example *Potamopyrgus* sp.(Mollusca) and Elmidae (Coleoptera) larvae. Other species were taken as they appear through the year, e.g. the Caddis larvae, or appeared less often as they diminished in numbers, e.g. *Sigara arguta* (waterboatmen). Table 2.5 also shows the

TABLE 2.6 MONTHLY AND YEARLY PERCENTAGE OF BIRDS TAKING EACH SPECIES AS PREY

Species	J	F	M	A	M	J	J	N	D	TOT.
Potamoprygus sp.	7 70%	6 75%	6 60%	10 100%	3 75	5 6.25	5 5.55		5 50	47 62.67
Elmidae Larvae	7 70%	1 12.5		5 50%	3 75	4 50	2 22.2		8 80	30 40.00
" adult	5 50	3 37.5			1 25	1 12.5	2 22.2	2 40.0	8 80	22 29.37
Chironimids	8 80	1 12.5	7 70	1 10	1 25	2 25	1 11.1	1 20		22 29.37
Sigara argata	9 90	2 25	6 60	5 50	2 50	1 12.5	1 11.1		3 30	29 38.67
Dytiscidae	1 70							1 20	2 20	4 5.33
Mollusc unknown	3 30	5 62.5	3 30	3 30	2 50	3 37.5	5 55.5	1 20	4 40	29 38.67
Coleopteran "	4 40	1 12.5	2 20		2 50	3 37.5	1 11.1	1 20	3 30	17 22.67
Sand case caddis	4 40	5 62.5		1 10		3 37.5	2 22.2	1 20		16 21.33
Olinga				2 20	1 25	2 25	2 22.2			7 9.33
Tipulids	2 20		1 10	1 10	2 50				3 30	9 12.00
Pyronota sp.									5 50	5 6.67
Megaloptera							1 11.1	1 20	1 10	3 4.00

Species	J	F	M	A	M	J	J	N	D	TOT.
Cicada		1 12.5							2 20	3 4.00
Oxyethiro						2 25	1 11.1			3 4.00
Physastra	2 20									2 2.67
Planorbis	1 10									1 1.33
Anisops		1 12.5	1 10							2 2.67
Free living caddis						1 12.5	1 11.1			2 2.67
Muscidae									2 20	2 2.67
Curculionidae									1 10	1 1.33
Culicidae									2 20	2 2.67
Dipteran unknown		1 12.5					1 11.1			2 2.67
Xanthocnemis								1 20		1 1.33
Elateridae									1 10	1 1.33
Ostracoda	1 10									1 1.33
Vertebrate							1 11.1			1 1.33

relative frequency with which the food was taken over the year as a whole and through the year. Thus Potamopyrgus sp. was taken by about 63% (47) of the birds sampled. Fragments of molluscs appeared in 39% (29) of the sample so it is probable that the figure for Potamopyrgus could be put somewhat higher than that given. Similarly Elmidae adult beetles occurred in about 29% of the sample and with known Coleopteran fragments occurring in 23% (17) the figure for Elmidae beetles could be higher.

Next to Potamopyrgus the most frequently taken food was Elmidae larvae being found in 40% of the sample, followed by Sigara arguta in 39%, then Chironimids (Diptera) consisting mostly of larvae but including some adults, in 29% of the sample. Sand-case caddis larvae also appear to be found throughout the year but were found in only 21% of the sample. The frequency of appearance of other species taken appears in Table 2.5 and the percentage of the monthly sample in which any given species occurs is also shown. Vertebrate prey was found on only one occasion; small unidentified vertebrae were found in the gizzard of one adult and may have belonged to a small fish such as a bullie (Gobiomorphus sp.), which Stead (1932) reports finding in stilts in the South Island.

The actual abundance of a given species found in the gizzard contents at different times of the year could not be determined as there was no way of estimating numbers. Considering only the more abundant species found in the diet, analysis of stomach contents shows a relative abundance of Potamopyrgus, Elmidae larvae and molluscan fragments found through autumn and winter. Chironimid larvae, water boatmen, Elmidae beetles and sand-case caddis larvae are found to be most abundant during the summer months.

The results were analysed in terms of the locality at which the birds were collected and the time of day, but in neither case was there any significant difference found between localities or times of day. A larger sample in each case, however, may reveal local and diurnal feeding patterns.

C. PARASITES.

The monthly sample was examined for both external and internal parasites. External parasites were found upon examination of the dead birds. These were a species of Mallophaga identified by Entomology Division, D.S.I.R. as being Saemundssonia platygaster (Denny, 1842). This is the first record of this species on Himantopus. It has been recorded on various Charadriidae, Tringa sp. (Sandpiper) and Arenaria sp.(Turnstone). There are slightly different races on various hosts and this is the closest to the population found on the Banded Dotterel (Charadrius bicinctus). Transfer from a different wader is unlikely in view of the number of specimens, including nymphs. Specimens of this feather louse were found essentially in the neck and head region at the base of the feathers.

Internal parasites of three types were found, namely nematodes, trematodes and cestodes. Nematodes were found in 4% of the sample but these could not be identified as they were all males. The trematodes were found generally in the posterior thoracic or abdominal air sacs and occurred in about 23% (17) of the sample. Some were found in the abdominal cavity itself but were presumed on other evidence to have come from the air sacs after these had been punctured. Numbers found in any one bird ranged from 0 to 6 though they most commonly occurred one in each of the posterior thoracic air sacs. These trematodes were identified as Harrahium halli (Dubois, 1959) which has not been previously recorded in Australasia, but have been found in North America in the genus Totanus (Yellowlegs). Relatively large and easily seen with the naked eye they average 8mm in length and 4mm in width.

Cestodes on the other hand were far more abundant occurring in 99% of the sample including all fledgling and juvenile birds. Generally there were at least two in each bird in the upper intestinal region and small immature cestodes were often found here as well as in the gizzard. The cestodes were of two species Acoelus vaginatus ((Rud.) Fuhrmann) and Diplophalus sp. (Dubois,1959) and occurred with about equal frequency, commonly two of one species in each bird, though sometimes one of each in the same bird. Acoelus vaginatus (Dubois, 1959) has been recorded from the same host in Australia. Both cestodes were large, measuring 150 - 200mm long by 6mm wide and filled almost the entire upper region of the intestine.

A third species appeared in a sample which had been sent to the British Museum of Natural History for confirmation of identification. This was identified by them as Diplobothrium sp. and not previously recorded from this sub-order Limicolae. They suggest that as this was the only specimen to appear that it might have been an accidental contaminant in the sample and not a parasite of the bird.

CHAPTER III

NON-BREEDING BEHAVIOUR

A. DISPERSION.

The dispersion of stilts in New Zealand was considered in relation to time of year. Records covering the period 1943-68 were obtained from Classified Summarised Notes in Notornis. The country was divided into five regions of approximately equal area (Fig.3.1) and monthly observations totalled for each region. These totals were calculated as a percentage of monthly totals for the whole country and then plotted as shown in Figure 3.2. The two northern most and two southern most regions respectively have been combined to level out small fluctuations in each region. Analysis of the numbers recorded each month and comparison of these for the combined regions 1 and 2, and 4 and 5, gave a -0.9 correlation coefficient. This indicates a trend, previously suggested by Stead (1932), toward migration from south to north during autumn and winter (March-July) and a reverse movement during spring and summer (September-February). Throughout the year, however, the numbers are on average greater in the north than in the south. Region 3 on the other hand, while showing some increase from November to January, follows broadly the trend of the southern areas in that numbers remain relatively constant throughout the year (Fig.3.2).

Dispersion was also considered within the study area which was contained in Region 3. Regular counts

FIG 3.1

ARBITRARY AREAS USED IN ANALYSING STILT DISPERSION

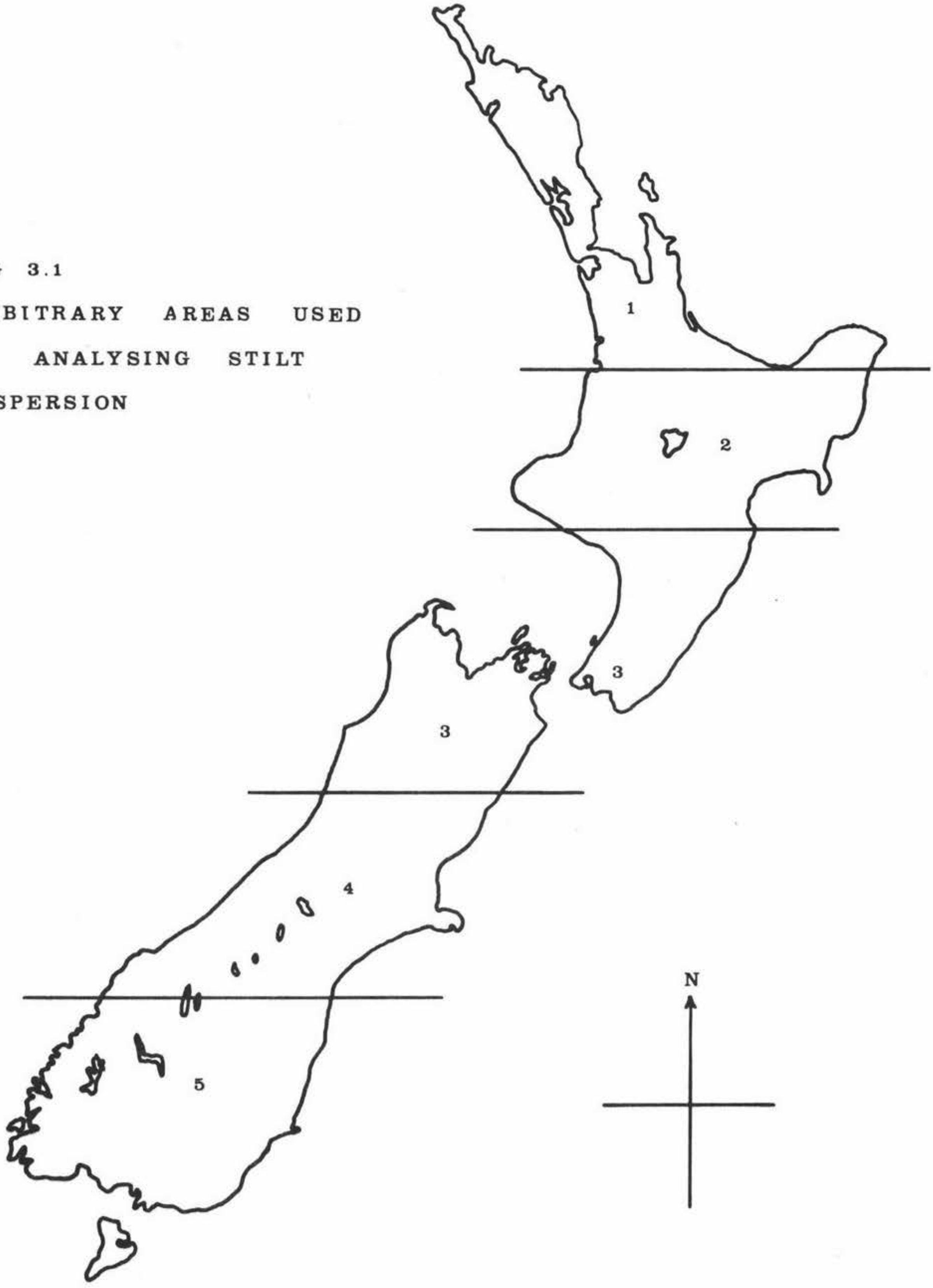


FIG 3.2 FLUCTUATIONS IN STILT POPULATION IN N.Z. (n = 139,941)

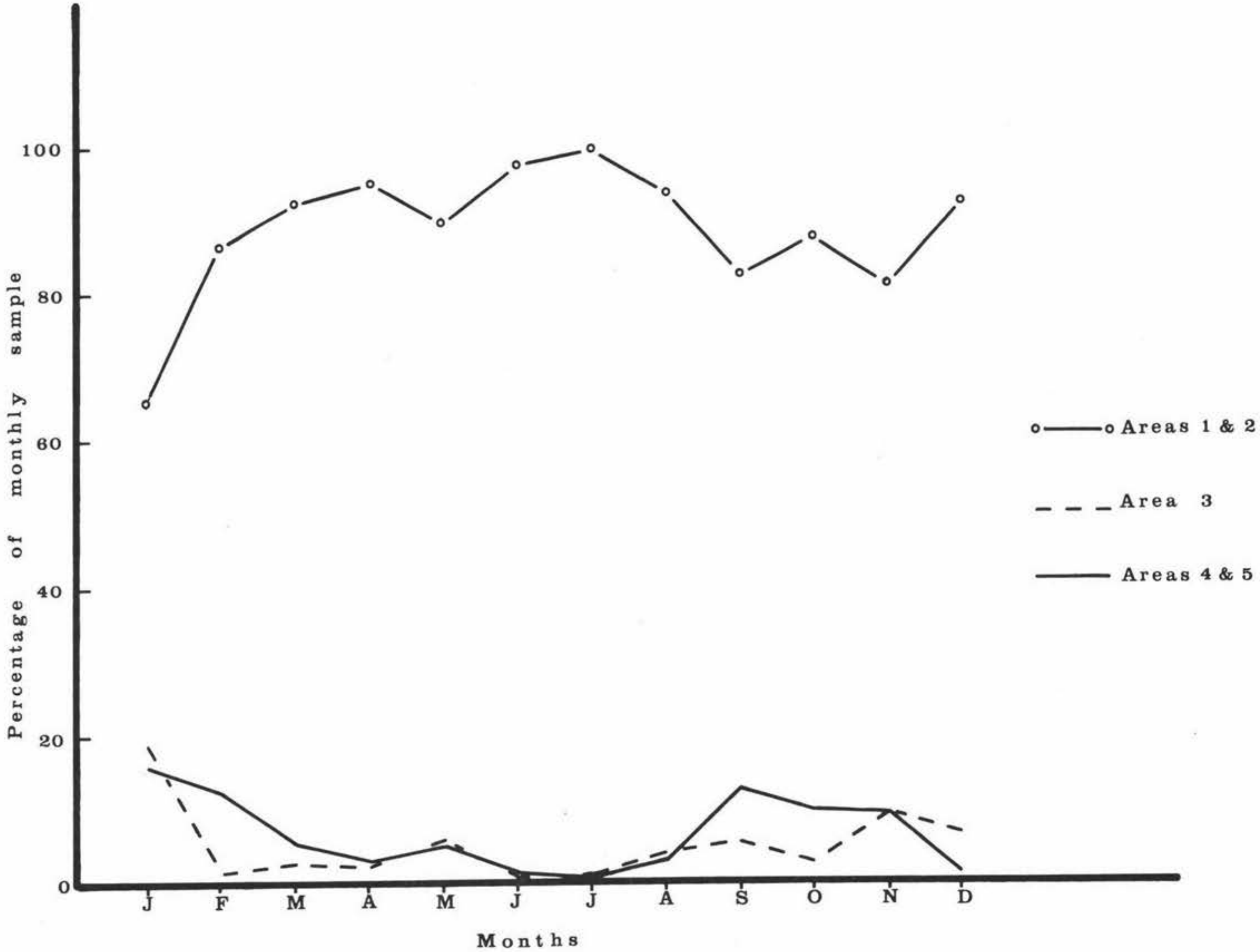
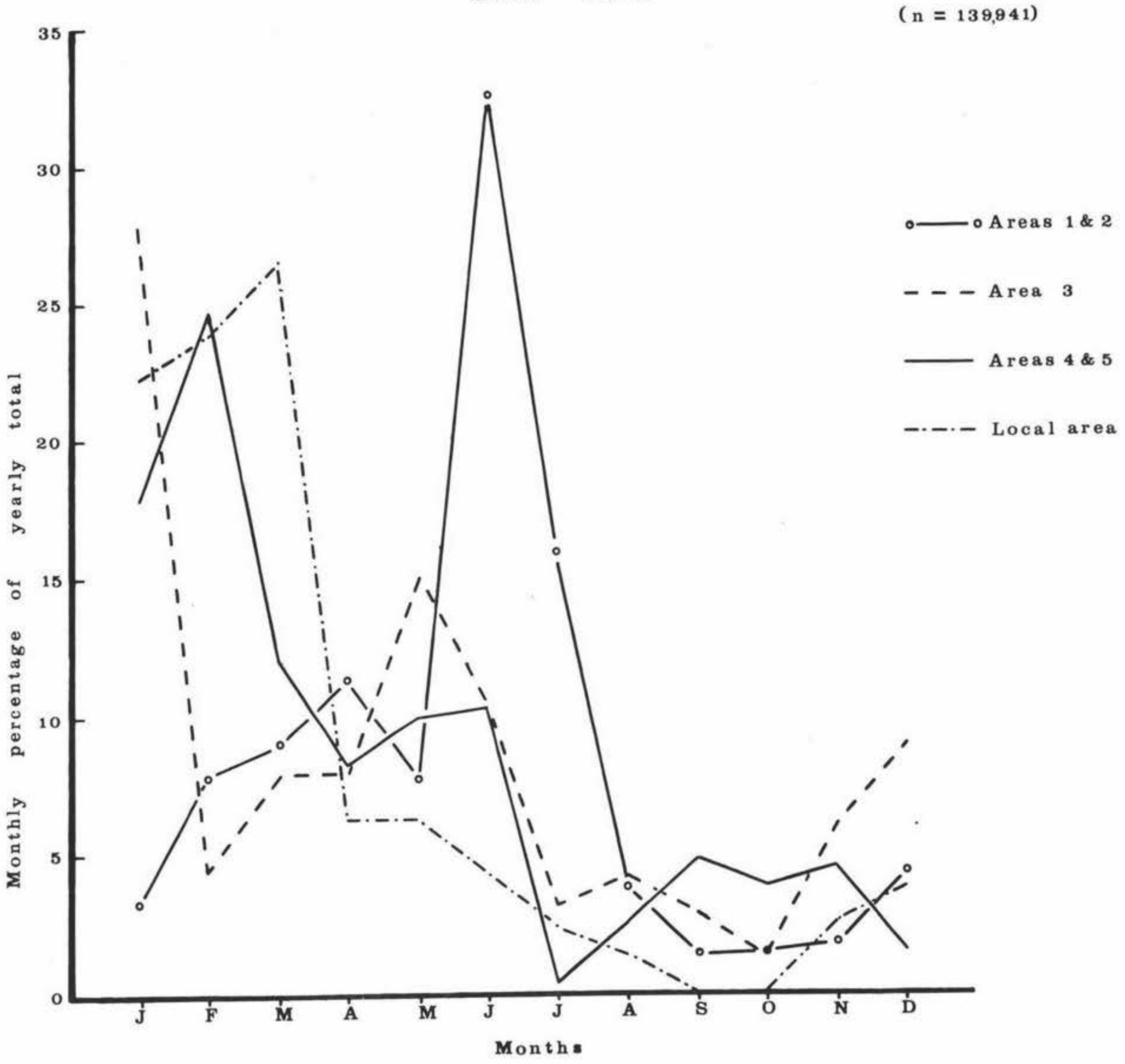


FIG 3.3 FLUCTUATION OF STILT NUMBERS IN EACH AREA



(2-3 times per week) were made at a given site throughout the year. In general the trend of this area is similar to that of the more southern regions (Fig.3.3). Figure 3.3 shows numbers observed at the given site calculated for each month as a percentage of the yearly total. There is an increase in numbers in spring and summer followed by a drop throughout autumn and winter. Further evidence from observations elsewhere in the study area indicates that the departed birds may not necessarily have migrated, but may have moved onto breeding colonies. Relatively large numbers were observed on inland breeding colonies from June through September when there were few on the rivers.

B. MAINTENANCE BEHAVIOUR.

i) Feeding.

When feeding in water (at no stage were they observed feeding on land) the stilt used quick pecking movements, taking food either off the surface or from below the surface of the water or mud, as reported in the Blacksmith Plover Hoplopterus armatus (Hall,1964). Occasionally the beak is swished sideways in the water, as if skimming food off the surface. This method appears most common in Avocets (Makkink,1936). Food is swallowed with a quick backward flick of the head. Contrary to some reports, stilts often put their heads completely under the water to feed, especially in deep water (6-8 inches) in which they very often seek food. I have observed some with their heads submerged for five seconds or more but I have not observed them swimming and feeding as Makkink (1936) reports is common in Avocets. Moreover I did not see swimming at any time except by a wounded bird, and the only report of swimming occurring is by Heather (1955) who reports a stilt swimming across a 25 yard wide channel during an aggressive situation. The foot stirring during feeding which Hall (1964) reports in the Blacksmith Plover and other members of the Charadriidae (European Lapwings (Vanellus vanellus)and Ringed Plovers (Charadrius hiaticula)) was not observed in Pied Stilts, neither has it to my knowledge been reported. Analagous behaviour has been noted in gulls (Tinbergen, 1962) and herons (Meyerriecks, 1966).

Feeding amongst Pied Stilts takes place individually, in pairs or in family groups, spread out along the edge of a river or in a shallow backwater. When an area is rich in food, however, the whole flock will feed together, although maintaining what appears to be individual distance. Crook (1965) suggests this flock feeding allows improved efficiency in food finding for individuals within the flock. Recher and Recher (1969) also report this in a number of waders (e.g. Western Sandpiper (Calidris mauri) and Semipalmated Sandpipers (Calidris pusilla)). Feeding ranges or territories also appear to exist, as on numerous occasions families or pairs have been observed chasing off other stilts which came into a certain area. This range appears to be only transitory and may change from day to day, possibly depending on the abundance of food. Once, what was taken to be the same pair, was seen to maintain approximately the same range over a period of 3-4 days. Similar behaviour is reported by Recher and Recher (1969) for a number of waders including Semipalmated Plovers (Charadrius semipalmatus), Sanderlings (Crocethia alba) and Willets (Catotrophorus semipalmatus). They note that feeding territories are most often established where (a) foraging sites are limited or food organisms are patchily distributed or (b) food organisms are scarce. From my observations it appears probable that the same situations may apply to the Pied Stilts. This may result in nomadism of the flock, i.e. birds range up and down the river in search of suitable feeding sites.

Times for feeding throughout the day vary depending on the size of the group involved and the prevailing weather conditions. It appears that family groups of 3-4 birds spend longer feeding than do larger flocks of 30-40 birds. For instance when large flocks are seen resting, generally two or three small groups remain feeding. Furthermore less time is spent feeding in hot fine weather than during cooler overcast weather. Out of 30 flocks observed on cool days, 22 of these were feeding,while only 5 flocks out of 20 were feeding on hot days. In general during spring and summer they may be considered to feed mostly between 0800 and 1030 hours, and 1430 and 1730 hours. Though a small number of small flocks were observed during late autumn and winter the birds appeared to feed at any time of day.

ii) Bathing.

Stilts may be seen bathing at any time of day although the frequency varies with the weather, i.e.

occurs with greater frequency on hot days as might be expected. It is an individual activity and does not appear to be under any social influence as Hall (1964) implies of the Blacksmith Plover. Bathing in stilts is similar to that of Avocets (Makkink,1936). Most typically the bird sits down in relatively deep water (5-6 inches) and begins frequent dipping under the water with closed wings. This is interspersed with springing in the air and splashing in the water with slightly open wings. It frequently rolls its head over its back and under its wings, but this may be part of the general preening movements as in Avocets (Makkink,1936). Waggling of the tail from side to side was also noticed occasionally as has been reported for the Blacksmith Plover (Hall,1964) but not the Avocet.

iii) Preening.

Preening may occur in the water as part of the bathing sequence or while standing on land and the manner of preening is the same in either case (Plate 8). The beak is rubbed initially over the back and rectrices, presumably to collect oil from the uropygeal glands. The stilt then preens over the back, along the wings, then over the breast with short quick movements. These movements are repeated a number of times on both sides. As described above, the bird may then rub its head and cheeks over the top of its back, and the inside of its wings over its head. Similar preening movements have been noted in the Avocet (Makkink,1936). Scratching and stretching are also part of the general body maintenance activities though may be performed along

PLATE 8

Preening showing a stilt rubbing its beak over its back and rectrices.

PLATE 9

Sleeping stilts showing the two typical positions.

with or apart from preening. The former is performed by lifting the leg over the wing to scratch generally in the head and neck region, as in other members of the Charadriidae, e.g. Charadrius, Vanellus, Haematopus but not in Tringa (Makkink, 1936). Stretching is performed by stretching the leg and corresponding wing backward, simultaneously with the body and neck almost horizontal in contrast to the bending of the neck downward in the Avocet.

iv) Sleeping.

Sleeping stilts normally have their beak tucked under their wing and more often than not rest only on one leg (Plate 9), as in most waders (Witherby et al, 1943). Occasionally, however, especially during hot weather they may sit on the ground with the whole of their chest and abdomen in contact with it. In such a position they may tuck their beak under their wing. At other times when merely dozing they assume a hunched posture, their head pulled right into their shoulders, generally standing on only one leg. Often if resting amongst a feeding flock, they will hop out of the way of an approaching stilt rather than put the other leg down and walk. On a few occasions I have noticed a bird fly off with its leg still tucked up and land again on one leg. Raising the leg to the tucked position may take a minute or two as the stilt flicks its leg often, shaking off water and mud, then allowing it to dry before tucking it under the feathers. Possibly for this reason the stilt is reluctant to place its leg down again.

v) Pseudo-sleeping.

This is a posture in which the stilt simulates the sleeping posture except that its eyes are kept open. It has been suggested (Simmons and Crowe, 1953) that this is a reaction of low intensity toward human intruders especially shown by breeding Avocets and Oystercatchers. Williamson (1952) suggests the primary function of this behaviour is to be found in the flocking behaviour of Oystercatchers. He reports that the activity appears related to each bird's need to maintain its individual distance which would be a "vital necessity for a quick unimpeded take-off should danger suddenly threaten the flock". In such a flock, he states (Williamson, 1953) normal rest would be out of the question and as a substitute "pseudo-sleeping has arisen as a secondary modification of the normal resting posture and has arisen to ensure (for) every member that his minute portion of territory within the flock does not diminish". This reaction was rarely noticed among breeding stilts as a reaction to humans, but usually occurred within a flock of non-breeding birds. In this situation it occurred as a reaction to conspecifics and approaching humans. I suggest, for Pied Stilts, that rather than being a true displacement activity as suggested for Avocets and Oystercatchers (Simmons and Crowe,1953) it is a low intensity reaction of watchfulness against intrusion. When threatened with dangerous intrusion (humans or conspecifics getting too close) then more active behaviour of fight or flight ensues. The situation in which it arises does not appear to be one of true conflict as required for a true displacement activity.

C. AGGRESSIVE BEHAVIOUR.

i) General.

Aggressive interactions between stilts occur in both breeding and non-breeding seasons and involve essentially the same displays, but may occur for different reasons and with different effects. During the non-breeding season aggression is primarily associated with interactions between feeding stilts. Recher and Recher (1969) in a study of 12 species of waders note that where interspecific aggression occurs it is usually with morphologically similar species. At no stage during the non-breeding season were stilts noted attacking other species. Intraspecific interactions were generally limited to low intensity threat postures, e.g. hunch pursuit (see below), rather than direct attacks, and occurred most often in large aggregations rather than small groups. In the Semipalmated Sandpipers, as with other similar species, Recher and Recher (1969) report that "the frequency of aggressive interactions is greatest at high population densities and decreases as the population density decreases". This they relate to the need to maintain individual distance and this becomes increasingly difficult as population density rises, resulting in increased aggressiveness in order to remain within a suitable feeding area. Lack (1954) shows that the numerical dispersion of a species throughout its habitat is related to the abundance of food. Where food is abundant and uniformly spread efficient foraging can probably take place within an area of high population density. On the other hand, where food is scarce waders, including stilts (see p. 53), set up feeding territories (Recher and Recher, 1969) and it is in these situations high intensity aggressive reactions take place. Thus aggression acts as a "population spacing mechanism" which enables individuals to maintain for their use a "portion of the environment (food and foraging space) which would otherwise be unavailable to them" (Recher and Recher, 1969).

ii) Intraspecific reactions.

Aggressive interaction with conspecifics among stilts involves three main displays. In order of increasing intensity these are :

(a) Hunch Pursuit. In this display one bird is chased by another which assumes a hunched posture with head and neck pulled into the shoulders and pointing down to the ground at a slight angle (Plate 10). Generally this threat is all that is required to chase off the interloper. On occasion, however, the aggressor may be highly stimulated and will continue to chase the intruding bird for 15-20 yards before breaking off. This continued chasing may also involve flying at the intruder (generally where the aggressor is territorial) which has the effect of hurrying its departure from the area. Most often there is no retaliation on the part of the offending bird. It is probable that such aggression is a result of encroachment on feeding ranges, but as it also occurs during flock foraging it

PLATE 10

Hunch pursuit posture.

PLATE 11

Aggressive upright posture.

may also involve violation of individual distance. One pair which left a resting flock to feed on the edge of a lake were continually harassed by two pairs in two separate areas before eventually landing in a less suitable area (as judged by the frequency of feeding there). Recher and Recher (1969) report similar findings in Sanderlings and note that non-territorial birds have to resort to less suitable foraging sites. The hunch pursuit appears analagous with the "pursuing" of Avocets (Makkink,1936) and the "quick-running hunched threats" of the Blacksmith Plover (Hall,1964).

(b) Aggressive Upright. Where two territorial stilts meet at their boundaries both generally assume a very erect posture side by side, their necks fully stretched while walking slowly around, parallel or sideways to each other (Plate 11). As the interaction continues they sidle toward or away from each other while watching each other closely. The same posture is adopted in defence of breeding territories (see p. 70). During the aggressive upright, feathers on the back of the neck and head are raised and the wings are held very slightly out from the body. Suddenly one will fly at the other and chase it off a few yards, or parachuting may take place (see below). So they oscillate back and forth, each being apparently dominant in his own territory (c.f.Hinde,1956). Hall (1964) notes a Blacksmith Plover "standing in the stiff-necked upright position before fly attacking a second bird", and this behaviour also appears analagous to the "thronging sideways" of Avocets (Makkink,1936).

(c) Parachuting. This term I have coined for what Makkink (1936) calls "springing and flapping" in Avocets. In an aggressive interaction one bird will suddenly jump into the air and float down again on open wings and with extended legs. As the bird floats close to its adversary it drops quickly toward it trying to kick with its feet. The aim of this appears to be to land on the opponent in order to force it onto the ground, and thence to peck it. This has been seen to happen on four occasions during the breeding season when the birds may have been very highly stimulated. Meanwhile the adversary attempts to do likewise in an attempt to evade the attacking bird and perhaps land on it also, which results in the two birds hovering in the air at the same time (Plate 12). The Blacksmith Plover also performs "jumps up and flying threats" (Hall,1964) as does the Ringed Plover (Mason,1947).

Parachuting may be performed in almost any aggressive situation where other methods of removing an intruder have failed. Generally, however, it appears to occur in violation of a territorial boundary. Often it appears to be contagious in a flock. If a pair of birds begin chasing or parachuting, otherwise peaceful birds nearby may soon follow suit. Stilts recently disturbed by a human intruder or predator, may also indulge in parachuting behaviour. In both cases this is possibly due to breakdown of individual distance and its re-establishment after the particular disturbance has finished. It may also be due to a lowered attack threshold resulting from an increased level of excitment.

PLATE 12

Parachuting display.

PLATE 13

Anxious or alert upright posture.

iii) Interspecific Reactions.

As previously indicated interspecific aggressiveness is seldom seen outside the breeding season, although as shown below (Chapter IV) it may continue while parents are watching over young at least up to four months' old, and even though the young may be flying strongly. Generally birds of other species are tolerated or ignored, and even Harrier Hawks arouse no reaction. No other predators of stilts apart from humans have been noted to arouse a reaction outside the breeding season.

Reactions to humans in the non-breeding season varies, often depending on the composition of the flock. Escape is the most common reaction to man and is generally preceded by the anxious or alert upright posture (Plate 13). Head-bobbing, as seen in many waders (Simmons,1955), is generally indicative of an excited state and may also be observed with the intrusion of man. One nervous stilt may scare the whole flock up while the intruder is still somewhat further away than normally tolerated before take-off. Frequently in the open one may approach within 40-50 yards of a flock of stilts though 30-35 yards is possible in a car. They become much more suspicious and remain on the alert if the intruder is known to be under cover. Some sort of watch system also appears to operate within the flock. On two occasions while observing a flock from under cover the bird nearest me (75 yards away) remained in the alert posture, bobbing and calling continuously for some 20-30 minutes while the rest of the flock continued resting or feeding nearby. During this time I had not moved nor could I be seen. When an aeroplane flew over on one occasion, the alert bird suddenly flew off followed immediately by the rest of the flock. Possibly this was due to the highly stimulated state of the alert bird resulting in a lower escape threshold and its flying off eliciting a similar response in the rest of the flock.

On most occasions, however, the whole flock would remain disturbed and suspicious, only ceasing their calling when I was observed leaving the immediate vicinity. Continual disturbances which posed no threat, such as metal trucks driving within 30-35 yards of the flock were habituated to. In this instance, as on other occasions, I was ignored and able to remain sitting 25-30 yards away from a small group which continued feeding toward me. Once I moved, however, they immediately became alert and began calling again.

CHAPTER IV

BREEDING BEHAVIOUR

A. PAIR FORMATION

The available evidence suggests that stilts first breed in the second year. Immature birds from the previous season were seen on the colony throughout the breeding season but were never observed breeding. Other charadriiform birds do not usually breed in the first year, e.g. some Oystercatchers breed at 3 years, but most do not breed until 4 years' old (Lack,1968).

Pair formation was difficult to determine and it appeared that birds arrived on the colony already paired. It is not known if the pair bond is permanent, though the occurrence of family groups and pairs throughout the year would suggest that it is. There were no signs of obvious pair forming behaviour, although at the beginning of the breeding season there appeared to be a considerable amount of preening in pairs on newly formed territories. Makkink (1936) suggests for Avocets "the way in which the pairs establish themselves cannot be a special performance different from the copulation or the fighting and nesting activities, for the Avocet has no other performances. Therefore the pair forming can only take place by means of one or more of these activities". If this is true also for stilts, it is probable that preening plays some part in pair forming, and is performed by both the sexes. Moreover it may be, as observed for some species of gulls (Carrick and Murray, 1964) that pairing territories are set up and later abandoned. Indeed many of the initial territories on which preening and nesting activities were observed, did not eventually contain nests. Those that did were built later in the season and may have been taken over by different pairs.

B. TERRITORIAL BEHAVIOUR.

i) Size of Territory.

Territories in the process of being set up were first noticed in the middle of June though these first sites subsequently contained no nests. Territorial boundaries were taken to be where territorial disputes, i.e. aggressive upright and choking, occurred frequently between neighbouring pairs. As suggested above, these may have been temporary pairing territories. More weight is perhaps added to this suggestion when size of territories is considered. Initially the territories were relatively small, being on average some 30-40 square yards. Often there were a number of territories in close proximity though there was also a considerable amount of "free space" between territories. Later in the season, however, territories were two or three times larger on average, particularly those containing nests. Size and shape of nesting territories varied depending on the terrain. These territories ranged from approximately 50 square yards to approximately quarter of an acre. The increase in size from prenesting to nesting territories is demonstrated by one pair which increased their territory gradually from a few square yards to a quarter of an acre and occupied at least 10 original prenesting territories. Nests were not necessarily in the centre of the territory but more often to the size farthest from the nearest neighbour.

The main colony site (Colony I) occupied approximately 2½-3 acres and nest territories were spread all over this though the territories were not always adjacent to each other nor were they all occupied at the same time. Twelve was the largest number of territories occupied at any one time, and free space between territories was common feeding ground.

Territories on the river (Colony II) spread over approximately half a mile of river shingle and a total of thirteen nest territories was the most occupied at any one time. Size of territories was on average of the same order as those on Colony I though there was not the range of sizes. All were in the order of 50-60 square yards. Most were situated on the edges of the shingle beds within a few yards of the water. As the water level subsequently dropped, however, some nests were left some distance from the water.

The function of the stilt's territory is not certain. As there was considerable free space around the colony from which any bird, including non-breeding birds, could and did obtain food it would appear that the territory is not necessary for food collection. Hinde (1956) states, however, that because a bird does not obtain the majority of its food from the territory, this does not mean that the territory has no importance as a source of food. Thus one factor may be that it provides a source of food in the immediate vicinity of the nest so that the incubating bird may come off periodically to obtain food. It does not appear necessary for copulation as a number of copulations and attempted copulations took place outside the territories without interruption from other birds, unless it was on another's territory. Armstrong (1965) indicates that this ignoring of copulating birds outside their territory is unusual for birds on the whole. Probably the main function is for the dispersal of the nests over a wider area for protection against predators (Lack,1968).

ii) Aggressive Upright.

Territorial disputes occur either when territories are being set up or when an intruder lands on an established territory. Usually the owner assuming a hunched posture (described in Chapter II) and chasing the intruder is sufficient to settle the dispute. In the event of the opponent not giving way, however, both generally assume an aggressive upright posture. This appears most common in disputes at territorial boundaries (see Chapter III) between members of adjacent territories.

iii) Parachuting.

As mentioned above this display occurs during territorial disputes and generally alternates with the aggressive upright. It is a general aggressive display and also occurs during the non-breeding season (Chapter III), although not as frequently, and follows exactly the same procedure.

iv) Choking.

Generally this display is performed only during boundary disputes between pairs with established territories. Perhaps this is an indication of its close association with nesting behaviour as its performance does show some similarity to "nest-showing" movements. Choking is resorted to where a dispute has become prolonged and has not been settled by parachuting and direct attacks. During choking the birds stand head downwards in an oblique position, with beaks almost vertical, pecking into the ground. When performed in pairs each pair stands side by side facing the opposing pair and pecking vigorously at the ground (Plate 14). On the other hand, when only one member of each pair is involved they stand side by side as for the aggressive upright (Plate 15). Moreover choking may follow directly on from the aggressive upright. Generally one bird begins choking and this appears to induce the other to choke also. When one assumes the aggressive upright again the other does likewise. This appears to be an indication of a refusal to give way as in gulls (Moynihan,1955).

Tinbergen (1952) notes this behaviour occurring among herring gulls (Larus argentatus) and considers it to be a displacement activity in aggressive situations and derived from nest building. His "surplus hypothesis", however, has since been superseded by the "disinhibition hypothesis" of Van Iersel and Bol (1958), which also fits the present case of the

PLATE 14

Neighbouring pairs choking toward each other.

PLATE 15

One member of each pair choking beside each other.

stilts. In the stilts choking appears as a displacement activity where a conflict arises between attack and escape in relation to a territorial intruder. When "effective equality" between the conflicting drives is reached the drive to nest-build is disinhibited and choking takes place. The similarity of choking to nest-showing movements has been noted above. Tinbergen (1952) considers that choking may be a derived activity itself and though apparently associated with nest building its origin is uncertain.

v) Grass-pulling and Sideways-throwing.

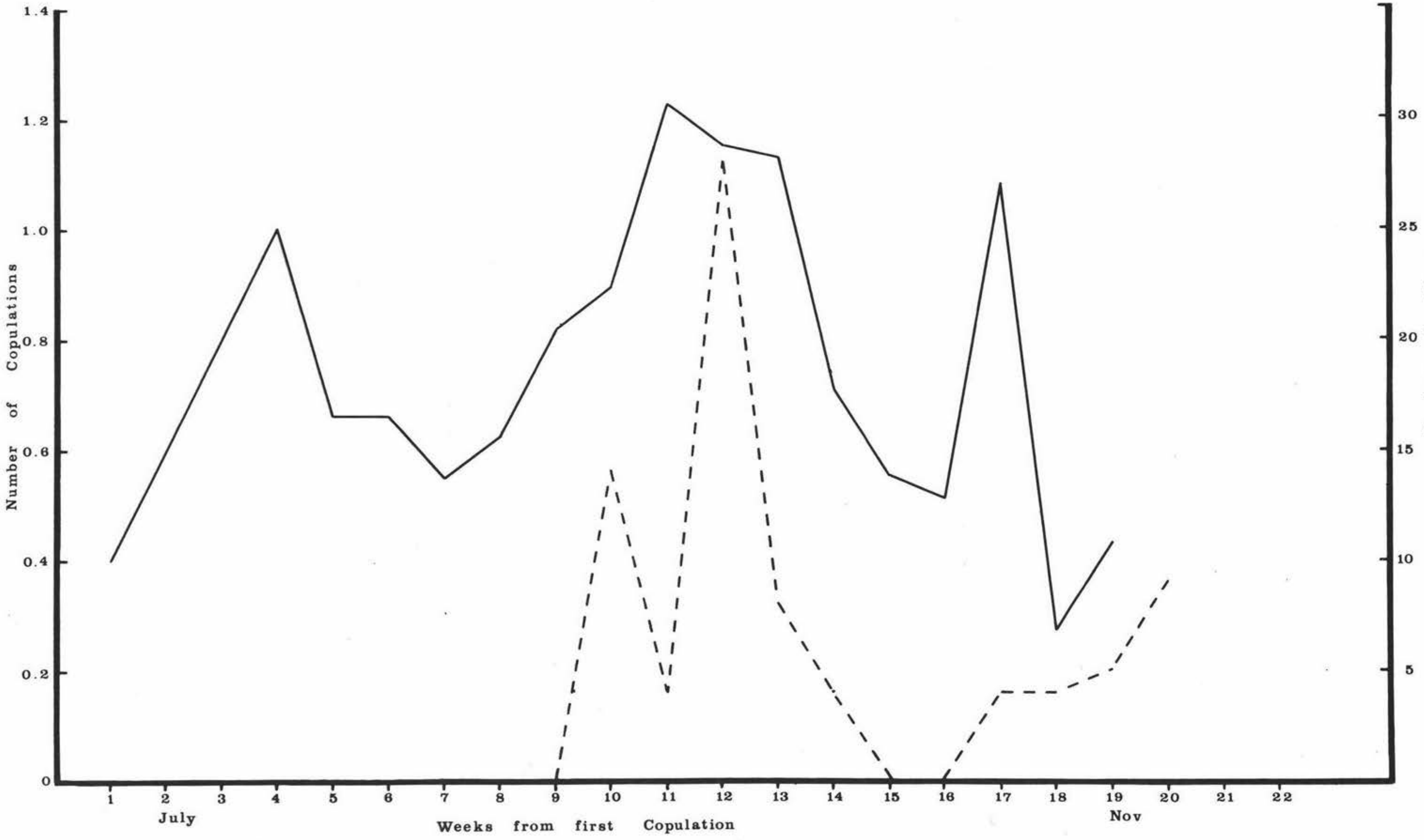
Most often this display occurs in conjunction with choking. During pecking at the ground a stilt may occasionally begin pulling off pieces of grass or vegetation and dropping them again. While doing this it may also begin throwing the grass back over its shoulder as in the sideways throwing movement of nest building. Makkink (1936) describes similar behaviour in the Avocet and attributes it to general sexual excitement. Occasionally because of a strong stimulus or perhaps a very much lowered threshold, one bird of the opposing pairs may actually sit down while performing choking and grass pulling movements. It may be noted again that these elements are present in nest building behaviour. Therefore while it may be argued that grass pulling may be redirected aggression (Bastock et al,1954), it could be suggested that other elements such as the settling and sideways throwing may be due to general sexual excitement associated with ownership of territory. On the other hand these elements contain the criteria of displacement activities. That is they occur as irrelevant acts in conflict situations, and that often the acts are incomplete in performance (Rowell,1961). While Tinbergen (1952) indicates that the external stimulus is not required for the displacement activity to occur, Van Iersel and Bol (1955) and Sevenster (1961) show clearly the need for some direct stimulation. They suggest that the required stimulation is most often the positive stimulation required to elicit the activity in its normal context.

On only a small number of occasions during the breeding season did I see actual physical contact between disputing pairs. Most of these occurred during parachuting when one bird successfully landed on another and trod it into the water or ground. Only on one occasion did I observe a bird pecking and holding another by wing, tail and beak. One of the opponents was an extremely aggressive male mated with what was believed to be a first year breeding female. They had extended their territory to one quarter of an acre but had failed to take at least two territories close by. As one territory was vacated when the eggs hatched and the brood moved away, another pair attempted to take over this territory. The aggressive pair harassed them continuously and they laid only one egg before deserting the territory. On one occasion the aggressive male trod one bird of the pair under water two or three times and pecked it vigorously, taking hold of wings, tail and beak of the opposing bird. In turn it was once trodden on and pecked about the head. Most disputes, however, were settled in a less violent manner,physical contact being slight if it occurred at all.

C. COPULATION.

Copulation was first noticed on Colony I on June 18th and observed periodically until October 22nd. However it must have occurred after this also to account for later nests, i.e. on the river colony as eggs were laid there through to the end of December. On Colony I, therefore, copulation occurred over a period of four months. It will also be noted that copulation occurred two months before the first egg was laid. It is not known whether the pair first seen copulating was the pair that laid the first clutch. Another pair,however, were first seen to copulate six weeks before their first egg was laid and during this time copulation or attempted copulation was observed at least fourteen times. Probably this figure could be put considerably higher. Moreover this pair is known to have copulated at least once after the full clutch was laid, as has been observed in a number of species including the Black-headed Gull Larus ridibundus (Kirkman,1937), Arctic Tern Sterna macrura (Bullough,1942) and Killdeer Plover Oxyechus v.vociferus (Gunther,1946). This pair was easily recognisable because of their distinctive markings. It is not known if any other pairs copulated after the full clutch was laid, as it was not possible to say if pairs copulating in a given area were the same pair in each case. Pairs do not necessarily copulate on their territory. Often they moved to deeper water in the central area of the colony which

FIG 4.1 NUMBER OF COPULATIONS(n=156) PER HOUR OF OBSERVATION PER WEEK IN RELATION TO NUMBER OF EGGS LAID PER WEEK ON COLONY I

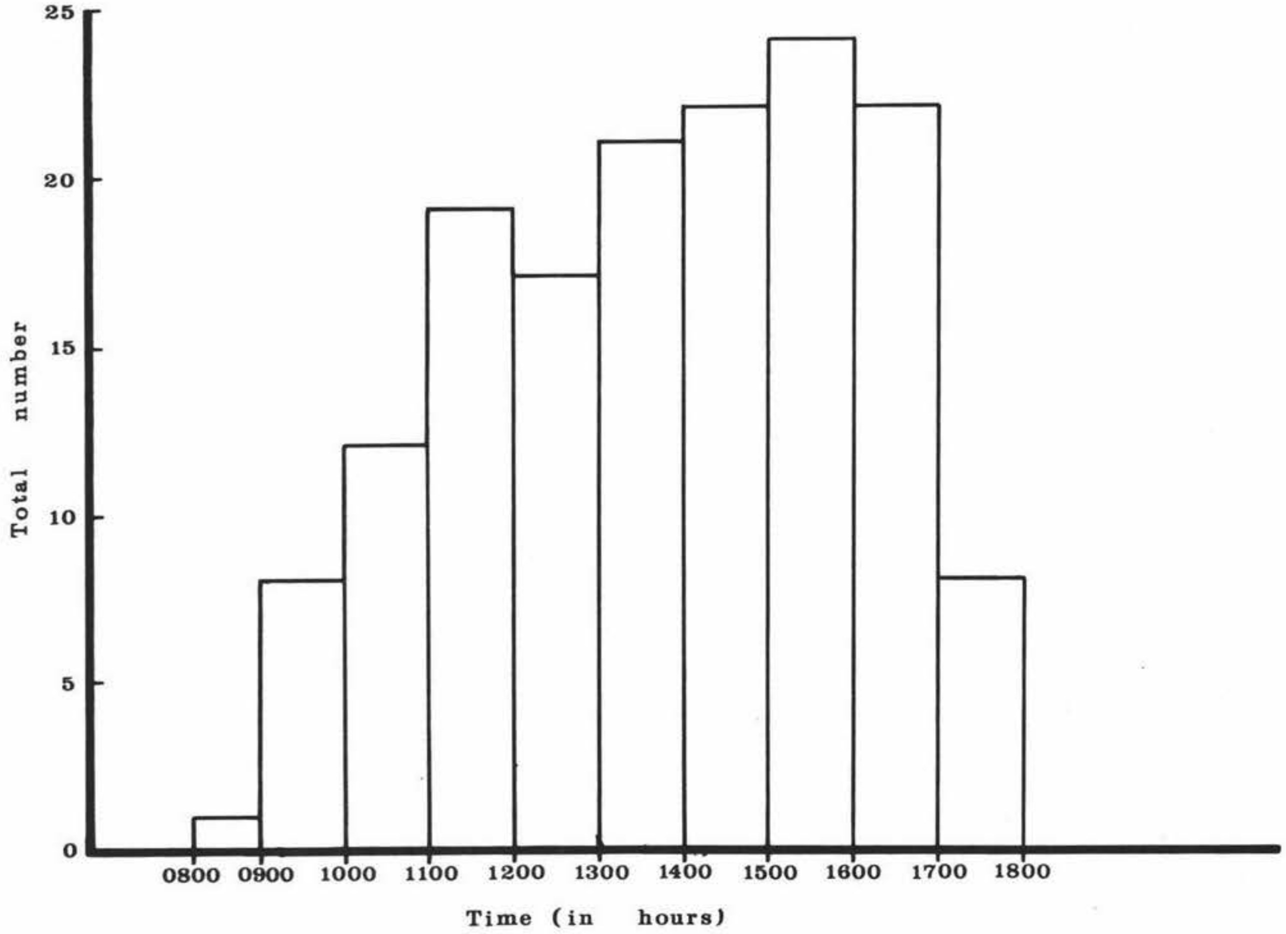


appeared to be free space, or attempted to copulate on another bird's territory. On the other hand another pair was seen to copulate at least 15 times in three weeks on their own territory before laying. This was a late nesting pair for which courtship may have been concentrated into a short period of time. It is obvious, therefore, that copulation can precede egg laying by a considerable time and that its function is not only fertilisation but also plays some part in the synchronisation of maturation of gonads and cementing of the pair bond.

In all 159 copulations or attempted copulations were observed over a period of four months and Figure 4.1 shows the mean number of copulations per hour of observation for each week of this period. It will be noted that the peak mean number of copulations per hour of observation coincides with the time when the greatest number of eggs were being laid on this colony, as might be expected as it appears that copulation occurs at least once before each egg is laid. Copulations did not appear to be concentrated at any particular time of the day but were fairly evenly spread although, as shown in Figure 4.2, they do rise to a maximum around 1500-1600 hours. Of 154 copulations, of known time 26% (40) occurred between 0900 to 1200, 39% (60) from 1200 to 1500 and 35% (54) from 1500 to 1800 hours. To a certain extent this correlates with time of egg laying which appeared to take place some time in the late afternoon or evening.

Copulation may be initiated by either the male or

FIG 4.2 OCCURRENCE OF COPULATION IN RELATION TO TIME OF DAY



female although in the majority of instances observed it appeared to be initiated by the female. That is, she was the first seen to engage in obvious copulatory behaviour. There may, however, be more subtle stimuli prior to engaging in copulation on the part of the male such as certain preening movements. Prior to copulation the female generally begins swishing her beak in the water, flicking water sideways, while remaining in a hunched position. Often as she does this she may give a low twittering call. The male walks over to the female and may remain feeding or preening for a short time while the female continues twittering and splashing. For Avocets, Tinbergen (1952) suggests this preening is a displacement activity due to excess of sexual drive waiting for the female to adopt the copulation attitude. In stilts, however, the male continues preening even after the female has adopted this position. According to the disinhibition hypothesis there must be two conflicting tendencies for displacement to occur and it is not clear what these might be in this situation. It is possible these are tendencies to approach and to draw away from each other. When the female assumes the invitation posture which is a flattening of the body with the beak almost horizontal to the ground (Plate 16) the male begins walking back and forth around behind her. The sequence here is variable, however, as the male may begin walking around the female just before she assumes the invitation posture. If the male should attempt to walk around in front of her the female begins pivoting,

PLATE 16

Copulation

Female assumes invitation posture.

PLATE 17

Male standing flicking and dipping beak in the water while female remains in the invitation posture.

to prevent the male doing so, until such time as the male begins walking around behind her. Thus she directs the male toward her tail and cloaca. On each side of the female the male stops and begins bowing, preening and flicking his beak in the water before walking back to the other side again (Plate 17). The number of times walking back and forth took place ranged from 5 to 18 with an average of 9 before mounting the female. When the male mounts the female he places his feet on her scapulars and with raised wings and beak slightly open lowers himself slowly, so the tarsus is lying right along the back, until the cloacae meet (Plate 18). As he does this the female rises to a slightly more horizontal position with her head moving quite rapidly from side to side. After copulation the male slides off, more often onto the female's right side, and with necks arched they cross beaks, the male's beak on top of the female's. At the same time the male spreads his wings out with one of them covering the females back. Together they walk like this for two or three steps (Plate 19) before breaking off and walking away from each other. Subsequent activities vary from bathing, generally by the female, to preening or feeding by either; there appears to be no standard behaviour following copulation.

In the cases where I assumed the male had initiated copulation the male was preening prior to the female assuming the preliminary hunched posture and swishing her beak. There were three occasions, however, when the male was on a mound nest-showing prior to copulation.

PLATE 18

Male mounts and copulates.

PLATE 19

Walking with crossed beaks after copulation.

Attempted copulations were indicated by the short time which the male was mounted (less than 5 seconds), and the absence of the crossed beaks element which characterised what I believed to be successful copulations. Burrows (1948) reports a copulation in which neither the walking back and forth nor the crossed beaks elements were observed. He reports also that this instance occurred on a windy day. I believe that this was probably an unsuccessful copulation as it appears so characteristic of the attempted copulations observed on Colony I on windy days, although on no occasion did I witness the absence of the male walking around the female. The most common causes of unsuccessful copulation was first, the presence of a strong wind which would blow the mounted male off and second, what appeared to be an inadequate stimulus as one or other of the pair would break off before copulation was complete (generally before the male had mounted). A third cause for unsuccessful copulation was breaking off to chase intruders from the territory, although no copulation was interfered with directly by another bird approaching the copulating pair.

D. NEST BUILDING.

i) Nest Site.

This varied considerably depending on the locality of the colony. On Colony I nests were generally on top of some sort of vegetation or on a low or high mound. Thus on this colony the nests were grouped into three classes depending on site. These classes were (a) on almost floating vegetation barely above water level,

(b) on a low mound close to the water level but on solid ground, (c) on a well raised mound. Of the 21 nests on this colony the distribution was 34%, 52% and 14% respectively. On Colony III on a swamp at Awahuri with a total of seven nests, all but one favoured a position in the crown of a low clump of rushes 6-8 inches above the water level. The exception was on a built-up mound of mud (Plate 20) which may have previously been the remains of a clump of rushes. Of the 25 nests built on the river, Colony II all were built among the rocks, but two sites were favoured. Sixty percent of these were laid amongst rocks alone and the other 40% laid close to a piece of driftwood or some vegetation.

As noted by Soper (1967) the Pied Stilt appears to be less particular in its choice of nesting place compared with the Black Stilt which prefers isolated river beds. Analysis of nest record cards of the Ornithological Society of New Zealand showed this to be the case, although there still appears to be some preference by Pied Stilts for river sites. Table 4.1 shows the analysis of 246 records. It should be noted that these records cover the whole of New Zealand and that for convenience only have they been grouped into the six categories shown in Table 4.1. For example nests by pools in a shingle pit were placed in the river category as they were considered to be on the same or similar terrain. Thus there is some variety within each category.

TABLE 4.1 NESTING HABITAT OF THE PIED STILT

	River	Farmland	Swamp	Sand Dunes	Mud Flats	Lakeside	Total
Number	96	68	53	22	4	3	246
Percentage	39.02	27.64	21.54	8.95	1.63	1.22	100

PLATE 20

Nest on built up mound of mud.

PLATE 21

Nest on river shingle bed showing lack of structure.

ii) Nest Materials.

In most cases on shingle beds nest material was sparse, most nests consisting essentially of a shallow scrape or depression lined with a few twigs or straw (Plate 21). Sometimes it was just a shallow depression among rocks. On the swamp colonies, however, the nests were of more solid construction, often incorporating large quantities of dry grass and rush stems (Plate 22). In cases which necessitated building up the nest, quantities of mud were also utilised (Plate 23).

iii) Nest Raising.

Such nest-raising behaviour as noted above was observed on a number of occasions on nests which were close to the water level of the swamp, especially after heavy rain. It was not noted on any occasion on the river probably because there was no suitable material in the close vicinity of the nests that were threatened. This behaviour has also been noted in the Black-necked Stilt (Truslow,1960) and the European Avocet (Makkink,1936). Cunningham (1970) reports that this behaviour has not been noted in Pied Stilts in New Zealand, but I suggest it probably has been seen but has not been recognised for what it is and thus not reported. It was possibly throught to be general nest building, as it occurs quite commonly. Makkink (1936) considers the behaviour to be instinctive, stimulated by rising water around the nest, and suggests it may be a typical reaction of birds in habitats where the danger of inundation of nests is common. Evidence, however, from three nests which were actually

PLATE 22

Nest on swamp composed of dry grass and rush stems.

PLATE 23

Built up nest on swamp showing quantities of mud incorporated.

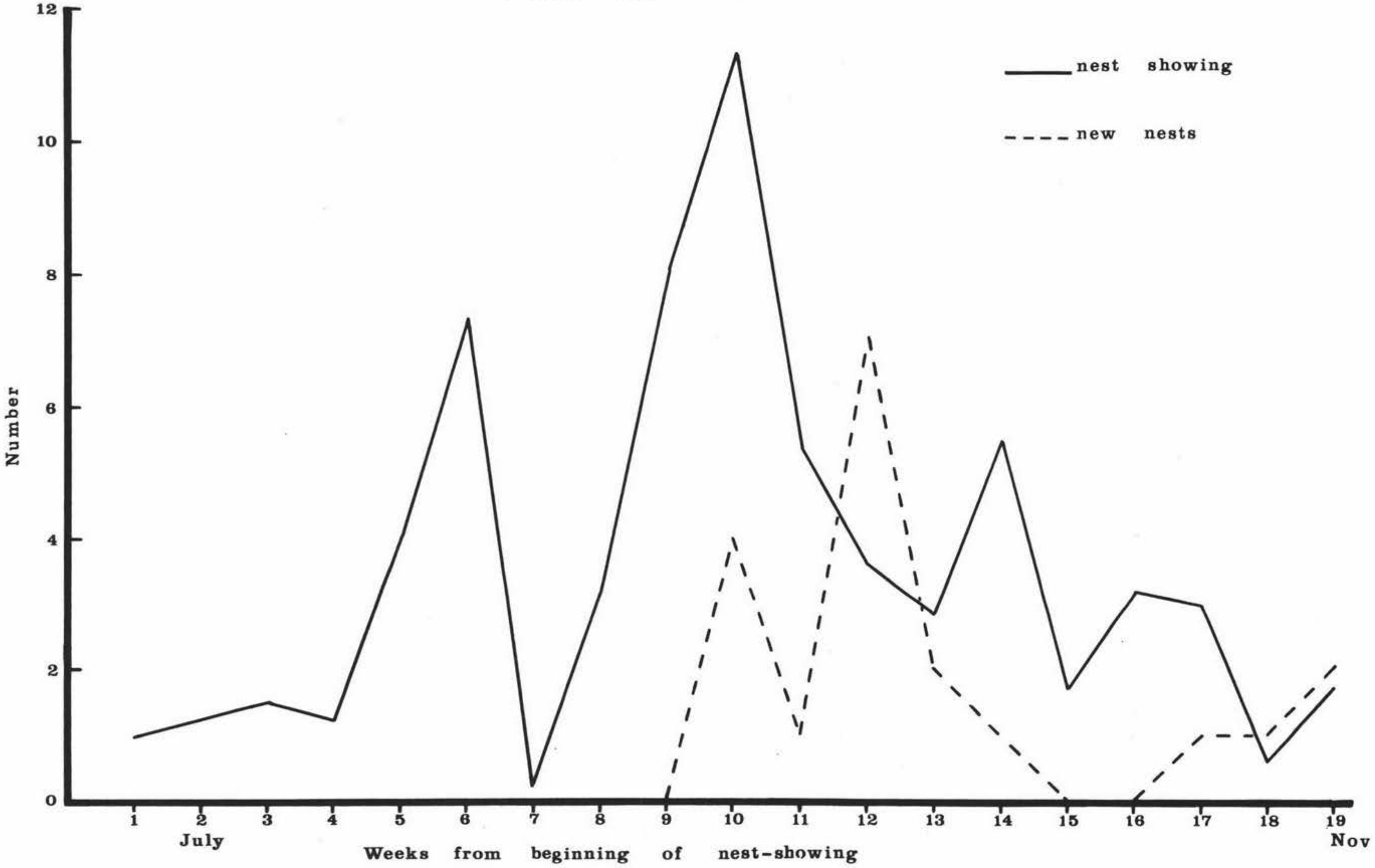
inundated with water without any apparent attempt to raise them. The age of the birds concerned is not known, but if it is a learned act it is possible they were young birds perhaps breeding for the first time.

Alternatively nest raising may occur as a result of displacement nest building from conflicting tendencies to incubate or to leave the nest. This does not explain why it occurs with some pairs and not others unless these tendencies differ in intensities between individuals.

iv) Behavioural Elements.

(a) Nest-showing. This term is applied to the initial behaviour engaged in at prospective nest sites. It takes the form of standing on the nest site and pointing or pecking into the nest mound or scrape, and giving a twittering call at the same time, with the beak held almost vertical to the ground. The bird may turn around in circles at the same time, its beak in the centre. In the early stages of nest site selection it is the male which appears to do the majority of the nest-showing and this is not limited to one site but may involve a number of such sites, as in the Blacksmith Plover (Hall,1964), European Avocet (Makkink,1936). Some gulls such as the Southern Black-backed Gull *Larus dominicanus* (Fordham,1964) and the McCormick Skua *Catharacta maccormicki* (Spellerberg,1966), also select one from a number of sites. Probably this is one of the nesting activities which stimulates the release of sexual behaviour in the female, as closer to the time of laying she engages in this behaviour more often,

FIG 4.3 MEAN NUMBER OF NEST - SHOWING BOUTS PER HOUR OF OBSERVATION IN RELATION TO NUMBER OF NEW NESTS PER WEEK



sometimes by herself but more often together with the male (Plate 24). When she starts by herself she is very quickly joined by the male. Nest-showing was known to have begun for one pair at least six weeks before they eventually laid. Other pairs were observed nest-showing at least 2-5 weeks before they laid eggs. It may have begun before this time but could not be determined as nest-showing could initially be carried out over a wide area and individuals could seldom be distinguished.

Figure 4.3 shows the mean number of bouts of nest-showing occurring per hour of observation for each week and this is related to the number of new nests per week. It will be seen that there are two major peaks in each line and the differences between the peaks in each case are roughly of the same order. This would suggest there may be some correlation between the two lines. In addition it may be noted that there is four weeks' duration between the first peaks in each case and only two weeks between the second peaks. I suggest that this is evidence for some sort of social stimulation in the development of breeding activities. Thus the activities of the early nesters while taking place over an extended period stimulate others in the colony so that the development of their activities is accelerated and the duration before nesting thereby compressed. The drop in number of bouts of nest-showing prior to each peak of new nests is in all probability due to an increasing amount of settling and sideways-building occurring as the number of nest sites become limited to one.

PLATE 24

Male and female nest-showing on nest site.

PLATE 25

Sideways building on nest mound.

(b) Sideways-throwing. Similar behaviour to this has been observed in other waders such as the Curlew Numenius arquata (Gordon,1936), Little Ringed Plover Charadrius dubius (England et al 1944), Blacksmith Plover (Hall,1964) and Avocets (Makkink,1936). Here the stilt picks up twigs, straws or grass and throws this material back over its shoulder alongside itself. Often it may involve large clumps of mud and roots dragged up from under water. Stilts do not carry this material from any distance back to the nest, but may be seen sideways-throwing sometimes up to six feet from the current nest site. More often they will stand in the nest, stretch out their necks, pick up material and throw it onto the nest. When sideways-throwing occurred away from the nest any material which had fallen close to the nest was picked up when the bird returned. Possibly this results in the more vigorous sideways-throwing when away from the nest. Sideways-throwing was most often seen in association with nest-showing and the two types of behaviour could be expected to be seen together except when sideways-throwing took place some distance from the nest. On other occasions such as territorial disputes (p. 73), during incubation (p. 127) and nest relief (p. 133) sideways-throwing was also observed and was performed in the same manner.

(c) Sideways-building. This behaviour which has also been observed in the European Avocet (Makkink, 1936), Black-headed Gulls (Beer,1963), McCormick Skua (Spellerberg,1966), White-fronted Tern Sterna striata

(L.Gurr,pers.comm.) and Red-billed Gulls (Mills,1967), involves the same elements as the sideways-throwing behaviour but is limited to a sitting position on the nest scrape. Instead of throwing the material alongside itself however, the stilt places it on the nest either beside or in front of itself and spends more time arranging it into position (Plate 25). Again the bird would reach as far out of the nest as possible to drag material in while remaining in the sitting position. Often this behaviour is adopted while incubating, and evidence of this was found in some experimental nests where large masses of vegetation slowly accumulated on top of the tambour (see Chapter V) and had to be removed periodically. It is possible that this is a displacement activity resulting in unintentional nest raising which serves to save the eggs from destruction in the event of flood, as Johnson(1941) reports for Northern Guillemots Uria aalge albionis. Such displacement behaviour could arise from conflicting tendencies to incubate and to leave the nest and the stimulus for the disinhibited action coming direct from the nest itself.

(d) Scraping. As seen in Plate 26 the stilt falls forward on its breast and wrists, its tail and wings pointing in the air at an approximate 45^{0} angle, its long legs tucked up at a similar angle and scraping backwards with its feet. The wings are held slightly out from the body as in Avocets (Makkink,1936). Scraping is generally quite vigorous and often showers of earth and grass can be seen being scraped out. The stilt does not turn around on its breast while scraping,

PLATE 26

Scraping in nest cup.

as does the Ringed Plover (Laven,1940) and Turnstone *Arenaria interpres* (Bergman,1946), but stands up and turns around to a new position before settling and beginning to scrape again. Thus each bout of scraping involves standing up and resettling a number of times before moving off again. Nest scraping may be performed initially by the male (as in the Red-backed Sandpiper *Calidris alpina*, Holmes,1964) on a number of sites (though fewer than nest-showing sites) which are gradually eliminated until finally only one site is involved. Analogous displays have been noted in several species of birds including the plovers (Hall, 1964), oystercatchers (Makkink,1942), avocets (Makkink, 1936), Red-necked Phalaropes *Phalaropus lobatus* (Tinbergen,1935), McCormick Skua (Spellerberg,1966) and gulls (Beer,1961,1963).

(e) *Settling*. Scraping is often followed by settling behaviour, where the stilt tucks its legs under itself and settles onto the nest scrape. It gradually works its legs under by rolling from side to side in the manner of an incubating gull (Beer, 1961), moving each leg a little at a time. When finally settled it gives a quiver of its tail. The settling movements involved here are similar to those of an incubating bird settling on eggs although performed a little quicker. In addition the bird does not settle for long in this early period, no more than two minutes on the average, but its period of settling lengthens, as the time for laying approaches. Settling may be performed by both sexes in the initial stages but towards laying the female does the greater amount.

E. DEFENCE OF NEST AND YOUNG.

i) Reactions to species other than man.

(a) Swooping. This term has been coined to distinguish it from the type of aerial attack used on man. When the colony is threatened by a Harrier Hawk flying overhead the breeding birds react by rising to meet it in the air. Attacking generally from behind, and either above or below they swoop in very close before pulling away sharply. Thus the stilts may be seen to be wheeling around the hawk and calling persistently. Hall (1964) reports similar "air-harrying" by the Blacksmith Plover. On only one occasion, however, was a hawk seen to be hit by a stilt although at other times they may have hit the tail feathers so close did they come.

During the first half of the breeding season in Colony I hawk scares were frequent, averaging some 6-8 scares per half hour of observation. This fact may account for the prolonged incubation period 27-28 days (compared to the normal 25 days) for some nests on the colony at this time. That is incubation may have been attenuated by frequent absence from the nest, although the birds were generally away for only 2-3 minutes. Moreover the bird incubating on any given nest did not necessarily rise with every threat but only when the hawk flew over the parts of the colony closest to its nest or when the non-incubating partner was absent. A similar reaction was also elicited by Black-backed Gulls although they were allowed to fly much closer in terms of altitude and distance before eliciting an attack.

In addition they were tolerated till eggs had been laid, whereas hawks were attacked from the beginning of breeding activities, indicating a lower attack threshold for hawks. Hawks and gulls were the only birds ever seen to be attacked in the air. Magpies Gymnorhina tibicen and pukekos Porphyrio porphyrio were also swooped on if close to a stilt's territory, but only when they were on the ground.

(b) Chasing. Pukekos which invaded a stilt territory early in the breeding season were initially chased by the stilt in the typical hunched posture used against conspecifics. Subsequently, however, in the presence of eggs or chicks the pukekos were swooped on until they left the vicinity of the stilt's nest. As a pukeko left the attacking stilt would continue to chase it, flying along just behind the pukeko with its feet stretched out in front as if trying to take hold of the pukeko's tail. Starlings Sturnus vulgaris which had previously been tolerated on the territory were also chased off as the time for laying approached.

When cows walked too close to the nest of a stilt the bird would assume an aggressive upright posture and call agitatedly, occasionally sideways-throwing and grass-pulling, remaining between the cow and the nest. The cow would take little notice of the stilt except to occasionally shake its head at the stilt if it got too close. Other species normally tolerated were also attacked if the stilts were sufficiently stimulated. A pair of mallard ducks Anas platyrhynchos which landed on a pond close to the spot where a pair of stilts were trying to get their chicks across, were at once attacked until they left the area completely.

ii) Reactions to Man.

Terminology for stilt reactions to human intruders will follow that used by Williamson (1952) for Oystercatchers Haematopus ostralegus. Most reactions to the intrusion of man result from conflict situations and thus contain elements of displacement or ambivalent behaviour, and these elements will be described where they occur.

(a) Aggressive flight. It appears that in the stilt this display is of high intensity as it is elicited only when the intruder is approaching and close to the nest. The bird flies directly and silently at the intruder at a shallow angle from about 50-70 yards away, breaking off sharply at about head height a few feet away. It flies up steeply and begins calling as it reaches the peak of its climb. Some stilts, perhaps more highly stimulated than others, may fly in very close, especially if attacking from behind, but on no occasion was I hit, even when standing over the nest and handling eggs or chicks. Moreover I know of only one record of a person having been hit by a stilt and this was recorded on a nest record card from Kaikoura in 1969. This would perhaps indicate greater aggressiveness in Oystercatchers as Williamson (1952) reports being hit by them a number of times. Hall (1964) records aggressive flight in the Blacksmith Plover, but only after the eggs have hatched, though he reports its occurrence in the Crowned Lapwing Vanellus during the egg stage.

(b) Furtive run. As for Oystercatchers (Williamson, 1952) this appears to be the display of lowest intensity. It appears that this behaviour occurs in a conflict situation where the stimulus to escape is slightly stronger than the tendency to attack. The bird assumes a hunched posture (Plate 27), similar to that used when chasing conspecifics, and runs with short quick steps away from the intruder, sometimes half sideways, looking back over its shoulder. It continues to do this as long as the intruder is following it, leading the intruder away from the nest or young. This posture is assumed when the intruder is still some distance from the nest but walking toward it. When the intruder has walked far enough away from the nest the stilt breaks off its furtive run and generally assumes butterfly-flight (see below). Should the intruder ignore the stilt, however, and continue to walk toward the nest or young, the bird will also assume butterfly-flight, but flying back toward the intruder quickly adopts the lure distraction display (see below). The furtive run may also be interspersed with displacement feeding as Williamson (1952) notes for Oystercatchers, though for stilts it does not appear to be an essential prerequisite to butterfly-flight and false brooding.

(c) Butterfly-flight. This term was coined by Huxley and Montagu (1925) who considered it to have no defined function. Williamson (1952) suggests that it may be a displacement activity serving as distraction to attract attention by advertisement flight. The present author suggests that this is ambivalent

PLATE 27

Furtive run posture (note similarity to hunch pursuit).

PLATE 28

Stilts hovering in butterfly flight.

behaviour showing signs of both attack and escape response. Subsequently it has become ritualised to incorporate the distraction function, but it is not true displacement behaviour as this particular activity is not part of the stilts normal behavioural repertoire, i.e. it is not an action occurring out of normal context. When a human intruder is spotted some distance from the colony the birds fly over and hover above with slowed wing beat, their legs hanging down, calling persistently (Plate 28). It is difficult, however, to determine which birds belong to which nest because many birds hover in butterfly-flight above any one nest site. Butterfly-flight is much more closely linked to the lure distraction displays of injury-feigning and false-brooding than is the furtive run. In most cases one merges into the other. There is a similar close relationship in the Avocet (Makkink,1936) and the same appears to be true for the Blacksmith Plover and Crowned Lapwing (Hall,1964). In comparison with the Oyster-catcher (Williamson,1952) the butterfly-flight of the Pied Stilts extends over a considerable period of time. It was observed from when the first eggs were laid until well after the young were flying. This protective instinct of the parents extends for at least four months after the young have hatched.

(d) Lure display. As the stilt drops to the ground from its hovering butterfly-flight it runs along the ground flapping its wings, apparently helpless, sometimes falling over rocks, occasionally giving small jumps in the air and calling all the time in an

PLATE 29

Lure distraction

(a) Running from predator and feebly flapping wings.

(b) Facing predator stumbling and holding wings out.

(c) Lying down feebly flapping wings.

(d) Springing in the air.

agonised manner (Plate 29). Every now and then the bird may sit down, flapping its wings rather feebly as it does so. Generally this occurs when the intruder stops moving but is close to the nest. With further movement of the intruder, especially toward the displaying bird, it will stand up and move off again. This may be analagous to the spread-out-wing behaviour of the Crowned Lapwing (Symmes,1952). Very often the stilt will seek some partial cover behind which to perform this sitting component of the display. Williamson (1952) suggests this "represents the most emotional condition, being the final resort to draw off an intruder who does not respond to the butterfly-flight". His observation of "how the tussle between the urge to continue flying and the impulse to fold the wings become united in the lure display" appears to occur also in the stilts (Plate 30) and therefore may be considered to be true displacement behaviour. Lure distraction display becomes more intense as incubation progresses, up to the point of hatching, when it appears to diminish in intensity, its place taken in intensity by aggressive flight. Due to the close proximity of the nests to each other a number of birds are generally displaying at the same time making it difficult to determine the parents of particular nests.

(e) False brooding. Often in the middle of the lure display a stilt will sit down in a brooding or incubating attitude amongst the rocks (Plate 31) or even in a few inches of water (Plate 32), as though covering eggs or young. It differs, however, from the

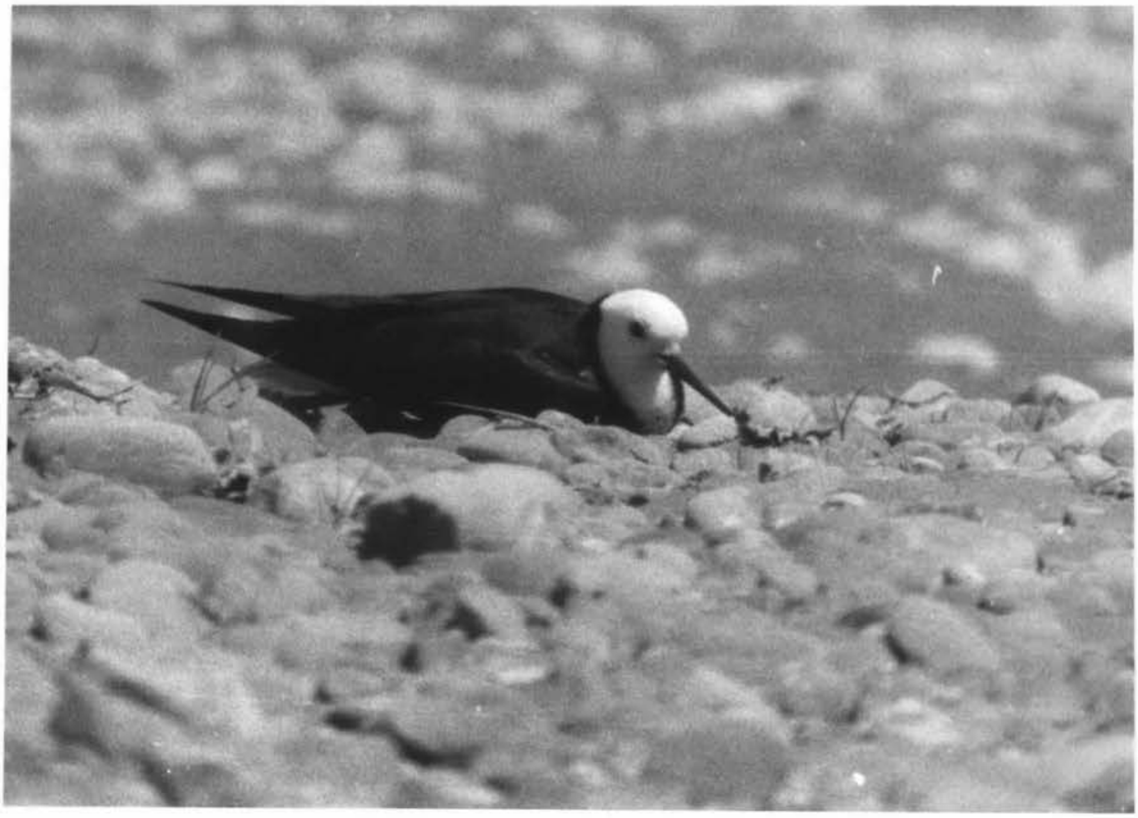


PLATE 30

Conflict Behaviour

(a) Standing with one wing folded and other flapping.

(b) Sitting down with one wing folded and other held stretched out.

PLATE 31

False brooding amongst rocks.

PLATE 32

False brooding in shallow water.

normal sequence in that the bird settles much more quickly. Following on from or interspersed the lure display, it is the last of these displays to develop, in contrast to the Oystercatchers (Williamson,1952) where its development proceeds that of the lure display. It is not known how long this display persisted after the hatching of the chicks, though it is known to survive at least for a short time but not as long as the lure display. In the Blacksmith Plover, Hall (1964) statesthat it is most likely to occur with human intrusion soon after hatching, is rarely seen before, and diminishes in intensity with increasing age of the young. Similar displays have been observed in Avocets (Makkink,1936) and Black-winged Stilts (Williamson,1965). Amongst all these species "the posture (has become) firmly established as an inherent behaviour pattern requiring only a minimal stimulus from the environment, (or) perhaps no extraneous stimulus at all" (Williamson,1952), the posture having become highly stereotyped. Other species, on the other hand, e.g. the Dunlin Calidris alpina schinzii (Thin,1942) require the stimulus of another nest or brood to act as releaser. Williamson (1952) disagrees claiming that false brooding is not a true displacement activity as defined by Tinbergen (1940) and he is supported by Makkink (1942). He claims that the activity that occurs is the dominant of two conflicting impulses, to escape and to brood. However it is probably more likely that the conflicting impulses are to escape and attack and that false brooding is the outcome of a disinhibited impulse to brood.

CHAPTER V

INCUBATION

A. EGG LAYING.

i) Dates of Laying.

The first nest, containing four dirty eggs was found on August 25th on Colony I. Since the eggs in a clutch are generally clean within two or three days of being laid it is probable that this first clutch was begun no earlier than August 20th. Stokes et al (1959) report laying as early as June 17th, while Foggerty (1968) reports the same but notes the hazards of such early laying. Laying in Colony II began on about the 20th October and 25 nests were eventually laid over a period of nine weeks until 29th December. In Colony I, however, laying in 21 nests in 14 weeks was completed by December 9th though the last clutch was laid a month after the penultimate clutch. The last nest, however, was subsequently destroyed. More clutches may have been laid in Colony I but it is possible that the observers continued presence on the colony induced them to change to the river site. Alternatively the lack, due to flooding, of possible preferred nesting sites on the river early in the season caused them to use the Colony I site. Later in the season nesting sites on the river again became available. In Colony III only 7 nests were laid in a period of about three weeks from the end of October to the middle of November. These were all subsequently destroyed so the actual laying date of some clutches could not be determined. An earlier attempt at laying in this colony was also hampered by flooding.

Two peaks appeared in the spread of laying (Fig. 5.1); one in the third week (September 5th-11th) after the first nest was discovered and the second in the twelfth week (November 7th-13th). The first peak consisted of seven nests, all in Colony I, while the second peak of nine nests was spread over the three colonies. A third small peak of four nests occurred in the fifteenth week (November 28th - December 4th) in Colony II and was the peak of laying for this colony.

The number of eggs laid per week is shown in Figure 5.2 and has a similar shape to Figure 5.1. Included in Figure 5.2 is the number of eggs hatching per week and it may be seen that again the graph has basically the same pattern, though lagging behind by about three weeks on average. This lag is an indication of the 23-27 day incubation period. The considerable drop in number of eggs hatching for weeks 11-14 is due largely to destruction of nests at this time by flooding (see p. 145).

ii) Time of Laying.

The time of day when eggs were laid could not be accurately determined without checking the nests at hourly intervals. This, it was decided was inadvisable due to the readiness with which stilts desert the nest. From general observation, however, it appeared that eggs were laid at the rate of one a day, though often at intervals of something more than 24 hours apart. The time between laying of successive eggs ranged from about 10 hours to something more than 48 hours. It appeared

FIG 5.1 NUMBER OF NEW NESTS PER WEEK FROM FIRST LAYING

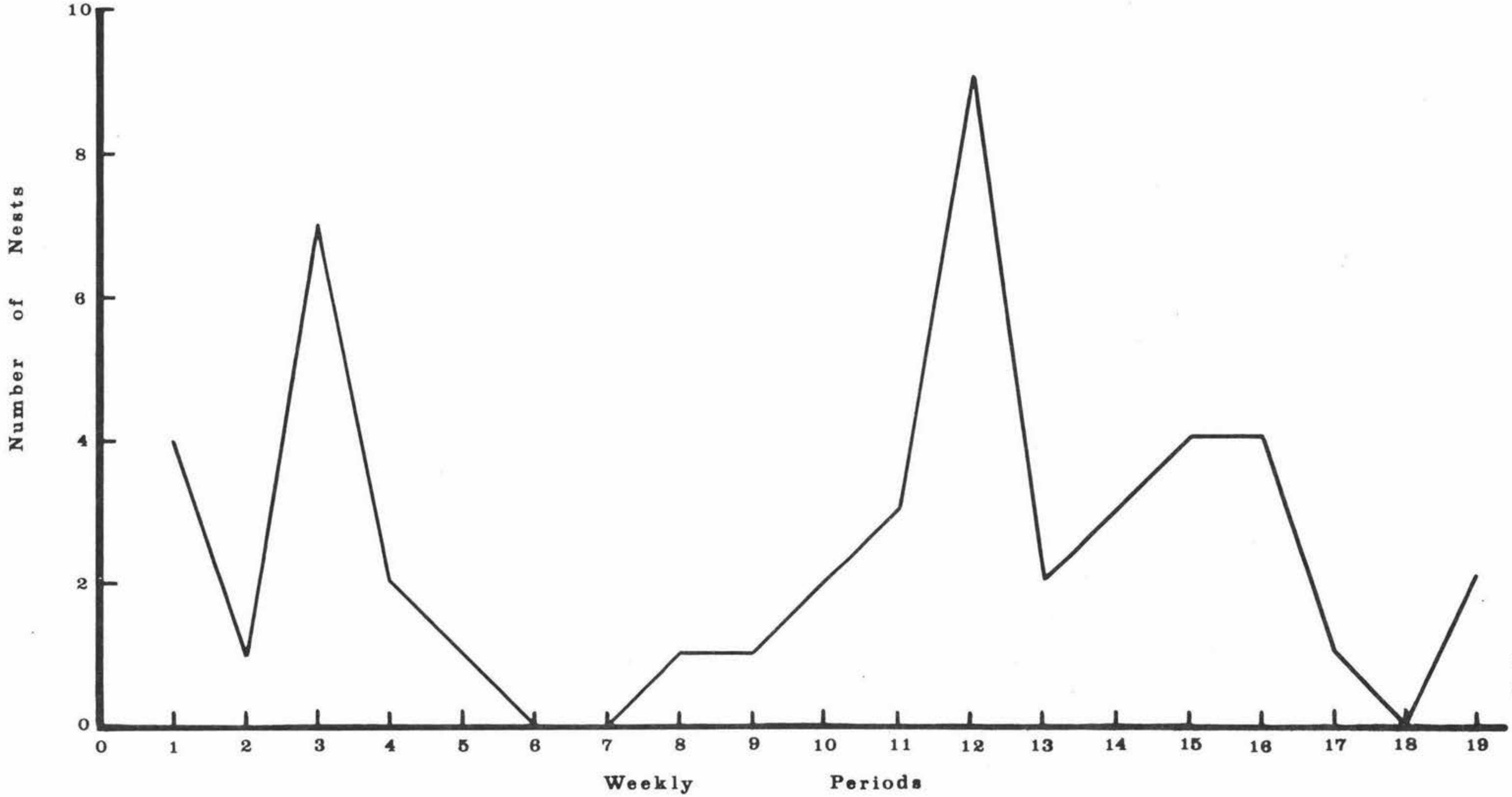
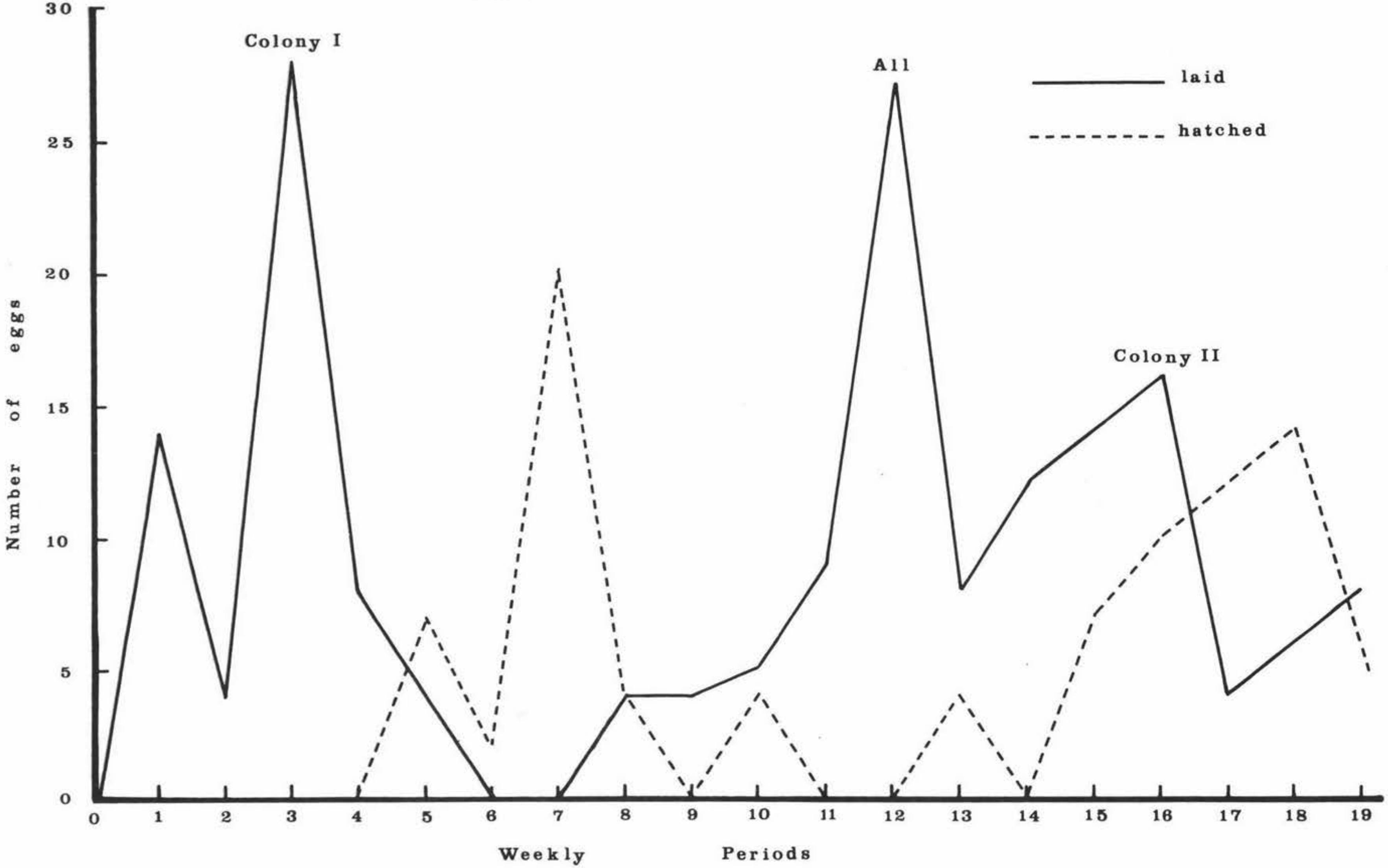


FIG 5.2 NUMBER OF EGGS LAID AND HATCHED PER WEEK THROUGHOUT BREEDING



that most eggs were laid between early evening and early morning, i.e. 1900-0700 hours during which time the author was generally absent from the colony. Lack (1968) reports for the Scolopacidae, e.g. Oystercatchers, that the interval between eggs is normally two days.

iii) Clutch Size.

From a total of 48 nests in three colonies the mean clutch size was calculated at 3.91 eggs. The distribution of these clutch sizes is shown in Table 5.1. Pullen (1967) gives an average clutch size of 3.85 based on 20 nests near Auckland. Analaysis of the nest record cards of the O.S.N.Z. yielded a mean clutch size of 3.82 from 213 nests. These results are shown summarised in Table 5.1. Clutch size ranged from one to five eggs, but there appeared to be no correlation with latitude, i.e. daylength. Only clutches of two to four eggs were found in the study area. It will be seen from Table 5.1 that the greatest percentage of clutches contained four eggs. A clutch size of four is normal for most species of the sub-order Limicolae (Witherby et al, 1943).

Lack (1968) states there is strong evidence that clutch size and hence brood size of some species is close to the number of young for which parents can find enough food in favourable conditions. Such does not appear to be the case with the Pied Stilt as there appeared to be an abundance of food available through the spring and summer, but the average number of young per family was only 2.4 from 43 observations of what appeared to be family parties. From the evidence of food samples and general observations all through the

TABLE 5.1 DISTRIBUTION OF CLUTCH SIZE

	Clutch Size					
Source	1	2	3	4	5	Total
Oroua	-	1	2	45	-	48
%		2.0	4.0	94.0		100
O.S.N.Z.	2	6	21	183	1	213
%	0.9	2.8	9.9	85.9	0.5	100
Total	2	7	23	228	1	261
%	0.8	2.7	8.8	87.6	0.4	100

breeding season no dearth of food or its availability was discerned. The mean number of young raised in these cases was much lower than the mean number of eggs laid. It would appear, therefore, that some factor other than food was involved in the determination of clutch size. Perrins (1965) in his study of the Great Tit Parus major suggested that the mean clutch was usually that which produced the most surviving young. This hypothesis fits the observed situation of the Pied Stilt better. That is, the observed mean clutch size was 3.91 but the observed surviving brood per family was 2.4. Applying Perrins' hypothesis means that it takes an average clutch of four eggs to produce a brood of more than two individuals. Considering the hazards other than the paucity of food that the young chicks are exposed to in the first two weeks or so of their existence, this constitutes a reasonable survival rate. Hazards which the parents have to contend with such as shelter from extremes of weather and protection from predators and territory-holding conspecifics limit the number of young which a pair can cope with. Thus it would appear that in the face of these hazards it is four eggs which produce the maximum number of young the parents can cope with.

On the other hand, Cody (1966) suggests a theory which incorporates both the postulates of Lack and Perrins. Cody's theory of clutch size is related to the amount of time and energy available for expenditure. Selection for utilization of this energy in different ways, e.g. avoiding predators or competition for food has caused the limitation of clutch size even in favourable circumstances. Thus the ability to avoid predators may increase when a large clutch is sacrificed for a slightly smaller one, or if more time is spent gathering food this limits the size of clutch the parents can cope with to produce the most surviving young. Although this appears a better general theory the information available on the stilt can neither support or refute this theory.

The Pied Stilt is a determinate layer in that generally a maximum of four eggs only are laid. In four nests, eggs were removed continuously after the appearance of the first, second, third and fourth eggs respectively. In all cases, except the first, a total of four eggs only were laid. Where the first egg was removed the pair immediately deserted the nest.

There does not appear to be any correlation between date of laying and reduction in clutch size as reported by Mills (1966) for Red-billed Gulls and Fordham (1964) for Dominican Gulls. They found that older birds with previous breeding experience laid earlier and laid larger clutches. Although age and previous breeding experience was not known in the case of Pied Stilts this pattern was not observed. It was unlikely that the colony observed consisted entirely of one age group. Consequently it appears that age and experience have little influence on date of laying or clutch size. Fordham (pers.comm.) suggests that the existence of such a correlation appears to be related to age composition of the colonies and dates of annual sexual maturation of birds of different ages.

iv) Egg Measurements.

Each egg was measured and weighed on a 100gm spring balance as soon as possible after laying. They were not weighed again for fear of disturbing the parents too much as stilts tend to desert the nest readily. From the length and breadth measurements the volume of each egg was calculated using the method recommended by Stonehouse (1966).

Table 5.2 shows the range in egg measurements and the mean size of egg. The order of laying was known only for 20 clutches, however, and it was from these that the positions of smallest and largest eggs in the clutch were determined. The smallest egg was at 1.9 and the largest at 2.95 in the clutch. These 20 clutches were also analysed for any significant differences between mean egg size of clutches. Considering linear measurements there was no significant difference between mean egg size of the three colonies, or between these colonies combined and 20 eggs from Alexandra, South Otago. Nor was there any significant difference between the mean of these colonies and the mean of 100 Black-winged Stilts' eggs given by Witherby et al (1943). Analysis of variance on the egg volumes of the 20 clutches showed there to be a significant difference between clutches and within clutches. A least significant difference test showed a significant difference (p=0.99) between seven clutches with the largest mean egg volume and the seven clutches with the lowest means. Within clutches a paired "t" test indicated a significant difference (p=0.95) between

TABLE 5.2 SIZE OF SMALLEST & LARGEST EGGS AND POSITION IN CLUTCH

	No. in Sample	Length	Width	Volume	No. in Sample	Position in Clutch
Smallest	192	3.85x2.95	4.35x2.86	17.564	20	1.9
Largest	192	4.85x3.24	4.38x3.34	26.014	20	2.95
Mean	192	4.33	3.08	21.11		

first and third eggs and the second and third eggs, but no difference between the first and fourth or third and fourth eggs although measurements showed a general decrease in size of the fourth egg. (Paludan (1951) has suggested this reduction in size of the final egg is linked with the physiological changes which are associated with termination of egg laying). Table 5.3 shows the egg volumes of these 20 clutches in order of size. It will be noted that clutches with the highest and lowest mean volumes are essentially all from Colony I and contain both early and late nests. Thus there appears to be no significant difference between egg size of early and late nesters as there is in Kittiwakes Rissa tridactyla tridactyla (Coulson,1963). It may be that the difference in mean egg size is due to the age of the breeding bird; younger birds laying smaller eggs as reported for the Kittiwakes (Coulson, 1963) and Red-billed Gulls (Mills,1966). This could not be determined in the present study because as stated above the birds were of unknown age.

v) Relaying.

Only two pairs were known to have relaid. The birds were recognised by their markings and their possession of the same territories. The first nest of both pairs was destroyed within a few days of laying and relaying took place 10-12 yards away within seven days. There was no significant difference between the first and second clutches though in both cases the relaying tended to have larger eggs. Gates (1962) noted in the Gadwall Anas strepera that ability to re-nest declined as the

TABLE 5.3 INCUBATION AND BODY TEMPERATURES OF STILT COMPARED WITH PENGUIN AND SKUA

	Incubation Temperature °F		Body Temperature °F		Difference °F
	Mean	Range	Mean	Range	
Stilt	92.2	85-97 (12.0)	105.3	103.5-108.5(5.0)	13.1
Penguin	92.7	84.5-98.2(13.7)	103.8	100.3-106.4(6.1)	11.1
Skua	96.6	87-103.5(16.5)	106.1	103.4-108.4(5.0)	9.5

stage of incubation advanced. It is possible that this is the reason no other stilts relayed after destruction of their nests later in the incubation period.

B. LENGTH OF INCUBATION.

Incubation does not generally begin until all eggs are laid. Beer's (1962,1963) investigations of the Black-headed gulls indicate that they show incubation responses in both the pre-egg and laying stages. He does state, however, that the presence of an egg in the nest during the pre-egg stage does increase the tendency of these gulls to perform some incubation behaviour, and this increases steadily as the date of laying approaches.

Stimulus to incubate in the stilts cannot be the presence of a full clutch (i.e. four eggs in the nest) as this does not account for two or three egg clutches being incubated. It would, therefore, appear that the stimulus is some internal factor perhaps related to hormonal levels and the presence of fertilised ova in the bird. Beer (1962) comes to a similar conclusion in the case of the Black-headed gull and suggests other factors such as learning, maturation, and brood patch development may also be involved. He also notes (1963) that the development of brood patches before laying may parallel an increasing tendency to incubate and that hormones known to be involved in the development of brood patches may influence the onset of incubation behaviour in other ways. Probably feedback stimuli from the egg (e.g. colour and size, Baerends,1959) are also important. No doubt stimuli relayed from the brood patches are important in determining incubation behaviour as in the Black-headed gull (Beer,1962). There is also little incubation by Herring Gulls (Drent,1967) and the Blacksmith Plover (Hall,1964) before the full clutch is laid, though the fact that hatching may be spread over two days suggests that some incubation occurs during the laying period (Paludan, 1951). The fact that there are shorter hatching intervals than laying intervals (Beer,1962, Kendeigh, 1963) and the "hatching sequence" may not correspond to the order of laying (Fordham,1964) as also noted in this study would cast doubt on this speculation. Beer (1962) and Kendeigh (1963) notes that if a certain minimum time of sitting is required for egg temperature to be raised above the threshold for promoting development, it is likely that a high proportion of short sitting spells in early laying effects little change in the embryo. A similar pattern for stilts can be seen in Figures 5.4 and 5.5. Lack (1968) states that in all Charadriiform waders incubation does not begin until the clutch is complete and such would appear to be the case with the Pied Stilt.

Assuming that incubation extends from the laying of the last egg to the hatching of the last young (Nice, 1937), the incubation period may be estimated only for those nests where the last egg hatches. From a total of 26 nests in which some eggs hatched only 15 nests yielded accurate data on the length of incubation. For these nests incubation lasted an average of 25.2 days (range 22-28); 47% (7 clutches) hatched in 24 days (25 days is usually quoted Moon, 1967; Oliver,1955; Stokes, 1961). Previously incubation periods of 22 or 23 days have only been reported once (Stokes,1961). An incubation period of 24 days is also given for the Hawaiian Stilt Himantopus h.knudseni (Berger,1967). One pair on Colony II continued incubating for at least 62 days before the eggs disappeared. Two eggs disappeared after 45 and 49 days respectively but the pair continued incubating until the last two eggs disappeared on the 63rd day. Harrier Hawk tracks were found near the nest and it was assumed that this was the cause of the eggs disappearance. Skutch (1962) notes that some species may continue incubating up to three times the normal period required for hatching. Where some of the eggs hatched within the normal period, however, the adult stilts generally left the nest within a day, deserting the unhatched eggs. In the case of one nest the female returned to the nest and incubated for short periods over the next day before finally deserting even though the fourth egg was hatching. Between the short spells of incubation the parent defended the first three chicks and moved them further away from the nest site. Probably at the stage of desertion the stimulus to protect the young was greater than that to incubate the last egg. It appears,therefore, that the length of the incubation period is determined, at least in part, by the hatching of the first chick and that the stimulus to incubate diminishes very rapidly thereafter until any eggs remaining after a day or so are deserted. When the eggs hatch, the parents transfer their attention to the chicks and the eggs are left uncovered more often. This may have the effect of delaying hatching even longer.

Beer (1962) believes that the new stimulus provided by a hatched chick disrupts the incubation behaviour pattern probably causing a rapid drop in the amount of effective incubation.

Pied Stilt chicks begin calling inside the egg before they hatch as Lack (1968) reports for Limicoline chicks. He suggests this habit presumably has survival value, possibly in synchronising hatching. Such synchronisation of hatching, however, did not appear to occur in many stilt clutches, so that hatching was spread over a period of up to two days. After hatching the chicks were seldom left unattended although sessions of attentiveness for chicks were much shorter than those for eggs. Generally in the first few days one parent keeps close watch over the chicks and seldom feeds while the other parent moves away feeding. As the chicks get closer to the fledgling stage they are attended less closely.

Stilts possess an instinct for egg shell removal. As each chick hatches, portions of the egg are removed, beginning first with the egg cap and then the rest of the shell. It was not noted whether there is a limited period of time in which this occurs as has been noted for some species of gull (Gurr, pers.comm.). The incubating stilt picks the shell up in its beak and flys off with it, but seldom drops the shell while in flight. Rather the bird lands and places the shell either on the ground or in the water some 40-50 yards from the nest. On four occasions, however, egg shell was found within a few feet of the nest. It was not known if the shell belonged to the adjacent nest or was dropped by another bird, except on one occasion when the shell belonged to the last chick of the adjacent nest. Makkink (1936) reports this instinct present also in Avocets and observes that the manner of shell removal is variable. Tinbergen et al (1962) consider this instinct to be of survival value in reducing the likelihood of predation. This instinct is aimed primarily at aerial predators in general and in the case of the Pied Stilt at the Harrier Hawk in particular.

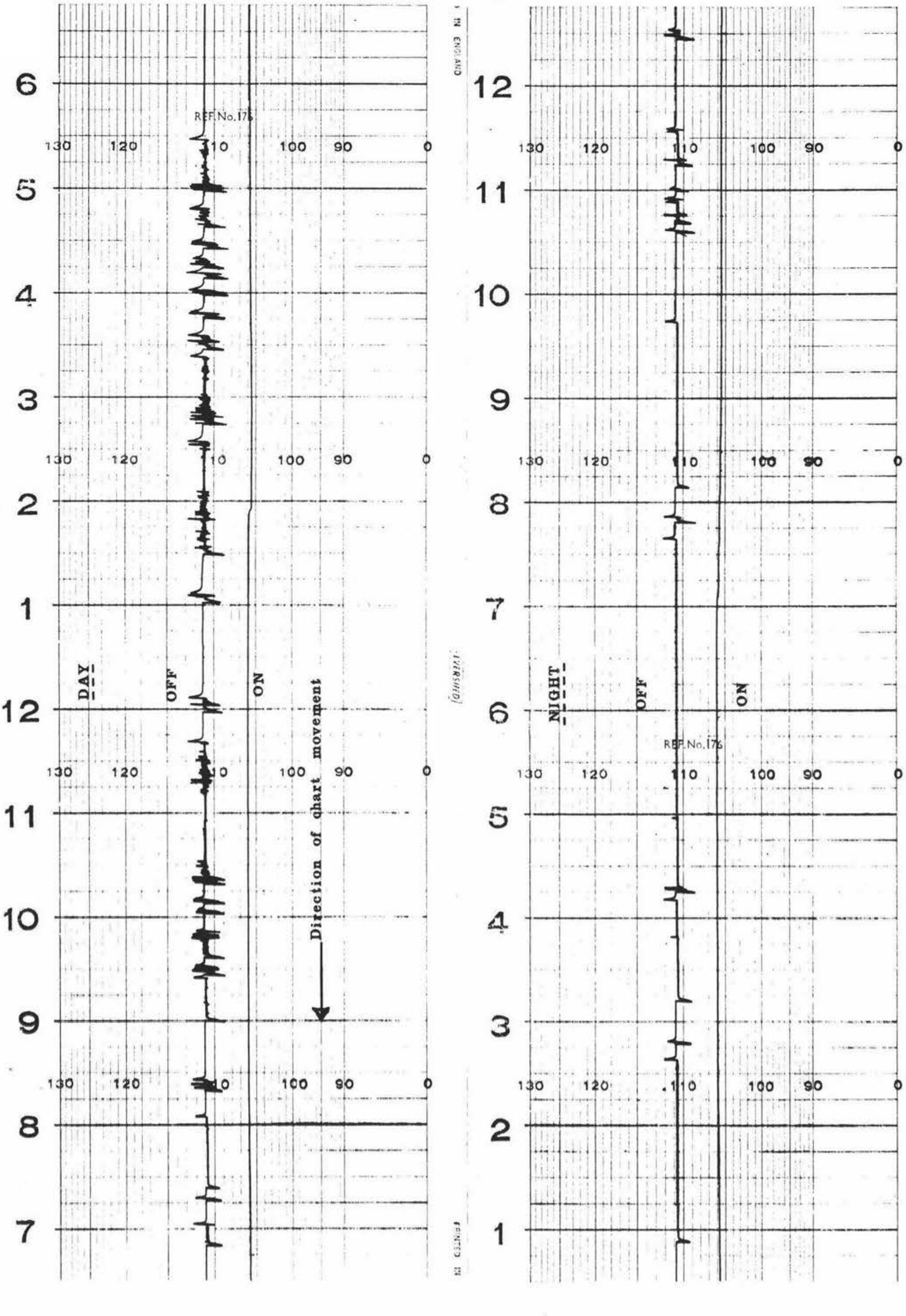
C. ATTENTIVENESS.

I have chosen in this section to follow the terminology of Skutch (1962) and Drent (1967) by using the terms "spells" and "breaks" for periods of uninterrupted incubation and periods off the nest during a session respectively.

i) Mechanical Recording.

Nest recordings were taken on two nests throughout their incubation periods and one nest for 10 days before it was deserted. The method used has been described in Chapter I and the equipment was placed in the nest during the period of laying. Typical records from the charts for both day and night periods are shown in Figure 5.3. Results were analysed in terms of average length of time spent on the nest and percentage of time the eggs were covered. From the automatic recording, however, it was not possible to distinguish the two sexes and therefore not possible to determine the actual length of sessions and recesses. This therefore had to be determined by direct observation. From fifty such observations on five nests, the mean time per incubation session was 75.9 minutes (range 8-184 minutes).

FIG 5.8 RECORDS OF INCUBATION SPELLS FOR DAY AND NIGHT PERIODS



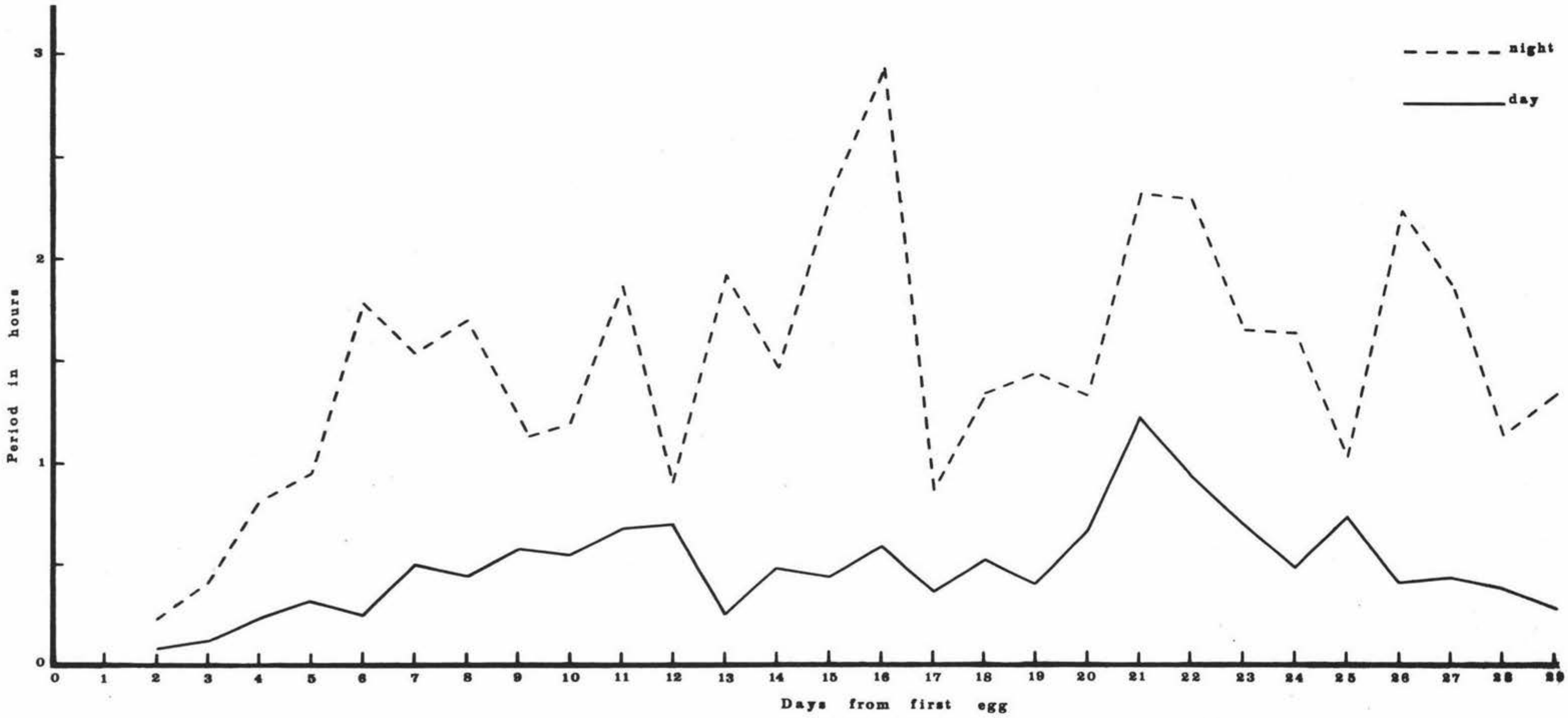
This is considerably less than the 120 minutes given by Soper (1967) for the Pied Stilt, though he does not saw how he obtained this figure. Beer (1961) also notes a considerable range in incubation for the Black-headed gull (13.7 - 169.5 minutes).

The stage in the incubation period of the above observations was not considered, but assuming they were randomly spread throughout the period the significance of the mean session should not be influenced. It seems, therefore, that the length of sessions are variable for the Pied Stilt although to some extent influenced by the stage of incubation as indicated in Figure 5.4 for three nests, tending to be longer through the middle of the incubation period. In addition there was no significant difference found between mean length of sessions for the two sexes. The Blacksmith Plover (Hall,1964) shows only a small range of 20-30 minutes per session. Bannerman (1961) reports for most members of the suborder Limicolae that incubation is shared equally by male and female.

During any given session the incubating bird may leave the nest for a few minutes to feed, build the nest or escape a predator. Beer (1961) in the case of the Black-headed gull attributes this to the bird not receiving satisfactory stimuli from the nest and eggs through the brood patches. The behaviour that results may be a displacement activity due to a conflict between the need to continue incubating and the desire to leave the nest. The incubating bird may return after a period ranging from 10 secondsto 5 minutes, but there was no way of telling from the chart whether it was the same

FIG 5.4 MEAN UNINTERRUPTED PERIOD ON THE NEST PER DAY THROUGHOUT BREEDING

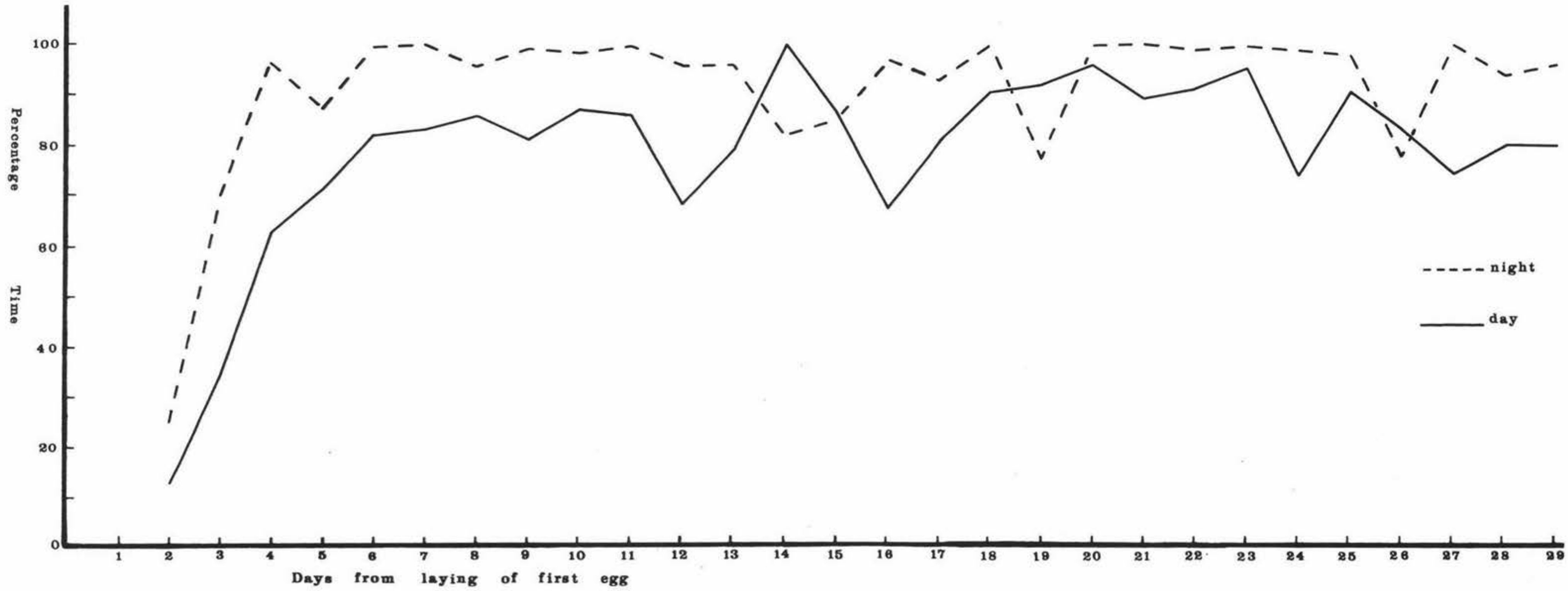
(for three nests)



bird. Change-overs at the nests generally took place within 30 seconds. Such breaks were shown in the chart records and thus Figure 5 .4 shows only spells and does not distinguish sessions as such. Figure 5.4 also shows the averages taken from three nests over the time intervals of official sunrise to sunset and official sunset to sunrise. I shall refer to these as day and night respectively. The time sequence is the number of days from the laying of the first egg. It will be seen that during the night the uninterrupted period on the nest is considerably greater than that for the daylight period as has also been indicated for the Blackbird (Gurr,1954). The figure also indicates the tendency for spells to increase as incubation progresses with a drop toward the end of incubation. Both these trends are reported as occurring in Herring Gulls (Drent,1967) and Black-headed Gulls (Beer,1961). The drop in length of spell toward end of incubation is best seen in the daylight period. Some of the fluctuations in the records were caused by failure of the equipment resulting in some days being represented by only one nest.

The percentage time the eggs were covered (Fig.5.5) rose rapidly to over 90% and remained fairly constant through the rest of the incubation period. Of note is the greater percentage time spent on the nest during the night, and also a slight drop off toward the end of incubation shown in the daytime percentage time on the nest. The total time the eggs are covered is of greater importance than how this is achieved, i.e. length of spell (Skutch,1962) and therefore less likely to be

FIG 5.5 MEAN PERCENTAGE TIME ON NEST THROUGHOUT INCUBATION
(for three nests)



influenced by individual differences. Thus the fact that some days are only represented by one nest in Figure 5.5 is less likely to influence the validity of the record.

The increase over the first few days of the time that eggs are covered, and the average spell, is in all probability an indication of the increasing tendency to incubate from the time the first egg is laid. Beer (1962) notes that in the Black-headed Gull the total amount of time spent sitting and the average duration of sitting spells are less in the one egg stage than in the two egg stage and less in both of these than in the incubation period. In this study the slower increase in mean spell is probably a better indication of this gradual increasing tendency to incubate. Baerends (1959) indicates that in the Herring Gull this tendency increases during the first two weeks, reaches a constant level, then drops again slightly in the last week. The importance of the total time for which the eggs are covered is indicated by the rapid rise to a high percentage of time the eggs are covered though the average uninterrupted period on the eggs remains relatively low. This dichotomy I suggest may be an evolutionary factor allowing gradual increase in incubating tendency, to allow relaying if necessary, but a rapid increase in incubating efficiency.

As indicated above the tendency to incubate is possibly related to the development of the gonads. Oestrogen output from gonads reaches maximum levels in the pre-laying period (Beer, 1963) and its subsequent decrease may prevent at some point the release of further ova. Thus if the clutch is destroyed within the first few days of incubation the stilt is still able to relay. (Two pairs which did relay had their first clutch destroyed within the first few days). Later in the incubation period if oestrogen levels have fallen too low relaying may not be possible. No pairs that lost a clutch late in the incubation period were known to relay and stilts are known to have only one brood per season.

The gradual decrease in mean spell toward the end of incubation is possibly related to the stimulus to end incubation. I suggest the stimulus to end incubation is the movement and chirping of chicks within the egg and their efforts to break the egg open. This could explain the behavioural changes observed in the final days of incubation and also the tendency to desert the remaining eggs a day or so after the hatching of the first chick. As mentioned above this change of behaviour is probably related to the changing stimulus to the brood patches.

ii) Nest Relief.

The length of incubation session appears to be determined by a decreasing tendency of the incubating bird to sit and a reciprocal build-up of the incubating tendency in the non-incubating bird as the session progresses. Beer (1963) considers in the Black-headed Gull that the incubating bird is responding to irritation in the brood patches or stiffness in muscles while the non-incubating is responding to a demand for stimulation from sitting on the eggs through the brood patches. Baerends (1959) notes that in Herring Gulls the tendency to sit drops gradually during the session. He also notes that a decisive factor in the termination of a session is the arrival of the mate. On at least one occasion in this study, however, the incubating female became very restless after one and a half hours incubating and left the nest every few minutes, calling and sideways throwing. Eventually she was relieved by the male who was standing 15-20 yards away. This may support Baerends (1959) observation that "the activation of the incubation instinct is lower in males than in females".

Generally the non-incubating bird is the one which initiates nest relief, though the incubating bird may do also. In the course of nest relief the non-incubating bird calls and walks towards the nest from some 10-15 yards away. Prior to this it may have called while flying in from some distance away. It walks directly to the nest without any ceremony apart from beginning to shake its feet when 3-4 yards away. As the relieving bird approaches the nest the incubating bird also begins calling. About the time the relieving bird begins shaking its feet the incubating bird rises and begins sideways throwing while continuing to call. Coming off the nest it may walk on average 2-3 yards away from the nest before moving away to feed. Similar nest relief ceremony has been noted in the Blacksmith Plover (Hall,1964). Once the nest is vacated the relieving stilt climbs onto the nest, shaking its feet vigorously, and rearranges the eggs before settling.

PLATE 33

Stilt settling on eggs (notice breast feathers ruffled to uncover brood patches).

PLATE 34

Stilt beginning sideways building after settling (notice piece of grass just dropped).

Generally two or three attempts are made before the bird settles finally. Probably this is to obtain the correct feedback stimuli from the eggs as noted by Beer (1961) in the Black-headed Gull. After settling the bird may continue sideways building for a few minutes. This agrees with Baerends' (1959) observation that rearranging of eggs, resettling and sideways building in the Herring Gull are more frequent at the beginning of the session when the incubation tendency is high. The stilts long legs are folded along the outside of the clutch rather than under it as in the Black-backed Gull (Fordham,1964). Plates 33 and 34 show the process of settling and sideways building by a relieving bird.

Rearrangement of eggs takes place at any time throughout the session, though it is more frequent at the start. The stilt stands on the nest, its feet straddling the clutch and rolls the egg toward itself with its beak (Plate 35). Arrangement of eggs in the nest is variable within and between nests. The two most commonly found patterns are shown in Figure 5.6.

Sideways building by the incubating bird may also occur at any time during a session. Thus frequently both parents are away from the nest, but never off the territory together. As indicated above, however, this tendency to leave the nest decreases as the incubation period progresses. The incubating bird also scrapes occasionally but most of the session is spent sitting quietly sleeping or preening while the non-incubating bird spends its time feeding, sleeping and guarding the

FIG 5.6 PATTERNS OF ARRANGEMENT OF EGGS WITHIN THE NEST DURING INCUBATION

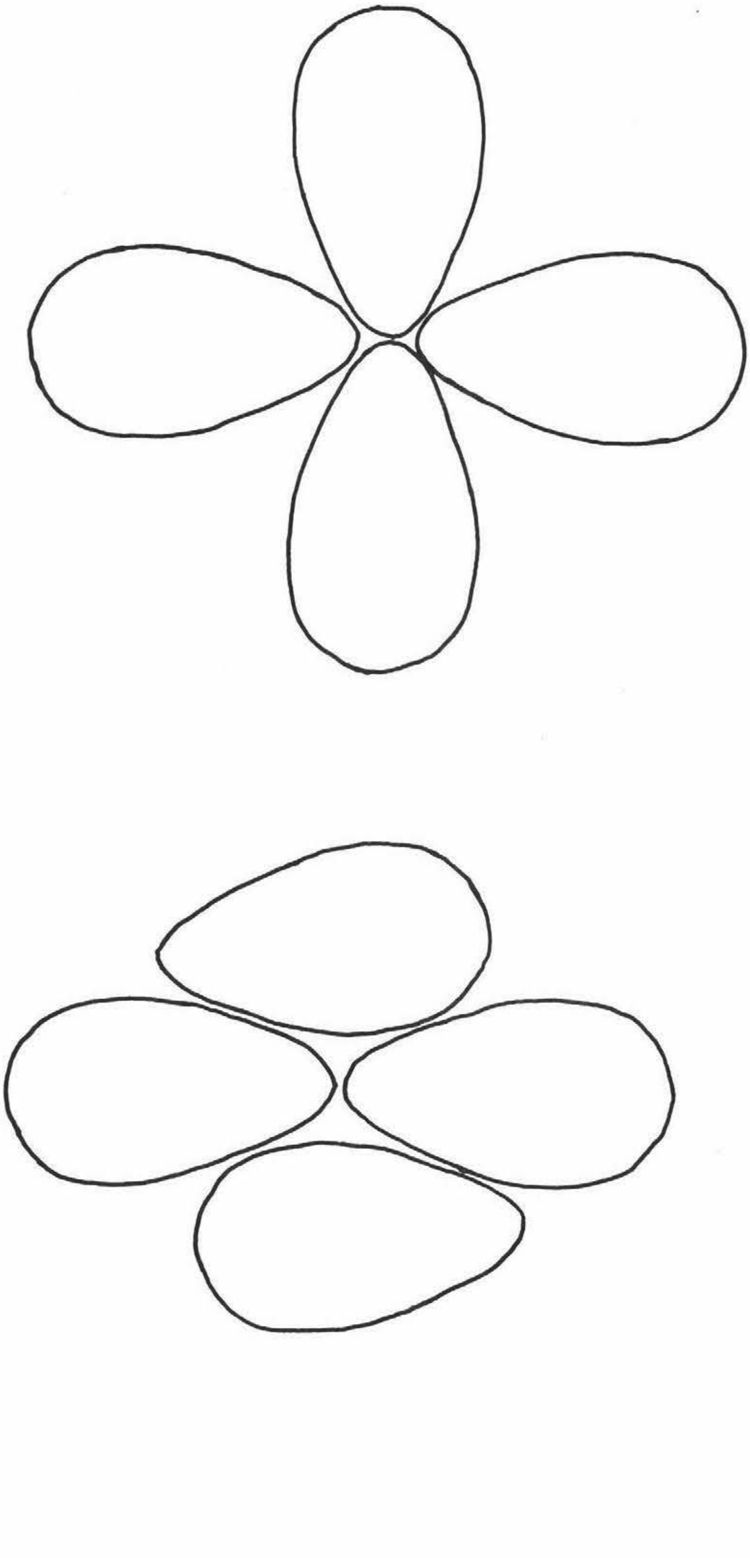


PLATE 35

Stilt turning eggs on the nest.

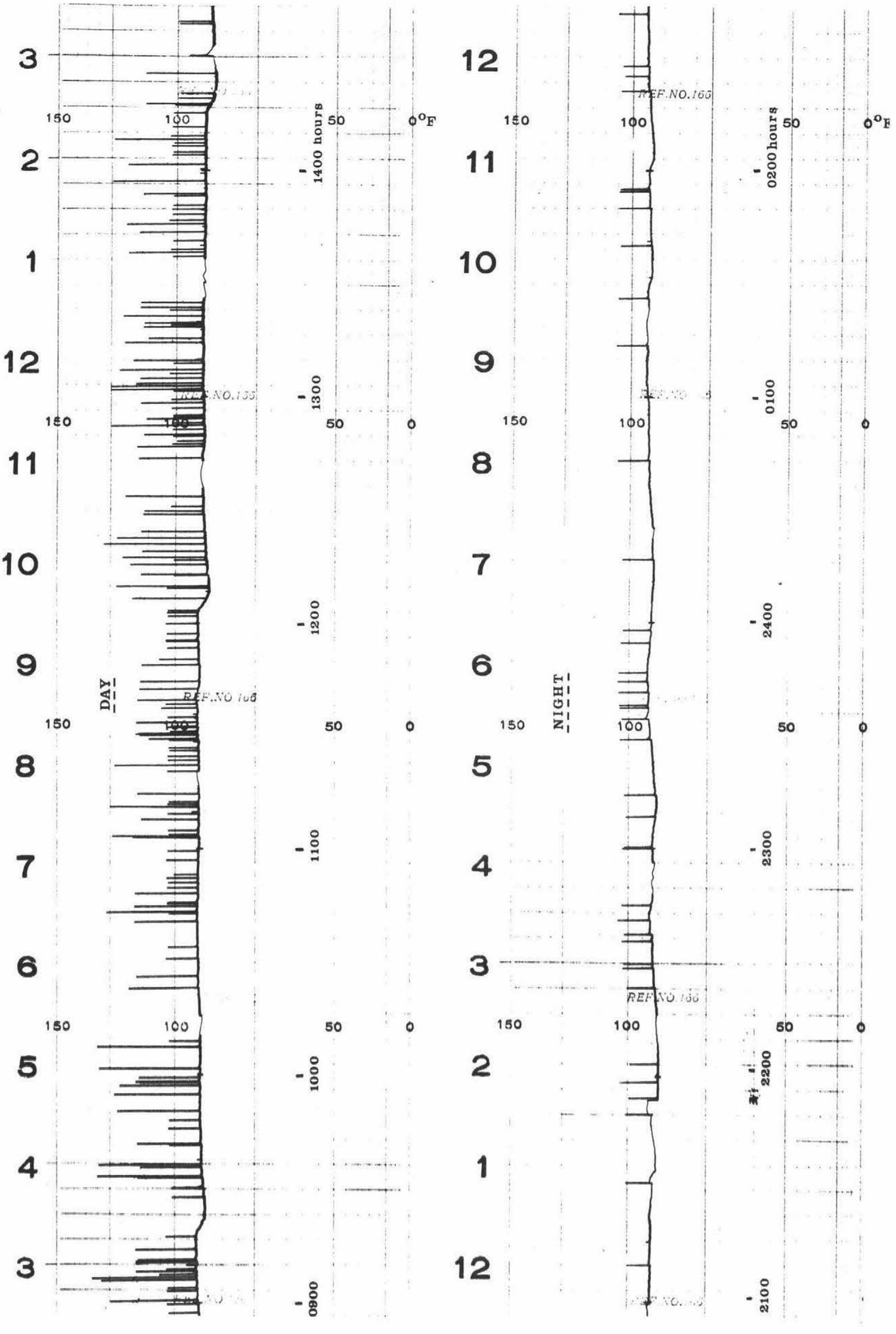
territory. All this movement is probably related to the type of stimulus being received through the incubation patches (Beer,1961).

Weather has some effect on incubation behaviour in the Pied Stilt which Beer (1961) does not note for the Black-headed Gull. Stilts tend to sit tighter during severe weather and spend more time off the nest during warm weather. Extreme heat, however, also causes them to sit tighter, possibly to prevent the egg overheating. (By "tighter" in this context I mean the stilt is less easily scared off and returns to the nest more readily). Both Skutch (1962) and Baerends (1959), however, note a general decrease in attentiveness with increase in temperature, even at high temperatures, especially in passerines. On the other hand, Drent (1967) reports a number of studies reporting close attention by parents during high temperature.

D. TEMPERATURE OF INCUBATION.

The temperature at which incubation takes place was measured continuously over a period of days by the method described in Chapter I. Recording of the temperature was automatic and Figure 5.7 shows the trace given for two periods approximately 12 hours apart. Because of difficulties with the apparatus only 36 hours of records were available for analysis. From these an average temperature of 92.2°F (range 85°F-97°F) was obtained from hourly readings. These records covered the last week of incubation. The mean body temperature of three stilts, measured immediately after shooting was found to be 105.3°F. Thus incubation was

FIG 5.7 INCUBATION TEMPERATURE RECORDS



maintained at a temperature approximately 13.1°F below body temperature. Eklund and Charlton (1959) carried out an experiment using a similar method of Adelie penguins *Pygoscelis adeliae* taken over a nine day period and the South Polar skua *Stercorarius skua maccormicki* taken over 57 hours at quarter hourly intervals. Their results can be seen summarised in Table 5.3 compared with those of the stilt. They consider that the range for the skua can be explained in terms of the greater number of incubation changes. The skua averages 2.36 changes every 24 hours. The stilt changes incubation considerably more often yet its range is much less. This, however, may be explained by the lower ambient temperature for the skua affecting the eggs much more rapidly. Eklund and Charlton (1959) indicate that there is a rise in the body temperature of the embryo after the tenth day of incubation and thereafter the heat production of the embryo increases rapidly. If a similar event takes place in stilts the temperature measured may not be the actual incubation temperature. Instead they may be a measure of the amount of heat applied to the egg at this stage of incubation. Air temperature at this time was 65-70°F, some 20-25°F lower than the incubation temperature.

CHAPTER VI

BREEDING SUCCESS AND CHICK BEHAVIOUR

A. EGG LOSSES.

Of 53 clutches only 26 (48%) reached the hatching stage and of the 193 eggs laid only 90 (46.6%) hatched. This number was, however, 89% of the eggs in those clutches which reached hatching. Thus 12 (11%) of the eggs from the 26 nests failed to hatch for some reason. Table 6.1 shows the fate of these eggs.

TABLE 6.1 FATE OF EGGS LOST FROM HATCHING CLUTCHES *

Fate	Number	Percentage
Chicks dead in egg	4	33
Taken by author	4	33
Taken by predator	2	18
Addled	1	8
Infertile	1	8
TOTAL :	12	100

* This table includes repeat clutches.

The fates of unhatched eggs from all nests appear in Table 6.2

TABLE 6.2 FATE OF EGGS LOST FROM ALL NESTS *

	Fate	Number	Percentage
A	Destroyed by flood	43	42
B	Deserted	21	20
C	Taken by predator	21	20
D	Destroyed by stock	8	8
E	Chicks dead in egg	4	4
F	Taken by author	4	4
G	Addled	1	1
H	Infertile	1	1
TOTAL :		103	100

* Includes repeat clutches.

Overall most losses occurred as a result of flooding, desertion and predation. Predation records were based on the sighting of a hawk taking eggs from two nests and hawk and pukeko tracks around other nests the day after those clutches were recorded intact. The hatching success and fate of eggs for each colony are shown in Tables 6.3 and 6.4

TABLE 6.3 HATCHING SUCCESS ON EACH COLONY *

	Number of nests	Total number eggs laid	Average clutch size	Number eggs hatched	%	Hatched per nest
Colony I	21	79	3.8	33	42	1.6
Colony II	25	94	3.8	57	61	2.3
Colony III	7	20	2.8	0	0	0
TOTAL :	53	193	3.6	90	46.6	1.7

* Includes incomplete clutches

TABLE 6.4 FATE OF EGGS IN EACH COLONY

Fates (as in Table 6.2)	A	B	C	D	E	F	G	H	Total
Colony I	-	15(33%)	17(37%)	8(17%)	2(4%)	3(7%)	1(2%)	-	46
Colony II	28(75%)	1(3%)	4(11%)		2(5%)	1(3%)		1(3%)	37
Colony III	15(75%)	5(25%)							
TOTAL :	43	21	21	8	4	4	1	1	103

It can be seen from both these tables that Colony II achieved the greatest hatching success of 63%, i.e. 2-3 eggs hatched per nest. Flooding mostly accounts for the poor hatching in Colony III and was responsible for spoiling 75% of the eggs that failed to hatch in Colony II. In Colony I most egg losses (70%) were due to desertion and predation.

Pullen (1967) found on a Pied Stilt colony of 20 nests with 77 eggs that 16 (21%) failed to hatch. Of these, 9 eggs (54%) were infertile or the chicks died in the egg, compared with 41% failing for similar reasons in the present study.

Two periods of heavy rain caused the flooding and egg losses in this study (see Chapter I). All the nests in Colony III were washed away twice, although the first nesting was not observed by the author. Egg losses as a result of predation were high, particularly in Colony I, where hawks often visited and were twice seen taking eggs from nests. Predation by hawks and pukekos has been previously reported on numerous occasions in Notornis (e.g. Foggerty,1968).

Desertion of the nests before hatching may have been influenced by the presence of the author. Certainly there was relatively more desertion on Colony I where most of the work was carried out.

The relative hatching success of clutches of different sizes was not considered as numbers of two and three egg clutches were too small.

B. CHICK LOSSES.

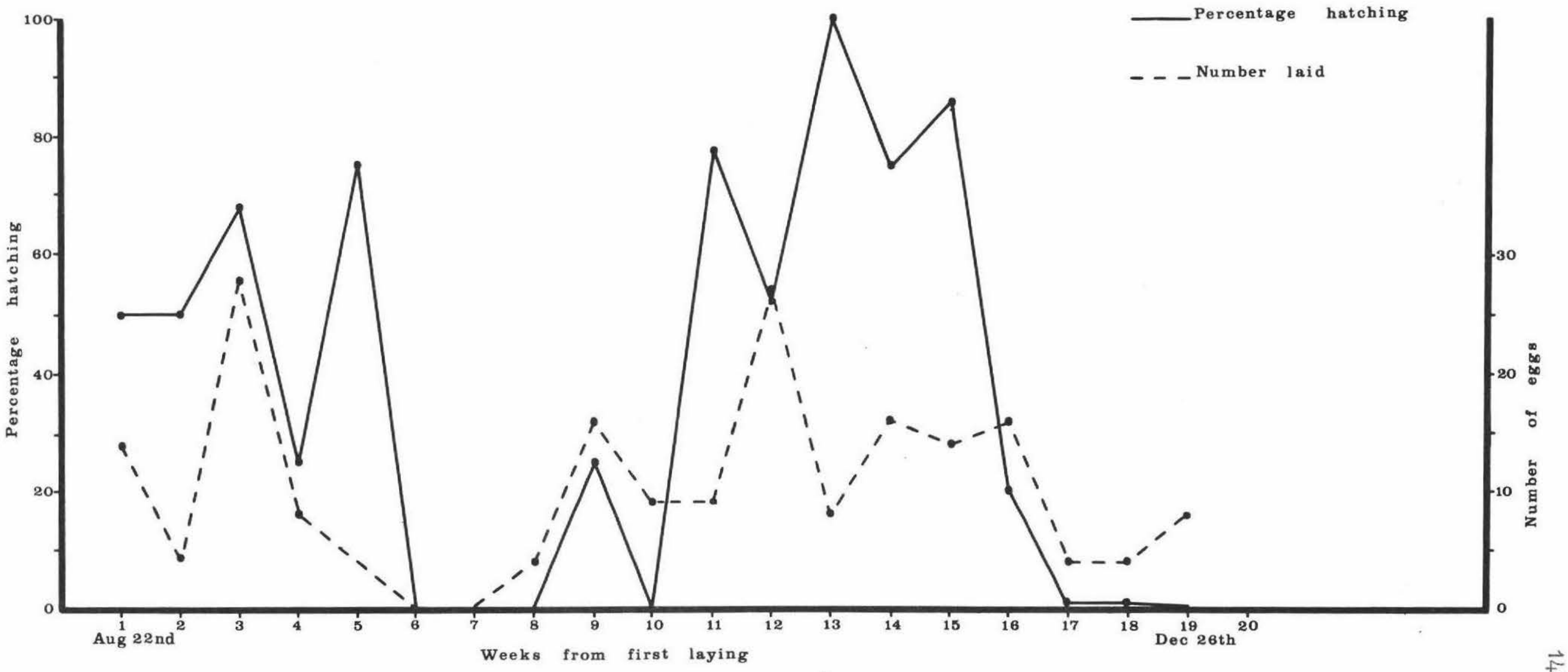
Chick losses were difficult to determine because the adults lead the chicks away from the territory almost as soon as they hatch. This makes individual clutches difficult to identify after hatching. In addition the vegetation around hatching time was long and the chicks difficult to see in it. When any attempt was made to actively search for them they "froze" into the vegetation in response to their parent's alarm call and finding them was almost impossible (see below). Finding chicks was a little easier on the river bed, though there was some success. Some pairs could be identified by their individual plumage patterns and chicks were marked with individual colour bands within two days of hatching. In at least six cases two chicks were lost within the first two or three days after hatching. The causes of loss were not known though in two cases neighbouring adults were seen to attack chicks during disputes. After one such attack one chick was found to be dead. At no stage were adults seen attacking fledglings or chicks more than 7-10 days' old. Other chicks were found dead close to nests within a day or so of hatching and in a number of cases parents were seen after a week or more with only one or two chicks. The most common number of juveniles observed in family parties was two (actual mean =2.4 young per family). If this figure is taken as the number of chicks per clutch surviving to the fledgling stage it suggests a maximum breeding success of 32% of the total number of eggs laid.

Nest record cards of the O.S.N.Z. were also analysed. Of 41 eggs in clutches that were observed through to fledgling 30 (73%) hatched, and of these 24 (80%) later died. For these nests therefore there was only a 15% breeding success. However these are only minimal figures and numbers hatching and surviving may actually be higher than those given. Discrepancy between the above two breeding success figures may be due to the fact that the O.S.N.Z. records are small and widespread, and the colonies studied may be in an optimum area for breeding. Pullen (1967) found that 27.3% of eggs laid (i.e. 34.4% of eggs hatching) reached the fledgling stage. The period from hatching to flying could not be determined but has been reported as being 27-42 days with an average of 32 days (Stokes *et al*, 1959; Stokes, 1961).

C. INFLUENCE OF LAYING DATE ON BREEDING SUCCESS.

In Figure 6.1 the 53 nests have been grouped according to laying date. The number of eggs laid each week is shown compared with the percentage of these which eventually hatched. While there is no marked correlation between the two or between percentage hatching and stage of season there is a tendency towards a higher hatching percentage later in the breeding season. If this is the peak laying period, as relative increase in number of eggs indicates, then the pattern observed is similar to that observed in other birds where the most successful birds are those laying during the peak laying period, e.g. the Red-billed Gull (Mills, 1967) and the Great Tit (Perrins,1965). Those laying

FIG 6.1 PERCENTAGE OF THOSE EGGS LAID EACH WEEK WHICH HATCHED SUCCESSFULLY



earlier or later are less successful.

No attempt was made to consider influence of clutch size on breeding success as there was insufficient data. Studies on other birds, e.g. Red-billed Gulls (Mills, 1967) indicate a correlation between optimum clutch size and breeding success.

D. CHICK BEHAVIOUR.

i) Anti-predator.

Pied Stilt are precocial and are born with very cryptically coloured plumage of blotched whitish-buff and brown (Plate 36). This enables the chick to blend in extremely well with its background. Within an hour or so of hatching the chick is led from the nest by one parent (in two cases this was known to be the male) while the other continues incubating. During any alarm situation in the first week after hatching, the chick "freezes" on the spot in response to the parent's alarm call. There it blends with its background and is difficult to see even when one knows where it is. When older, however, it will run a few yards before freezing amongst rocks or long vegetation. Families of chicks generally scatter and run in different directions before freezing. This makes it difficult to pinpoint chicks from a hide to find them later. Thus it was not possible to keep one clutch under observation long enough to determine fledgling period.

If picked up the chicks remain motionless in the hand, but after a minute or two begin to struggle. If the chicks are set down again they almost immediately resume a frozen position and continue to remain

PLATE 36

Chick on nest just hatched showing cryptic colouration.

motionless. However if handled for a few minutes and then released while still struggling a chick quickly runs some distance before freezing on the ground again. When disturbed at the early fledgling stage they are capable of flying only short distances before running and hiding.

ii) Aggressiveness.

The only aggressiveness observed amongst young Pied Stilts was just after fledging. Fledglings were seen to attack and chase off adult Pied Stilts which landed in what appeared to be the family feeding area during a disturbance. This was observed while the author was walking through the colony and the parents of the fledglings were flying overhead attacking and performing distraction displays. Thus it would appear that some sort of territorial instinct is present in the young birds. It is probable that this has survival value in defence of a feeding range or territory while the adults are absent. Evans (1968) reports intraspecific aggressiveness present in two and three day old domestic chicks, but this was not observed in the stilt chicks.

iii) Feeding.

Pied Stilt chicks appeared to be able to feed themselves within a day of hatching. Lack (1968) reports that this is common among Recurvirostridae. At no stage in this study were parents seen feeding chicks nor was any food begging behaviour observed in the chicks.

SUMMARY

(a) General Biology

Measurements of adult birds indicate that although there is slight separation of male and female in some characters these are not significant enough to be used as sex distinguishing characters. Both body and gonad weight vary throughout the year with body weight highest in winter and gonad weight highest just prior to and during breeding. General development of gonads coincides with formation of territories and nesting.

Plumage patterns and their changes are discussed with the implications these have as to the status of the Black and Pied Stilts. I suggest that both should be included in the same sub-species on the basis of measurement and plumage patterns and the fact that they interbreed and produce viable offspring.

Stilts appear to feed almost exclusively on fresh water insects and especially fresh water molluscs.

Endoparasites consisting of trematodes and cestodes were found in almost 100% of the sample. Ectoparasites of a species of Mallophaga not previously recorded from this host were found on a small proportion of the sample.

(b) Non-breeding Behaviour.

Pied Stilts are widely dispersed throughout New Zealand. However because they feed exclusively on aquatic animals they are never found far from permanent water. They are found at estuaries, along rivers and on swampy farmland throughout the year. A slight trend toward migration from south to north in the breeding season was detected. Pied Stilts remain in family parties or pairs for much of the non-breeding season. Their general maintenance behaviour is described.

In general Pied Stilts are fairly tolerant of most other species of birds in the non-breeding season. During this time aggression is primarily associated with interactions between feeding conspecifics. The various agonistic postures are described.

(c) Breeding Behaviour.

Indications are that Pied Stilts do not breed until two years' old. Birds arrive on the colony already paired and it is possible that the pair bond is permanent. Nesting territories are 90-120 square yards on average, with an average distance between nests of 10 yards. Behaviour associated with defence of territory is discussed. Copulation was observed over a period of four months and began two months before the first egg was laid on 20th August. Nest site and construction varies depending on the habitat of the colony, those on the swamp being of more solid construction than those on the river bed. The elements of nest building described are similar to those of other waders. Defence of nest and young takes the form of distraction displays similar to that exhibited by many other wading birds.

Egg laying continued until the end of December and was spread over a period of 17 weeks. The spread of laying differed on the two colonies being 14 weeks and 9 weeks for Colonies I and II respectively. Laying on

Colony II began on 20th October. Successive eggs in each clutch are laid approximately 24 hours apart, generally during the night. The mean clutch size is 3.91 with a range of 2-4 eggs. Egg measurements show a decrease in size of the fourth egg and a significant difference (p70.95) in size between the first and third eggs. Relaying only occurred where the first clutch was destroyed within the first few days of incubation. Incubation period is between 22-28 days with a mean of 25 days. Incubation is shared by both male and female. No significant difference between the time each spends incubating was discerned. The average length of spell on the nest is approximately 75 minutes. The nest relief behaviour is described.

The temperature at which incubation takes place was 92.2°F which is approximately 13°F below body temperature. In this study there was only an estimated 32% breeding success as against 46.6% hatching success. Flooding is the greatest factor responsible for destruction of eggs, followed by desertion and predation. It was not possible to determine causes for chick losses. Breeding success appears to be influenced by laying date only so far as the most successful birds are those laying during the peak laying period. Chick behaviour is also discussed.

ACKNOWLEDGEMENTS

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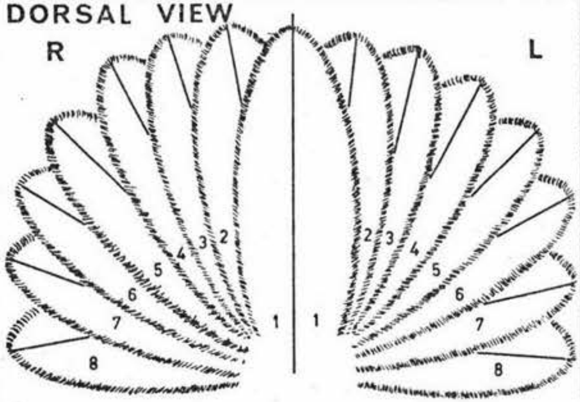
Thanks are due to Mrs F.Rabone for typing the manuscript.

Finally I wish to thank my wife without whose patience and encouragement this study would not have been possible.

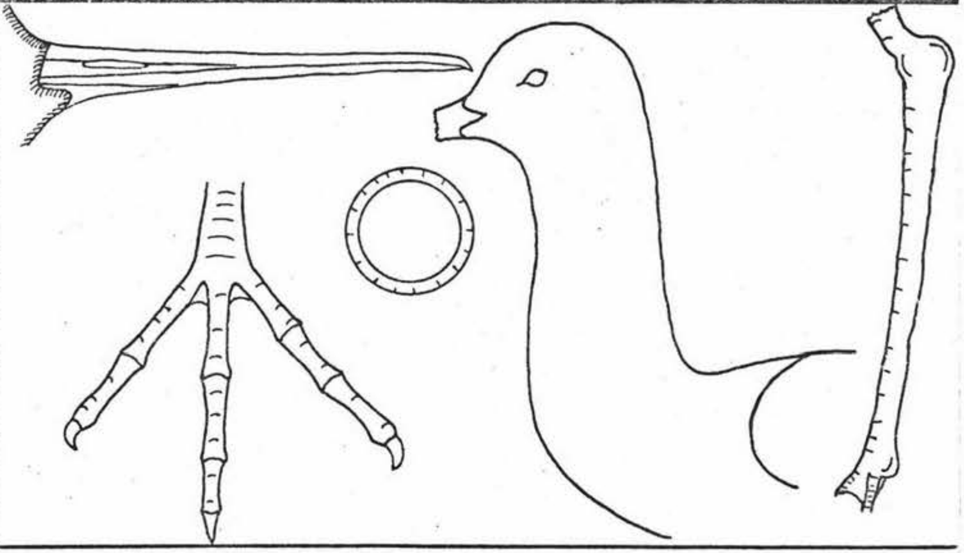
APPENDIX 1

LOCALITY		
BEAK	L.T.	L.Ex.C
L.L.M.	W.	D.
WING 1st P.		
TARSUS	TOE	TOENAIL
TAIL	WEIGHT gms	
GAPE COLOUR		

DORSAL VIEW



COLLECTOR	AGE	SEX	DATE



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GENERAL REMARKS

APPENDIX II

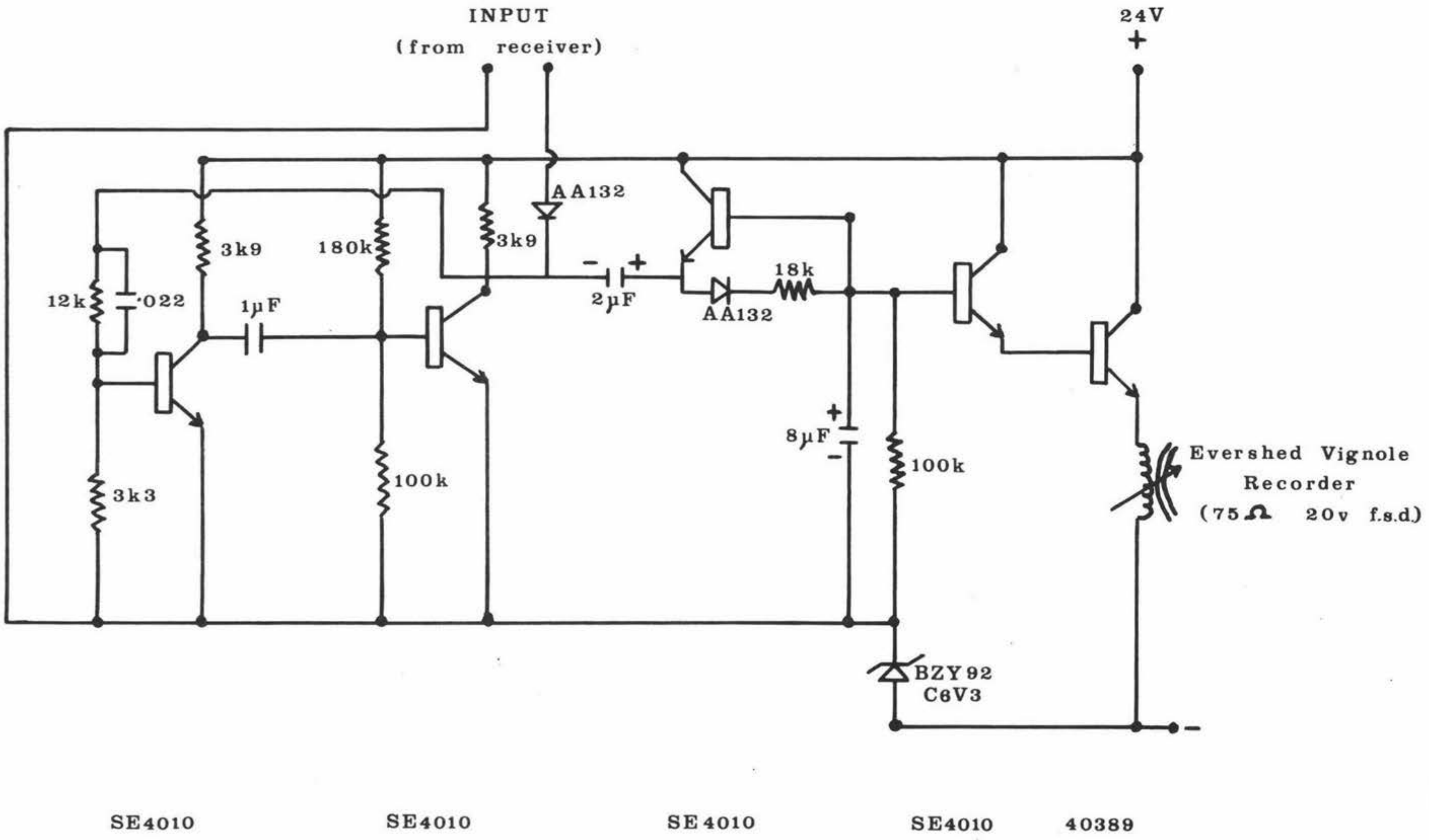
TECHNICAL DATA

The temperature recording circuit consisted of a pulse shaping network fed from a high impedance source. A shaped pulse chain is fed into a simple frequency to voltage converter, a compound emitter follower and hence to the recorder. Power requirements were minimal (less than 4 watts), but the supply was split so that full scale deflection could be achieved. Calibration was from 0 to 150°F.

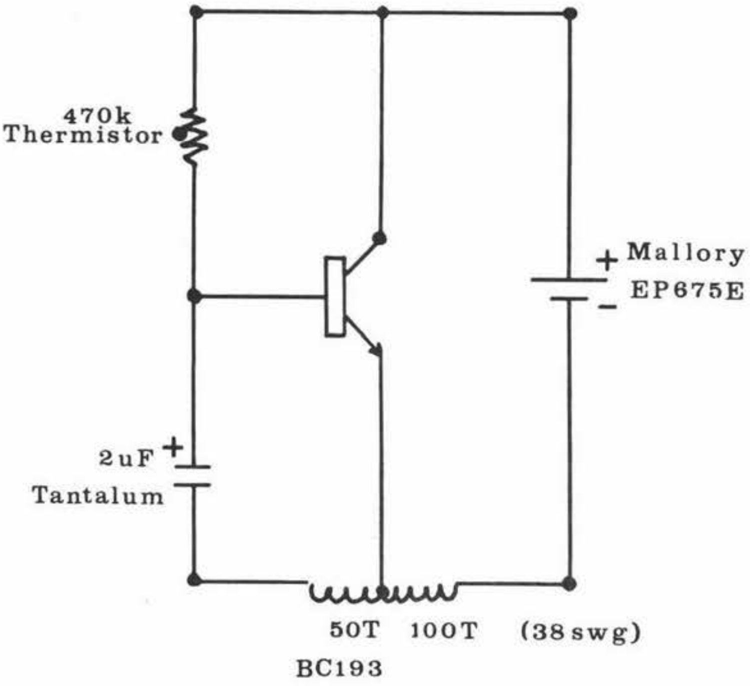
The transmitter was a conventional blocking oscillator, the pulse rate of which was thermistor controlled to give an output rate proportional to temperature. To maintain transmission over a considerable period two batteries were connected in parallel. The size of the device was approximately 7/8" x 1/2" diameter. The range of transmission was to 1-2 meters under laboratory conditions but in the field the range was reduced to 30 cms.

The receiver was a commercial model with a modified aerial and the output taken across the volume control.

TEMPERATURE RECORDING CIRCUIT



THERMISTOR CIRCUIT



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