THE SOCIAL ORGANIZATION OF THE PUKEKO
Porphyrio porphyrio melanotus
Temminck, 1820

A thesis presented in partial fulfilment
of the requirements for the degree
of Doctor of Philosophy in Zoology
at Massey University

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ABSTRACT

The social organization and behaviour of the pukeko, *Porphyrio porphyrio melanotus*, is described for two different habitats. The study shows that pukeko breed in pairs or communal groups with the proportion of these varying according to habitat. All breeding pairs and groups defend territories, but the degree of maintenance varies. In some defence occurs at all times of the year; of the remainder and outside the breeding season, some restrict defence to a core area while with the rest defence ceases. Outside the breeding season also, part of the population form flocks. A hierarchy exists among members of groups and flocks. Furthermore, a hierarchy is found between pukeko of adjacent territories as is demonstrated by differential boundary positions. In group territories, all adults participate in breeding and often more than one female lays in the same nest. Breeding success varies, in this study, pairs are more successful than groups

CONTENTS

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SUMMARY

1. The year-round social organization of the pukeko, Porphyrio porphyrio melanotus, was investigated in two areas of differing habitat; a dune lake at Pukepuke and a small stream valley at Linton. Special emphasis was given to assessing the interaction of social hierarchy and territory, and the role of communal breeding. The study was carried out between March 1970 and April 1973.

2. Pukeko were sexed and aged from body measurements (Williams and Miers, 1958) which varied with reproductive state but were adequate when repeated several times during the year. Nares-to-tip was the most reliable measurement with males exceeding 30 mm. A frontal shield less than 23 mm wide coupled with an olive colouration in the iris indicated a bird less than one year old.

3. The overall dispersion of pukeko was territorial during breeding but varied from territorial to flocking in autumn and winter. Most (79%) of territories were held by communal groups of 3-6 birds, the remainder (n = 7) were held by pairs, with six of these at Linton. Sex ratios within territories were equal except in those formed by flock birds: here males predominated. Flocks had a preponderance of males (63-64%) and juveniles (63-69%).

4. Pukeko are mainly herbivorous although quantities of animal food were taken in the breeding season and fed mainly to chicks. Most territories contained both pasture and swamp. Pasture provided most of the food outside the breeding season but when nesting or caring for young chicks, pukeko confined their activities to the swamp where they fed mainly on raupo.

5. Pukeko that failed to join a territory dispersed radially as did chicks at Linton that were expelled

from the pair territories prior to nesting. Most chicks in group territories remained in their natal territories. Dispersal accelerated during the shooting season when small numbers were shot.

6. The behavioural repertoire of the pukeko is described and analysed quantitatively. Agonistic displays centred around the head or tail. In the most aggressive displays, the head was held in a pecking position with the red beak pointed at the opponent, but with increasing conflict between escape and aggression, the beak was lowered towards the ground and finally pointed at it. Alternatively, the beak was turned away from the opponent. The red frontal shield is believed to accentuate the beak as the aggressive releaser. Submissive displays focused on the white under-tail which was directed at the opponent. The wings were raised to expose a greater amount of white in the more submissive displays, and infrequently sexual displays were used for signalling submission.

7. Social hierarchies were investigated in all territories and within the flocks, with artificial feeding used to increase the number of interactions. A linear hierarchy existed between all members of all territories and flocks. Status was dependent on sex, males dominating females; on age, adults dominating juveniles; and in the flock alone, on prior residence. Where territories broke down outside the breeding season, the same birds were still dominant over pukeko of similar age and sex in their previous territorial ranges.

8. All breeding groups established defended territories, but maintenance varied outside the breeding season. In some, defence continued unchanged, in others defence became restricted to a core area, while in the remainder, it broke down completely. All members of the territories helped in defence although the greater proportion (75%) was done by males. Territory size varied from 0.5 to 3.2 hectares and appeared to be

unrelated to the number of birds in the territory.

9. Territorial boundaries were constant between group territories but varied markedly between pairs, apparently as a result of fewer birds being available for defence during breeding. The length of boundary requiring defence was short in pair territories. A hierarchy between members of adjacent territories was demonstrated by the existence of different boundary positions for different opposing pairs although the presence of more than two birds at the boundary complicated results. Inter-territorial status correlated with intra-territorial status.

10. Courtship and copulations occurred between all adult members of a territory regardless of sex although male-female copulations were the most common. Participation in copulation by more than two birds was common and is believed to help synchronize sexual cycles allowing several females to lay in the same nest at the same time. No relationship between frequency of copulation and status was obvious although low ranking yearlings were excluded.

11. Clutch size correlated directly with the number of birds in a territory with an overall mean of 6.0. Dominant and older females tended to lay more eggs and also contributed more to the more successful earlier clutches. Most territories were double brooded.

12. All adults incubated with frequency of incubation dependent on status: the dominant male and female each tended to spend more time incubating than lower ranked birds did. Incubation time varied from 23 to 29 days as hatching was asynchronous. All full-grown birds cared for the chicks with the proportion of care dependent on status: the dominant male did a greater amount than the dominant female who in turn did more than the lower ranking adults. Where yearlings were present, these cared for chicks more than any other bird,

while in pair territories, early chicks fed later ones.

13. Hatching success varied but was higher (not significantly) in groups. Overall reproductive success was significantly higher in pair territories than in group territories and there was a significant difference between the two study areas. Most groups were found at Pukepuke where low summer water levels dried the territories, thereby reducing the amount of animal food for the chicks and so leading to the loss of almost all the young of second clutches. In contrast, water levels at Linton were constant and survival was high in all broods. Breeding success of individual territories appeared to be related to the amount of cover, and to water depth.

1. INTRODUCTION

1.1 General

The pukeko, Porphyrio porphyrio melanotus (Temminck) ranging throughout eastern Australia, Tasmania and New Zealand, is one of 22 sub-species of a species with world-wide distribution (Peters, 1934; OSNZ, 1970). Its arrival in New Zealand from Australia is estimated at the late Pleistocene (Fleming, 1961). The pukeko inhabits mainly swamps and marshes, as is typical for most members of the Rallidae and, possibly because observation in such areas is difficult, few detailed studies have been made of any rails, except for the more aquatic species such as coots (Fulica spp.).

Early New Zealand authors (Buller, 1882; McLean, 1902; and see Carroll, 1969) recorded the abundance of pukeko and referred to it as an agricultural pest. Pukeko have been blamed for carrying Salmonella, destroying root (potato, kumara, swede) and grain crops, fouling pasture and water troughs, and raiding waterfowl nests to eat eggs and kill ducklings (Oliver, 1930, 1955; Bell, 1955; McKenzie, 1967; Carroll, 1969; and many farmers, pers. comm.). Pukeko predation on eggs and young of pied stilt, Himantopus leucocephalus, has also been recorded (Pullen, 1967; Fogarty, 1968; McConkey, 1972).

Carroll (1969) records fluctuations in numbers of pukeko and its history as a game bird. The pukeko ranks third on the game list in numbers shot per season following mallard, Anas platyrhynchos, and grey duck, Anas superciliosa (T.A. Caithness, pers. comm.). It would probably be taken in greater numbers were it not for imposed bag limits.

Because of the pukeko's reputation as an agricultural pest, Muggeridge and Cottier (1931) and Carroll (1966) investigated feeding habits and found the pukeko to be mainly herbivorous. On the other hand, there are numerous reports (e.g. McLean, 1902; Oliver, 1955; McKenzie, 1967) of pukeko taking animal food, especially during the breeding season. McLean (1902) and Guthrie-Smith (1927) gave accounts of the general biology of the pukeko, and these have been added to by Tunnicliffe (1965). Tunnicliffe (in preparation) is concluding a more detailed study of behaviour and ecology but this study has not followed the social organization throughout the year mainly because of the size of the study area and the sheer number of birds present.

McLean (1902), Guthrie-Smith (1927) and Tunnicliffe (1965) record a long breeding season (August to March) and Oliver (1955) reports eggs as late as June. These authors also described co-operative breeding where several females laid in the same nest and Tunnicliffe (1965), Stidolph (1971) and P. Morrison (pers. comm.) record females laying in immediately adjacent multiple nests. Feeding of younger chicks by older ones has been observed in the wild (Tunnicliffe, 1965) and in captivity (Guthrie-Smith, 1927).

Pukeko are territorial only during the breeding season (Tunnicliffe, 1965), forming large flocks of up to 250 birds in autumn and winter (see also Carroll, 1969). At Lake Ellesmere all breeding territories held three or more birds (Tunnicliffe, pers. comm.) but many reports (e.g. McLean, 1902; Andrew, 1967) record pairs although it is suspected that many of these may have been groups. Tunnicliffe (1965) reported 37 monogamous nests based on a clutch of less than eight with eggs of uniform colour, but gave no figures for the number of birds in the territory.

A single male was held to be involved in co-partnership nests (Guthrie-Smith, 1927; Tunnicliffe, 1965), but later research with banded birds showed that more than one male may have been involved and that the overall sex ratio favoured males (Tunnicliffe, pers. comm.). Both authors suggested that most of the incubation was done by the male, at least during the day, and this was accepted by Oliver (1930, 1955) and Falla, Sibson and Turbott (1966), but McLean (1902) considered that females did most of the incubation.

1.2 Aims

Previous workers have been concerned mainly with the feeding and breeding biology of pukeko and very little examination has been made of year-round social organization, or its relation to ecological aspects such as habitat and reproductive output. This study was intended to fill such gaps.

In the voluminous literature on avian social organization, most studies have dealt with passerines and colonial seabirds, have concentrated on breeding organization, and also on a single concept - territory. A number of recent papers (e.g. Emlen, 1957; Pitelka, 1959) have challenged Noble's (1939) classical definition of territory of 'any defended area' which was accepted by Hinde (1956). More recent criticism has been applied to the validity of assessing territory as an isolated social phenomenon and a link between social hierarchy and territory has been proposed (e.g. Davis, 1958, 1959; Brown, 1963; Willis, 1967).

Davis (1959), working on house mice, Mus musculus, regarded social hierarchy and territory as two extremes of a continuum of social organization. The position along this continuum depended on population density, tending towards territoriality at low densities. This was upheld by Kinsey (1971) with wood rats, Neotoma fuscipes. A number of other studies (Sabine, 1959; Kikkawa, 1961; Willis, 1967; McBride, Parker and Foenander, 1969) have demonstrated an interaction between territory and social hierarchy where rank was dependent on distance from nesting territory.

Studies of mammals (e.g. Etkin, 1964; Hornocker, 1969; and Leyhausen, 1971) have similarly linked home range, territory and social hierarchy. More recent studies (Brereton, 1966, 1971; Leyhausen, 1971) have brought together these previously isolated concepts of social organization. Thus, one of the main objects of the present study was to investigate the inter-relation, particularly of territory and social hierarchy, within the social organization of pukeko throughout the year.

Animal social organization has been widely linked with different selective advantages; as by Wynne-Edwards (1962) with regulation of population size in relation to resources: Brereton (1966, 1970, 1971) with habitat type and food;

Brown (1963, 1969) and Brown and Orians (1970) with distribution of resources; and Crook (1965) with resource distribution and predation. In an attempt to evaluate these separate theories, ecological aspects of pukeko social organization were investigated at two different study areas in the Manawatu. The larger of these was a coastal dune lake at Pukepuke and the smaller was an inland stream gully and surrounding areas at Linton.

Pukeko have been previously reported as both monogamous and co-operative breeders, and an attempt was made to ascertain the ecological factors that could have produced these differences. In the small amount of previous work on communally breeding species, authors have either shown a selective advantage in reproduction (e.g. Parry, 1968; Ridpath, 1972; although in the latter case, kin selection was invoked; Ridpath and Maynard-Smith, 1972), or linked the communal habit with population regulation (Carrick, 1963).

To establish the gross behavioural strategies of the pukeko, an attempt was made to describe the behavioural repertoire and to analyse quantitatively all agonistic and courtship postures.

It was hoped that information gained might assist in the future management of the pukeko both as a game bird and as a reputed agricultural pest, and also help in the management of related takahe, *Notornis mantelli*. Observations were made on captive takahe at Mt Bruce Wildlife Reserve to further this link.

Feeding (at present being studied by R.A. Fordham and also covered by Carroll, 1966), maintenance activities, growth and development of young, moult and anatomy (covered by Tunnicliffe, in preparation) were not investigated further. Incidental observations, however, were made where necessary to interpret other results better.

1.3 Description of Study Areas

1.3.1

Pukepuke Lagoon is a Game Management Reserve under the control of the Wildlife Branch, Department of Internal Affairs, with total area of swamp and open water of approximately 90 hectares. Observations were concentrated in the south-eastern corner of the reserve and the adjacent pasture.

The lagoon vegetation forms a hydrosere of four basic communities:

(i) Floating plants - *Lemna minor*, *Azolla rubra*, *Wolffia arrhiza* and *Spirodella oligorrhiza*.

(ii) Submerged plants - *Chara* spp., *Potamogeton crispus* and *Ranunculus fluitans*.

(iii) Seasonally emergent rooted plants - *Veronica anagalis-aquatica*, *Ranunculus scleratus*, *Nasturtium officinale* agg., *Polygonum decipiens* and *Polygonum hydropiper*.

(iv) Tall emergent macrophytes:

- (a) raupo, *Typha orientalis* and *Carex secta*
- (b) flax, *Phormium tenax* and cabbage tree, *Cordyline australis*.

All these communities were present in the area studied although cabbage trees were sparse and *Mariscus ustulatus* was common in the flax zone.

Adjacent paddocks were entirely different. The 'Hay Paddock', (Fig. 39) (so named because it was shut for hay in the 1970-71 summer) had a pasture of *Trifolium fragiferum*, *Agrostis tenuis*, *Juncus articulatus*, *Juncus bufonius*, *Bromus mollis* and other grasses. In the 'Rough Paddock' (Fig. 39) which was poorly drained and had never been ploughed and sown, the main pasture species were *Festuca gigantea*, *Festuca arundinacea*, *Trifolium fragiferum*, *Juncus articulatus*, *Agrostis* spp., *Lotus pedunculatus*, *Holcus lanatus*. As well as these, large areas of *Mariscus*, *Cortaderia toetoe* and

Juncus pallidus were present. *Cordyline* and flax were also common.

Pukepuke Lagoon is fed by a catchment of approximately 2600 hectares and although the outlet is controlled, water levels fluctuate widely (Fig. 2a). In the summer of 1969-70, immediately prior to the start of this study, the lagoon dried up completely. After refilling in April-may 1970, the lagoon became choked with dense growth of the 'seasonally emergent plants' and *Chara*. Another drought in the summer of 1972-73 almost dried the lagoon, producing dense growth of *Bidens pilosa* among the raupo. Cattle grazed in the Reserve until November 1970, cropping much of the 'seasonally emergent vegetation' and raupo. Sambar deer, *Cervus unicolor*, also present in the Reserve, were rarely seen and had a negligible effect on the vegetation of the area under observation. In March 1971 the New Pond (Fig. 40) was constructed and one year later the Cloverleaf Ponds (Fig. 41) were excavated. Minor changes to the leading edge of the raupo were made by duck shooters before each season. More extensive cutting by duck shooters and the Wildlife Branch occurred early in 1973.

1.3.2

The stream gully at Linton (Fig. 38) had basically the same floating vegetation as Pukepuke with emergent *Typha*, *Carex* and *Mariscus*, forming both pure and mixed stands. There was only one small area of open water. The surrounding paddocks supported a wetland pasture of *Trifolium repens*, *Plantago lanceolata*, *Lolium* spp., *Festuca* spp., *Cynosurus cristatus*, *Holcus lanatus* and *Juncus articulatus*. Water levels were almost constant as the area was fed by a bore at the top of the valley.

The vegetation of adjacent areas at Linton (Fig. 38) was varied: Linton 3 had almost pure *Typha* with a small area of open water; Linton 4 had mainly *Festuca* spp. and *Carex* and Linton 5 pure *Carex*. Linton 3 had a relatively constant water level; Linton 4 and 5 were subjected to periodic flooding in winter but, except for the drain in Linton 4, dried out completely in summer.

1.4 Methods and Materials

Pukeko were observed for a total of 1160 hours between April 1970 and May 1973 (Appendix I) from three permanent hides with the aid of 7 x 35 and 10 x 50 binoculars and a 15-60 x zoom telescope. Most of the interactions observed occurred within 150 metres of the hides, which were elevated on 4.5 m legs. Supplementary observations were made from vehicles, portable hides and, less frequently, other permanent hides at Pukepuke. Watches were typically kept for three to five hours but shorter and longer watches were also made, the longer watches being usually employed for photography. Initially, watches were made at all times of the day but, except when observing nests, were later restricted to periods of peak activity, from dawn to mid-morning and from mid-afternoon to dark. To facilitate observation, small areas of raupo were cleared in the immediate vicinity of the hides, but in many of these regrowth occurred during the breeding season.

All activity was recorded on a portable tape recorder and later transposed. Initially all behaviour was described and frequently recorded by sketches. Direct observations were supplemented with approximately 1850 frames of 35 mm film (using a Pentax S1 and Pentax with motor drive and 135 and 500 mm telephoto lenses), 1200 feet of 8 mm colour movie (using a Bolex and Cannon with zoom lens) and 500 feet of black and white 16 mm (using a Bolex). The majority of 8 mm film was exposed during the operation of an automatic nest recorder (Craig & Craig - in press - Appendix II). A Nagra IV portable tape recorder was used in an attempt to record calls.

Birds were trapped in standard funnel-entrance traps baited with maize and barley. A rocket net was used once in May 1972. All trapped birds were individually marked with numbered metal leg bands, individual combinations of coloured leg bands and also numbered and lettered patagial wing tags (c.f. Anderson - 1961 -) made of heavyweight PVC with plastic marking ink. All birds whenever caught were measured and weighed.

Artificial feeding was used. From January to September, a double pile of maize and barley was put in the hay paddock at Pukepuke to increase the number of interactions and so determine a hierarchy. The food was put in a different area at each watch and to assist discovery of the food, a large metal disc was displayed. The piles were 30-50 cm apart and contained sufficient food for intermittent feeding by one bird for 1-2 hours. To facilitate observation of boundary behaviour, food was evenly spread up to ten metres on either side of the suspected boundary position. These boundaries were pegged at one metre intervals by numbered pegs. Young chicks were kept near cover: so small patches of food were occasionally put in an easily observed part of the territory to entice the families out and allow the chicks to be counted.

Such artificial feeding was never more than spasmodic, was insufficient to form any significant part of any bird's diet and totalled less than 20 kg over the three years. The majority of watches during the breeding season and many outside the breeding season were made without recourse to artificial feeding. Except for the winter months, natural food was so abundant that the birds remained at the artificial food only for brief periods. Food remaining at the conclusion of watches was removed.

Artificial aids were also used to follow nesting behaviour. A tambour (Gurr, 1955) was used in one nest, and a thermistor (McConkey, 1972) in another. Incubation was followed by means of an automatically triggering 8 mm camera (Appendix II), while telemetry was also tried unsuccessfully for the same purpose. All eggs were numbered and measured, and chicks were individually toe-clipped on hatching. In September 1971, miniature patagial tags (0.3 g in weight) were attached to one wing of 11 newly hatched chicks. However, most were lost or had to be removed because they hindered movement. Coloured tape on chicks' legs was also tried unsuccessfully as most of these markings were lost within hours of application.

For comparison with the pukeko data, 39 hours were spent making similar observations on captive *Notornis* at Mt Bruce. All watches were from a permanent hide and were supplemented by photography.

2. GENERAL BIOLOGY

2.1 Morphology

2.1.1 General

The morphology of the pukeko has been adequately described by Oliver (1955) and need not be repeated. The species is particularly prone to albinism; one bird outside the study area at Pukepuke had wholly white wings as well as numerous white body feathers. Five of the birds banded at Pukepuke had a small number (less than 10) of white thigh feathers, obvious only when in the hand. A purple-buff coloured variety, termed isabelline by Oliver (1955), has been recorded in the Wairarapa (Cunningham, 1955), and is being bred at the Mt Bruce Wildlife Reserve. The colour is apparently controlled by a single recessive allele.

2.1.2 Sex and Age Determination

Measurements and morphological notes were taken at first banding and subsequent recaptures. Pukeko are monomorphic but can be sexed from external measurements (culmen length and body weight) with accuracy of 94% (Williams and Miers, 1958) or 92% (Tunnicliffe, 1965). Males have a culmen length of 70 mm or more and weigh above 950 g; the figures for females are lower but show some overlap with males (Williams and Miers, 1958). Most birds banded were caught and measured more than once, and sex was determined by measurement and behaviour. Only four birds (n = 133) fell outside their sex range for both measurements and in each case these measurements fell within the range on at least one subsequent recapture (Table 1 and Fig. 1).

Both measurements were variable. The weight of breeding females increased rapidly in early spring but decreased after laying. For example, 00* weighed 970 g in August 1970

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* Reference to individual birds is by their patagial tag number.

Table 1 **PUKEKO BODY MEASUREMENTS**

Juvenile Female

	Mean	s.d.	n
Tibia Length	90.3 mm	2.84	26
Tarsus Length	91.7 mm	2.80	26
Culmen + Shield Length	63.3 mm	2.10	26
Shield Width	21.1 mm	2.33	26
Bill Depth	27.1 mm	0.97	26
Nares-to-tip Length	28.1 mm	0.79	26
Body Weight	814.6 gm	61.22	25

Adult Female

Tibia Length	91.2 mm	3.21	22
Tarsus Length	91.8 mm	3.02	21
Culmen + Shield Length	64.5 mm	1.65	29
Shield Width	25.7 mm	1.61	29
Bill Depth	28.0 mm	0.99	27
Nares-to-tip Length	28.8 mm	0.78	29
Body Weight	875.9 gm	70.7	29

Juvenile Male

Tibia Length	95.3 mm	3.50	37
Shield Length	97.3 mm	3.91	37
Culmen + Shield Length	67.7 mm	3.53	37
Culmen Width	21.9 mm	2.50	37
Bill Depth	28.8 mm	1.62	37
Nares-to-tip Length	30.3 mm	1.57	37
Body Weight	924.6 gm	113.7	37

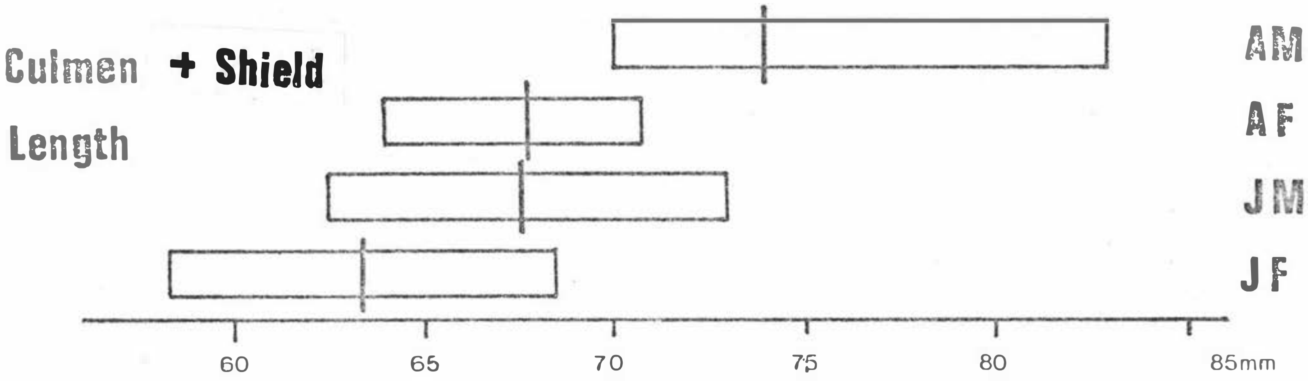
Adult Male

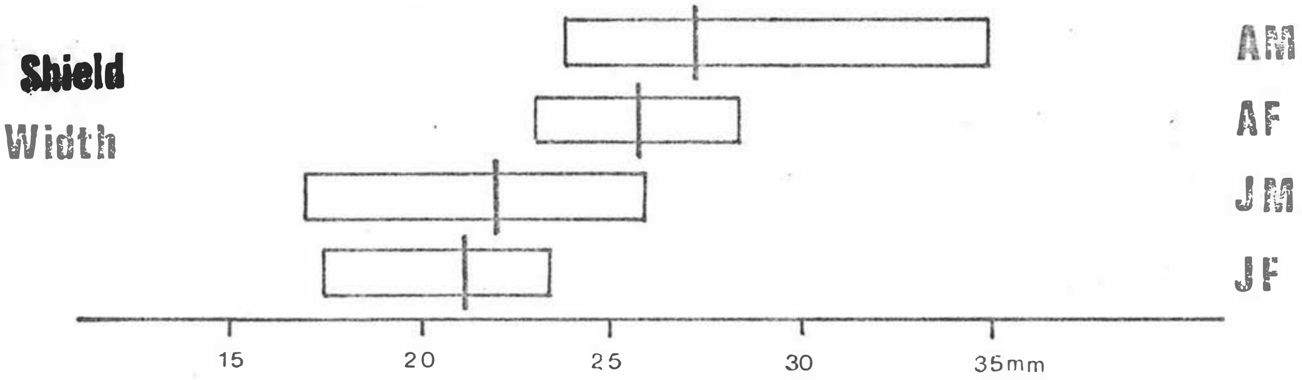
	Mean	s.d.	n
Tibia Length	98.4 mm	2.73	37
Tarsus Length	98.8 mm	3.49	37
Culmen + Shield Length	73.9 mm	2.58	42
Shield Width	27.2 mm	2.00	42
Bill Depth	30.4 mm	0.88	42
Nares-to-tip Length	31.8 mm	1.12	43
Body Weight	1052.6 gm	63.9	40

Figure 1 Measurements Used for Sexing and Aging Pukeko

(a) Mean and range of body measurements in relation to age and sex.

A = adult J = juvenile
M = male F = female


Culmen + Shield
Length
AM
AF
JM
JF
60
65
70
75
80
85mm


Shield
Width
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AF
JM
JF
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20
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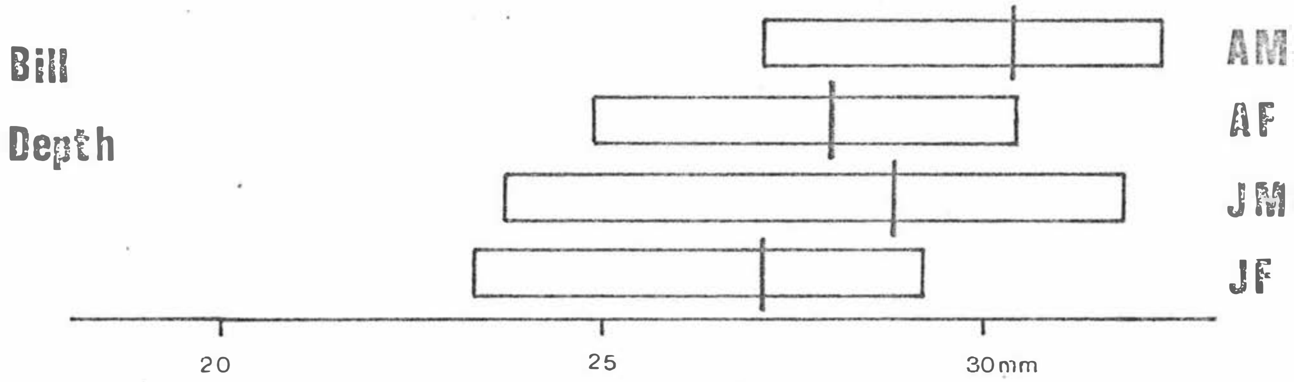
30
35mm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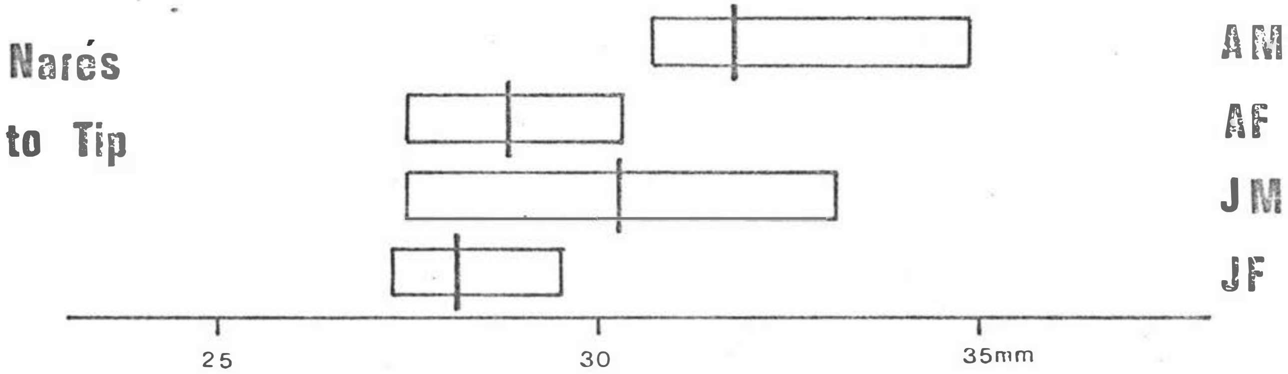
Depth
AM
AF
JM
JF
20
25
30mm


Narés
to Tip
AM
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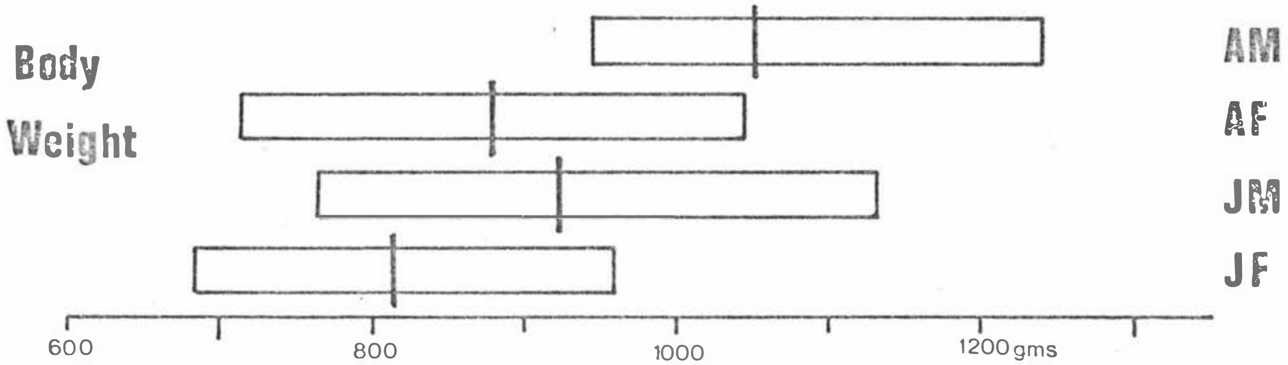
25
30
35mm


Body
Weight
AM
AF
JM
JF
600
800
1000
1200gms

but was only 806 g three months later. The frontal shield width of Ew was 34.88 mm in February but only 31.64 mm in July. Expansion of the shield also affected culmen + shield length and for most breeding adults this measurement expanded up to 2 mm.

Failure to establish age may have been a source of error in the data of other workers. The bill, frontal shield, iris and legs of adults are red, whereas chicks hatch with a white bill except for a black tip, a black shield and browny-black iris and legs. The bill colouration undergoes a series of changes varying the proportion of black to white before becoming red. This reddening begins at the shield and progresses forward until only the tip remains black, by which time the body plumage resembles the adult apart from white-tipped feathers between the legs. Finally the bill reddens completely. These changes are illustrated by Tunnicliffe (1965). The leg reddens more slowly than the bill but resembles the adult's at 5-6 months. After the colour change of the bill and legs and the disappearance of the white-tipped feathers between the legs, age can still be estimated by iris colour and shield width.

The iris begins to redden at about the same time as the bill and shield but more slowly. When the bill is completely red, the eye is still olive-red but at about nine months only a fine inner ring of olive next to the pupil remains. This olive ring can persist for 18 months.

The shield does not attain adult width until the bird reaches breeding condition (Table 1). In non-breeding yearlings, the shield remains narrow and very horny as distinct from its fleshy expansion in breeding birds. Eye colour and shield width and condition can be gauged only in live or freshly killed birds as both structures contract when frozen. 9y was an exception to both these age indicators, having a large shield width (25.86 mm) and a fully red iris at six months.

If juvenile birds (identified by an olive eye or shield width of less than 23 mm) are omitted from a sexing sample, a higher proportion could probably be sexed accurately by the method of Williams and Miers (1958). (A juvenile is defined as a bird less than ten months old, the youngest age at which a bird was known to breed.) This would not, however, include females which exceed 70 mm culmen + shield length and/or 950 g weight, but would only separate the juvenile males whose measurements resemble those of adult females (Table 1). The difficulty of sexing juveniles also remains.

Two other bill measurements: Nares-to-tip and depth (Fig. 1b) were used to overcome this. The former measurement was found to be extremely reliable, lacked seasonal variation and operator error, and was less than 30 mm in females with two exceptions. Behaviour was used to sex these two females. The bills of juveniles reached adult dimensions for nares-to-tip at about 5-6 months of age, whereas culmen length frequently took 8-10 months and in non-breeders even longer. Bill depth paralleled nares-to-tip in juvenile females whereas in males the latter measurement usually increased at a greater rate. Thus, using nares-to-tip in relation to depth, it was possible to sex most birds over four months of age.

2.1.3 Discussion

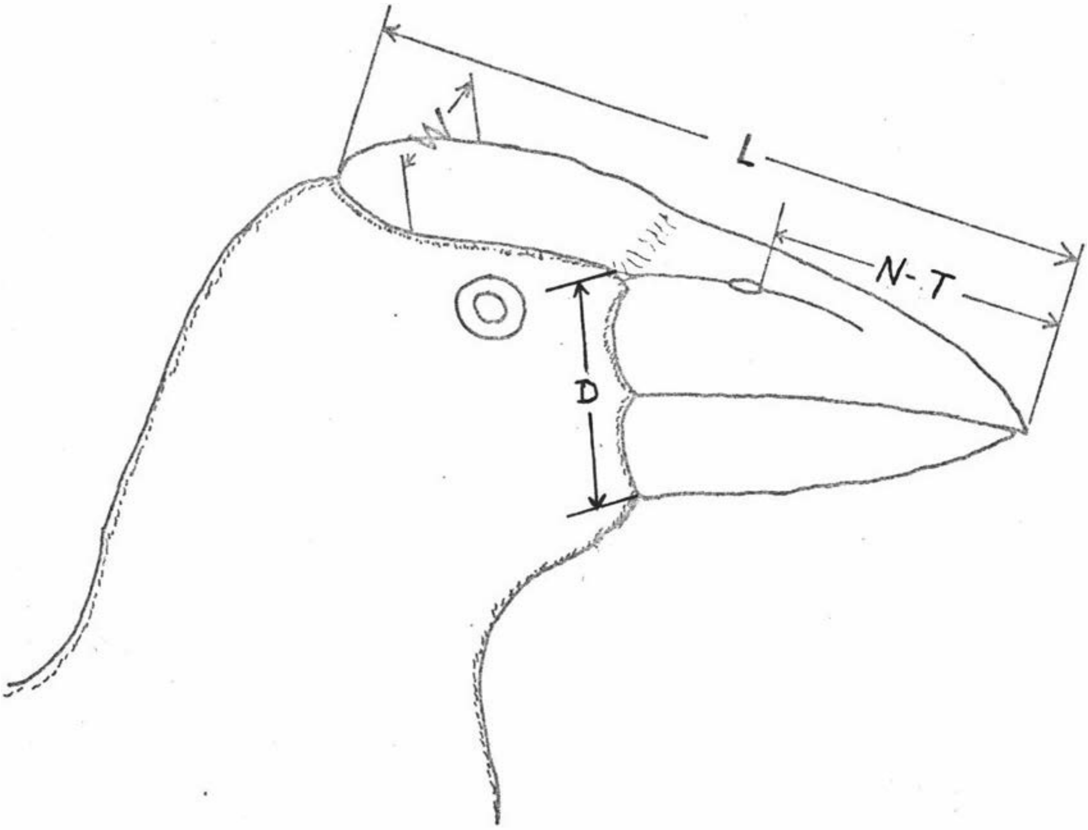
The sexual monomorphism of the pukeko leads to some uncertainty in sexing. Culmen + shield length and body weight, suggested by previous workers for separating the larger males from the females, vary seasonally. Culmen + shield length and shield width expand with the onset of breeding, a change that has been linked in coots with sex hormone concentrations (Gullion, 1951). In pukeko, the weight of breeding females increased markedly before laying and the body weight of males could also change greatly in a short period as shown by 10y (see p. 99). A further problem was the similarity of measurements of juvenile males and adult females. These factors must have led to much discrepancy by previous workers in the matter of sex determination. Error in culmen + shield length measurements is also likely in live birds. Williams and Miers (1958) recommended the use of body weight because of reduced operator error, but this is countered by wider natural variability.

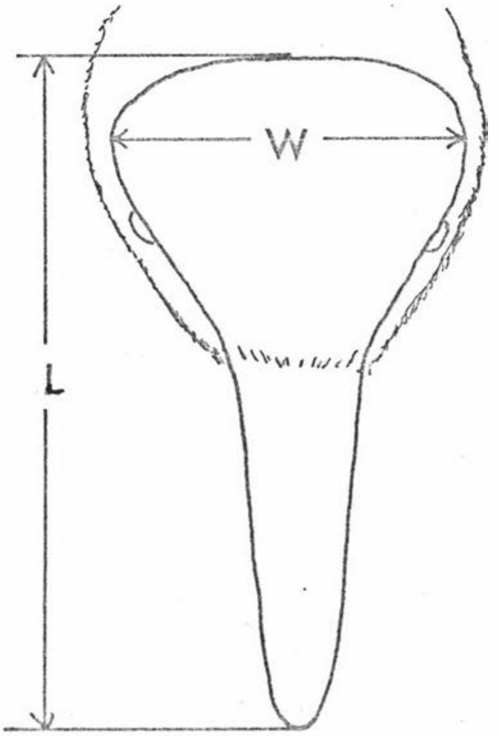
Figure 1 Measurements Used for Sexing and Aging Pukeko

(b) Head measurements used

(i) As viewed from the side
(ii) As viewed from above

L = Length of culmen + shield
W = Width of shield
D = Depth of bill
N-T = Nares-to-Tip length


L
W
N-T
D


W
L

Nares-to-tip does not vary with breeding status and hence was found to be a more reliable guide to sex than culmen + shield length or body weight. Operator error was negligible because callipers can be rested on hard and non-fleshy end points. This measurement moreover reaches adult range sooner than culmen + shield length or body weight, thereby allowing earlier sexing. Accordingly its use is strongly recommended for estimating sex. Despite the objections to culmen + shield length and body weight, these allowed ultimate sexing of all adults in the study territories, since measurement at different times of the year gave opportunities to check sexing at all stages of the breeding cycle. Behaviour (Chapters 3 and 6) was a reliable check of sex although homosexual matings caused difficulty for the observer.

A major difference of this study from previous work is the small number of females (4) which exceeded the maximum female culmen + shield length and the small extent of this overlap (0.72 mm). Tunnicliffe (1965) had 49 of 128 females with a culmen + shield length greater than 70 mm, and Reid (pers. comm.) found 14 out of 68 females in this category. The figures of Williams and Miers (1958) (2 out of 38 females greater than 70 mm) compared more closely with the present results. Differences between the studies probably arose from incorrect sexing and/or different measuring techniques. The marked advantages of the present study were that all birds were able to be aged, were alive and measured more than once, in contrast to the un-aged and shot samples of other workers.

Gullion (1952a) found overlap of body measurements of males and females in the American coot, <u>Fulica americana</u>. Midtoe length was the most reliable but can involve considerable sampling error, and in pukeko, this measurement showed large male/female overlap. Kornowski (1957) also found considerable overlap of body measurements in the European coot, <u>Fulica atra</u>, including nares-to-tip but, unlike Gullion, was using an un-aged sample. Body measurements were also unreliable for sexing Tasmanian native hens (Ridpath, 1972). All these species, however, lack the large frontal shield found in the pukeko and it is assumed that this may affect the differences in the reliability of the measurements. Gullion (1952) found voice to be the most accurate means of sexing coots, but this was not reliable for pukeko which do not duet like some other rails.

Age is more difficult to determine than sex. Bill and leg colour, and the presence of white-tipped feathers between the legs were reliable age indicators in very young pukeko, but other characteristics were needed for birds over five months. Eye colour appeared to be very reliable: the presence of olive in the iris was found only in birds less than one year old apart from a small number of non-breeding yearlings, which had a fine olive inner-ring. Culmen width was also helpful for aging birds but was complicated by breeding condition: non-breeding yearlings were similar to juveniles, but a shield width of less than 23 mm appeared to be a reliable indication of a juvenile. Birds with a width greater than 23 mm and a totally red iris could still be juveniles however, as for example, 9y , whose adult shield and eye condition could have been related to the great amount of territorial defence undertaken by this young bird when both parents were renesting.

The leg of the coot does not attain adult colour until it is two years old, and thus is a reliable indicator of age (Gullion, 1952a). There are no published age criteria for other rails.

2.2 Feeding

The pukeko studied had two major feeding times, early morning and late afternoon. Birds roosted until dawn, then moved out to feed in swamp or pasture, before returning nearer to cover about mid-morning to preen and sleep. During mid-afternoon they returned to open feeding areas where they remained until dusk, at which time they moved back to cover to roost. A number of observers have noted pukeko flying at night, and two birds were seen at Pukepuke flying back to the swamp from a barley field three hours after dusk on a moonlit night.

2.2.1 Food

All the study territories contained both swamp and pasture. The birds fed mostly in the pasture in late summer, autumn and winter but in spring and early summer, when chicks were present, they fed mostly in the cover of swamp vegetation, chiefly - as often observed - on raupo. When water levels dropped at Pukepuke, many holes were apparent where raupo shoots had been removed. As well as shoots, fully grown raupo plants were attacked but only the inner apex was eaten, a hole being torn through the outer leaves to gain access. At Linton, water levels were relatively constant and cows grazed the outer edges of the raupo; thus raupo shoots were less accessible and were rarely eaten, but grass was readily available instead.

Claims by farmers of extensive damage to grain and root crops could be partially substantiated at Pukepuke only when crops were planted within 350 m of the swamp, where in 1973 much of the pukeko flock fed in and trampled the barley.

Animal food was insignificant in the diet except during the breeding season when much of such material taken was fed subsequently to chicks and juveniles. Animals observed to be eaten included: annelids, isopods, insects, molluscs, three eels (Anguilla spp.), two frogs (Litoria aurea), three ducklings (Anas spp.), one sparrow (Passer domesticus), one black-backed gull (Larus dominicanus) as carrion; birds' eggs, one rat (Rattus spp.) and three rabbits (Oryctolagus cuniculus) as carrion. On only one occasion was a duck nest observed under attack by pukeko although many other successful duck nests were found in pukeko territories. Moreover, one deserted duck nest was found in Linton 4 and the eggs were still intact three months later.

Animal remains were frequently found around pukeko nests and included 30-40 snail shells (Helix aspersa) and duckling remains. Pukeko were never observed to attack ducklings, nor were ducks with young seen to take protective action when near pukeko.

2.2.2 Feeding Behaviour

Raupo was always held up to the beak in one foot. Grass was usually eaten by pulling a single tiller out with the beak, to be transferred to one foot to eat the succulent stem base; the blade normally being discarded. Whole plants were occasionally pulled up and washed before being eaten. Grass seeds were stripped in the same manner as described for takahe by Williams (1960).

Ground invertebrates were picked up directly in the beak but low flying insects were chased. Worms were eaten when encountered in pasture, and at Linton were actively sought, cattle faeces being ripped open or overturned to yield large numbers of worms and other invertebrates. Frogs, eels and small birds were actively hunted, though most vertebrates were probably dead before they were found.

2.2.3 Discussion

Pukeko are primarily vegetarian as shown by Carroll (1966), but raupo appeared to be relatively more important (at least at Pukepuke) than her study indicated (see also McKenzie, 1967). Raupo is a seasonal food, with use dependent on water levels, which may explain these different observations.

The amount of animal food in the diet of pukeko is also in dispute. Carroll (1966) reported very little, but McKenzie (1967), G. Tunnicliffe and C. Roderick (pers. comm.) also found pukeko taking live young, especially birds. The present study suggests that duck eggs and young are rarely taken nor are they actively sought, and that animal food, while recorded frequently, formed only a small proportion of the diet, with most of it fed to the young. Gurr (1951) recorded a high proportion of animal matter in the diet of young takahe. In pukeko, most larger items of animal food were dead when found and, as suggested by Caithness (1972), the major effect of pukeko predation occurs under unnatural conditions. This could explain the larger numbers of ducklings killed at Mt Bruce (C. Roderick, pers. comm.).

2.3 Overall Pattern of Dispersion

2.3.1 Territory

If Noble's (1939) classical definition of territory as 'any defended area' is accepted, pukeko held territories during the breeding season. Those at Linton held territories all the year round while most pukeko at Pukepuke showed varying degrees of tolerance of non-territorial birds outside the breeding season (see Chapter 5). Some territories at Pukepuke completely broke down at this time, presumably due to 'swamping' by large numbers of non-territorial birds, and others were abandoned after unsuccessful breeding.

There were variable numbers of birds within territories. The numbers recorded (Table 2) were from counts made at the hatching of the first egg or, where breeding was unsuccessful, at the laying of the first clutch. Participation in breeding was not a pre-requisite. In the study areas, 22% of the territories contained monogamous pairs, but, of all territories where numbers were known accurately, only 19% were pairs. Most of these pair territories (six out of seven) were found at Linton. The number of birds in group territories varied (three to six) but showed an increase in the mean as the study progressed, this being caused mainly by the retention of young in the territory. Monogamous pairs expelled their young prior to the subsequent breeding season. In all group territories, and in pair territories when juveniles were present, a hierarchy was established.

The sex ratio was equal in territories with an even number of birds (two, four or six) with the exception of the Peninsular Territory 1972-73 (see Fig. 40) where there were five males and a single female (Appendix 3). The sex ratio in four group territories with uneven numbers was ascertained: two had an extra female and two an extra male. Thus the overall sex ratio for all territories was approximately equal (48 males : 44 females; $X^2 = 0.087$).

2.3.2 Flocking

Non-territorial birds began to flock in the Hay Paddock

Table 2

NUMBERS OF BIRDS WITHIN A TERRITORY*

Recorded at the hatching of the first egg or, where breeding was unsuccessful, at the laying of the first clutch.

	No. of Birds Per Territory					Mean
	2	3	4	5	6	
Year						
1970-71	1	2	4	1	-	3.6
1971-72	3	-	4	5	-	3.9
1972-73	3	2	2	-	5	4.2
Total	7	4	10	6	5	4.0
Extra Territories +		1	2	2		4.0
Overall Total	7	5	12	8	5	4.0

* From Appendix 3

\+ From adjacent areas

in November and December each year. Building to a peak in April, the flock then gradually decreased until all birds had dispersed by the following breeding season (Fig.2a). The size of the flock fluctuated, containing only 29 birds in April 1971, but exceeding 50 (maximum = 72) in other years. The build-up was also variable, being faster in 1972-73 than in other years possibly because of the low water levels caused by the drought. Comparison of water levels with flock size (Fig. 2a) shows a negative correlation in 1972 and 1973. (Most territories were dry when the lagoon level dropped below 6.25 m a.s.l.). The assembly of the flock also appeared to be related to breeding since, each year, the first major increase in flock size occurred approximately one month after laying began in the last study nest although there was a gradual increase before this.

Flock composition was not constant and banding showed that some birds remained in the flock for only a few days or weeks: these movements were partially reflected in the sudden decreases and increases in flock size shown in Fig.2a. A few birds (*Ow*, *Vy* , *IVw*) were present in the flock in more than one year, *Vy* returning in all years, and this number would probably have been greater had all birds been banded. As in all territorial groups, a hierarchy existed in the flock.

May shooting affected flock numbers. In all years numbers fell after the shooting season but always by more than those known to have been shot (see p. 32). The decrease observed before shooting in 1972 may have been caused by shooters going to the lake to prepare maimais (shooting stands) and to clear raupo. Shooting in 1971 resulted in the original flock splitting into two parts (Fig.2a), one remaining in the Hay Paddock and the smaller one shifting to the Rough Paddock, with some interchange occurring. In 1973, the flock divided prior to the shooting season.

Sex and age ratios of the 1970-71 and 1971-72 flocks were skewed (Table 3). These two flocks had a high proportion of both males (64% and 63% respectively), and of juvenile birds. Since no new birds were banded in the

Figure 2 (a) Number of Pukeko in the Pukepuke Flocks in Relation to Breeding and Lake Levels

Numbers in the flock are shown by two lines where the flock was split. The upper line represents the total numbers in the flocks in both the Hay Paddock (lower line) and the Rough Paddock. The number of nests initiated per month is included as a reference to breeding. Lake level depths below 6.25 m represent substantial drying of the study territories.

Note: The number of birds recorded in the flock was the maximum seen during each watch.

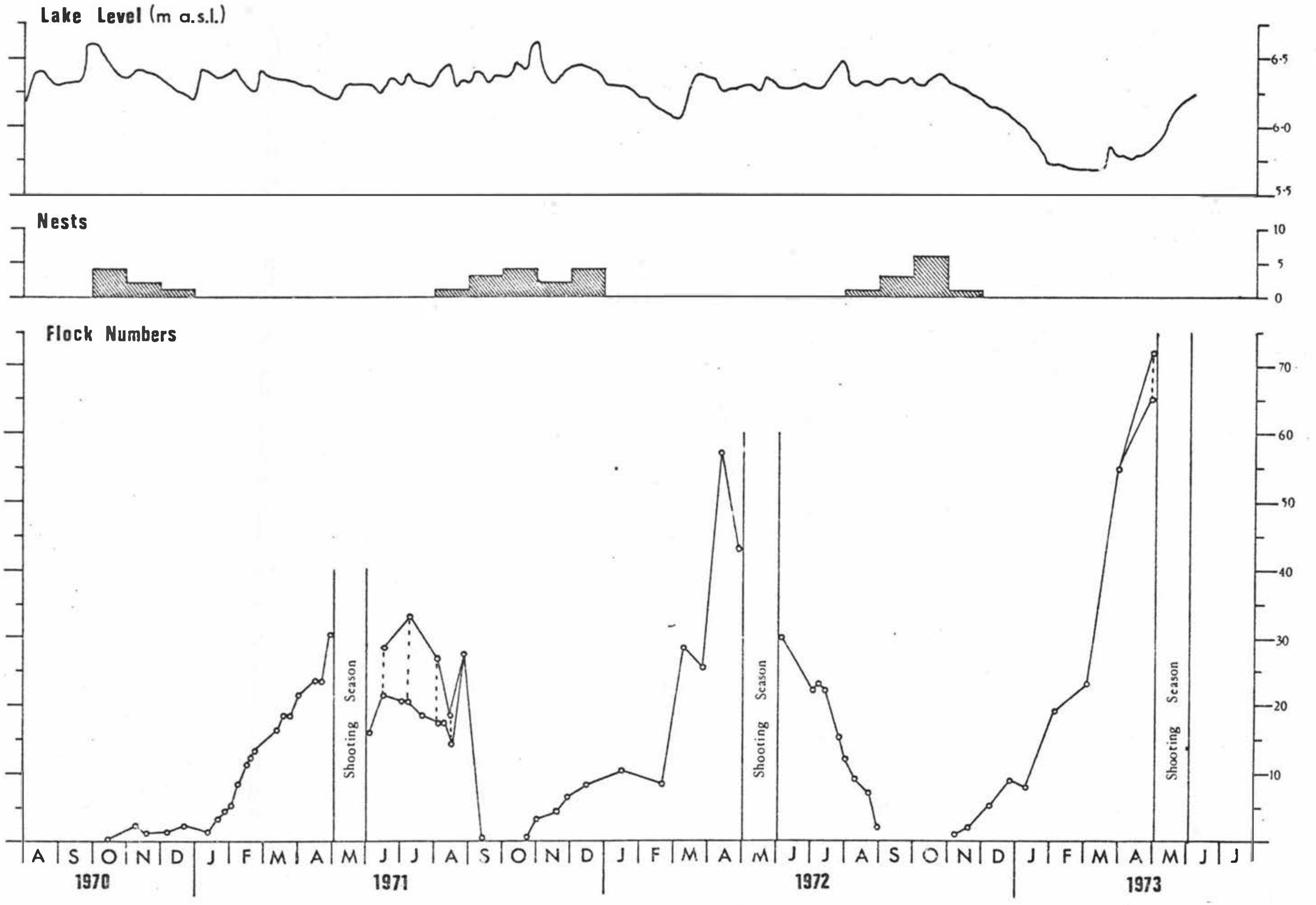

Lake Level (m a.s.l.)
6·5
6·0
5·5
Nests
10
5
0
Flock Numbers
70
60
50
40
30
20
10
Shooting Season
Shooting Season
Shooting Season
A
S
O
N
D
J
F
M
A
M
J
J
A
S
O
N
D
J
F
M
A
M
J
J
A
S
O
N
D
J
F
M
A
M
J
J
1970
1971
1972
1973

Table 3

AGE AND SEX COMPOSITION OF PUKEKO FLOCKS

1970-71

	Adult	Juvenile	Total
Male	9	14	23
Female	2	11	13
Total	11	25	36

Unitary Age Ratio = 1 Adult : 2.3 Juv.   Unitary Sex Ratio = 1 ♀: 1.8 ♂♂

1971-72

	Adult	Juvenile	Total
Male	6	13	19
Female	5	6	11
Total	11	19	30

Unitary Age Ratio = 1 Adult : 1.7 Juv   Unitary Sex Ratio = 1 ♀: 1.7 ♂♂

1972-73 flock, little is known regarding the sex and age ratios. Four birds were caught, however, all of which were juveniles and the only one sexed was a male. Another bird, banded as a chick at the end of the 1971-72 breeding season, also appeared in the flock and was found to be a male. The preponderance of young birds especially males in the previous two flocks could thus have been repeated in the 1973 flock.

Flock numbers slowly diminished until few birds remained in August when most breeding territories were re-established as defended areas. In 1971 the remaining birds (7) moved to the Rough Paddock where five eventually defended a territory and bred. In August 1972 more birds remained and the flock in the Hay Paddock split into two groups which then established the Trap and Peninsular Territories. As already seen (Appendix 3), these territories had a high proportion of males. The Trap Territory formed first and expelled the remaining nine birds (6 male : 3 female) which nested and laid. After losing the first two nests, these nine were reduced to the final six of the Peninsular Territory. The second flock in the Rough Paddock also formed into two groups: one remaining and establishing the Corner Territory forcing the rest to a neighbouring drain. This group later disappeared.

Apart from the birds which established breeding territories in the study area, little could be found about dispersal of flock members. A small number were known to have moved to other areas (see p. 31) and a few remained in the study area as solitary non-breeding birds. *Vy* and *Fly* from the 1970-71 flock were seen frequently in the study territories throughout the following breeding season. Both birds were extremely 'furtive' in their habits, moving between territories in a crouch with tail flicking, keeping close to cover and away from the territorial birds. *Vy* reappeared in both the 1972 and 1973 flocks. *Ow* was also present in the flock in two years but its whereabouts in the intervening (1971-72) breeding season were not known. *Ky* , a member of the 1971 flock, was still at Pukepuke and non-territorial in February 1972, but did not rejoin the flock.

IVw from the 1972 flock joined the Corner Territory which dissolved after unsuccessful breeding and IVw reappeared in the flock in April 1973.

Some of the flock birds managed to join established territorial groups, but most did so only temporarily. For example, on April 28, 1972, ILy was fully accepted in the Hide Territory but was gone by June 12, 1972, but by July 6, 1972, IJy was a member of the same territory. Vy was accepted into the Western Territory on August 15, 1972, but the territory dissolved after unsuccessful breeding. Kw joined the Hide Territory in 1971 and became a permanent member.

An attempt was made to determine the origin of flock birds by banding and following two territorial groups outside the study area at Pukepuke. Both territories contained very small areas of pasture. These two banded groups, however, remained in their territories all the year and did not move to the flock area at any time. Periodic observations were also made around the Reserve, but these failed to demonstrate the existence of other flocks. They did, however, show that outside the breeding season birds were still associated in small groups - suspected to be territorial.

2.3.3 Discussion

Pukeko populations appeared to have two forms of social organization: territories and flocks. All pairs and groups were territorial during the breeding season and while some were defended throughout the year, others broke down either partially or completely. This will be further documented and discussed in Chapters 5 and 7.

Numbers of birds within a territory were variable, but over 80% of study territories contained more than a pair. The disproportionate occurrence of pairs at Linton suggests a relationship between territory type and habitat, which will be discussed further in Chapters 5, 6 and 7. The increase, during the study, in the mean number of birds per territory appears to be a reflection of an overall population rise which showed further in an increase in the number of territories and an increase in flock size. The increasing number of birds in a territory was caused in almost every case by the retention of young. It is unlikely that numbers within a territory would have continued to increase indefinitely but it is not known when this process breaks down and birds are expelled from the territories. Further investigation is needed.

Tunnicliffe (1965) gave no figures for the number of pukeko per territory but found no pairs at Lake Ellesmere (pers. comm.). Ridpath (1972) reports approximately equal numbers of pairs and trios (26 and 19 respectively), five territories with four birds and one of five in the Tasmanian native hen. Ridpath also recorded four *Porphyrio* trios in Tasmania. The coot is listed as being monogamous by Gullion (1952) and Kornowski (1957) but there is some evidence (Fredrickson, 1970) that more than one female may occasionally lay in a nest. Howard (1940) also recorded the moorhen (*Gallinula chloropus*) as being monogamous although there are reports of a juvenile helping with breeding, including incubation (Robertson, 1972).

Takahe are generally considered monogamous and territorial (Williams, 1960; Reid, 1967). However, Williams and Miers (1958) reported two cases of yearlings remaining within their parents' territory and another possible case of three birds in a territory. Seven of the ten chicks banded by Reid (1967) were still in their natal territory as yearlings, and another was found associated with another pair. Of seven birds caught as two-year olds, one was within, and another on the margin of its home territory. It was not known if any of these takahe bred communally. Williams and Miers (1958) reported one yearling incubating in its parents' territory but Reid (1967) suggested that this was more likely to be 'an example of family-sharing incubation', but it would still constitute a group territory as defined in my study. Guthrie-Smith (1927) recorded one weka (*Gallirallus australis*) trio with two females laying in the same nest.

Gullion (1952) considered monogamy to be general for Rallidae, assuming it to be a necessary condition in birds where both sexes incubate. The well documented cases of communal breeding in Tribonyx and Porphyrio, however, and the occasional instances in takahe, weka, coot and moorhen suggest that group territories and communal breeding may be as frequent as pair territories and monogamy. Detailed studies of more rails are needed to verify this.

Sex ratios within the study territories were balanced with the exception of the Peninsular Territory (1972-73). Guthrie-Smith (1927) referred to pukeko as being polygamous but he sexed by observation only, while Tunnicliffe (pers. comm.) considered pukeko to be polyandrous. The findings of the present study do not necessarily conflict with those of Tunnicliffe as, although sex ratios are not known for Tunnicliffe's study, all his territories were held only in the breeding season and were set up by flock birds. The sex ratio is known for two territories (Peninsular and Trap, 1972-73) at Pukepuke which were formed in a similar way and in both cases males predominated. It is possible that other territories (e.g. Rough Paddock 1971-72, and Corner 1972-73) that were also formed from the flock may have had a preponderance of males but sex ratios were not known.

Ridpath (1972) found Tribonyx to be polyandrous with permanent territories in which sex ratios favoured males in all but three cases. Of these, two favoured females and the third had an even ratio. However, Ridpath's method and accuracy of sexing is questioned (see p. 203).

Because most study territories were occupied all the year, it is difficult to explain the origin of the flocks at Pukepuke. In each year, some of the first birds to appear in the flock seemed to be family groups, and initially remained coherent, but as flock size increased these became fragmented and indistinguishable. These groups suggested that the flock was partly formed from birds that held territories only in the breeding season. It was suspected that the territories most likely to break down after breeding were those lacking adjacent paddocks for feeding, but the only evidence available conflicts with this.

The very high proportion of young birds in the flock suggests that it may be formed from juveniles and yearlings expelled from natal territories. However, the juveniles banded in the two territories lacking pasture remained with their parents, as did all juveniles in the study territories at Pukepuke. One bird banded as a chick by the New Pond did join the flock as a yearling.

The return of birds to the flock in subsequent years indicates the origin of part of the flock. The records of *Vy* and *IVw* suggest that at least part of the flock was formed from non-breeding itinerants and birds from unsuccessful breeding territories. However, opposing this was the failure of *Ky* and *Fly* and the other banded birds from the unsuccessful territories to rejoin the flock. Thus the origin of the majority of birds in the flock remains unsolved, but the preponderance of young pukeko in the flock points to expulsion of young as a likely factor in its formation.

The sex ratio of the 33 chicks banded in study territories (see Table 25) was equal (16 males : 17 females) which suggests that the strongly imbalanced sex ratio of the flock was not due to an unbalanced chick sex ratio. It is perhaps unrealistic to extrapolate from the study territories which apart from the Peninsular territory did not contribute to the feeding flock, but it is possible that whatever the conditions that prevailed in the territories contributing birds to the flock, they may have resulted in a differential survival of male offspring or differential retention of female offspring. In fact, Table 25 shows that of the seven juveniles produced and retained in permanent territories at Pukepuke, five were females. This favours the suggestion of differential retention of females and coupled with a preponderance of males in the territories which broke down to form the flock (assuming this to occur as shown by Peninsular and Trap territories), may explain the unequal ratios of the flock. The very low number of adult females in the flock may have been partly due to biased trapping (see p. 125), but in 1972 the rocket net caught all except two of the unbanded birds, so this bias was not large, and was insufficient to explain the unbalanced ratios.

Tunnicliffe (1965) observed up to eight non-territorial flocks at Lake Ellesmere and many other large aggregations have been observed by others (e.g. Carroll, 1969) but no sex or age ratios are available.

American coots are partially migratory and in some areas, form large winter flocks with a high proportion (90%) of young birds but with a sex ratio close to 1 : 1 (108 males : 100 females) (Gullion, 1952a). European coots (Kornowski, 1957) and moorhens (Anderson in Dunnet, 1965) also form large winter flocks after breeding territories break down but takahe (Williams, 1960; Reid, 1967) and Tasmanian native hens (Ridpath, 1972) do not form flocks. The sex ratio of Tasmanian native hens heavily favoured males (111 males : 74 females) in Ridpath's study area but a neighbouring population (shot and internally sexed) had a more even distribution of the sexes which tends to lay doubt on Ridpath's method of sexing (see also p. 203). However, the sex ratio of surviving Tribonyx chicks (internally sexed) also favoured males (50 : 18) and may have affected adult ratios. As discussed earlier, pukeko chick sex ratios were even although no chicks were killed for sexing in my study in order that chick dispersal could be followed.

2.4 Dispersal

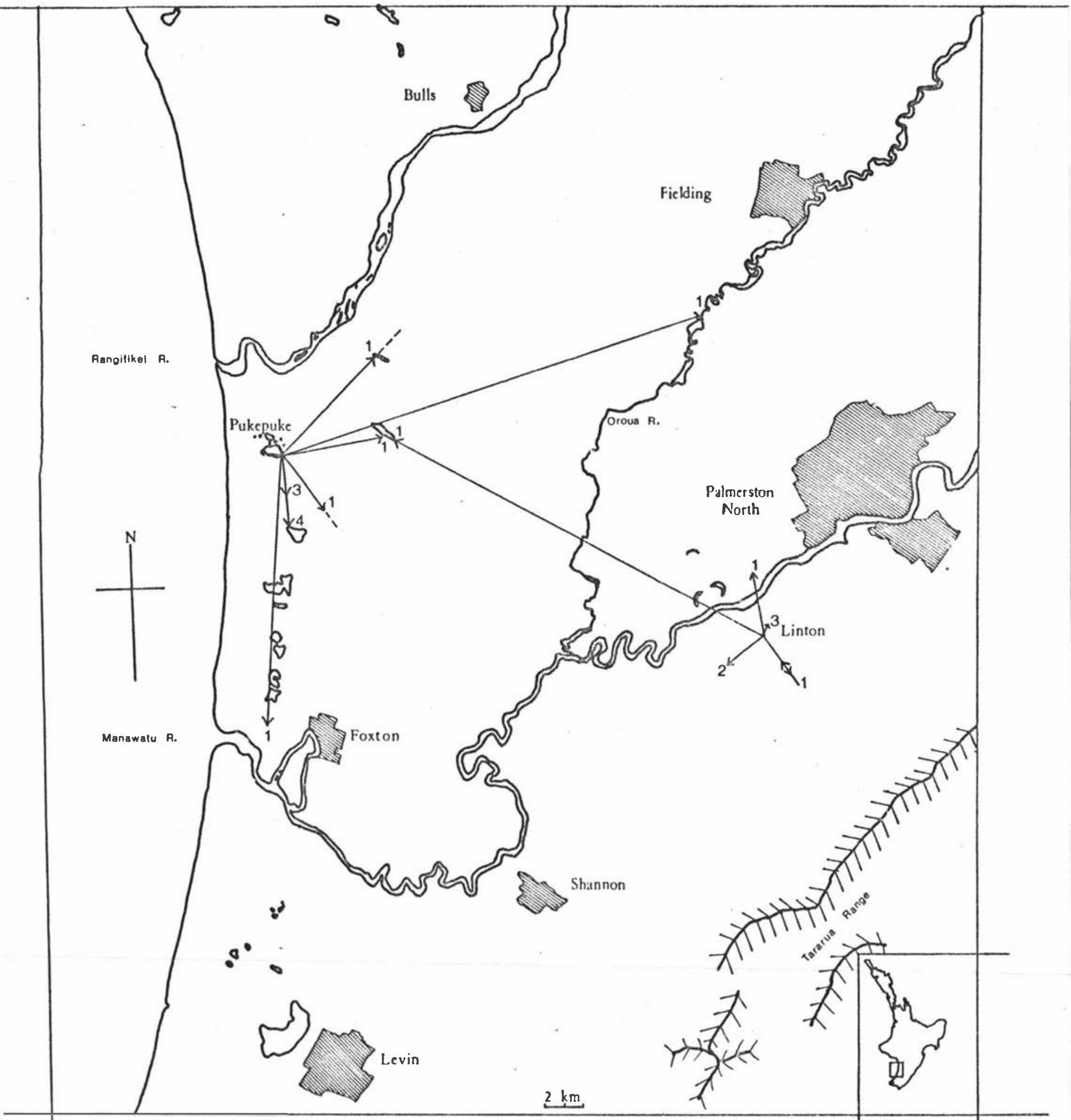
2.4.1

Much of the evidence for dispersal comes from shooters' returns, but because pukeko form a very small proportion of bags in the Wellington District (3% in 1971 and 2% in 1972; Caithness, 1973), only a small number of bands were returned. In order to obtain records from the 1973 shooting season, an appeal for the early return of pukeko bands was mailed to all shooters in the Wellington District.

Known returns showed that most birds moved only short distances (Fig.2b), the longest being 24 km from Linton to Omanuka. As already stated (p. 20) juveniles from the pair territories at Linton were expelled prior to the hatching of the first egg or more usually before laying, and dispersed

Figure 2 (b)   Dispersal of Pukeko from Study Areas

Arrows represent the places where birds from the study area were found or sighted. Totals are shown at the tip of each arrow. Dotted lines show that the bird(s) subsequently dispersed further.


Bulls
Fielding
Rangitikei R.
1
1
Pukepuke
Oroua R.
1
1
3
1
4
Palmerston North
N
1
3
Linton
2
1
1
Manawatu R.
Foxton
Shannon
Tararua Range
Levin
2 km

mostly to neighbouring areas. *05* ,*06* and *Ow* from Linton 1 all moved to Linton 3 in August 1972. *21w* was known to have left Linton 2 and moved to an area 2 km East in September 1972, but then returned to Linton 2 before dispersing again to an unknown area. When Linton 5 broke down, two of the birds were seen in Linton 2 but were expelled. *7y* from Linton 2 was found breeding in a group territory 2 km South-west in October 1972.

Birds from Pukepuke were occasionally sighted in adjacent areas, and after the breakdown of the flock in 1972, four banded birds were seen briefly in surrounding areas. *1Fy* was observed in early November 9 km North-east of Pukepuke one week after leaving the flock, but was gone three days later. Three other banded birds were seen 1 km South of Pukepuke in September but subsequent visits to this area failed to find the birds which, like *1Fy* , were apparently still dispersing.

Fifty-four band returns from all operators throughout New Zealand showed no general trend in dispersal. Distances moved varied from 0 to 240 km: 15 moved more than 50 km and six more than 100 km. Sutton (1967) recorded a pukeko returning 97 km to its point of capture in eight days, and band records also showed two pukeko moved more than 180 km in three months in late summer and autumn, while another moved 121 km in 52 days in autumn.

Pukeko may also remain in the same place for a long time; one banded bird was recorded at its place of capture seven years later. While the brevity of my study prevented accumulation of such data, at the conclusion (April 1973) 12 birds were still resident in the territories where they were banded in 1970, and one other, *Ew* , had moved to an adjacent territory. Also seven of the young raised in the 1970-71 or 1971-72 breeding seasons were still in their natal territories at the conclusion of the study.

One bird, *ISw* , which had been captured as a chick at Opiki and held in captivity for one year, was released at Pukepuke in March 1972. It was shot three months later just 100 m from where it was released.

2.4.2 Discussion

Pukeko appear to radiate from their natal areas stopping at intervening swampy areas until eventually they find a place suitable to breed. Most birds dispersing from the study areas were juveniles or yearlings, but some adults also moved, especially after unsuccessful breeding (see p. 25). Other reports demonstrate that pukeko are capable of moving long distances in a short time and that of Sutton (1967) shows that breeding birds will return to a successful territory if moved, while non-breeding birds may adopt new areas (cf. 1Sw). Most long distance dispersals occurred outside the breeding season.

Ridpath (1972) found that flightless Tasmanian native hens, mostly juveniles, radiated short distances to adjacent areas, and Gullion (1952) recorded coots returning to the point of capture after being moved to other areas.

2.5 Shooting Pressure

2.5.1 Results

Pukeko are third on the game list in terms of numbers shot, but in 1972 formed only 7% of the total bag for New Zealand (T.A. Caithness, pers. comm.). Shooting pressure varies from area to area as do bag limits: e.g. in the West Coast Acclimatization District, pukeko comprise up to 35% of the shooters' bags (Caithness, 1972).

In the study area, pukeko were protected in 1968 and 1969, but in 1970, 1971 and 1972, shooters (n = 28-33) were allowed two pukeko per day for the opening and closing weekends only - a maximum bag of ten. Despite this only 42, 11 and 10 were shot in the three seasons respectively (Caithness, pers. comm.) but this may have been affected by requests not to shoot banded birds. In 1973, when shooters were allowed two birds per day for the whole season, only 20 were shot. Measurements were taken in 1971 and 1972 to gauge the age and sex ratios of the shot birds. These results (Table 4) suggested that more males than females are shot.

Table 4

AGE AND SEX OF BIRDS SHOT

Sex	1971		1972		Totals	
	Adult	Juvenile	Adult	Juvenile	Adult	Juvenile
M	3 2*	1	2 2+	1	5 4	2
F	1	1 1*	1 1*	–	2 1	1 1

\+ Birds shot by W.J.P. at Wanganui

* Verified by internal sexing

2.5.2 Discussion

Shooting pressure is extremely variable throughout New Zealand, and the numbers shot appear to depend on the availability of more sought-after species such as ducks and swans. At Pukepuke it appeared that insufficient pukeko were shot to affect the population size, but this may have been partly due to requests to leave banded birds. When questioned, most shooters considered them easy to shoot and poor to eat. It is not known whether the greater harvest of male pukeko was simply a reflection of the overall sex ratio or whether shooters actively took larger birds. The large number of adult males taken suggests the latter may be more likely.

As pukeko are considered poorer game but cause considerable crop damage in certain areas, it is suggested that a special shooting season (over crops) in March would be the most effective means of controlling pukeko. The present study has shown that flock pukeko (those most likely to cause damage) were mainly non-territorial and non-breeding birds whose elimination would have little effect on the overall population.

3. GENERAL BEHAVIOUR

3.1 Introduction

In order to interpret correctly the gross behaviour of a species, it is necessary to begin with description and categorization of individual units thus establishing an ethogram or behavioural repertoire. If the temporal relationships of descriptive units are analysed, causal and functional relationships can be inferred. Observation should, ideally, be on a wild population, be unbiased, and direct observation should be accompanied by film recordings to ensure that all aspects are recorded (Eibl-Eibesfeldt, 1970). As Marler and Hamilton (1966) point out observation must to some degree be selective, but this can be partially overcome by the use of objective terms to describe behaviour. Therefore in the formation of the original description of behaviour, no presumptions were made concerning function of the different patterns. This was determined later by analysis.

The problem of subjective description further arises from fitting observed behaviours into previously named displays. To overcome this, no account of prior work was recorded until all behaviour had been fully assessed. Consequently all patterns of behaviour were given original and purely descriptive terms, but to prevent unnecessary duplication many postures have been equated with previously described behaviour. Many of the terms used in earlier research were inadequate or inaccurate; so my original terms are retained.

As previously mentioned (p. 4) no attempt was made to record maintenance behaviour or ontogeny of behaviour already covered by Tunnicliffe (in prep.)

3.2 Locomotion

Locomotory activities have no signal function but are included to provide related information for the better understanding of the overall behaviour of the pukeko.

3.2.1 Flying and Walking

The pukeko is capable of long sustained flight. However, its flight appears 'laboured' and birds resorted to flying in few situations, e.g. escape from predators and crossing of drains. In the latter situation, birds rarely flew when crossing to open fields but did so readily when crossing back to cover. At all other times walking was 'preferred' and running was frequently accompanied by wing flapping.

3.2.2 Swimming

Pukeko do not have webbed feet, but swim well with wings and tail raised. Chicks can swim from the day of hatching and can also dive in response to predators. Adult pukeko are also reported to dive (Tunnicliffe, 1965).

3.3 Interspecific Behaviour

3.3.1 Alert

The bird stood completely still and erect, all body feathers were sleeked, and the neck was elongated. The head might be tilted especially when watching a predator and the tail was normally flicked. A bird in an Alert appeared 'anxious' and 'ill at ease' (Fig. 6). The Alert was also used frequently in intraspecific occasions.

3.3.2 Grouping

When actively threatened by hawks, Circus approximans, pukeko grouped in very compact aggregations in the Alert posture. A harsh alarm call was given and if the hawk swooped, one or more birds flew up at it. Grouping was independent of territory and status and thus large groups of birds, even from adjacent territories, formed and consequently much fighting and pecking occurred after the danger was past (Fig. 3a).

Figure 3 Flock Pukeko

(a) Flock birds slowly dispersing into the Hay Paddock.

(b) Flock birds grouped beside the drain. Note the small distance between individuals.

As well as the above behaviour, pukeko actively hunted and attacked mustelids and rats when seen.

3.4 Calls

The lack of a directional microphone prevented the recording of all calls and hence none are presented in detail, but a number of calls were easily recognisable. No attempt is made in the following descriptions to use phonetic symbols which are of very limited use.

3.4.1 Territorial Long Call

This call was the longest of the calls and was usually repeated up to five times. The initial call was harsh and the notes gradually tapered away. This call was frequently heard at night and was given by most territorial birds when flying out to feed at the conclusion of a territorial defence or after Wing Clapping.

3.4.2 Wing Clap Call

This, as the name suggests, always accompanied the Wing Clap and was a harsh, short, staccato call. Like the Long Call it was partly a territorial call but was also used in distraction of predators (p. 55).

3.4.3 Location Calls

Very soft 'ding' calls were given by birds when in dense cover. These were especially common when adults were calling and leading chicks.

3.4.4 Juvenile Calls

(a) Cheeps: These were given by very young chicks and were similar to domestic chick calls.

(b) Immature 'Miaow' (Following Ridpath, 1972): This was a high pitched monotonous whining call, given by juveniles when begging or when attacked.

3.4.5 Yelling

A very loud raucous call occasionally given in a territorial dispute.

3.4.6 Precopulatory Hum

A very nasal monotonic call given by the male when approaching or following the female prior to mounting.

3.4.7 Grating Low Pitched Call

A very deep staccato grating call given by subordinates in a Bow.

3.4.8

Many other very soft calls were given between birds at the nest. These were particularly frequent prior to nest relief.

No call equivalent to the 'See-Saw Aggressive Call' (Ridpath, 1972) of the Tasmanian native hen was heard but similar dueting is common in takahe (pers. observation) and other rails (e.g. coots - Gullion, 1952).

3.5 Agonistic Behaviour

The following behaviour patterns form distinct units of a continuum of behaviour with extremes representing attack and escape. Apart from the extreme, the remainder were ambivalent containing elements of attack and escape. Few patterns appeared in isolation but formed complex chains of reaction. No attempt is made to describe the integration of these displays in inter- or intra-group interactions. These will be detailed in the relevant chapters (4, 5 and 6). What follows is solely description and analysis of postures. The head, neck, body, tail, wings, and the total orientation of the bird were used separately and in combination in signalling. Apart from the initial description of wing and tail positions, displays are presented in a sequence based on head position and body orientation, but this is not meant to be a functional sequence.

3.5.1 Wing and Tail Positions

Pukeko have white undertail coverts which contrast strongly with the surrounding black tail and wing feathers. Wing and tail positions varied greatly both as components of all displays and as separate displays. The wings and tail formed a continuous gradation where the wings varied from being closely against the body to being vertically raised and laterally extended, and the tail varied from fully down and closed to vertical and expanded. These were divided into units that were readily distinguishable in the field.

A. Tail Postures

(a) At Rest: The tail was held down at an angle from the body, was completely closed, and no white was obvious.

(b) Tail Up: This was recognized as a separate display as well as accompanying other postures. Five grades were recognized according to the angle of the tail to the body axis. These were Tail One Third Down, Tail Horizontal, Tail One Third, Two Thirds and Fully Up, and showed increasing amounts of white behind. The tail was either closed or expanded to some degree.

(c) Tail Flick: The tail was rapidly flicked from a lower to a higher position and then returned. Rates and amplitude of flicking were variable.

B. Wing Positions

(a) At Rest: The wings were folded and lay close to the body and along the back.

(b) Wings Partly Up: The wings were partially raised but fully closed. The tip of the tail feathers still projected above the wings.

(c) Wings Fully Up: The wings were raised while still closed, completely covering the raised tail from side view.

(d) Wings Exaggerated Up: The wings were held at extreme elevation, still fully closed and with the tips touching.

(e) Wings Out: This accompanied any of the preceding wing positions and took the form of the wings held out laterally on either side of the body. It was usually accompanied by Yelling.

C. Combination of Wing and Tail Positions

In general increased elevation of the wings was accompanied by greater elevation and expansion of the tail. The tail was normally Fully Up when the wings were Partly Up but tail expansion was at a maximum when wings were Fully or Exaggerated Up. The postures described above form a gradation that from the rear exposed increasing amounts of white undertail coverts but from the front and side made the bird appear increasingly large. The dark wings were a sharp contrast to the white tail and framed and accentuated it when viewed from behind (Figs 4-25).

3.5.2 Fighting

Normally all actions were very fast indeed. Opposing birds jumped at each other feet first, attempting to rip violently with their claws. The leg actions occasionally pushed the birds apart and onto their backs. One bird then managed to get astride the back or belly of the other and violently pecked it. Birds occasionally locked together sitting on their rumps ripping at each other's breasts with their free legs. The main element of fighting appeared to be getting into a position to deliver a downward peck. This was achieved by jumping above the other bird, getting it off balance or in a position where it could be pecked but was unable to return a peck (Figs 4 and 5). Most fighting was very swift and involved as many as four birds (Fig. 5). However, occasionally two birds stood perfectly still and slowly sparred at each other with one foot (Fig. 4). Fighting was never observed between members of the same group but was frequently seen on territorial boundaries or, less often, between members of large winter flocks.

3.5.3 Pecking

This was normally a simple downward peck with slightly opened beak usually directed at the opponent's head, neck or back (Fig. 35). Pecking was most common between adults and juveniles in the same group.

3.5.4 Charge

Here a bird ran at another with the position of the neck depending on the speed of running (Fig. 7). With increasing speed, the neck was lowered further towards the horizontal for balance. The beak pointed downwards and if the opponent was reached, a violent peck was delivered. Wing and tail positions were variable but tended towards the more raised positions with the increasing status of the opponent and the proximity of the territorial boundary.

A second form of charge, the 'Splatter' (cf. Gullion, 1952b) was recognized. In this the wings were flapped to increase the speed of charge and to retain balance.

3.5.5 Head Flick

In this posture the head and bill were flicked vertically upwards and backwards (Figs 8 and 10a). Body feathers were normally sleek. In extreme cases, the neck was elongated and curved up and back so that the beak lay along the back. The head posture was held for varying lengths of time but was frequently only a simple flick. Accompanying wing and tail positions were variable but the tail was almost always Fully Up and the wings were Fully or Exaggerated Up.

Figure 4 FIGHTING

Two pukeko sparring with feet on a territorial boundary. Both birds are in 'Aggressive' Uprights.

Figure 5 FIGHTING

Multiple fight between four birds on a territorial boundary. Note pegs demarcating the boundary zone.

Figure 6

1Bw in an ALERT. Note the very erect stance.

Figure 7

Pukeko CHARGING during a territorial dispute.


18

3.5.6 Upright

This posture was so named because of its similarity to the Upright of gulls, Larus spp. (Tinbergen, 1959). Like the posture in the gull, it was extremely variable but with two easily distinguishable extremes, the 'Aggressive' Upright and the 'Anxiety' Upright.

(a) Aggressive Upright: The head and bill were pointed downwards at approximately 45 degrees, and the neck was either vertical or forward. The neck varied from being fully stretched to being unextended and fattened. Where two birds faced each other, both usually extended their necks presumably to get their beaks above the other to deliver a downward peck (Figs 9 and 10b). A bird in an Aggressive Upright nearly always faced its opponent and occasionally advanced towards it. Because of this orientation, the red frontal shield and bill were prominently displayed, and probably acted as releasers (Figs. 9 and 11).

Rarely this posture was adopted when the body was side on or turned away from the opponent. This was observed only when a low status bird from one territory was near the boundary and the displaying bird was a high ranking male who was feeding while facing away from the boundary. If this part-adoption of the posture was ineffective in producing the retreat of the opponent, then the bird adopted the full frontal orientation.

(b) Anxiety Upright: As in gulls, this posture differed from the above in that the head and bill were horizontal or pointing slightly upwards. The neck was usually unstretched and vertical, and was rarely inclined forward. Plumage was usually sleek and flattened (Fig. 10c).

Orientation was variable but the bird never moved towards an opponent. The higher angle of the

Figure 8

Male (H1w) in an 'AGGRESSIVE' UPRIGHT, Tail One Third Up approaching a female which is HEAD FLICKING, Wings Partly Up, Tail Fully Up. Note tip of tail still visible above the wings.

Figure 9

Two males in a territorial dispute. Male on right in an 'AGGRESSIVE' UPRIGHT, Wings Fully Up and Out, Tail Fully Up. Second male has just jumped up and back.

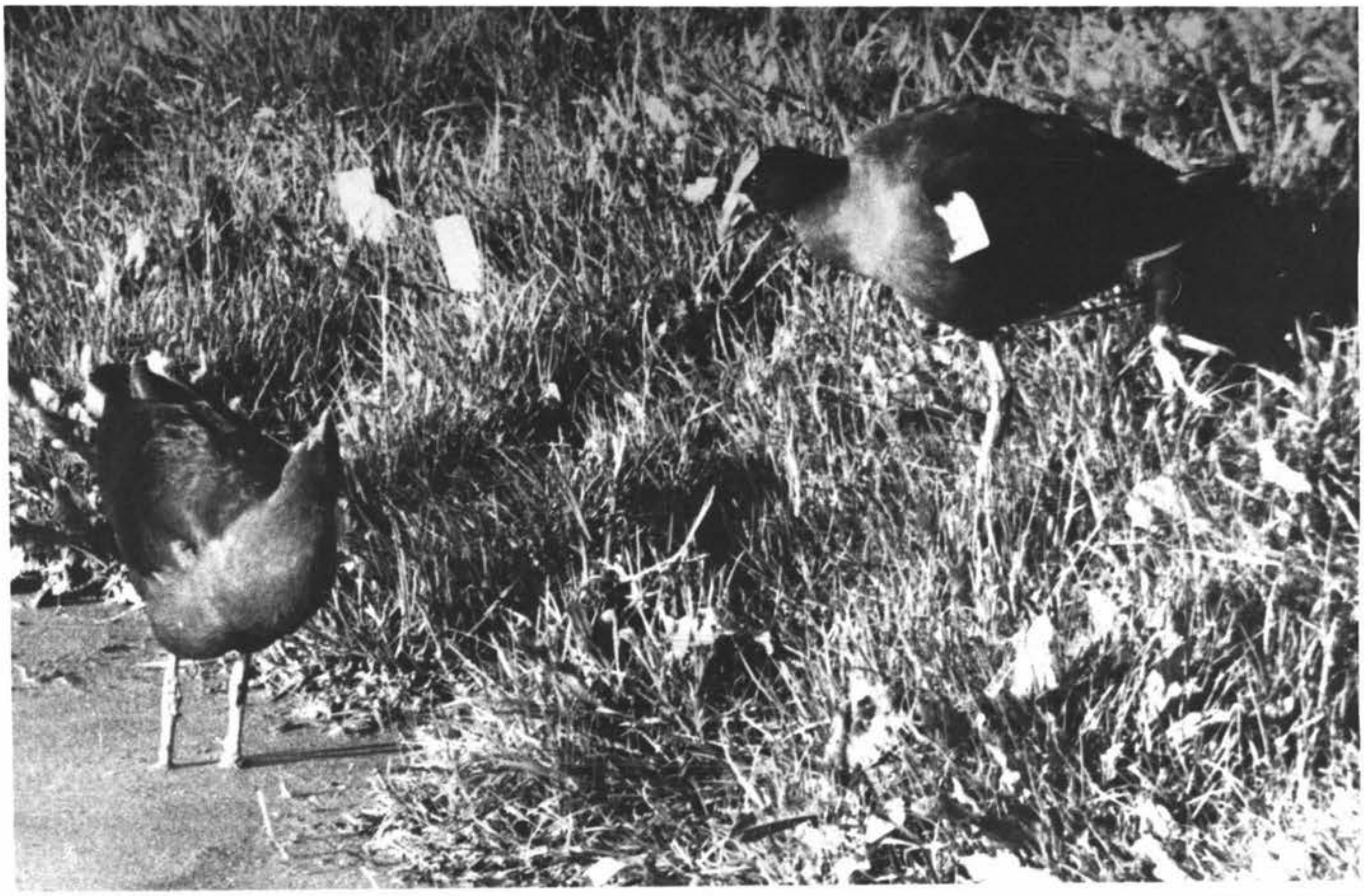
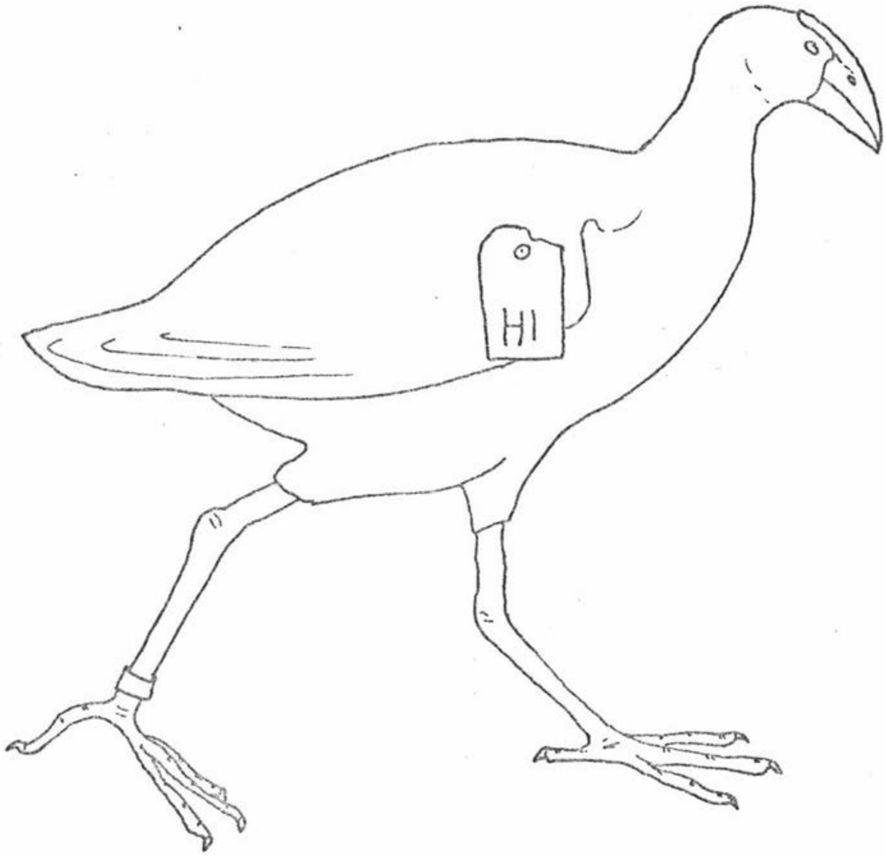


Figure 10   Head Flick and Uprights

(a) Head Flick, Wings and Tail Fully Up.

(b) 'Aggressive' Upright, Wings Fully Down Tail Horizontal.

(c) 'Anxiety' Upright, Wings and Tail Fully Up.



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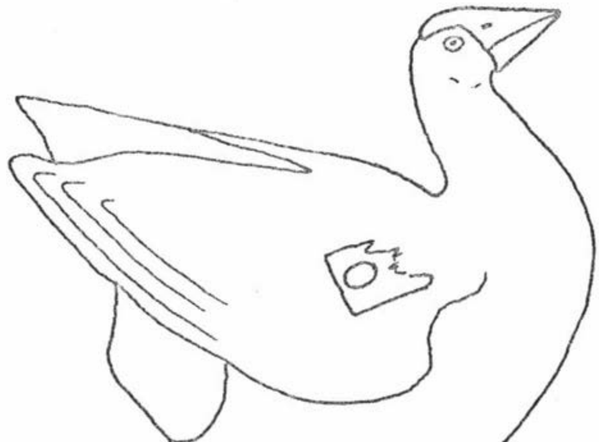

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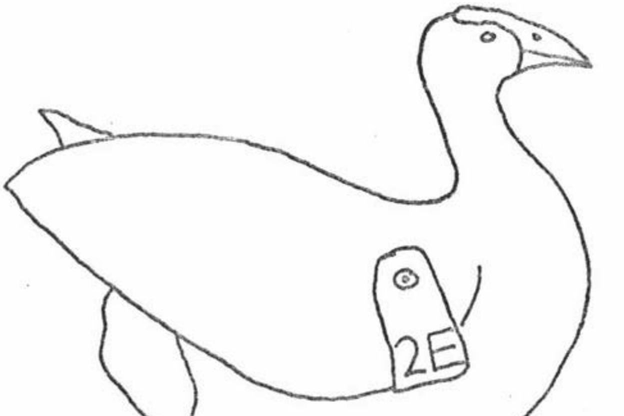


c

head tended to minimize or obliterate the opponent's view of the frontal shield.

(c) Comments: Intermediate positions between the two extremes were common. Wing and tail positions were also extremely variable but paralleled changes in head and neck postures. At the 'Anxiety' extreme, the wings and tail were usually at their extremes of elevation, but the converse usually applied at the 'Aggressive' extreme. However, most combinations of head, neck, tail, wings and feathers were possible and depended on the status of the opponent, and the distance from the opponent and/or territorial boundary. The 'Anxiety' Upright was never accompanied by Wings Out. Body feathers, especially of the back and neck, were frequently erected but the amount of fluffing was less with the more exaggerated wing postures.

3.5.7 Forward

This posture graded from the previous one and was named after the similar posture found in gulls (Tinbergen, 1959). It was extremely variable with the two extremes, Horizontal and Depressed Forward.

(a) Horizontal Forward: In the Horizontal the bill was horizontal or slightly depressed, the head and neck were held low, roughly horizontal or angled slightly above the horizontal and the neck was forward and frequently stretched. The body and vertebral column were approximately horizontal or tilted slightly forward. A bird in the Horizontal always faced directly at the opponent and so extended the red bill and frontal shield towards it. Because of the neck position, the bill and shield were surrounded and offset by the dark plumage of the bird. The bird remained completely motionless, gradually moved towards its

Figure 11

Two males in a territorial dispute. Male on the right is in an 'AGGRESSIVE' UPRIGHT, Wings and Tail Fully Up. Male on the left is in a DEPRESSED FORWARD, Wings and Tail Fully Up.

Figure 12

Tw (Northern Territory) and Aw (Southern Territory) less than 50 cm apart during territorial dispute. Tw is in a HORIZONTAL FORWARD, Wings and Tail Fully Down while Aw is in a FULL BOW, Wings and Tail Fully Up.

opponent, or charged. The posture was not usually accompanied by a call.

Wing and tail postures were variable but were usually at least Partly Up and were occasionally Out. Body feathers were almost always fluffed (Figs 12 and 13a).

(b) Depressed Forward: The main difference between this posture and the Horizontal was that the head and bill were nearer the ground but still horizontal, and the important feature was that the bill was pointed at the opponent. The vertebral column was tilted forward and down so that the body formed an angle of 20°-60° with the ground.

As in the Horizontal, a bird in the Depressed Forward almost always faced its opponent but occasionally moved slowly forward or backward, or in rapid short jerks forward. Wing and tail postures were variable but tended towards the more elevated, although all variations were possible. Body feathers were almost always fluffed (Figs 11, 13b and 14).

3.5.8 Bow

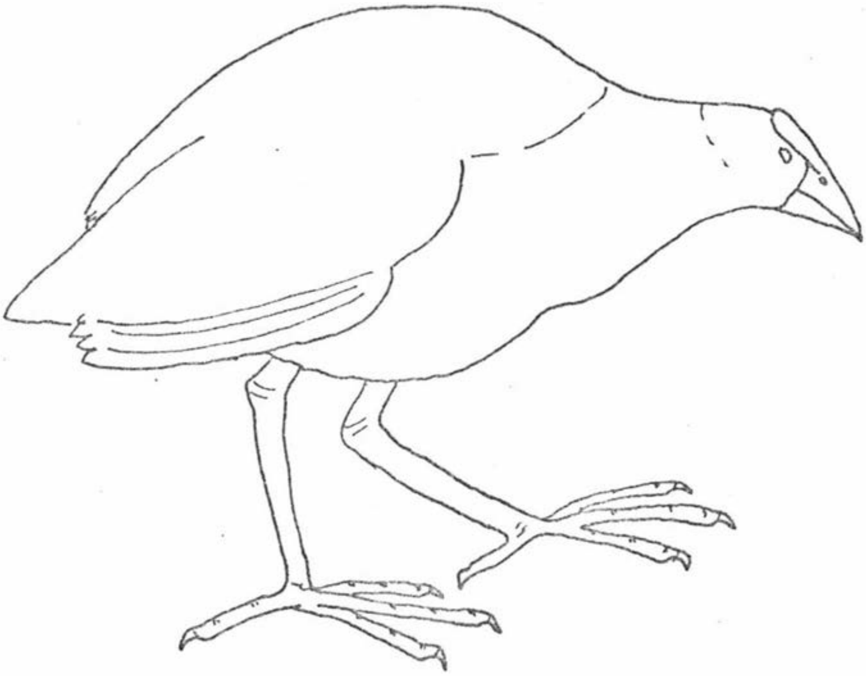
This posture was extremely variable but has been divided into three readily distinguishable units. The important unifying feature was that the bill pointed vertically downwards at the ground.

(a) Head Bow: This posture was basically similar to the Horizontal except for the important feature of beak orientation which was vertically down. This was achieved by turning the head downwards, lowering the neck and pointing the head downwards, or more rarely by arching the neck through 90° so that the bill pointed vertically downwards (Figs 15 and 18a).

Figure 13 FORWARDS

(a) Horizontal Forward Wings and Tail Fully Down.

(b) Depressed Forward Wings and Tail Fully Up.



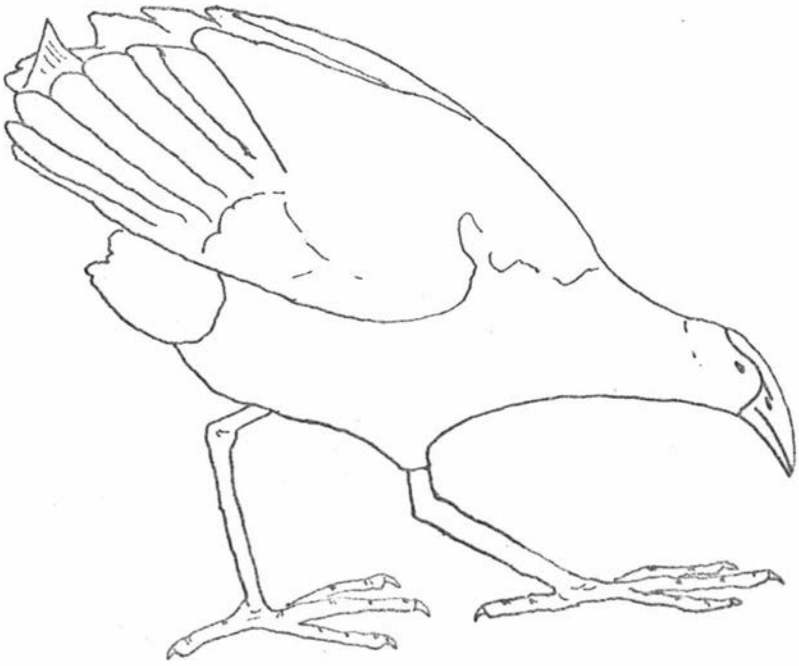


Figure 14

Ey (Southern Territory) in a DEPRESSED FORWARD, Wings and Tail Fully Up and Ew (Northern Territory - wing tag lost) in a HEAD BOW, Wings and Tail Fully Up during a boundary dispute.

Figure 15

Unbanded pukeko on the left in a HEAD BOW, Wings and Tail Fully Up, TURNING AWAY from Pw (centre) who is in a HORIZONTAL, Wings Partly Up Tail Fully Up. Bw on the right is in a FULL BOW, Wings and Tail Fully Up.

Orientation was initially frontal but in the majority of cases the bird 'Turned Away' to side on or Facing Away from the opponent.

(b) Full Bow: The bill again pointed directly at the ground or back between the legs. The vertebral column was tilted well forward with the neck held at the same angle as the body or further depressed and the body and neck formed an angle of 60^{o}-90^{o} with the ground (Figs 12, 18b and 32).

A bird in a Full Bow usually remained extremely rigid. However, occasionally one foot was repeatedly stamped on the ground or rapid 'pecking' movements occurred. An extremely low grating sound was occasionally uttered by a bird in this posture. A Dip Bow occurred where a bird was moving towards its opponent, and alternated between an Upright and a Full Bow giving the impression of rapid pecking or dipping its beak into the water.

(c) Body Bow: This posture represented the extreme form of the Bow. The vertebral column was tilted well forward almost to the vertical but also downward so that the breast rested on, or near, the ground. This meant that the neck was extended forward and like the head and beak rested on the ground. A bird in this posture was usually rigid, but if facing the other bird, frequently backed away (Figs 16, 17 and 18c).

(d) Comments: Intermediate variations between the above Bows did occur but usually only when the bird was changing from one Bow to another, and were therefore only transitory.

Wing and tail postures were variable but tended towards Fully or Extremely Up, especially in the case of Full and Body Bows. The wings were never Out and, body feathers were rarely fluffed.

Figure 16

Kw (β male, Hide Territory) in a BODY BOW, Wings and Tail Fully Up backing away from H1w (α male) who is approaching in a HORIZONTAL FORWARD, Tail Horizontal.

Figure 17

Bw (β female, Northern Territory) in a BODY BOW, Wings and Tail Fully Up as Tw (β male) approaches in an 'AGGRESSIVE' UPRIGHT, Wings and Tail Fully Down.

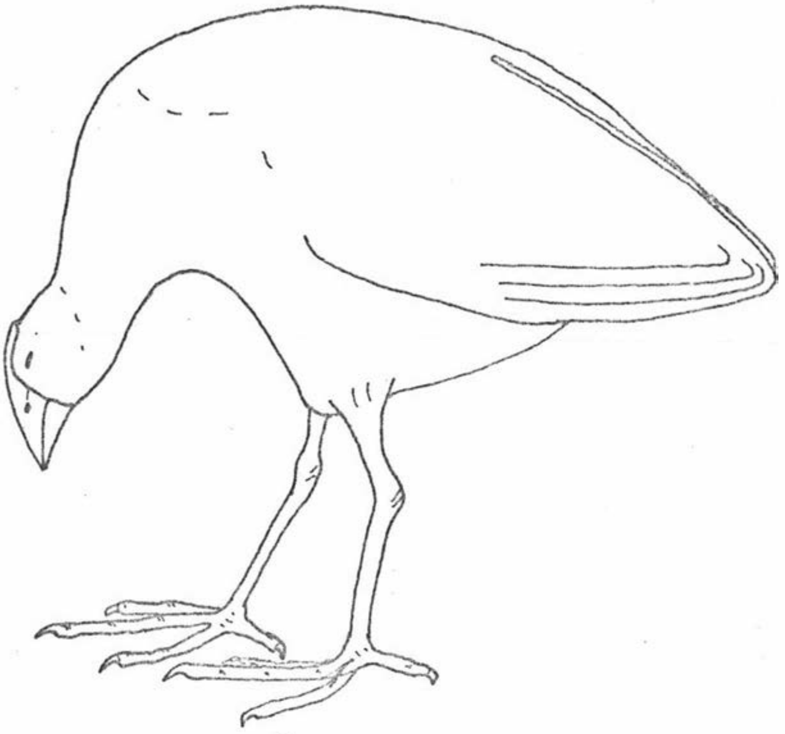

B

Figure 18 Bows

(a) Head Bow, Wings Partly Up

(b) Full Bow, Wings and Tail Fully Up

(c) Body Bow, Wings Exaggerated Up Tail Fully Up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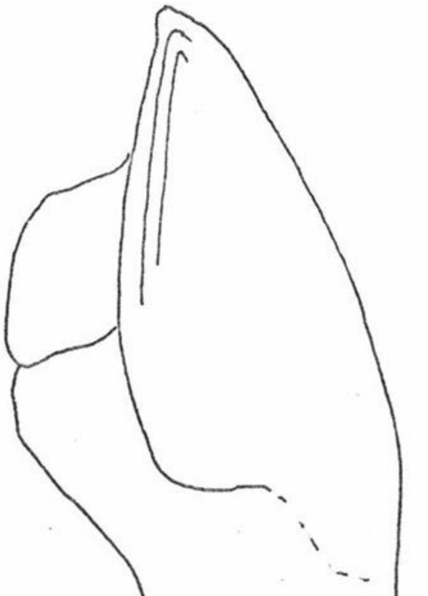
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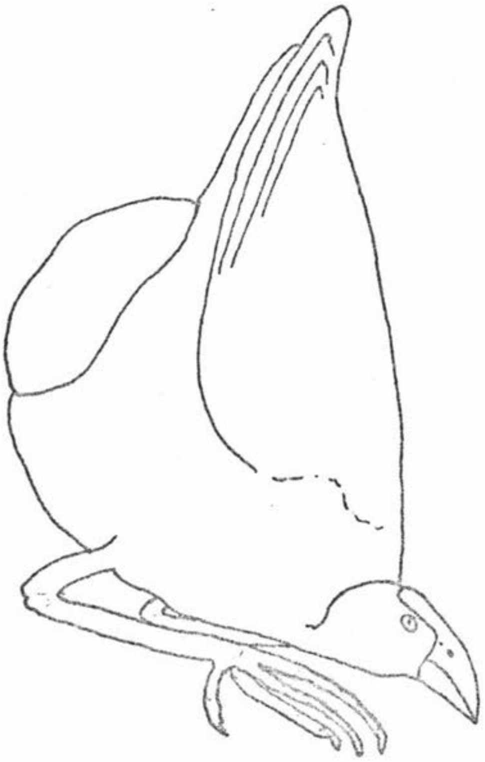
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3.5.9 Crouch

The head and bill were horizontal or depressed and even partly tucked under the body, the body feathers were sleeked and the bird crouched lower and lower, with the neck withdrawn and hunched. Wings were held close to the body and the tail position was variable but usually down. Orientation was extremely variable. This posture nearly always involved birds of very low status, or juveniles, in which case the posture was accompanied by very loud juvenile 'miaow' calls (Fig. 19).

3.5.10 Facing Away

In this simple movement, the bird merely turned its head and bill away from the other bird. The reacting bird was at any orientation to its opponent but the head was always turned away from the opponent. The important point was the removal of the bill and shield from view.

Facing Away occurred in many of the above postures but was more common in the Bow, Depressed Forward, Crouch, Headflick and Upright. Facing Away almost always preceded 'Turning Away' where the bird turned from its frontal orientation prior to 'Moving Away' (Fig. 20). Wing and tail postures were usually well raised and frequently Wings Extremely Up.

3.5.11 Head Flagging

This was alternate Facing Away to either side of the body and usually occurred when birds were facing each other. This only occurred in Bows and the Crouch.

3.5.12 Erect Hunch

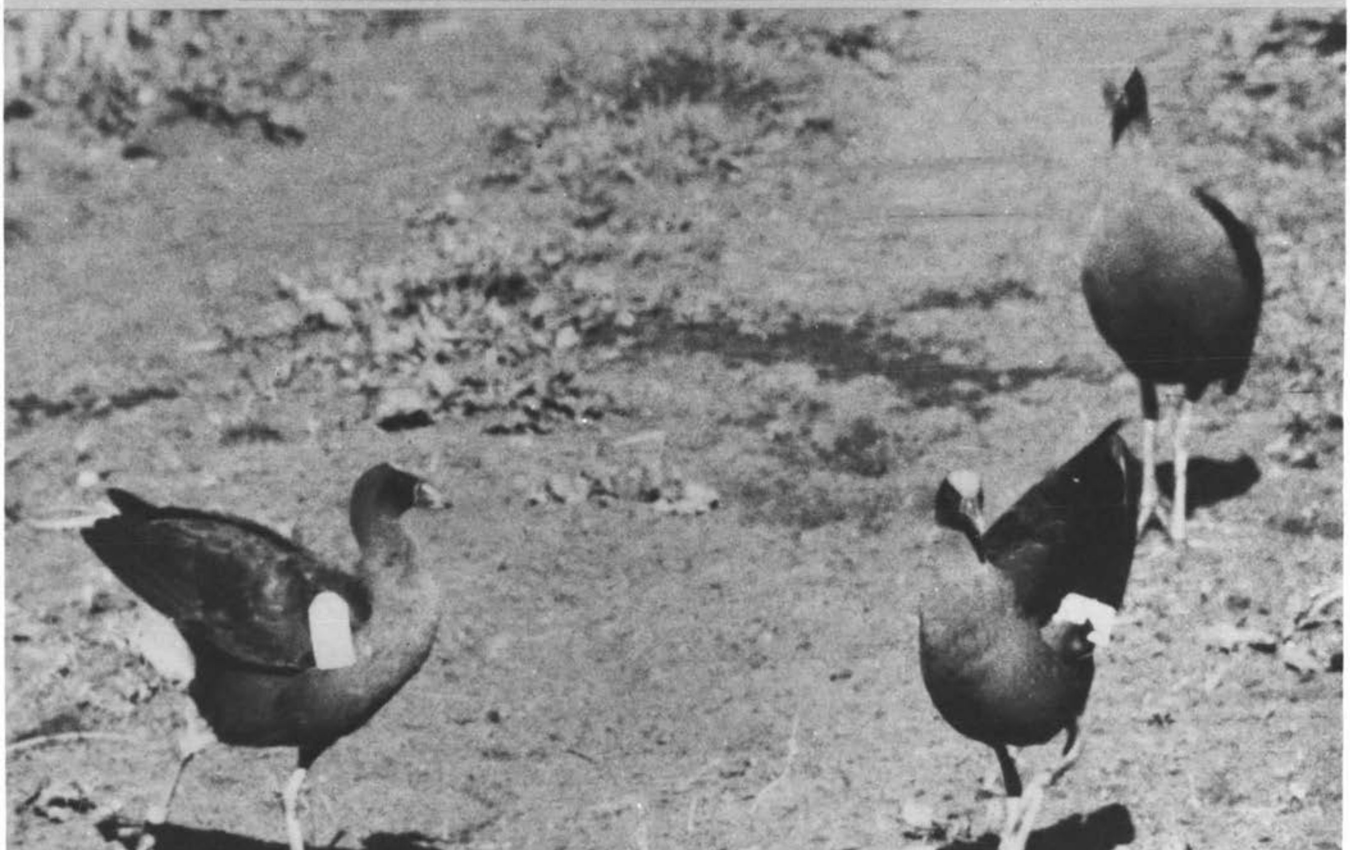
In this position, the head and beak were depressed and the neck was hunched, the vertebral column was held almost vertical with the wings close to the body and the legs well spread. Orientation was always away from the opponent. The tail was depressed and the bird usually shuffled away from the other bird. The bird appeared hunched and its head and

Figure 19

An adult male in an 'AGGRESSIVE' UPRIGHT standing over a juvenile (note narrow culmen) which is CROUCHING.

Figure 20

Pukeko on the right starting to FACE AWAY from the left hand bird which is in an 'AGGRESSIVE' UPRIGHT. Note the lower ranking bird in the background in an 'Aggressive' Upright and that the wings of the bird Facing Away are more elevated than the bird in the 'Aggressive' Upright.



beak were hidden from the opponent. The posture closely resembled the pre-copulatory posture of the female differing only in its extreme vertical stance (Figs 21 and 23a).

3.5.13 Wings Expanded Hunch

This posture differed from the preceding one only in the position of the wings. In the extreme case the primaries were fully extended and expanded. The bird occasionally 'looked over its shoulder' while in this posture and only if the opponent had moved did it drop the posture (Figs 22 and 23b).

3.5.14 Wings Drooped

A bird in the Wings Drooped posture differed from the normal feeding posture only in the position of the wing primaries, which were drooped and hung beside the body. Orientation was always side on. Only dominant males were observed in this posture and no bird reacted aggressively toward it while this posture was held (Fig. 26).

3.5.15 Wing Clap

The bird giving a Wing Clap was usually in an Upright. Orientation was variable and the posture was rarely given by an isolated bird. The wings were partly spread and rapidly lifted to meet above the back. The posture was accompanied by a loud call with every clap. The wing clap was also used interspecifically and appeared to function in leading a predator from the nest or young. Birds wing clapping in this situation gave the impression of losing balance and gradually led the predator from the nest, but the birds did not feign injury.

3.5.16 Escape

Various forms of pure escape behaviour occurred.

(a) Move Away: This was a very broad category of behaviour in which the essential element was that the bird moved away from its opponent. Body

Figure 21

Male pukeko (Aw) in an ERECT HUNCH as viewed from the side.

Figure 22

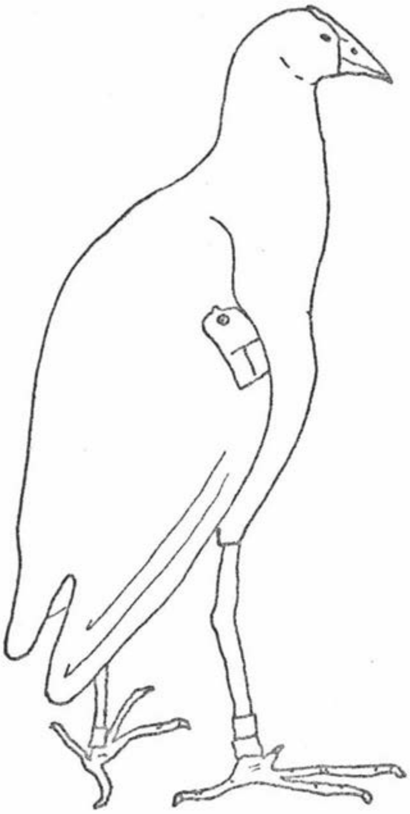
Pukeko in a WINGS EXPANDED HUNCH during a territorial dispute as viewed by its opponent.

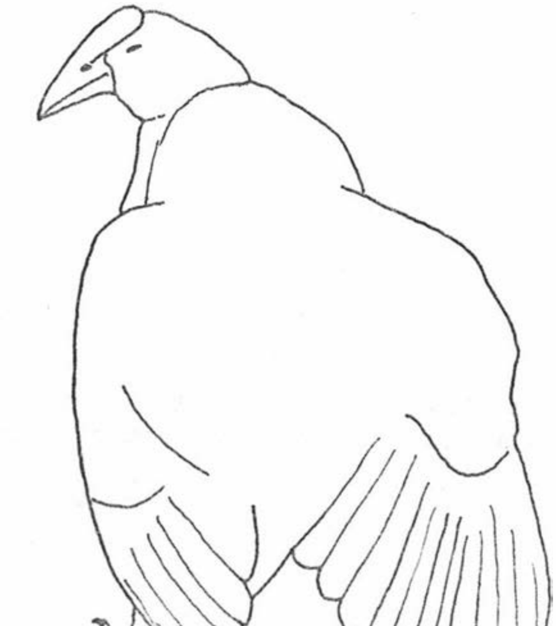

A

Figure 23 Hunch Postures

(a) Erect Hunch

(b) Wings Expanded Hunch





position usually depended on the posture held prior to moving away. For example, a bird in a Bow usually moved away with its beak still held near the ground and only slowly raised it as it moved further from its opponent. The one factor common to all displays grouped under Moving Away was the high elevation of Wing and/or Tail position. Because the tail was the feature most obvious to the opponent, it was considered justified to group all variations of the posture regardless of head and bill position which were hidden from the opponent (Figs 24 and 25).

(b) Splatter Escape: This was identical to the Splatter Charge with the exception of orientation which was away from the other bird.

3.5.17 Grass Pulling

On four occasions in a territorial dispute where both birds were facing each other in Forwards, one bird (*Ey* in three cases) was seen to peck violently into a flattened Carex clump immediately in front of it and then throw the resultant beakful of grass to one side and backwards. The number of times this action occurred in each case varied from one to four. In all cases this bird then retreated.

3.6 Sexual and Courtship Behaviour

3.6.1 Allo-preening (Cullen, 1963)

Pukeko are unable to preen their own head and neck but this was frequently done by other members of the group. The bird wishing to be preened usually presented itself in the form of a Bow, with eyes closed. Facing Away was frequently involved. The position of wings and tail and the form of Bow of the presenting bird depended on the status of the bird. The more elevated the wings and tail were, the lower the status of the bird. Only the lowest ranking birds assumed a body bow; all others adopted a full bow.

Figure 24

Two male pukeko MOVING AWAY, Wings and Tail Fully Up in response to the male on the left from the adjacent territory who is in a HORIZONTAL FORWARD, Wings Fully Down.

Figure 25

Pukeko MOVING AWAY WINGS EXAGGERATED UP, Tail Fully Up.

Orientation was variable but usually frontal (Fig. 27).

3.6.2 Courtship Feeding

Postures were similar to Allo-preening but eyes were always open. Orientation was always frontal and wings and tail were normally down. Actual passing of food, usually small pieces of duck weed, occurred only when the birds were standing in water. Much courtship feeding appeared purely symbolic with the two birds standing beak to beak 'nibbling'. Passage of 'food' was usually from male to female, although female to male or female to female did occur (see p. 163).

3.6.3 Sexual Upright

This posture resembled the 'Aggressive' Upright with the beak strongly depressed. The neck was usually elongated and the posture was accompanied by a Humming call. A male in this posture walked towards the female with a high stepping gait and then followed behind her. Wings and tail were always down (Figs 28 and 47).

3.6.4 Sexual Forward

This posture usually followed the 'Sexual' Upright. The head and neck were withdrawn, the beak depressed, and the male's body was held slightly above the horizontal. The same Humming Call was given (Fig. 47).

3.6.5 Precopulatory Hunch

This posture of the female varied little from the Erect Hunch except that the vertebral column was held at a more horizontal angle (Figs 28 and 47).

3.6.6 Precopulatory Position

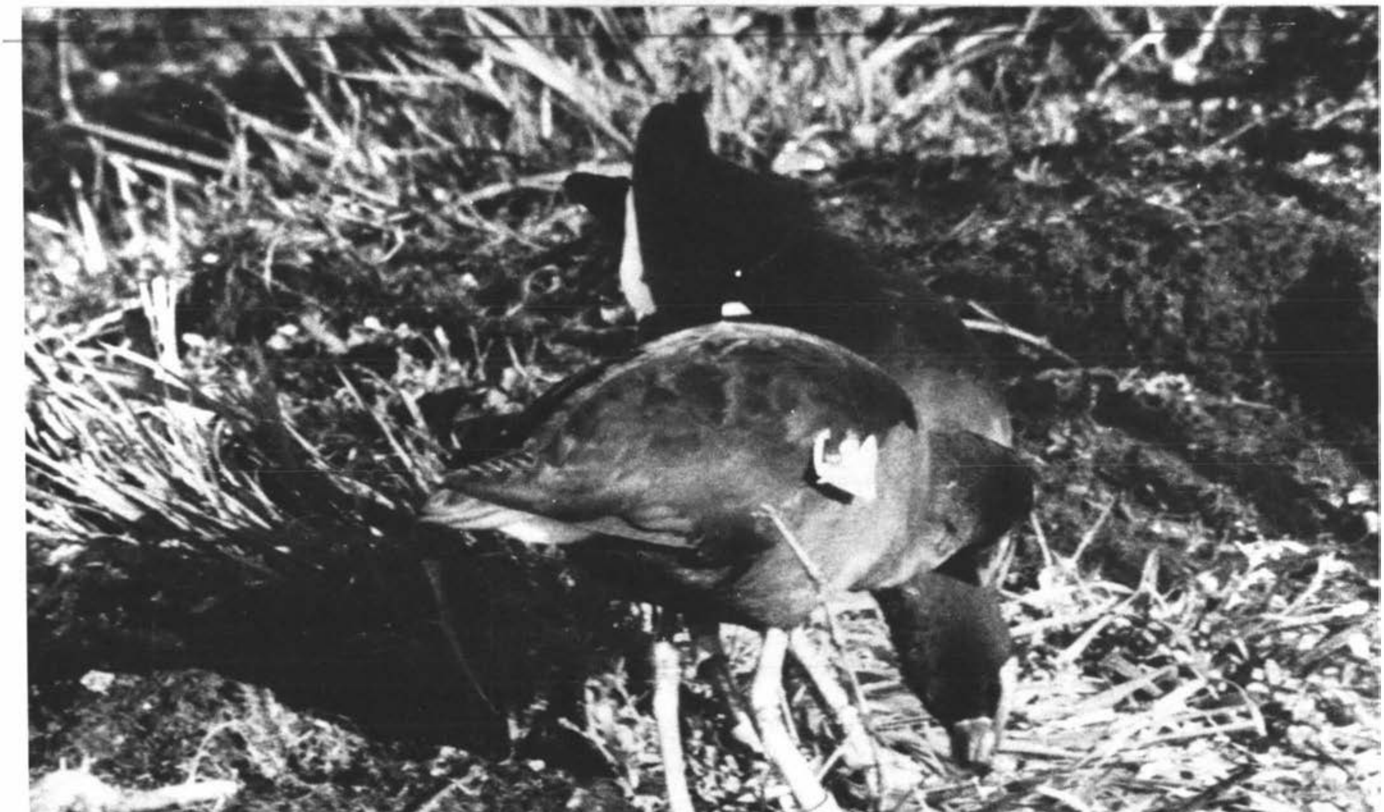
This graded from the Hunch. The neck was elongated and curved downwards with the head pointing at the ground, and the wings were held out from the body but the primaries remained closed. As the male mounted, the head and neck

Figure 26

Dominant male standing in territorial boundary zone with WINGS DROOPED.

Figure 27

COURTSHIP ALLOPREENING. Note the presenting bird is in a Bow with eyes closed.



were pointed back between the legs and the body was inclined until horizontal (Figs 29 and 30).

3.6.7 Copulation

The male typically placed one foot on the back of the female and mounted still giving the Humming Call. He then trod the back of the female and slowly lowered until his metatarsi lay on either side of the female's back. The toes appeared to curl over the front edge of the female's partly extended wings. The male, flapping his wings to help maintain balance, slowly became vertical, the female raised her tail, and the male side-swiped his tail attaining cloacal contact and ejaculating (Fig. 30). The male then dismounted over the head of the female with Wings and Tail Fully Up (Fig. 31).

3.7 Chick Postures

3.7.1 Food Begging

This posture was adopted by chicks and juveniles attempting to solicit food from older birds. The young bird was in a crouched hunch posture with head and neck extended horizontally forward, with the wings held at right angles from the body and rapidly twirled. A soft begging call was given and Head Flagging could also occur. The food when offerred was taken from the edge or tip of the adult's bill.

3.8 Quantitative Analysis

With the various behaviour patterns now described in isolated units, it is necessary to demonstrate interrelationship between them and thus determine their signal function. Then by determining common components of linked displays, form an overall pattern of the components important in aggression and in escape.

Figure 28

Male in a SEXUAL UPRIGHT with beak open giving the Humming Call approaching a female in a PRECOPULATORY HUNCH.

Figure 29

A male still giving the Humming Call MOUNTING a female in the PRECOPULATORY POSITION.

Figure 30

Cloacal contact during a copulation. Male is flapping wings to retain balance and has his tail to the side, female has her beak back between her legs.

Figure 31

Male in POSTCOPULATORY POSITION with Wings Exaggerated Up Tail Fully Up as he steps off the front of the female after copulation. Female still has tail fully raised but not expanded as when used in submissive display.

3.8.1 Intergroup Spacing Behaviour

(a) Sequential Ordering of Displays by a Single Bird:

Temporal correlation of the different displays of a bird involved in territorial defence was obtained by recording the frequency with which one display preceded another in any bird. Territorial displays of all adult birds regardless of sex and age were combined but because males were responsible for the greater proportion of territorial defence (see p. 137) the displays of males form the greater part of the sample (Table 5). Apart from this, no differences were observed in the display sequences of males and females. The analysis excludes incomplete records and some made early in the study. Statistical analysis follows Davies (1963) where if the expected value differed from the observed by more than three times its own square root, the difference was taken as significant. (This approximates to a probability level of 0.01.) A positive significant link demonstrates that postures followed each other more often than expected at random and hence the postures were of similar motivation.

Displays did not occur at random (Table 5) but a large number of significant links (both positive and negative) occurred between displays. The main positive trends are illustrated in Fig. 32. Starting from the most commonly observed posture (from Tables 5,8,14+15), the 'Aggressive' Upright, there are three main sequences: two of these end in pure escape and therefore include increasing elements of escape. One sequence leads to an 'Anxiety' Upright and then to Moving Away. The second and longer integrated sequence of displays leads from the 'Aggressive' Upright to a Horizontal Forward to a Depressed Forward to a Bow to Moving Away. The

Table 5

SEQUENTIAL ORDERING OF TERRITORIAL DISPLAYS OF A SINGLE BIRD

(The expected value is given below the observed value.)

FOLLOWING DISPLAY

PRECEDING DISPLAY

	Fight	Splat.	Charge	Anx. Up.	Agg. Up.	Horiz. Fwd	Depr. Fwd	Head Bow	Full Bow	Body Bow	Face Away	Erect Hunch	Exp. Hunch	Move Away	Splat. Away	Wings Droop	Total
Fight		1 4.56	3 6.18	– 2.77	35 * 9.33	10 15.30	4 10.69	– 2.93	1 10.09	– 0.11	– 0.11	– 2.60	– 1.19	34 26.96	6 * 0.81	– 0.38	94
Splatter	3 1.47		– 1.70	– 0.76	1 2.56	4 4.19	1 2.93	– 0.80	– 2.77	– 0.03	– 0.03	– 0.71	– 0.33	17 * 7.39	– 0.22	– 0.10	26
Charge	19 17.75	80 15.06		9 9.14	36 30.84	85 * 50.56	6 + 35.32	– + 9.68	11 + 33.35	– 0.35	– 0.36	2 8.61	– 3.94	59 + 89.10	– 2.69	1 1.25	308
'Anxiety' Upright	– 4.22	– 3.58	1 4.36		5 7.34	– + 12.03	– 8.41	– 2.30	2 7.94	– 0.08	– 0.09	3 2.05	– 0.94	65 * 21.21	– 0.64	– 0.30	76
'Aggressive' Upright	32 19.38	3 + 16.45	56 * 22.32	37 * 9.98		98 * 55.21	19 + 38.57	16 10.57	21 36.42	– 0.39	– 0.39	– + 9.40	– 4.31	43 + 97.30	– 2.94	– 1.37	325
Horizontal	22 22.23	– + 18.86	9 + 25.59	4 11.45	35 38.62		149 * 44.23	36 * 12.12	66 * 41.76	– 0.45	1 0.45	3 10.78	– 4.94	23 + 111.58	– 3.37	– 1.57	348
Depressed Forward	16 10.66	– 9.04	– + 12.27	1 5.49	11 18.52	22 30.36		2 5.81	79 * 20.02	– 0.22	– 0.22	4 5.17	– 2.37	41 53.50	– 1.61	– 0.75	176
Head Bow	– 2.95	– 2.50	– 3.40	– 1.52	– 5.13	7 8.41	4 5.87		– 5.54	– 0.06	– 0.06	3 1.43	1 0.66	38 * 14.82	– 0.45	– 0.21	53
Full Bow	– + 10.59	– 8.98	– + 12.19	– 5.45	– + 18.39	8 + 30.15	8 21.06	– 5.07		2 * 0.21	– 0.21	6 5.13	1 2.35	151 * 53.14	– 1.60	– 0.75	176
Facing Away	–	–	–	–	–	1	–	–	–	–		–	–	–	–	–	1
Erect Hunch	– 2.11	– 1.79	– 2.43	– 1.09	3 3.66	3 6.01	– 4.20	– 1.15	1 3.96	– 0.04	– 0.04		19 * 0.47	12 10.59	– 0.32	– 0.15	38
Expanded Hunch	– 1.20	– 1.02	3 1.39	– 0.62	3 2.09	3 3.43	1 2.39	– 0.66	– 2.26	– 0.02	1 0.02	– 0.58		11 6.04	– 0.18	– 0.08	22
Move Away	5 12.61	– + 10.70	31 * 14.52	– 6.49	41 * 21.90	40 35.91	5 + 25.09	– 6.88	5 + 23.69	– 0.25	– 0.25	27 * 6.11	1 2.80		9 * 1.91	6 * 0.89	170
Splatter Away	2 0.44	– 0.37	– 0.50	– 0.22	2 0.76	1 1.24	– 0.87	– 0.24	– 0.82	– 0.01	– 0.01	– 0.21	– 0.10	3 2.19		– 0.03	8
Wings Drooped	– 0.60	– 0.51	11 * 0.69	– 0.31	– 1.04	– 1.70	– 1.19	– 0.33	– 1.12	– 0.01	– 0.01	– 0.29	– 0.13	– 3.00	– 0.09		11
Total	99	84	114	51	172	282	197	54	186	2	2	48	22	497	15	7	1832

Statistical test following Davies 1963

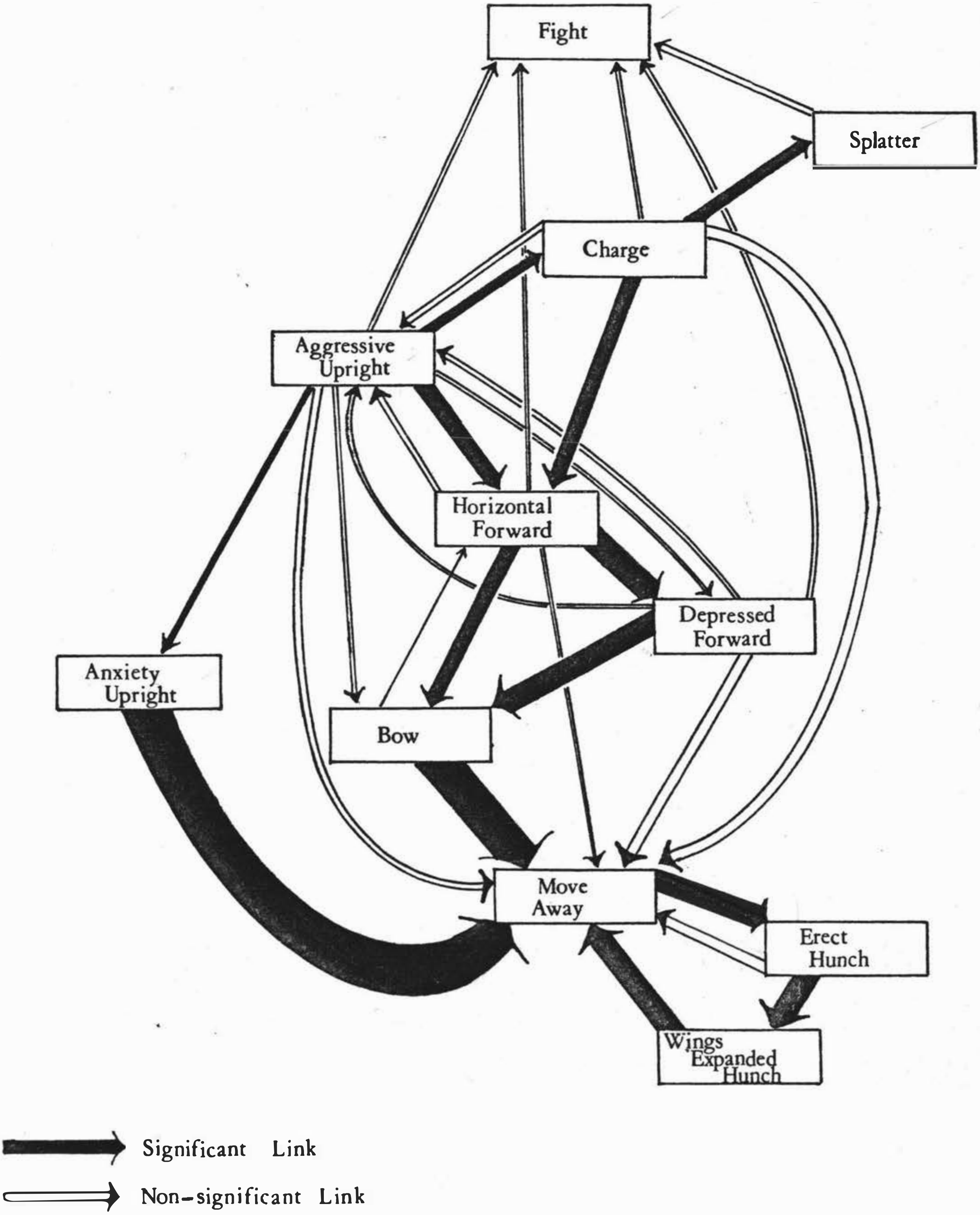
‖ * ‖ = positive significant difference

\+ = negative significant difference

Figure 32 Flow Diagram of Display Sequences during a Territorial Dispute

The proportion of any display which led to any other is represented by the width of the connecting arrows.

(For simplicity, displays and non-significant links observed less than 15 times are omitted.)


Fight
Splatter
Charge
Aggressive Upright
Horizontal Forward
Depressed Forward
Anxiety Upright
Bow
Move Away
Erect Hunch
Wings Expanded Hunch
Significant Link
Non-significant Link

positive link between Horizontal and Bow shows that the Depressed Forward may be by-passed.

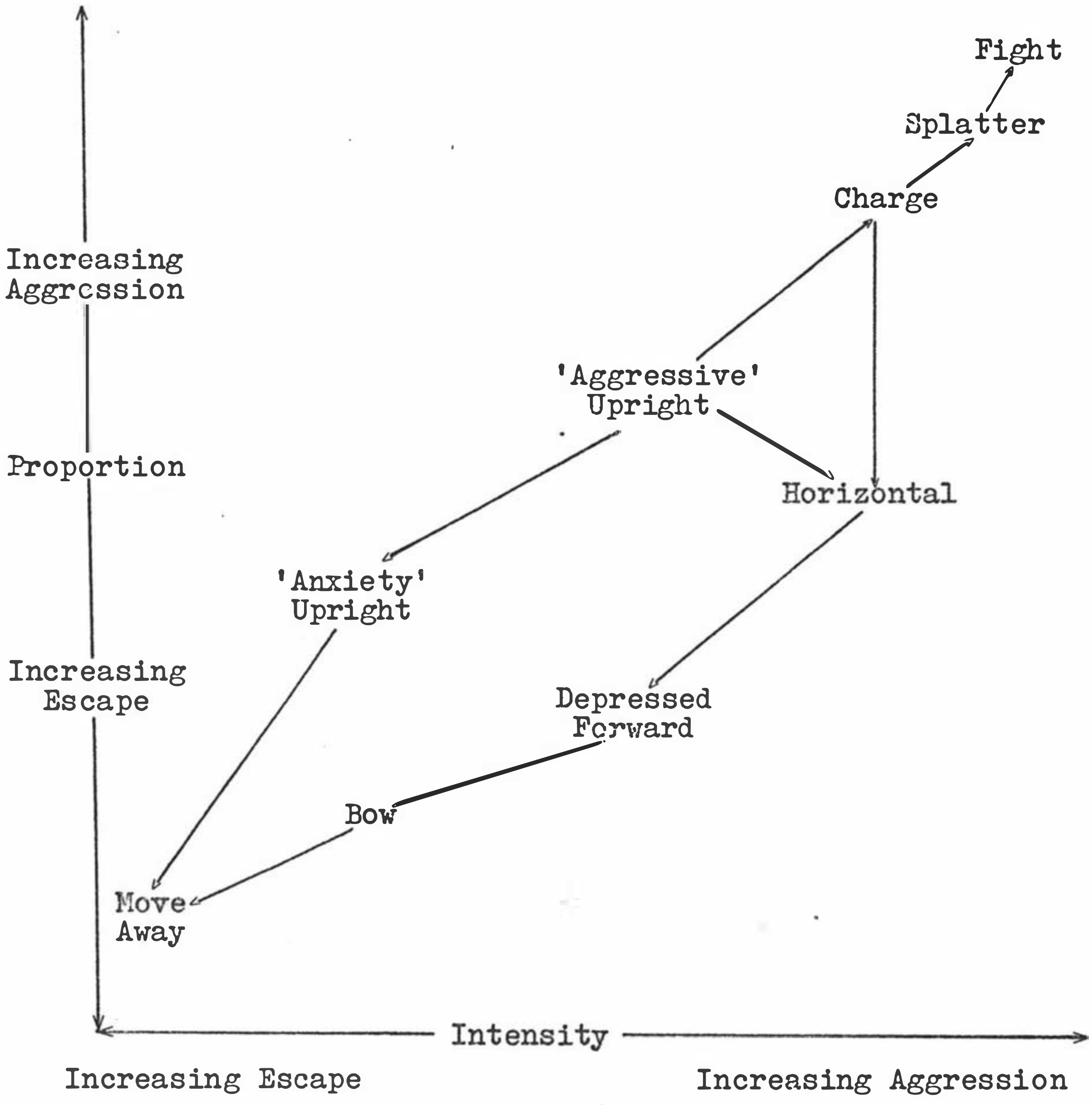
Both of these sequences involve changes in the position of the head so that it becomes increasingly less orientated for pecking and more hidden from the opponent. The first line of 'Aggressive' to 'Anxiety' Upright to Move Away involves a lifting of the head to remove the bill and shield from the opponent's view. The second more complex sequence involves a progressive lowering of the head. This does not remove the bill and shield from the opponent's view, but puts the bird in an increasingly difficult position for pecking, until the bird finally Turns Away and Moves Away. However, it should be noted that the lowering of the head also takes the head nearer the opponent, suggesting a greater aggressive tendency as well as the increased escape tendency. This increased aggressive tendency is also demonstrated by the negative links between Horizontal and Move Away.

A third sequence of displays leads from the 'Aggressive' Upright to the Charge and then to the Splatter. This series involves increasing speed of movement towards the opponent and thus an increasingly aggressive tendency. The significant link between Charge and Horizontal shows that the 'Aggressive' Upright can be by-passed and also adds further evidence of the highly aggressive content of the Horizontal. These main postural sequences can be summarized in a motivational hierarchy (Fig. 33).

Apart from these main display sequences, a number of smaller significant links between displays can be found. An extension to the main sequence involves the Erect and Wings Expanded Hunch. Moving Away led significantly more times than expected to an Erect Hunch which then led to the

Figure 33 Motivational Hierarchy of Territorial Displays of Pukeko

Most displays appear to be the outcome of conflict between tendencies to attack and to escape. To demonstrate the inter-relation of these tendencies the proportion and intensity of these tendencies are plotted against each other.



Wings Expanded Hunch. A positive link also exists between Moving Away and Splatter Away which is only to be expected as this involves increasing movement away from the opponent i.e. higher escape tendency.

Move Away also has expected positive significant links with more aggressive displays, because Moving Away must lead the bird further back into its own territory where it is more likely to act aggressively, thus starting a new sequence. For this reason these are not shown in Fig. 32. Similarly the large number of Move Aways following a Splatter Charge is likely if the Splatter took the bird past its boundary, especially when more than two birds were interacting. Negative significant links add further evidence to the above interpretation by demonstrating the infrequency with which highly aggressive displays led to displays with high escape tendencies.

Wing and tail postures are disregarded in Table 5 for simplicity. However, because the wings and tail form an important part of most postures, it is necessary to investigate these as well. There are several ways of doing this, but now that the postures have been arranged in a motivational hierarchy, it is easier to compare the wing and tail postures of each display.

Tabulation of the frequency of the different wing and tail postures seen in each display (Table 6) shows an increasing frequency of the more elevated wing and tail positions with increasing escape motivation of the display. Thus the more aggressive the display, the more likely it is to be accompanied by low wing and tail postures while the higher the escape tendency, the more likely a bird's wings and tail will be elevated.

Table 6

FREQUENCY OF WING AND TAIL POSTURES SEEN IN EACH DISPLAY (ONE BIRD)

Posture	% Frequency of Posture Seen With					n
		Tail Up				
	Tail Down	Wings Down	Wings Partly Up	Wings Fully Up	Wings Exaggerated Up	
Charge	24.0	7.1	21.2	31.3	16.4	422
'Aggressive' Upright	6.9	5.6	22.8	18.1	46.7	497
Horizontal Forward	2.5	1.1	29.3	31.2	35.9	630
Depressed Forward	1.1	0.5	3.0	53.0	42.4	373
Bow	0	1.1	2.3	43.7	52.9	471
'Anxiety' Upright	0	1.6	1.5	20.5	76.4	127
Moving Away	0.1	1.4	0.6	10.7	87.2	667

Note: where the wings are up, the tail is also up, and with increasing raising of the wings, more of the white undertail is exposed.

The high frequency of Wings Exaggerated Up but low frequency of Wings Fully Up in the 'Aggressive' Upright may have been partly due to observational errors. Either some of the Wings Fully Up could have been interpreted as Wings Exaggerated Up or some Wings Exaggerated Up 'Aggressive' Uprights could have been Wings Exaggerated Up 'Anxiety' Uprights. The latter is a probable explanation because it is less likely that a highly aggressive bill position would be accompanied so frequently with the most extreme wing position which appears from Table 6 to show a high escape tendency. Thus some of the 46.7% of the 'Aggressive' Uprights seen with Wings Exaggerated Up were probably 'Anxiety' Uprights or intermediates.

Further evidence for the motivational state underlying the different wing and tail positions can be obtained from the frequency with which one posture led to another with a higher escape tendency and

(i) a higher wing and tail posture, or

(ii) a lower wing and tail posture.

This is given in Table 7 and as expected from the results of Table 6, (i) was more frequent than (ii).

(b) Sequential Ordering of Displays Between Birds: Further evidence for the motivational basis of displays can be obtained from the 'effect' of a display in a territorial dispute. By scoring the display of any bird elicited by a given display of another bird, it is possible to obtain a measure of the 'effectiveness' of any display and thus confirm or disprove the previously calculated motivational basis of the displays (Table 8). On the assumption that the previous motivational hierarchy is correct, it would be expected that

Table 7

WING AND TAIL POSITIONS ASSOCIATED WITH A CHANGE TO A DISPLAY OF HIGHER ESCAPE MOTIVATION

Posture	Subsequent Posture of Higher Escape Motivation With			Sample Size
	Lower Wings and Tail	Same Wings and Tail	Higher Wings and Tail	
Charge	3.4%	40.7%	56.3%	206
'Aggressive' Upright	3.4%	73.1%	23.5%	234
Horizontal Forward	1.8%	78.1%	20.1%	274
Depressed Forward	1.6%	74.3%	23.8%	122
Bow	0.5%	60.3%	39.2%	189
'Anxiety' Upright	0%	76.9%	23.1%	65

Table 8

SEQUENTIAL ORDERING OF DISPLAYS BETWEEN BIRDS IN TERRITORIAL DISPUTES

(The expected value is given below the observed value.)

DISPLAY OF SECOND BIRD

DISPLAY OF FIRST BIRD	Fight	Charge	Anx. Up.	Agg. Up.	Horiz. Fwd	Depr. Fwd	Head Bow	Full Bow	Body Bow	Face Away	Erect Hunch	Exp. Hunch	Move Away	Splat. Away	Crouch	Total
Fight	45 * 1.11	– 1.05	– 0.85	– 3.60	– 6.36	– 3.06	– 1.24	– 4.11	– 0.23	– 0.14	– 1.07	– 0.89	1 + 20.27	– 1.88	– 0.14	46
Splatter	– 2.38	– 2.25	– 1.83	– 7.74	– 13.69	– 6.59	– 2.68	– 8.85	– 0.51	– 0.30	– 2.30	– 1.91	4 43.63	95 * 4.04	– 0.30	99
Charge	– + 11.02	10 10.43	7 8.46	32 35.80	21 + 63.35	8 + 30.49	2 12.39	8 + 40.92	– 2.36	– 1.38	6 10.62	2 8.85	362 * 201.85	– 18.69	– 1.38	458
'Anxiety' Upright	– 0.07	1 0.07	– 0.06	1 0.23	– 0.41	– 0.20	– 0.08	– 0.27	– 0.02	– 0.01	– 0.07	– 0.06	1 1.32	– 0.12	– 0.01	3
'Aggressive' Upright	7 18.06	19 17.10	31 * 13.87	110 * 58.71	105 103.88	32 50.00	21 21.32	55 67.10	10 3.87	7 2.26	20 17.42	12 14.52	315 330.98	– + 30.65	7 * 2.26	751
Horizontal Forward	– + 12.97	13 12.27	2 9.96	18 + 42.14	164 * 74.55	65 * 35.89	26 14.59	75 * 48.16	2 2.78	– 1.62	18 12.50	18 10.42	138 + 237.55	– + 22.00	– 1.62	539
Depressed Forward	4 4.84	4 4.58	3 3.71	12 15.71	15 27.80	49 * 13.38	9 5.44	48 * 17.96	– 1.04	– 0.60	6 4.66	3 3.89	50 + 88.59	– 8.20	– 0.60	201
Head Bow	– 0.22	– 0.20	– 0.17	– 0.70	1 1.24	– 0.60	5 * 0.24	2 0.80	– 0.05	– 0.03	– 0.21	– 0.17	1 3.97	– 0.37	– 0.03	9
Full Bow	– 1.68	– 1.59	– 1.29	7 5.47	2 9.68	3 4.66	– 1.89	18 * 6.25	– 0.36	– 0.21	1 1.62	– 1.35	39 30.85	– 2.86	– 0.21	70
Body Bow	–	–	–	–	–	–	–	–	–	–	–	–	3 1.32	–	–	3
Erect Hunch	– 0.24	1 0.23	– 0.18	– 0.78	– 1.38	– 0.67	– 0.27	– 0.89	– 0.05	– 0.03	1 0.23	4 * 0.19	4 4.41	– 0.41	– 0.03	10
Expanded Hunch	– 0.51	– 0.48	– 0.39	– 1.64	– 2.90	– 1.40	– 0.57	– 1.88	– 0.11	– 0.06	– 0.49	6 * 0.41	15 9.26	– 0.86	– 0.06	21
Move Away	– 2.84	5 2.69	– 2.18	2 9.23	14 16.32	– 7.86	– 3.19	2 10.54	– 0.61	– 0.35	2 2.74	– 2.28	93 * 52.11	– 4.82	– 0.35	118
Total	56	53	43	182	322	155	63	208	12	7	54	45	1026	95	7	2328

Statistical analysis following Davis, 1963.

‖ * ‖ = positive significant difference

\+ = negative significant difference

in a territorial dispute, the first bird to act would assume a posture of highly aggressive motivation and the responding bird would adopt a display of higher escape motivation. But where a dispute was more closely contested, the postures adopted by the two birds would be more equally motivated. Thus significant links would be expected

(i) between highly aggressive displays by the first bird and highly submissive displays by the second bird and

(ii) between displays of similar motivation.

The data bear out these expectations.

A good measure of the aggressive content of a given posture can be obtained, therefore, from the frequency that the display was seen to elicit escape (Move Away or Splatter Away) in the other bird. The results (Table 9) are as expected and show the highest frequency of escape was elicited by the Splatter Charge and the lowest by the Bow and 'Anxiety' Upright.

A second measure of the effectiveness of any one display can be obtained by calculating the frequency with which an opponent was observed to reply in a display of higher escape motivation. These results (Table 10) confirm the previously calculated motivational hierarchy.

Just as evidence for the motivational basis of displays has been obtained from the effect of the display in a territorial dispute, so further evidence regarding the motivation underlying wing and tail positions can be gained from the same source. If a more elevated wing and tail posture

Table 9

FREQUENCY WITH WHICH EACH DISPLAY LED TO PURE ESCAPE (MOVE AWAY OR SPLATTER AWAY) BY THE OPPONENT

Posture	Frequency Leading To Moving Away	Sample Size
Splatter Charge	100.0%	99
Charge	72.0%	510
'Aggressive' Upright	34.0%	933
Horizontal Forward	17.7%	861
Depressed Forward	14.0%	356
Bow	12.6%	366
'Anxiety' Upright	2.1%	48

Table 10

PERCENTAGE FREQUENCY OF OBSERVED POSTURE, WITH THE OPPONENT IN A POSTURE OF HIGHER ESCAPE MOTIVATION, IN RELATION TO THE NUMBER OF TIMES THE POSTURE WAS SEEN

Posture	Frequency of Opponent in Posture of Higher Escape Motivation	Sample Size
Charge	97.8%	458
'Aggressive' Upright	81.1%	751
Horizontal Forward	63.5%	539
Depressed Forward	57.7%	201
Bow	21.6%	79
'Anxiety' Upright	0%	3

was due to a higher element of escape it would be expected that where an opponent gave a posture of higher escape motivation in reply to any given display, its wing and tail posture would be the more elevated. Results (Table 11) confirm this. The converse is also true, i.e. that a reply posture of lower escape motivation is more likely to have a lower wing and tail posture (Table 11). The exception is the 'Aggressive' Uprights but this may be partly due to the small sample size and/or may be the result of observational errors (p. 71).

Further indication of the motivational basis of wing and tail postures can be obtained from the frequency with which each display was seen with the two extremes - Wings and Tail Down and Wings Exaggerated Up Tail Fully Up (Table 12). As expected, the former was most commonly found in the more aggressive displays and the latter in the escape-motivated displays.

3.8.2 Intragroup Spacing Behaviour

Sequential analysis of postures used in the establishment and maintenance of hierarchies (Table 14, 15 and 16) can also be used to provide further evidence for the motivational hierarchy of postures already established from intergroup spacing behaviour. As expected, postures given by the more dominant pukeko were the more aggressive (Charge and 'Aggressive' Upright), while displays given by submissive birds were all high in escape content. The wing and tail postures of the submissive birds were more elevated than those of the dominants in all cases.

3.9 Colour Experiments

Two birds were painted in an attempt to investigate the role of the red colouration of the bill and shield and the white of the undertail. The paint and dye used were first

Table 11

RELATIONSHIP OF WING AND TAIL POSTURE TO DISPLAY MOTIVATION

Posture	Opponent in Higher Escape Motivated Posture			Sample Size
	Higher Wings and Tail	Same Wings and Tail	Lower Wings and Tail	
Charge	68.6%	23.28%	8.1%	481
'Aggressive' Upright	62.0%	31.70%	6.3%	599
Horizontal Forward	55.7%	40.20%	4.1%	338
Depressed Forward	33.6%	66.40%	0%	107
Bow	91.1%	5.60%	4.4%	45

Posture	Opponent in Higher Aggressively Motivated Posture			Sample Size
	Higher Wings and Tail	Same Wings and Tail	Lower Wings and Tail	
'Aggressive' Upright	35.29%	35.3%	29.4%	51
Horizontal Forward	15.30%	51.6%	33.1%	157
Depressed Forward	6.60%	57.4%	35.0%	136
Bow	4.70%	33.8%	61.5%	275
Moving Away	2.30%	25.3%	72.5%	931
'Anxiety' Upright	0%	22.7%	87.3%	44

Table 12

FREQUENCY OF THE EXTREME WING AND TAIL POSITIONS OBSERVED IN EACH DISPLAY

Posture	Frequency of Posture seen with		Sample Size
	Tail Down	Wings Exaggerated Up	
Charge	26.67%	9.02%	510
'Aggressive' Upright	27.44%	29.50%	933
Horizontal Forward	1.40%	33.10%	861
Depressed Forward	1.69%	45.22%	356
Bow	2.73%	58.74%	366
Moving Away	0.87%	55.87%	1260
'Anxiety' Upright	2.17%	47.83%	46

tried on two captive birds to test for possible side effects.

The bill and frontal shield of one male (*H1w*) were painted black with a fast drying commercial lacquer in the expectation that this bird would lose status with the colour change. Several subordinates challenged *H1w* after it was painted but all were successfully repelled. *H1w* continued to dominate all subordinate birds and appeared as effective in display as before (see p. 117). In the second case, the undertail of a low ranking female from the feeding flock (*N1w*) was blackened with Durafur R Flakes (I.C.I. Ltd) in the expectation that *N1w* would be chased more often without a white tail to signal submission. No detectable change in behaviour occurred.

The failure of the experiments to produce the expected result is, in the case of *N1w*, possibly due to the fact that although the shield and bill were black like the surrounding feathers, their smooth texture made them still fairly obvious. The experiment may have been affected by the fact that status of resident birds was partially dependent on the presence of other members of the territory (see p.148), and that individual recognition may have involved characters other than the bill and shield. It is difficult to see how these factors could have been avoided. The failure of the tail blackening experiment was due mainly to the inability to detect small changes in distance run in the flock situation. Circumstances prevented the repetition of the experiment at a marked territorial boundary where small changes could have been measured.

3.10 Discussion

Most pukeko displays appear to be centred around two anatomical features - the red frontal shield and bill and the white undertail coverts. These features contrast markedly with the dark colour of the plumage and thus are ideal signalling structures and obviously act as releasers. Presentation of the main fighting weapons occurs in the threat displays of many animals (Marler & Hamilton, 1966).

Tinbergen, 1959 and Andrew, 1961 gave the bill and wings as the main weapons of many birds. The frontal shield of the Rallidae appears to function as an extension of the bill, consequently serving to magnify the opponent's view of the main weapon - the bill.

The main element of attack appeared to be the positioning of the bill so that a downward peck can be delivered. Because feet were also used in fighting, the upright stance adopted in the more aggressive threat postures was expected so that the feet could also be used for striking. Thus the 'Aggressive' Upright is the simplest and therefore the most common threat posture found in pukeko. The main element of escape is movement away from the opponent, therefore most postures were ambivalent in that the bird continued to face its opponent but increasingly removed the focus of attention from its beak.

With increasing conflict between escape and aggression the bill is still orientated towards the opponent, but in a position from which it would be increasingly difficult to peck. Hence the sequences 'Aggressive' Upright-Horizontal Forward-Depressed Forward-Bow and 'Aggressive' Upright-'Anxiety' Upright-Head Flick. On the other hand it should be noted that in the Forward, while the bill was put in a position where pecking was unlikely, the bill was taken nearer the opponent suggesting an increase in aggression as well as an increased element of escape. The fact that both Forwards led to fighting tends to confirm this. Thus the Forwards convey maximum threat on the one hand, and on the other the intention that the bird will not attack unless attacked as Tinbergen (1959) suggested for the Forward and Choking in Gulls. Finally the bill is directed away from the opponent (Facing Away and Turning Away) and the sequence terminates in pure escape (Moving Away). The very high number of 'Aggressive' Uprights seen is readily explained if it is assumed that a bird in an aggressive encounter will initially adopt the aggressive posture involving the least expenditure of energy. Its future action will then depend on the action of the other bird.

The extension of the main sequence from aggression to escape into the Hunches and then back to Moving Away is interesting because of the obvious similarity between the Hunches and the female Precopulatory Position. In most cases, these Hunches were adopted by males when involved in a dispute with a male from the opposite territory, but were adopted by either sex when reacting to an opponent of either sex. This posture may serve to motivate the opponent sexually, and because of the similarity of the displays, the Hunches have probably developed by ritualization from the precopulatory sexual postures. It should be noted that sexual inversion (Hinde, 1970) occurs in pukeko (see p. 167) and therefore female precopulatory postures were part of the male's behaviour repertoire. As a bird was rarely attacked while in this position it appears to be a very effective submissive posture. However, the body feathers were fluffed and the wings spread, suggesting an element of aggression. This could account for the Wings Expanded Hunch leading to threat display as frequently as it led to Moving Away.

The Wings Drooped posture is also of interest in that it was adopted only by males and the bird was never attacked while in this posture. The significant link from Wings Drooped to the Charge suggests it is an aggressive posture. Pukeko and other rails sunbathe in similar postures (Holyoake, 1970).

The small number of observations of Facing Away as a separate display distinct from Turning Away may be due to the open nature and large size of pukeko territories. Species which live in colonies and hence in very close contact, for example gulls (Moynihan, 1955; Cullen, 1957; Tinbergen, 1959), tend to have developed Facing Away to a greater degree. On the other hand pukeko do not need to rely on appeasement displays relatively as much because they can readily escape from each other. Similarly the absence of a display equivalent to the choking of gulls may be due to the large size of pukeko territories and the consequent ability to escape.

Aggression has been frequently linked with an increase in size; hence the fluffing of feathers (although this may also be submissive (cf. Morris, 1970), erection of crests, raising of wings, and other similar acts. In pukeko, the erection of body feathers appeared to be related to aggression, as it was most common in the 'Aggressive' Upright and Forwards. However, it may have been due to thwarting (Morris, 1956) in the conflict situation that these displays occur. Sleeking of feathers was most common immediately prior to and during escape.

Wing raising by pukeko does not seem to include an element of aggression (i.e. by increasing the apparent size of the displaying bird), for the more elevated the wing posture, the higher the escape element in the display. Also sleeked body feathers invariably accompanied an extremely elevated wing posture which would not be expected if raised wings signified increased aggression. However, the increased apparent size gained by lowering the wings as in the Wings Drooped and the Wings Expanded Hunch definitely appears to be linked with aggression. It follows that if the wing posture cannot be explained by the conventional argument of enlargement for aggression (Tinbergen, 1959), another postulate must be made.

Higher wing and tail postures were more frequent in displays of high escape motivation, and an elevation of wings followed the adoption of a display with high escape content more often than did a less elevated posture. Elevated wing postures were always accompanied by an extremely elevated and expanded tail posture. Also (see p. 91) a submissive bird almost always maintained a more elevated tail posture when near a more dominant bird. This suggests that elevated wings and tail are more closely linked to escape and submission than to aggression. It is therefore postulated that the white undertail coverts are a submissive signal and that the elevation of the wings serves to expose more of the white tail and provide a contrasting frame. A similar theory for white mammalian rump patches has been formulated by Guthrie (1971). Guthrie, however, explained the evolution of mammalian rump patches by suggesting that the presentation of the white rump remotivates the aggressor sexually towards the presenting animal. This explanation is unlikely in pukeko, because the female does not raise the tail until after the male has mounted for copulation. So it is postulated that the white undertail coverts have evolved more as the direct opposite of the aggressive weapon. Thus not only does the white undertail occur at the opposite end of the pukeko to its beak but the white is in direct contrast to the red of the shield, bill and eye. The elevation of the wings therefore is not acting to increase the apparent size of the bird, but serves only to expose more of the subordinate signal, and also provide a contrasting frame.

If this postulate is true, and all evidence appears to support it, then all the postures of the pukeko involving frontal orientation and elevated wings and tail must be ambivalent. The frontal orientation and presentation of the bill are elements of aggression while the raised wings and tail are elements common to submission and escape.

The only apparent contradiction to the theory is the high incidence of highly elevated wing and tail postures in the 'Aggressive' Upright. Some of this may have been due to an observational error where 'Aggressive' and 'Anxiety' Uprights were difficult to distinguish, and while the 'Aggressive' Upright is thought to be low in escape motivation, it is also considered to be lower in aggressive content than the Charge or even the Horizontal. If it was very high in aggressive motivation, it would be unlikely to lead immediately to such a strong appeasement posture as the 'Anxiety' Upright. Selection would tend to produce a greater difference between the Uprights if the signal was so completely different. Also most of the 'Aggressive' Uprights with elevated wings and tails were accompanied by sleeking of feathers and were given when opponents were in very close proximity.

This theory that wing postures are linked with escape rather than aggression is contrary to most previous work (e.g. Gullion, 1952; Tinbergen, 1959). However, my results suggest that the posture needs to be evaluated quantitatively in rails, and the occurrence of exposed carpal joints in every submissive begging posture of gulls (Tinbergen, 1959) suggests that the significance of raised wings needs wider quantitative evaluation in birds. This theory also differs from the conventional idea that white undertail coverts in the pukeko and most other rails act as a warning signal in times of danger (e.g. Oliver, 1955; Tunnicliffe, 1965; Howard, 1940; Gullion, 1952; Williams, 1960; and many others). However, tail flicking was seen whenever a bird was agitated, which included sighting of predators, but neighbouring birds reacted only if the bird also assumed the Alert. Accordingly the function of white undertail coverts as a warning signal is disputed.

The problem remains as to the possible derivation of wing and tail postures. As noted on page 35, pukeko raise wings and tail when swimming, presumably to prevent unnecessary wetting. The elevated wings and tail are also movements of intention to fly and it is likely that ritualization of intention movements of flight for escape is the source of the posture.

Daanje (1950) suggested that the raised wings and tail in most birds, including the coot and moorhen, are intention movements for flight. He also suggested the tail postures of coots and moorhens were ritualized intention movements for jumping, and noted that the moorhen will tilt its tail towards the opponent and hence implied that the jumping movement must be away from the opponent.

3.11 Comparison with Work on Other Rails

Various workers have given brief accounts of the displays of other rails but most were vague, confused, and tended to follow the work of Gullion (1952b). None has employed quantitative analysis. Display terms used by other workers are listed in Table 13.

Fighting appears to be the least confused of the behaviours. Tunnicliffe (1965) reports actions similar to those described and Tasmanian native hens appear to fight

Table 13

TERMS FOR POSTURES OF RAILS USED BY OTHER WORKERS

TERM USED IN THIS STUDY FOR PUKEKO	TERMS USED FOR OTHER RAILS	AUTHOR
Charge	Charge Swimming Attack Aggressive Run	Gullion (1952b) Kornowski (1957) Ridpath (1972)
Splatter	Splatter Flying-run Attack Chase	Gullion Kornowski Ridpath
Forward Bows Moving Away	Paired Display Paired Display Ostentatious Display Extreme Threat	Gullion Tunnicliffe (1965) Kornowski Williams (1960)
Horizontal Forward	Gaping Threat Posture	Holyoake (1970)
Depressed Forward	Hunched Threat Posture Ready	Holyoake Ridpath
Bow	Bow Arch Bow Greeting Display	Howard (1940) Gullion Ridpath Ridpath
Tail Up	Greeting Display Swimming rch	Howard Gullion
Wings Up	Wing Arching Wing Arching	Gullion Tunnicliffe

in an identical manner to pukeko (Ridpath, 1972). The accounts of fighting in American and European coots (Gullion, 1952b and Kornowski, 1957) and in moorhens (Howard, 1940) appear similar except that, being water birds, they do not jump at each other but sit on their tails propped against their wings on the water and spar with their feet. Takahe attempt to peck the cheek of the opponent and hold on, twisting and pulling with the beak and pushing and ripping with the feet (pers. observation).

Charging has been described by all workers but under differing names. I have followed Gullion (1952b) in using the term Charge but Kornowski (1957) termed it a Swimming Attack and Ridpath (1972) referred to the 'Aggressive Run'. The two latter terms were considered unsuitable because they include a reference to intent.

For the same reason, Gullion's term Splatter is preferred to Kornowski's term 'Flying-run Attack'. Ridpath used Chase to describe the same display, but Chase implies the involvement of more than one bird whereas pukeko were frequently seen Splattering towards another which was unaware of the action and did not Splatter away till the last minute. Takahe also Charge and Splatter (pers. observation).

A posture similar to the 'Aggressive' Upright was described and illustrated by Holyoake (1970), and the Still of the Tasmanian native hen is also similar. Both authors illustrate the birds with tails up. No previous records of 'Anxiety' Upright and Head Flick are known for other rails, although both have been observed in takahe (pers. observation).

Accounts of Horizontals, Depressed Forwards and Bows are confused. Gullion (1952b) and Tunnicliffe (1965) confuse these with Moving Away Wings Exaggerated Up Tail Fully Up, lumping all under the term Paired Display, as does Kornowski (1957), who used the term Ostentatious instead of Paired. Gullion and Tunnicliffe state that the bird's head is held low and the wings are arched. The bird then pivots to bring the undertail coverts into prominence. Tunnicliffe (1965) illustrates a bird in a Horizontal Wings and Tail Fully Up under the caption Paired Display and Kornowski also states that the head is held low during the Ostentatious Display. Williams (1960) uses the term 'Extreme Threat' for takahe. Takahe do have Horizontals, Depressed Forwards and Bows as described for pukeko (pers. observation). Holyoake (1970) also illustrates a bird in a Horizontal, calling it a Gaping Threat Posture. He also describes a Hunched Threat posture which may be equivalent to a Depressed Forward or Bow but the description is vague. Ridpath (1972) refers to the 'Ready' which appears to be the equivalent of the Depressed Forward especially as he states that it frequently preceded a fight.

The majority of workers (Howard, Gullion, Kornowski, Tunnicliffe, Ridpath) record the Bow, although most only in courtship. Ridpath does illustrate it in an intragroup encounter but interpreted it as a 'Greeting Display' (see p. 122 for further discussion). Howard (1940) and Gullion (1952b) refer to Arching which appears to be the equivalent of Bowing. Moorhens and coots are monogamous and Howard and Gullion confused this Bowing (Arching) with a sexual display, but, because it was given by the female without nibbling or copulation, it is more likely a submissive display. The 'Squat Arch' (Gullion) appears equivalent to the Body Bow, Howard (1940) also illustrated Body Bows and Bows and Kornowski (1957) describes Bowing in a similar situation to Gullion's but does not name it.

Gullion (1952b) also referred to 'Bowing' as a display distinct from Arching and reported it was normally associated with nibbling. The distinction was that Bowing occurred in the water while Arching occurred on platforms or on land. But because the essential element of beak pointed at the ground (or water) is common to both the two should be combined. Gullion (1952b) appeared to be partly aware of the significance of the display as he stated: 'the submissive bird goes into a Bow'. Tunnicliffe used the term Bowing for the land display.

Tunnicliffe (pers. comm.) also recognised the Bow as a threat display, and explained the Dip Bow as a ritualized displacement activity - namely displacement drinking which became relevant because it also washed the bill and frontal shield, the primary organs of attack. Displacement pecking at the ground by pukeko was also common during Bows and was noted in moorhens by Howard (1940). It is possible, therefore, that the display may be derived by ritualization of feeding and/or drinking.

No previous author recorded the use of the Erect Hunches in disputes, although Howard (1940) illustrated males 'in the form of a Bow' in front of females. Howard's 'form of a Bow' is the equivalent of the Precopulatory Position. Similar behaviour was observed in takahe.

The least confusion in previous descriptions occurs in regard to sexual and courtship displays. All accounts appear very similar.

The greatest contradiction with previous work is the interpretation of the elevated wing and tail postures. As mentioned, all referred to Tail Flicking as a warning display. Howard (1940) described Tilting in the moorhen where the tail was tilted towards the other bird exposing the white undertail coverts. Howard described it as a 'Greeting Display' but said it could occur 'out of context' and often was an isolated act or even appeared at the end of coition. Gullion (1952b) described a 'Swimming Arch' where the female swam immediately ahead of the male displaying her undertail coverts. The equivalent is not found in European coots (Kornowski, 1957) which have black undertail coverts. Ridpath (1972) did not record a separate Tail Up display in the Tasmanian native hen but the tail was still raised in many displays even though the native hens also lack the white undertail coverts.

Wings Up was termed Wing Arching by Gullion (1952b) and by Tunnicliffe (1965). Both recorded it as an 'antisocial' display and Gullion stated that it 'supplements' the frontal shield and ruff 'when a more aggressive display is required'. Both also recorded the 'Paired Display' where two (or more) birds swam away from each other with wings and tails raised and the birds 'present their tails to each other'. Gullion recorded this as the 'final act of aggression'. This 'Paired Display' is obviously Moving Away with Wings and Tail Fully or even Exaggerated Up. However, as already stated, the accounts are confused. Gullion's description stated that the white undertail coverts and the frontal shield are prominent - an impossible combination for a single display. Gullion did record the Paired Display in non-territorial disputes and Howard (1940) illustrated birds in Bows and Wings and Tail Fully Up.

To summarize, in the displays of the pukeko, most ritualization has occurred in connection with the head and bill, the latter being the primary aggressive weapon. Ritualization has also occurred in respect of the wings and tail which have assumed the function of submissive signals. Consequently in the most aggressive display, the bill and frontal shield are clearly presented, and with decreasing aggressive motivation, the bill is increasingly removed from focus until it is completely hidden in the submissive displays. To prevent ambiguity, the white undertail coverts have evolved as a distinct submissive signal, being markedly different in colour and location to the aggressive weapon, the bill. The development of the white tail as a submissive signal may have paralleled the development of the large frontal shield which serves to maximize the aggressive releaser. Ritualized female sexual postures serve as secondary submissive displays.

4. SOCIAL HIERARCHY

4.1 Introduction

When the existence of a social order in territorial groups was suspected, artificial concentrations of food were provided to force crowding and induce an increase in interaction between individuals. The food was placed so that if more than one bird fed at a single pile, the distance between individuals was less than 10 cm. Two piles, 50 cm apart, were usually provided so that more than one bird could feed at the same time, but could easily supplant one another. Artificial feeding was infrequent during the breeding season.

All interactions between birds at and away from the food were recorded as were those when no artificial food was provided. Avoidance and aggressive displacements were worked up separately to give two indices of status.

4.2 Behaviour Associated with Hierarchy in Territories

The hierarchical behaviour of pukeko within territories (both at and away from food piles) is summarized in Table 14.

4.2.1 Without Artificial Food

The existence of a hierarchy was first suspected in Linton 1 in 1970 when birds in close contact with each other were observed to have different tail postures; subordinates always raising their tails more than those of birds of higher rank. When approached by a dominant bird, a subordinate raised its tail, directed it at the dominant and moved away. The subordinate then fed with its tail elevated but gradually lowered it.

Subsequent observations with artificial food confirmed the hierarchy in Linton 1 suggested by tail positions. However, attempts to apply the hypothesis to all territories were not completely successful for the subordinate did not always adopt the more submissive posture. This was

Table 14

HIERARCHICAL BEHAVIOUR WITHIN TERRITORIAL GROUPS

(The subordinate's posture recorded was the first and usually the only posture given.)

DOMINANT'S POSTURE	SUBORDINATE'S POSTURE											
	'Anxiety' Upright	Head Flick	Dip Bow	Full Bow	Body Bow	Face Away	Erect Hunch	Wings Expanded Hunch	Crouch	Head Flag	Move Away	Splatter Away
Charge	-	1	-	-	-	-	1	-	1	-	51	6
'Aggressive' Upright	27	42	34	100	21	24	-	2	39	16	192	-
Peck	1	-	-	-	-	-	-	-	17	2	9	-
Foot Up	-	-	-	-	-	-	-	-	3	-	6	-
Dip Bow	-	1	-	15	-	-	-	-	-	-	-	-
Full Bow	1	-	-	2	-	-	-	-	-	-	1	-

especially evident in the breeding season, when a dominant bird was occasionally seen to raise its tail when walking past an immediate subordinate of either sex.

The difference between Linton 1 and other territories in the reliability of tail positions as indices of status may have been related to differences in the membership of the territories. Linton 1 in 1970 consisted of an adult male (04), an adult female (07) and a yearling female (06). All other territories had at least two adult males, most had two adult females, and thus subordinates were greater rivals for status.

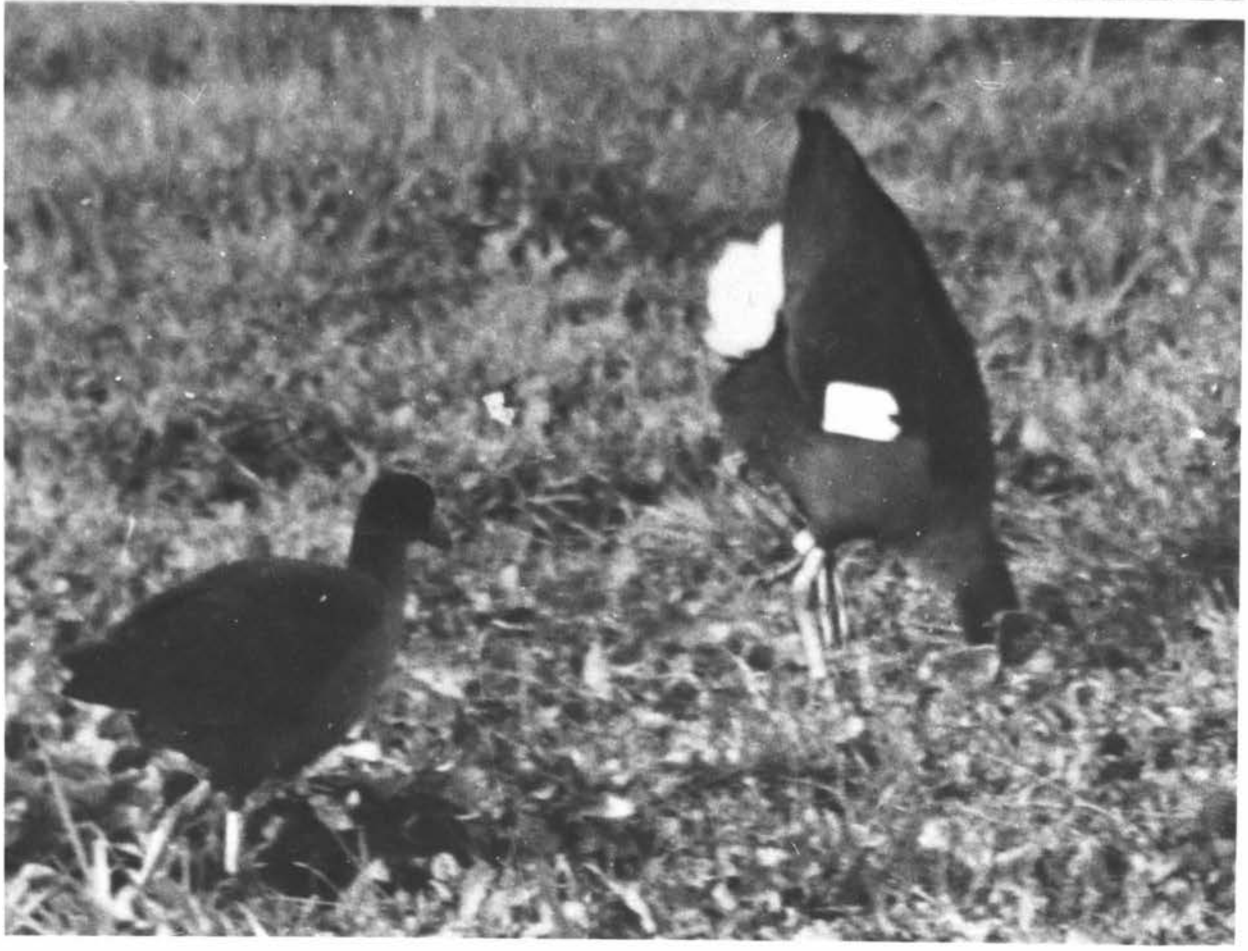
When birds from the same territory met, one normally assumed a submissive or appeasement posture while the other remained in an Upright. Apart from the raising of the tail, the most common posture assumed by a submissive bird away from food piles was a Bow (Table 14). The bird initially raised its tail, then its wings and finally when the more dominant was close, it dropped to a Bow and held this until the dominant had passed (Fig. 34). Occasionally a Bow led into a Body Bow. Other common submissive or appeasement postures adopted by adult subordinates were the 'Anxiety' Upright and the Head Flick, but where the subordinates were juveniles or yearlings, Crouching and Head-Flagging were the most common.

The 'Aggressive' Upright was the posture most commonly adopted by the dominant bird (Table 14), although pecks and foot displacements were seen but were usually directed at juveniles. The use of the submissive Bows by dominant birds appears contradictory, but these were Dip Bows, where the bird rapidly alternated between a Bow and an Upright. In almost all cases, the subordinate assumed a Permanent Bow as the dominant approached from a distance. As well as the above postures, birds occasionally supplanted other members of the territory and then fed on the captured food supply. Less frequently a dominant took food, usually raupo shoots, from a subordinate.

Figure 34 BOWING during Hierarchical Interaction

(a) Subordinate (right) has Wings Partly Up, Tail Fully Up and is beginning to Bow to the approaching dominant.

(b) Subordinate in Full Bow, Wings and Tail Fully Up as the dominant approaches in an 'Aggressive' Upright, Tail One Third Up.



4.2.2 At Artificial Food

Only two birds were usually present at the food at any one time although other birds, unable to feed because of the presence of dominants, circled and occasionally dashed in and grabbed food from under them. Most interactions at the food involved the subordinates Moving Away, usually with wings and tail raised in reply to an 'Aggressive' Upright by the dominant. Facing Away and Head Flicks were also common, although juveniles usually Crouched or Head Flagged. Food begging was also seen from juveniles and even yearlings in reaction to an aggressive adult, and this frequently resulted in feeding and/or aggressive pecking. Results of artificial feeding were less conclusive in the breeding season as male and female occasionally fed at the same pile of food.

4.3 Behaviour Associated with Hierarchy in the Flock

4.3.1 Without Artificial Food

Normally the flock maintained relatively large individual distances and dispersed gradually through the Hay Paddock. Occasionally one bird displaced another when in close contact but sometimes displacement was deliberately initiated from further away. Crowding occurred naturally, before and when the birds first appeared in the paddock, when they flew back to the lake after being disturbed by stock or humans, when birds went to the drain to drink, and also when the birds grouped in reaction to a circling hawk (Fig. 3b). Apart from times when the hawk was still present, this crowding produced intense interaction and birds were actively displaced by both Peck and Foot Up, (Figs 35 and 36) while others Moved Away, with Wings and Tail Up. Charges and Splatters were also seen, but eventually the birds dispersed and interactions ceased.

4.3.2 At Artificial Food

Once the food was found, pukeko usually grouped around

Figure 35

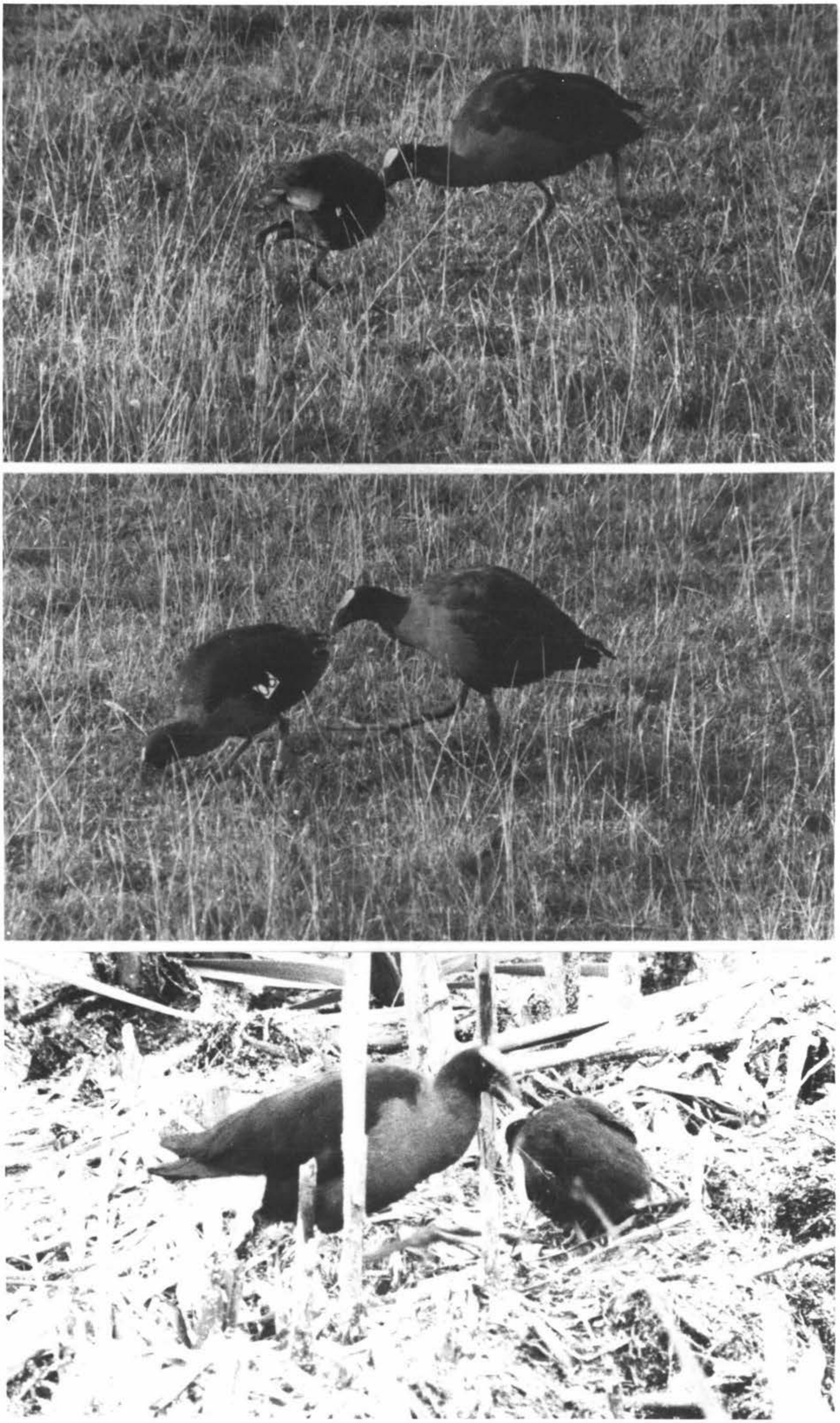
Subordinate in a crouch being PECKED by a dominant.

Figure 36

FOOT UP displacement by a dominant. The dominant bird on the right has just run its foot down the back of the subordinate.

Figure 37

Initiation of a chick into the hierarchy. 1Nw pecking Vw when the latter begged for food. Vw in a crouch.



it displacing those of lower rank and circling those of higher status. Low ranking birds frequently dashed in and snatched a single grain from under the feeding birds and then took it away to eat it. As these birds ran from the food, they avoided more dominant pukeko and displaced subordinates. Similar interactions were observed when birds moved to or from the drain to drink which they did frequently presumably because of the low moisture content of the grain. All this provided a large number of active displacements and avoidance interactions which were usually very brief; the dominant bird simply adopted an aggressive posture while the submissive pukeko Moved Away or assumed an appeasement posture. A sample of the behaviour of the feeding flock observed around artificial food concentrations is given in Table 15.

Head Flicks, Pecks, and Foot displacements were common, probably reflecting the extreme crowding observed around the food, and subordinates always Moved Away with a higher wing and tail posture than the dominant bird. When you consider the large number of juveniles in the flock (see Table 3) it is interesting to note the relatively low frequency (2.9%) of Crouching. In rare cases a pukeko challenged a more dominant bird causing a short fight which usually ended in a Splatter chase. The majority of charging, however, was the result of redirected aggression which was common. For example, a bird supplanted from, or unable to gain access to, the food Charged or Splattered the nearest subordinate(s). Redirected aggression occasionally produced a chain reaction where a displaced bird supplanted another which in turn attacked another, and such chain reactions could involve up to five birds.

4.4 Behaviour Associated with the Establishment of a Hierarchy

4.4.1 Within Territories

Most territories were permanent and membership was

Table 15

HIERARCHICAL BEHAVIOUR WITHIN THE FLOCK

	SUBORDINATE'S POSTURE								
DOMINANT'S POSTURE	'Anxiety' Upright	Head Flick	Dip Bow	Full Bow	Face Away	Crouch	Head Flag	Move Away	Splatter Away
Splatter	-	-	-	-	-	-	-	-	18
Charge	-	-	-	-	-	-	-	64	4
'Aggressive' Upright	53	76	6	22	25	9	-	374	-
Peck	-	-	-	-	-	13	1	46	-
Foot Up	-	-	-	-	-	-	-	48	-

constant throughout the year. Six territories were observed being set up but in each case the pair, or group, had an established hierarchy before the territory formed. One case of a bird being admitted to an established territory was recorded in detail, however.

In early March 1971, an unbanded male (later 10y) appeared in the main valley at Linton, and was treated as a trespasser, being alternately driven from Linton 1 and Linton 2. It finally remained in Linton 1 and was Charged and Splattered by all members of the group, but contrary to its initial behaviour, 10y did not run directly away from the attacking bird(s) but ran in circles, and at times, up to four birds were seen running in file after it. The amount of Splattering slowly decreased and by 24 March 1971 the dominant male (04) had ceased attacking 10y , which assumed a submissive posture and almost constantly Tail Flicked whenever near 04. Other members of the territory continued to attack it. By 28 March 1971, 10y had begun attacking the juvenile members of the territory and by 18 April 1971, was completely accepted into the territory and submissive only to 04 . 10y dominated the juvenile female (08) first, then the juvenile males (0w and 4w) and finally the adult female (07) and when recaught on 13 June 1971, 10y had dropped from 1055 grams at 11 April 1971, to 895 grams.

Other evidence for the establishment of a hierarchy within a territory comes from the initiation of chicks into the hierarchy. Most chicks remained in their natal territory until eight months of age and in group territories many stayed permanently. Pukeko were usually double-brooded (see p. 182) and when renesting began, the first chicks were frequently pecked as they begged for food, but were still fed, the pecking becoming more frequent and subsequent feeding less common. Chicks from the second brood were treated similarly once they were two or three months old. Where yearlings were present in the territory, they assumed much of the role of feeding the chicks (see p. 193) but when the chicks were two to three months old, the yearlings pecked and chased the chicks as frequently as they fed them. In the Southern Territory, 1972, the three surviving chicks from the first nest were fed mainly by the yearling female (*INw*). One of these chicks was banded (*Vw*) and was immediately attacked whenever it begged from *INw* (Fig. 37), long chases frequently resulting. None of the adults reacted in this way to *Vw* and *INw* did not treat the other two chicks similarly until three weeks after *Vw* was banded. It is interesting to note that once *INw* was chasing *Vw*, other birds from the territory joined in the attack on *Vw*. Chicks began pecking each other from about three months when both were begging from the same adult, although food stealing was occasionally observed between younger chicks, especially where they were different in size (see Fig. 49).

4.4.2 Within the Flock

When the flock first formed early in the year, fighting between members was common. Some disputes were settled by sparring with the feet (Fig. 4) until one bird retreated, but most were decided after a single Splatter. Other disputes were protracted, occasionally involved more than two birds, and strongly resembled territorial interactions as the birds displayed to each other in Forwards and Bows. Full fights sometimes resulted. Most birds were unbanded at this time of year; so relationships between individuals were unknown.

4.5 Behaviour Associated with Expulsion from the Hierarchy

As noted previously (p. 25), the Hide Territory absorbed a number of males, three of which (*JIw*, *ILy* and *IJy*) were later expelled prior to the breeding season. After *IJy* was expelled in 1972, it was frequently seen in other territories. Initially the Peninsular Territory 1972-1973 contained the remaining nine flock birds (p. 24), two of which (*Ky* and *Iy*) were subsequently ejected while the third (*Qw*) left after two unsuccessful breeding attempts. The behaviour of the other members of the groups when they expelled these birds is shown in Table 16.

Table 16

BEHAVIOUR OBSERVED WHEN A BIRD WAS EXPELLED FROM THE HIERARCHY

		POSTURE OF EXPELLED BIRD							
		'Anxiety' Upright	Head Flick	Dip Bow	Full Bow	Body Bow	Crouch	Move Away	Splatter Away
DOMINANT'S POSTURE	Splatter	-	-	-	-	-	-	2	71
	Charge	3	-	-	2	-	-	116	
	'Aggressive' Upright	2	2	9	5	5	2	8	-

Submissive or appeasement displays on the part of the ejected birds were infrequent but escape, especially Splatter Away, was common. In direct contrast to the behaviour associated with admission of pukeko to the hierarchy, these escapes and Splatters were initially in circles, but gradually the attacked bird took more and more to running directly from the attacker, spent less and less time in the territory and eventually disappeared.

A more violent expulsion of a juvenile pukeko occurred at Linton. On 29 September 1972, 17w was dominant over 11y in Linton 2 and persistently attempted to drive it from the territory. On 4 October 1972 the roles were reversed and many of the other birds from the territory also tried to evict 17w. Extracts from my field notes read:

> 0812 Lot of calling from first bay. 11y in raupo at the end of the bay, moving in an 'Aggressive' Upright W & TFD at 17w which is in a Body Bow W & TFU. 17w remained in Bow as 11y approached. 11y got on 17w and pecked rapidly at the top of its head. 17w ran off in sleek crouch with 11y charging after it. 11y kept pecking 17w and hitting it with its foot. 10w, 03 and 21w also charged over and held, kicked, clawed and pecked 17w hard on the head. 17w limped into raupo, 00 flew after it and vigorously pecked its head. Calling brought 61y and 71y (Linton 1) to the boundary. 0825

17w was still in the valley on 24 October 1972 but appeared blinded in one eye and spent most of its time at the Linton 1/Linton 2 boundary.

4.6 Quantitative Results

Brown (1963) has stressed that different criteria of dominance are applicable to different species and it is necessary to establish criteria based on the behaviour of the species in question. Much of past emphasis has been placed on measuring the more dominant individuals' priority to incentives such as food, water, space, sexual partner, roost, etc. Food has been the most common (Guhl & Allee, 1944; Ritchey, 1951; Wood-Gush, 1955; Marler, 1955; Brown, 1963; Dixon, 1965: McBride et al, 1969; Watson, 1970;

Minock, 1971; Meeze & Ewbank, 1972; and many others). Other workers e.g. Sabine (1959) and Rowell (from Bernstein, 1970) have concluded that responses of subordinates were better indices of rank.

Bernstein (1970) stated that while feeding order or acquisition to presumed incentives is a popular and simple objective measure of dominance, 'it may not be clear exactly what is being measured, in-as-much as this measure may correlate poorly with other presumed dominance measures such as direction of agonistic episodes.' He concluded that it was important to show significant positive correlations between two independent scoring techniques. For example:

(1) Agonistic dominance (such as aggressive displacement from food)

(2) Priority of access to food (as demonstrated in avoidance by subordinates).

In the present study, these were:

(1) Aggressive displacement where the dominant bird
    (a) gave a unidirectional peck,
    (b) gave a unidirectional displacement with a Foot Up,
    (c) adopted a threat posture which produced escape or appeasement in the other bird.

(2) Avoidance where the subordinate bird
    (a) moved out of the way with no apparent threat display by the other bird,
    (b) circled a feeding bird,
    (c) snatched food from under a feeding bird.

4.6.1 Within Territorial Groups

Interactions between territorial members of the Hide, Northern, and Southern Territories are presented in Tables 17-19, where monthly interactions are given for 1972 and overall results for 1971 are presented for the Hide and Northern Territories. Results for the 1970-71 breeding season for the Hide Territory are also included.

Table 17 HIDE TERRITORY HIERARCHY

Figures represent the number of times a bird won or lost an encounter with the score recorded against the loser.

August 1970-January 1971

WINNER

LOSER	Ew	H1w	2B	2C	2J	2E
Ew		-	-	-	-	2
H1w	5		2	-	1	1
2B	2	2		-	-	2
2C*	2	-	-		-	-
2J	4	10	3	3		1
2E	11	12	15	4	5	

March 1971-August 1971

WINNER

LOSER	H1w	Kw	J1w	2E	P1w
H1w					
Kw	28				
J1w	13	13			
2E	32	14	8		
P1w	12	7	1	24*̣	

March 1972

	H1w	Kw	2E	P1w	R1w
Hw					
Kw	3				1
2E	10	5			
P1w	13	3	4		
R1w	2	1		2	

April 1972

	H1w	Kw	1Ly	2E	P1w	R1w
H1w						
Kw	10					
1Ly	10	9		1	2	
2E	12	5	4		6	
P1w	11	10	15	7		
R1w	16	5	12	15	11	

June 1972

	H1w	Kw	P1w	2E	R1w
H1w					
Kw	6				
P1w	12	1			
2E	6				
R1w	14				

July 1972

	H1w	Kw	P1w	2E	R1w	1Jy
H1w						
Kw	20					
P1w	17	14				7
2E	18	9	7			5
R1w	24	17	13	7		
1Jy	42	38	8	2		

August 1972

	H1w	Kw	P1w	2E	R1w	1Jy
H1w						
Kw	5					
P1w	12	1				
2E	14	4	5			
R1w	9	6	2	9		
1Jy	3	1				

September 1972

	H1w	Kw	P1w	2E	R1w	1Jy
H1w						
Kw	9		1			
P1w	3	1				
2E	3	1				
R1w	2	1				
1Jy	2		2			

October 1972

	H1w	Kw	P1w	2E	R1w
H1w					
Kw	2				
P1w	1	2			
2E					
R1w	1				

TOTAL

	H1w	Kw	1Ly	P1w	2E	R1w	1Jy
H1w							
Kw	55			1		1	
1Ly	10	9		2	1		
P1w	69	32	15		11		7
2E	62	24	4	18			5
R1w	68	30	12	26	31		
1Jy	47	39		8	2		

* Left territory, 16 October 1970

*̣ Most of these occurred during July when 2E appeared to attempt to expel P1w

Table 18 NORTHERN TERRITORY HIERARCHY

Figures represent the number of times a bird won or lost an encounter with the score recorded against the loser.

March 1972

WINNER

LOSER	Ew	Tw	Pw	Bw	1Bw	L1w
Ew						
Tw	4					
Pw	2					
Bw	2	2	4			
1Bw	5	1	2	1		
L1w	10					

April 1972

WINNER

LOSER	Ew	Tw	Pw	Bw	1Bw	L1w	1Xw
Ew		1					
Tw	3		1				
Pw	2	4		2			
Bw	1	1	3				
1Bw	4	3	5	2		2	
L1w	2	5	5	2	1		
1Xw	5	4	5	2	1	1	

June 1972

	Ew	Tw	Pw	Bw	1Bw	L1w
Ew						
Tw	5					
Pw						
Bw			6			
1Bw	3	2	1	1		
L1w	4	3		1	1	

August and September 1972

	Ew	Tw	Pw	Bw	1Bw	L1w
Ew						
Tw	1		1			
Pw	3	1				
Bw	1		2			
1Bw		3				
L1w	4	3	5			

October 1972

	Ew	Tw	Pw	Bw	1Bw	L1w
Ew						
Tw						
Pw		2				
Bw	1	1				
1Bw	2	3		1		
L1w	1	2			1	

November 1972

	Ew	Tw	Pw	Bw	1Bw	L1w
Ew						
Tw	3					
Pw						
Bw	2					
1Bw	3	2	2	2		
L1w	3	3			2	

TOTAL 1972

	Ew	Tw	Pw	Bw	1Bw	L1w	1Xw
Ew		1					
Tw	16		2				
Pw	7	7		2			
Bw	7	4	15				
1Bw	17	14	10	7		2	
L1w	24	15	10	3	5		
1Xw	5	4	5	2	1	1	

Table 19 SOUTHERN TERRITORY HIERARCHY

Figures represent the number of times a bird won or lost an encounter with the score recorded against the loser.

March 1972

WINNER

LOSER	Aw	Ey	By	S1w	1Nw	1Pw
Aw		1				
Ey	14					
By	23	16				
S1w	9	11	8			
1Nw	4	3	7			
1Pw	4	3	4	2	2	

April 1972

WINNER

LOSER	Aw	Ey	By	S1w	1Nw	1Pw
Aw						
Ey	2					
By	7	8				
S1w	6	17	13			1
1Nw	4	3	5	3		
1Pw	3	7	5	7	1	

June 1972

	Aw	Ey	By	S1w	1Pw	1Nw
Aw		1				
Ey	3					
By				1		
S1w		4				
1Pw	3	1	2	1		
1Nw	2	8	4	2	2	

August and September 1972

	Aw	Ey	By	S1w	1Pw	1Nw
Aw			1			
Ey	1					
By						
S1w		1	1			
1Pw	1			2		
1Nw	3	1	3		1	

October 1972

	Aw	Ey	By	S1w	1Nw	1Pw
Aw						
Ey	2					
By	2	1				
S1w						
1Nw	3	2	1	1		1
1Pw	1	4	1	3		

November 1972

	Aw	Ey	By	S1w	1Pw	1Nw
Aw						
Ey						
By						
S1w						
1Pw	1	1		1		
1Nw						

TOTAL 1972

	Aw	Ey	By	S1w	1Pw	1Nw
Aw		3				
Ey	21					
By	32	25		1		
S1w	15	29	26		1	
1Pw	13	16	12	16		3
1Nw	16	17	20	5	4	

In general, a simple linear or absolute (Leyhausen, 1971) hierarchy existed in all territories and no triangular relationships occurred. A small number of hierarchical violations were recorded, but usually these were between birds immediately adjacent in status and were far outweighed by interactions in the other direction. The only exceptions to this involved females during the breeding season. A number of reversals of status were observed e.g. *2E* (chick in 1969-70) and *Plw* (chick in 1970-71) of the Hide Territory reversed positions in April 1972. The four chicks of 1971-72, of the Northern and Southern Territories, *IBw* and *Llw*, and *IPw* and *INw* respectively, also reversed positions between April and June 1973, although numbers of interactions were small.

Hierarchies at Linton are given in Tables 20 and 21 for Linton 1 and Linton 2 respectively. Both territories included chicks and juveniles which in all cases were subordinate to adults, although by the time the young left the territory they had scored a number of violations that suggested a change in status might eventually have occurred.

Results for other territories were similar to the above, were few, and are not given.

4.6.2 Within the Flock

Failure to capture and band most of the pukeko in Autumn 1971 flock, despite intensive trapping, meant that little work could be done on a hierarchy, but by June a number of birds were banded and a hierarchy was calculated (Table 22). A simple linear hierarchy appeared to exist in the flock but interactions between some pairs of birds were not observed. Violations also occurred between many of the birds but results were too few to record monthly and so were inconclusive.

In 1972 a concentrated effort to investigate a flock hierarchy led to intensified banding culminating in the use of a rocket net in June, and resulted in all except two of the flock birds being caught and banded. Later, a metal

Table 20

LINTON 1 HIERARCHY

July 1970-July 1971

Figures represent the number of times a bird won or lost an encounter with the score recorded against the loser.

	WINNER						
LOSER	04	10y	07	06	Ow	4w	08
♂04		4	3	-	1	-	-
♂10y	18		3	4	-	-	1
♀07	12	5		2	4	-	1
♀06	12	8	4		1	4	-
♂Ow	14	11	8	2		-	1
♂4w	6	-	1	3	-		-
♀08	13	10	10	2	14	-	

Juveniles are underlined

Table 21

LINTON 2 HIERARCHY
1972

Figures represent the number of times a bird won or lost an encounter with the score recorded against the loser.

	WINNER								
LOSER	03	00	0y	10w	21w	14w	11y	17w	6w
♂ 03									
♀ 00	8		2						
♂ 0y	8	6		1			1		
♂ 10w	6	11	5						
♂ 21w	5	6	2	2					
♀ 14w	1	3	2	4	1				
♂ 11y	4	7	3	1		4		4	
♀ 17w	5	10	2	5	2	3	7		
♀ 6w	2	1							

Juveniles are underlined

Table 22

FLOCK HIERARCHY
March-July 1971

Figures represent the number of times a bird won or lost an encounter with the score recorded against the loser.

LOSER

	Ub	Oy	Ky	Xw	K1y	Nw	Vy	F1y	Sw	Ub
♂Ub		1	2							
♂Oy	2		1	2			1			
♂Ky	4	6		3			1			
♂Xw	6	2	6							
♀K1y		1	2	2				1		
♂Nw			1				1			
♂Vy	1	3	12	10	1	2		1		
♀F1y	3		9	7	2		6			
♀Sw			3		2		1	1		
♀Ub	4		4	1			1	1		

Juveniles are underlined

disc was placed in the paddock (see p. 8) to help pukeko find the artificial food and thus to provide a maximum number of interactions. The birds readily associated the disc with the food and ran to it whenever it was out. A sample of results (Table 23) demonstrates the existence of a linear hierarchy among the flock members even though a small number of violations occurred. The hierarchy was also complicated by the rebellion of *Plw* against *2E* already referred to (Table 17). Table 23 also demonstrates the frequently observed redirected aggression. The large number of interactions involving *2E* were the result of redirected aggression after *2E* was unable to gain access to the food or was driven from it.

Many of the violations were apparently due to mistaken identity, as in the extremely crowded situation around the food, a pukeko occasionally pecked a more dominant bird from behind. This bird made a short dash away, then turned and immediately attacked the bird that had displaced it.

In June 1972 *Tly* received a severe injury to its right leg and had a pronounced limp, but was still able to maintain its position in the hierarchy even when it was forced to hop for a short period. The injury gradually healed and *Tly* became the dominant male in the Trap Territory.

4.7 Interaction Between Territory and Hierarchy

The flock formed in the Hay Paddock and fed in a number of former breeding territories (see p. 20). Initially the resident birds attempted to defend their territorial boundaries against the intruders but by March 1972 and 1973 the Peninsular Territory had completely broken down as had the Trap Territory in 1973. Defence of the Hide Territory was also restricted to a 'core' area ('nucleus area, centred about the previous season's nesting sites', Gullion, 1952) by April in all years and the flock fed freely in all areas of the Hay Paddock previously included in all these territories. To investigate the effects of territory, prior residence and distance from nest site, on the status of the

TABLE 23 FLOCK HIERARCHY APRIL 1972

Food in Hide Territory

WINNER

LOSER

	Hlw	Ow	Kw	Ky	2E	Plw	Tly	1Tw	Rlw	1Zw	Qw	Lly	1Fy	1Ey	1Lw	Vly	1Vw	Vy	1Cy	Zw	Nlw	Iy
Hlw																						
Ow	$^{2}2$							$^{1}1$						$^{1}1$								
Kw	$^{3}10^{7}$																					
1Ly	$^{5}10^{5}$		$^{3}9^{6}$		$^{1}1$																	
2E	$^{6}12^{6}$		$^{2}5^{3}$	$^{3}4^{1}$		$^{4}5^{1}$																
Plw	$^{11}11$	1^{1}	$^{3}10^{7}$	$^{9}15^{6}$	$^{2}7^{5}$		$^{2}3^{1}$	$^{1}2^{1}$		$^{2}2$			$^{1}1$									
Tly	$^{1}2^{1}$	$^{2}2$	$^{1}1$	$^{1}2^{1}$	$^{6}6$	$^{4}4$			$^{1}1$													
1Tw	$^{2}4^{2}$	$^{6}8^{2}$	$^{1}1$		$^{11}12^{1}$	$^{9}10^{1}$	$^{14}14$															
Rlw	$^{8}16^{8}$		$^{2}3^{1}$	$^{7}12^{5}$	$^{4}15^{11}$	$^{6}11^{5}$	$^{1}1$	$^{1}1$			$^{2}2$											
1Zw	$^{4}6^{2}$	$^{3}5^{2}$	$^{7}9^{2}$	$^{1}1$	$^{14}16^{2}$	$^{5}6^{1}$	$^{5}7^{2}$	$^{4}5^{1}$			$^{1}3^{2}$			1^{1}								
Qw	$^{2}4^{2}$	$^{6}8^{2}$	$^{5}7^{2}$	$^{1}1$	$^{11}11$	$^{5}5$	$^{5}7^{2}$	$^{3}6^{3}$	$^{3}3$	$^{2}3^{1}$												
Lly	$^{3}5^{2}$	$^{3}4^{1}$	$^{6}6$	$^{2}2$	$^{15}15$	$^{7}7$	$^{7}9^{2}$	$^{10}12^{2}$		$^{1}1$	$^{3}4^{1}$			$^{1}1$		$^{1}1$						
1Fy	$^{3}4^{1}$	$^{2}3^{1}$	$^{4}5^{1}$	$^{7}8^{1}$	$^{18}20^{2}$	$^{11}12^{1}$	$^{5}8^{3}$	$^{4}5^{1}$	$^{3}3$	$^{1}2^{1}$	$^{6}7^{1}$	$^{4}4$		$^{1}1$								
1Ey	$^{3}5^{2}$	$^{1}5^{4}$	$^{4}4$	$^{1}1$	$^{19}20^{1}$	$^{7}7$	$^{15}16^{1}$	$^{6}9^{3}$	$^{4}4$	2^{2}	$^{3}5^{2}$	$^{3}4^{1}$	$^{7}7$						$^{1}1$			
1Lw					$^{2}2$	$^{1}1$		$^{2}2$														
Vly	$^{4}8^{4}$	$^{2}3^{1}$	$^{5}6^{1}$	$^{2}2$	$^{17}19^{2}$	$^{6}6$	$^{6}13^{7}$	$^{1}3^{2}$		$^{1}2^{1}$	$^{5}7^{2}$	$^{1}1$	$^{6}7^{1}$	$^{1}1$	$^{1}1$							
1Vw		$^{3}3$	$^{1}1$		$^{2}2$	$^{5}5$		$^{1}1$		$^{1}1$	$^{1}1$					1^{1}						
Vy	$^{2}5^{3}$	$^{1}2^{1}$	$^{3}3$	$^{1}3^{2}$	$^{12}14^{2}$	$^{5}6^{1}$	$^{4}5^{1}$		$^{4}5^{1}$	$^{1}2^{1}$	$^{5}6^{1}$	$^{3}3$	$^{2}2$			$^{6}7^{1}$						
1Cy	$^{5}10^{5}$	$^{4}4$	$^{4}5^{1}$	$^{6}12^{6}$	$^{23}27^{4}$	$^{11}13^{2}$	$^{1}5^{4}$	$^{4}5^{1}$	$^{4}6^{2}$	$^{1}1$		$^{1}1$	$^{4}5^{1}$			$^{3}3$		$^{2}2$				
Zw	$^{1}3^{2}$	2^{2}	$^{5}5$	$^{3}6^{3}$	$^{13}13$	$^{5}6^{1}$	$^{2}2$	1^{1}	$^{1}2^{1}$		1^{1}		$^{3}3$			$^{1}1$	1^{1}		$^{2}2$			
Nlw	$^{5}7^{2}$	$^{1}2^{1}$	$^{3}4^{1}$	$^{2}2$	$^{15}16^{1}$	$^{7}7$	7^{7}	$^{1}3^{2}$	1^{1}	$^{1}1$	3^{3}	$^{3}5^{2}$	$^{5}7^{2}$	$^{5}7^{2}$		$^{1}1$		$^{1}3^{2}$	$^{2}3^{1}$	$^{2}2$		
Iy	1^{1}			$^{3}3$	$^{7}7$	$^{1}1$	$^{1}1$				$^{4}4$	$^{1}1$				$^{1}1$		$^{2}2$	$^{2}2$		$^{2}2$	

Food in Hide

Territory

a = Aggression

$\begin{array}{cc} a & b \\ \multicolumn{2}{c}{T} \end{array}$ b = Avoidance

T = Total

The results are set out with the displacements scored against the loser. Active aggressive displacements are entered in the top left corner and passive avoidance in the top right corner of each square. These are then totalled. Thus the very left hand square second from the top shows that Kw was actively displaced by Hlw three times and avoided Hlw seven times.

birds in the flock, artificial food was placed in different areas of the Hay Paddock on different days and results tabulated monthly (Table 23, Appendix 4). Most feeding was done in either the Hide or Peninsular Territorial areas but food was also placed on the old boundary between these territories and in what later became the Trap Territory.

The results show a strong correlation between territorial membership (and thus prior residence) and status in the flock. (Membership of all study territories is given in Table 25). The regular members of the Hide Territory, *Hlw*, *Kw*, *2E* and *Plw*, were higher in status in their own territorial area than they were in the Peninsular territorial area where *Mlw* and *Qw* were dominant. This applied particularly to the dominant male from each territory who was completely dominant over all birds (territorial and flock) in his own territorial area. This included *Ry* when the 1972 flock divided (see p. 22) as, although most flock members were not banded, *Ry* was able to hold artificial food against all birds in the Western 'Territory', part of the Rough Paddock.

Temporary male members of the Hide Territory (*Jlw*, *lLy* and *lJy*) also ranked higher in their own territory than in the Peninsular territorial area. The Hide Territory birds were lowest in status when the food was far from their territory (e.g. June), and did not go to it when it was in the area that later became the Trap Territory.

The females of the territories did not have constant status throughout the year. When the flock first invaded their territories, they ranked highly but slowly dropped in status. However, dominant females in each territory dominated all other females in their area at all times. At first, birds from the same territory acted together to displace other birds, and thus low status birds gained access to the food in the presence of higher ranked non-territorial birds. This would explain the frequent violations between the Hide Territory and flock birds, especially the juvenile *Rlw*. Dominant males occasionally tolerated their own juveniles and females at the same pile of food in March and April. For example, *Hlw* allowed *Rlw* and occasionally *2E* at the food with it; and *Mlw* tolerated *Lly* and *Nlw* and occasionally *Qw* also. Some evidence for combined action of birds from the same territory was seen when the dominant male (*Hlw*) did not appear at the food (Appendix 4g). On that day, *Kw* was the only Hide Territory bird to spend any time at the food and suffered status violations to *Qlw* and *1Zw*, which were not repeated at any other time. Similarly, the few observations of *Hlw* displacing *Mlw* when the food was in the Peninsular Territory were believed to be due to the presence of *Kw* at the food with *Hlw*.

By August, Hide Territory birds were again able to defend their territory and artificial feeding in this part of the Hay field produced only territorial interactions. Artificial food in the Peninsular Territory still attracted most of the Hide Territory birds although even *Hlw* was attacked by previously subordinate birds which later became members of the Peninsular Territory.

Apart from the above, interactions between members of the flock were relatively constant, although minor changes of status did occur among birds at the bottom of the hierarchy - especially *ly* . The only triangular relationship evident involved *Plw*, *lZw* and *2E* when food was put on the boundary between the Peninsular and Trap Territories.

4.8 Relationship of Status to Sex and Age

As a general rule, within territories males dominated females, but there were exceptions. In the Hide Territory in 1970 (Table 17), *2J* was dominated by the two adult females, *2B* and *2C* . However, while *2J* was definitely an adult male, its previous history was not known and it was expelled from the territory before the chicks hatched. In 1972, *1Jy* which was similarly expelled during the breeding season (although it was after the chicks hatched), was subordinate to the adult females, *Plw* and *2E* , during the breeding season. *lJy* had dominated *2E* prior to the breeding season and had been admitted to the territory during the previous winter. In all other cases, adult males dominated all females.

The evidence of the Northern and Southern Territories (Tables 18 and 19) suggests that juvenile females initially dominated juvenile males but that this was reversed at about eight months of age. Interactions are few and results differ from Linton (Tables 20 and 21) where all males dominated all females in the same age class. Older chicks dominated younger chicks of the same sex at both Linton and Pukepuke (Tables 18, 20 and 21).

Males dominated females in the flock as in territories, but this was complicated by the effects of territory and prior residence. Thus in the Hide territorial area, *2E* and *Plw* were able to dominate adult males (Appendix 4) but only in the months immediately after territorial defence ceased. Adults dominated initially, but juvenile males (e.g. *lWw* and *lZw*) were able to dominate adult females in later months (Appendix 4). The exception to these generalizations was *Rlw*, a juvenile female, which at first was able to dominate both adults and juveniles, but only in its natal territorial area.

4.9 Relationship of Status to Weight and Shield Size

The weights and shield measurements of all birds in the territorial and flock hierarchies are given in Table 24. There is correlation between body weight and status although other factors such as prior residence complicate this and have already been discussed. Using culmen length x shield widths as an index of shield area, the correlation between shield size and status is more evident but it is again affected by prior residence. Juveniles are excluded as their measurements were continually changing.

4.10 Experimental Results

Because the red colour of the shield and bill was

Table 24

CULMEN SIZE AND BODY WEIGHT IN RELATION TO STATUS

Birds are listed in order of status with juveniles and yearlings underlined. Measurements were taken at different times of the year for different birds.

Hide Territory 1972-73

	Culmen Size		Body Weight
	Length mm	Width mm	gm
H1w♂	76.95	31.05	1120
Kw♂	75.54	28.36	1010
P1w♀	65.32	23.34	985
2E♀	65.30	23.06	860
R1w♀	64.48	18.92	820

Northern Territory 1972-73

	Culmen Size		Body Weight
	Length mm	Width mm	gm
Ew♂	81.68	34.88	1160
Tw♂	74.12	29.52	1070
Pw♀	68.70	25.72	956
Bw♀	69.22	23.64	920
1Bw♂	70.34	21.84	940
L1w♀	66.48	25.88	870
1Xw♂	59.52	17.00	750

Southern Territory 1972-73

	Culmen Size		Body Weight
	Length mm	Width mm	gm
Aw♂	75.10	30.36	1060
Ey♂	70.16	25.94	995
By♀	68.40	26.50	880
S1w♀	68.84	24.86	825
1Pw♂	68.96	24.72	945
1Nw♀	60.20	20.92	770

Flock 1971

	Culmen Size Length mm	 Width mm	Body Weight gm
Gy♂	67.46	20.62	980
Ky♂	66.66	23.34	870
Xw♂	69.80	24.92	925
K1y♀	62.68	23.44	920
Nw♂	66.78	24.82	860
F1y♀	61.70	19.64	725
Sw♀	64.62	21.84	785

Flock 1972

H1w♂	76.95	31.05	1120
M1w♂	75.46	29.26	1020
Kw♂	75.54	28.36	1010
Ow♂	70.58	24.24	985
T1y♂	71.78	24.60	1020
1Tw♂	71.18	25.54	1060
Q1w♂	71.68	26.86	1035
1Zw♂	70.48	25.38	1030
1Ww♂	69.28	23.64	1030
Qw♀	68.64	28.18	880
P1w♀	65.32	23.34	985
2E♀	65.30	23.06	860
L1y♂	70.42	24.88	930
1Fy♂	67.12	21.12	890
1Ey♂	65.78	23.24	955
V1y♀	66.94	21.76	880
Vy♀	65.94	22.88	875
Zw♀	65.48	22.60	800
Ky♀	62.74	21.02	875
N1w♀	62.82	20.92	760
Iy♀	66.92	21.58	895

assumed to be important in aggressive displays (p. 80), these parts of *Hlw*, the dominant male of the Hide Territory, were painted black. It was expected that:

(i) This would make *Hlw* less effective in aggressive displays.

(ii) It would alter a characteristic used for individual recognition and hence cause a change of status.

On the day of painting, *Hlw* did not appear in the Hay Paddock (Appendix 4g) but interacted with the other members of the Hide Territory, all of whom reacted submissively. The morning following painting (Appendix 4h), *Hlw* moved out as usual with the other members of the Hide Territory and went to the food in the Peninsular territorial area. Six birds from the flock initially displaced *Hlw* but were immediately attacked and defeated. *Mlw* , usually dominant to *Hlw*, even avoided it when it was feeding with *Kw* at the second pile of food. The afternoon after the painting, food was put in the Hide territorial area and *Hlw* successfully dominated all birds and was not attacked by any (Appendix 4f). Within eight days, much of the black paint had worn off and it was completely gone 20 days after application.

4.11 Relationships Between Rank and Departure Dates of Juveniles

These results apply only to Linton because juveniles at Pukepuke were retained in their natal territories. In 1971, only one chick (*7w*) survived in Linton 2, the other being killed on the road. In Linton 1, three chicks were still alive in June, and the territory dissolved in August. *Ow* which appeared to be the dominant juvenile (Table 20) left the territory in June and moved to Linton 3. *4 w* departed when the territory dissolved but *08* remained for a further three weeks.

In Linton 2, 1972, six chicks were successfully raised (the seventh again killed on the road) and the most dominant, *Oy*, left the territory on 19 September 1972. The remaining juveniles left between 24 October 1972, and 2 November 1972, although *2lw* left the territory, returned and finally departed with the others as discussed earlier (p. 31). Two of the chicks in Linton 1 in 1972 were not banded. However, the most dominant juvenile, *9y* , left the territory a month before the two unbanded ones. The youngest three juveniles were the last to leave - almost six weeks after *9y* . Thus, in general, the most dominant juveniles left the territory first but the remainder usually left within a short time of each other.

4.12 Relationship Between Rank and Leadership

Results were kept of the order in which flock pukeko appeared in the Hay Paddock and their positions were mapped at quarter-hour intervals. No pattern of entry to the Hay Paddock emerged other than that *Mlw* was consistently one of the last to appear, but, in general, all birds emerged within a few minutes of each other and in groups. The composition of these groups appeared arbitrary and changed constantly. Once in the Hay Paddock, the birds dispersed throughout the area, usually feeding in groups which were inconsistent in membership. The lowest ranking birds, especially *Nlw* , *Zw* and *1Cy* , were always furthest from the drain while *Mlw* was nearly always closest to the drain. When artificial food was supplied, the lowest ranking birds, *Nlw* , *Zw*, *1Cy* and *ly* , were frequently unable to gain access to it and dispersed into the paddock. As the piles decreased in size, more and more birds drifted out further into the paddock forcing the lower ranking birds still further from cover. In July and August, *Nlw* was at the greatest distance from the drain in all watches and was frequently 15-25 metres further than the next bird.

Thus, in general, the dominant bird was the last to appear and the lowest ranking birds dispersed furthest from cover but for the majority of the flock no obvious pattern emerged.

4.13 Discussion

The use of artificial food to investigate hierarchies has been criticised (e.g. Ridpath, 1972) as an unnatural situation which produces abnormal behaviour and the fabrication of a hierarchy which does not exist in natural uncrowded situations. However, birds frequently do crowd around natural food (Willis, 1967; Raveling, 1970) and pukeko did naturally crowd in barley fields (p. 18). Also, a hierarchy was suspected prior to artificial feeding and was simply confirmed by it. Many interactions were seen away from food or in the absence of it and these agreed with the order obtained using artificial food.

The behaviour seen around the food was as expected where individual distance was greatly reduced in that appeasement postures involving the rapid removal of bill and shield from the opponent's view, such as Head Flick and Facing Away, were common. The posture most seen in all situations was the raising of the tail, and frequently the wings as well, and Moving Away from the opponent. In a territorial situation where the birds were in constant contact, this was shortened to simply raising the tail to a dominant.

The high frequency of Crouching and Head Flagging in the territorial situation, even when the young were more than eight months of age, and the low frequency of the same displays in the flock, which contained a large number of juveniles of similar age (see Table 3), suggests that young retained in territories extend the use of juvenile behaviour patterns. This retention of juvenile behaviour is presumed to produce tolerance on the part of adult members of the territory and hence allow continued residence in it.

The Bow was the most common and most submissive frontally orientated posture in the territorial situation and the use of Bows, Head Flicks, 'Anxiety' Uprights and Facing Away in all hierarchical interactions confirms the prior evidence (p. 82) that these are extremely submissive displays involving a large element of escape. Similarly, the high frequency of 'Aggressive' Uprights by the more dominant bird substantiates the view that this was the simplest low intensity aggressive display. This is assumed because in a hierarchy interaction where status was already determined, a display of low aggressive intensity was all that was required to displace a subordinate. Only if this display involving the minimum expenditure of energy was ignored, did the dominant resort to a more aggressive display.

The fact that the wing and tail posture of subordinates was always more elevated than that of the more dominant birds is further evidence that tail colour has evolved for appeasement and that the raising of the wings serves only to increase the dominant's view of this signal.

The observation that dominants sometimes raised their tails when passing subordinates does not necessarily conflict with the theory of wing and tail postures, because such behaviour occurred mainly in the breeding season and was correlated with the partial disappearance of hierarchical behaviour. It is obvious that individual distance and aggression between the sexes needs to decrease at this time in order to facilitate successful breeding. This would explain why dominant males tolerated females at the same food pile during this period. This theory could also be extended to explain the out-of-context tail raising between males of the same territory, as all adult males help with incubation (see p. 188). Therefore, it is assumed that aggression on the part of the dominant male towards subordinate males would also need to be reduced or the subordinate male(s) would not approach the nest for incubation when the dominant male was present. In fact, where males were actively displaced by dominant males during the breeding season, e.g. *J/w* and *I/y* , they did not incubate or took very little part in incubation (see p. 188).

Another factor likely to produce the raising of the tail by a dominant when passing a subordinate may have been an ambivalent attitude on the part of the dominant towards a strong rival. Thus it could be deemed advantageous for the dominant to display a submissive signal to an immediate subordinate when the dominant is in a defenceless situation such as walking immediately ahead of the subordinate. Failure to do this could provoke attack by the subordinate at a time when maximum energy and co-operation were required for breeding. These postulates would explain why a dominant raised its tail in the immediate vicinity of a rival or a member of the opposite sex, but not to a bird of markedly lower rank. McBride et al (1969) found that fowls 'lost status' in a number of situations, one of which was running, when birds were frequently attacked by subordinates from behind. Thus the dominant pukeko could lose status when immediately in front of the head of another and hence resort to submissive tail raising.

Further evidence for the previously estimated motivational basis of displays is obtained from the behaviour associated with admission to and expulsion from a hierarchy. Birds entering a hierarchy used a high proportion of appeasement displays that were not given by expelled birds which reverted more and more to higher intensity escape. This is correlated with the dominant bird's behaviour which declined in aggressive intensity when a new bird was admitted, and rose in aggressive intensity (as shown by a high frequency of Charges and Splatters) when a bird was expelled.

Collation of all behavioural interactions demonstrated a linear hierarchy within all groups. Movements of birds were not at random with regard to neighbours and total agreement was obtained from the two criteria - avoidance and aggression. Many other authors (see p. 124) have demonstrated a similar hierarchy in other birds.

A number of hierarchical violations were recorded. However, it is possible that some of these were observational errors, the most likely one being the misinterpretation of situations where a dominant left food of its own accord and a subordinate immediately took its place. Sabine (1959) records a similar problem. Another source of violations was mistaken identity and this further stresses the disadvantage of a dominant close to, and with its back turned towards a subordinate. This would be likely if the characteristics used for individual identification are all centred on the head and the attacks on *Hlw* by six subordinates after its shield and bill were painted suggested these characters are important for recognition. Guhl and Wood-Gush (1953) and Guhl and Ortman (1953) have shown that combs and other head features are important for recognition in fowls. A few violations were the result of attempted rebellions, while others were the result of the combined effect of members of the same territory. Raveling (1970) also found interaction between members of the same family in Canada geese: the goose families remained and fought as distinct units whereas with pukeko, families (or territorial groups) never reacted together as a unit and only rarely did one member help or tolerate another.

As far as is known, Ridpath (1972) is the only other worker to investigate a possible hierarchy in a rail, Tribonyx. Although he described a hierarchy where more than one bird held the same status it is suspected that this may have been caused by experimental method. Ridpath (pers comm.) used artificial food piles large enough for all birds from the territory to feed together. Thus it is assumed that even though a complete hierarchy existed, the birds were able to feed where they chose and hence interactions between many birds were not observed and a partial hierarchy resulted. Use of smaller food piles where birds were forced to supplant each other could be expected to give a different result.

Ridpath did not see any obvious hierarchical interactions away from artificial food but as mentioned previously (see p. 93), bowing between members of the same territory was observed and because this usually happened when birds met at a distance, Ridpath assumed this bowing to be a 'Greeting Display' of unknown significance. Pukeko frequently Bowed to a dominant member of the territory, this being most common when birds were at a distance, and this therefore suggests that the 'Greeting Display' of the Tasmanian Hen could have been an interaction between a subordinate and a dominant. If this analogy is correct, further doubt is thrown on Ridpath's sexing of Tasmanian Hens. He recorded that male Tasmanian native hens bowed to females as frequently as the converse occurred. In pukeko the female was almost always subordinate to males in the same age class which is also true for Tasmanian native hens judging from the partial status results obtained by Ridpath (1972). So the anomalous situation occurs where the dominant males gave a subordinate display to females as frequently as the subordinate females gave the same display to the higher status males. It is therefore possible that many of the birds that Ridpath assumed were males were in fact females.

Gullion did not quantify status in coots but noted that subordinate females Bowed at the approach of the more dominant male, (discussed on p. 88) and described females in a Swimming Arch (Tail Up) in front of males. This is in total agreement with my results but conflicts with the behavioural observations of Ridpath.

4.14 Interaction of Hierarchy and Territory

At any one site a linear or absolute social hierarchy existed in the pukeko, but status varied with site and hence in reality a relative social hierarchy (Leyhausen, 1971) existed. Thus at Pukepuke, the flock invaded part of the Hide Territory in all years, part of the Western Territory in 1972, all of the Peninsular Territory in 1972 and 1973 and all the Trap Territory in 1973. While it is possible to state that the Hide Territory and Western Territory were held all the year round because an inner 'core' area was always defended, this cannot be claimed for the Peninsular or Trap Territories which were completely invaded. But even though trespass was common, the results show that the dominant male of the territory was able to dominate all the trespassing birds, and the dominant female was able to defeat all trespassing females. In many months, especially early in the year, the other members of the territory were able to dominate all trespassers of the same sex and age class. Therefore, if territory is defined as 'a space in which one animal generally dominates others which become dominant elsewhere' (Willis, 1967), the territories can be said to have been permanent because there was a reversal of dominance, with birds dominant in their previous territorial area but subordinate in the territorial area of others. This will be discussed further in chapter 7.

Other workers (e.g. Dixon, 1965 and other references in Willis, 1967) have demonstrated a dominance order related to distance from the nest site. In all cases, the higher status near the nest site may have been due to prior residence, or may have been a relic of 'territorial' behaviour, or may have been caused by both of these. Because status of the previous territorial members declined with time and territory was re-established suddenly at the beginning of the breeding season prior residence appears the more likely. Prior residence has been shown to affect status in caged birds (e.g. Guhl & Allee, 1944; Collias, 1952; Wood-Gush, 1955; and many others).

Various factors have been shown to influence the status of a bird. These include sex, age, size, weight, plumage and other bodily characteristics, prior residence, sexual state and physiological state.

In most studies, males dominate females but this may be altered by the sexual state of the female. Male domination has been demonstrated in domestic hens, *Gallus gallus* (Guhl & Allee, 1944; Guhl, 1954; and others), feral hens (McBride *et al*, 1969), chaffinch, *Fringilla coelebs* (Marler, 1955), mountain chickadees, *Parus gambeli* (Dixon, 1965), blackcapped chickadees, *Parus atricapillus* (Hartzler, 1970), Australian magpies, *Gymnorhina tibicen* (Carrick, 1963), white wagtails, *Motacilla alba* (Zahavi, 1971), red grouse, *Lagopus lagopus* (Watson & Jenkins, 1968), American robin, *Turdus migratorius* (Young, 1956) and many others, in most primates (Bernstein, 1970) and, in fact, in most vertebrates (Allee, 1950). However, sex status reversals are reported at the beginning of the breeding season in some birds: e.g. chaffinch (Marler, 1956 and other references in Allee, 1950). In other species, males cease to exert dominance over females during the breeding season (Allee,

1950) or females assume the same status as their mates (McBride et al, 1969). In primates, females in oestrus assume the same status as their mates (Yerkes, 1943; Cambell, 1966; Bernstein, 1970; and others). Similar results were obtained for pukeko in that there were fewer interactions during the breeding season and females were frequently tolerated at the same food by a male, as discussed earlier (p.113).

The existence of hierarchies with status related to sex may have affected trapping of pukeko. As traps were baited and subordinates avoided dominants, it is possible that trapping could have been biased in favour of males. This is thought to have been overcome by repeated trapping in the same area.

The age of pukeko affected status in that young were always subordinate to adults until full breeding status was obtained, but little is known regarding the effect of age on status in other birds as most studies have confined results to birds of similar age in artificial pens (Guhl & Allee, 1944; Guhl, 1950; Wood-Gush, 1955; Ritchey, 1951) or restricted observations to adults only (e.g. Sabine, 1959; Dixon, 1965; Brown, 1963; Hartzler, 1970). Emlen (1939) reports that older quail Lophortyx californicus, generally rank higher, and Raveling (1970) demonstrated that adults dominated juveniles in Canada geese, Branta canadensis, although the situation was complicated by family group status. The dominance of adults over juveniles was also shown for feral fowl (McBride et al, 1969), and in kookaburra, Dacelo gigas (Parry, 1973). In primates, adults clearly dominate juveniles (Bernstein, 1970; Kummer, 1969; Sugiyama, 1969; Kaufusen, 1969; Sade, 1969; and others) although in Hanuman Langurs, Presbytis entellus, the situation is complicated by filial tolerance (Sugiyama, 1969). In free ranging Rhesus monkeys, Sade (1969) demonstrated that even though young start fighting as infants or yearlings, their rank is predetermined by their mother's rank. Similarly, on reaching maturity, the adult female's rank is still determined by her mother's rank. No similar results were found with pukeko although juveniles in the flock tended to rank highest when in their natal territory area, and status was affected by the presence of other members of the territory (cf. *Rlw*).

Domestic chickens begin fighting for status at 5-7 weeks of age and have a stable dominance order at about 8-10 weeks (Guhl, 1964). However, as these were isolated flocks of chicks, nothing is known about the effects of parental status or other factors in the development of the hierarchy. McBride *et al* (1969) record hierarchies developing within broods of feral domestic fowl and Cullen (1957) reports a peck order between nestling kittiwakes, *Rissa tridactyla*. van Lawick-Goodall (1968) reported the interesting phenomenon of juvenile chimpanzees, *Pan troglodytes*, hiding behind adults (especially mother) of high status when fleeing from a juvenile of higher status and in many cases even threatening the more dominant individual while sheltering. Similar cases of sheltering behind individuals of higher status have not been reported in birds although there is some comparison in Canada geese (Raveling, 1970) where a hierarchy exists between family groups with status partly dependent on that of the adult male but more on the size of the family group. Here all members of the family shared equal dominance status but the dominance position decreased on separation and increased upon unification. (It should be noted, however, that in the case cited by Raveling, it was not known whether the 'family' groups were actually related individuals). However, from these cases it is obvious that an individual's status can depend on the presence of other individuals near it. No comparable results were obtained for pukeko in intra-group behaviour, but similar results were obtained in inter-group encounters (see p. 148).

The initiation of dominance in chicks of feral fowls was followed by McBride *et al* (1969). Fighting (both play and dominance) began at four weeks but McBride did not state if a hierarchy was formed within each brood. After weaning, the broods tended to remain distinct until about 17 weeks when males changed rank; pullets (juvenile females) were integrated into the adult female hierarchy on reaching sexual maturity. Hierarchies have been reported in young mammals in the form of teat orders for pigs (McBride, 1963) and cats (Leyhausen, 1971).

The correlation of rank and weight has also been demonstrated for other species e.g. Adelie penguin, Pygoscelis adeliae (Spurr, 1972) but is not universal (Wynne-Edwards, 1962), and may be a reflection of age. Culmen size in the pukeko was also related to status and is assumed to be one of the most important characteristics used in individual recognition. Comb size is correlated with status in domestic hens and presence and size of horns is linked to status in mammals (e.g. Geist, 1966; Bouisson, 1972).

There was only a partial relationship between status and flock leadership. The observed pattern of distribution of birds when feeding was believed to be related to the fact that subordinates were forced to feed further from cover and water possibly due to a 'pushing effect' (Leyhausen, 1971) of the dominant male. Hafez (1962), and Leyhausen (1971) have shown a partial correlation between rank and leadership in mammals.

4.15 Function of Hierarchy

One of the most important functions that have been postulated for hierarchy is reduction in aggression (Guhl & Allee, 1944; Raveling, 1970). Thus the rank of neighbours is constantly recognised, and behaviour is regulated preventing overt aggression. Accordingly memory and habit reinforce and may replace aggression which is so important in the origin of the social order, and 'social inertia' (Guhl, 1968) results. Social inertia of stable flocks has also been noted by other authors (McBride et al, 1969), and occurs because birds learn and accept dominant-subordinate relationships. When these relationships become habituated social inertia is operative and promotes stability of the hierarchy. The resulting dispersion means birds can feed in groups without loss of food or injury because of fighting. This may explain the ability of some sick or injured birds to maintain their status provided factors for recognition are unaltered (Guhl, 1964). For instance *Tly* was able to maintain its rank despite a severe leg injury.

In the pukeko, dominants gained priority to food and water and also were able to feed in areas closest to cover. Subordinates were forced to feed in areas furthest from cover in order to feed undisturbed, but were able to join the flock when predators (hawks) attacked, and had the opportunity to join a group for breeding. This subject will be discussed further in chapter 7.

5. INTER-GROUP USE OF SPACE
(TERRITORY)

5.1 Introduction

Territory defined as 'any defended area' (Noble, 1939) is with birds one of the most common inter-group divisions of space (Brown and Orians, 1970), and is an important aspect of pukeko social organization. The criteria applied to determine the existence of territories were those listed by Hinde (1956) and Brown and Orians (1970), namely:

(a) restriction of some or all types of behaviour to a more or less clearly defined area,

(b) defence of that area.

With these criteria all breeding groups and pairs of pukeko defended a set area during spring and early summer, but most of these territories broke down partly or completely at other times of the year.

Fifteen territories (Appendix 3) were observed during the study and eight were followed in detail (Table 25). Six territories were at Linton (Fig. 38) and the remainder at Pukepuke (Figs 39, 40 and 41). At Linton three of the territories, 1, 2, and 4, were adjacent, whereas the others, 3, 5, and 0, were semi-isolated swamp areas. The Hide was placed on the boundary between territories 1 and 2, both of which were defended at all times of the year. Adult membership of Linton 2 was constant, but all birds from Linton 1 left in August 1971, and in all the territories chicks dispersed prior to breeding each year.

At Pukepuke all territories adjoined another on at least one boundary and varied greatly in membership and degree of breakdown. Territories formed from flock birds - Peninsular, Rough Paddock, Trap, and Corner (see p. 24) - broke down completely after breeding. The Hide and Western Territories partially broke down outside the breeding season and trespassing was tolerated outside a 'core' area

Table 25

MEMBERSHIP OF MAIN STUDY TERRITORIES

TERRITORY	SEASON			
	-1970	1970-71	1971-72	1972-73
Linton 1	04♂ 07♀ 06♀ * 05♀	* 04♂ * 07♀ * 06♀ *10w♂ * 4w♂ * 08♀ * 0w♂	Ub♂ 41y♀ * 9y♂ *2Ub *61y♂ *71y♂ *81y♀	Ub♂ 41y♀ 3Ub 2Ub
Linton 2	03♂ 00♀ * 01♂ * 02♀	03♂ 00♀ * 7w♂ + 5w♂	03♂ 00♀ * 0y♂ *10w♂ *11y♂ + 6w♀ *14w♀ *17w♀ *21w♂	03♂ 00♀ 4Ub
Hide	Ew♂ H1w♂ 2J♂ 2B♀ * 2C♀ 2E♀	Ew♂ H1w♂ ' 2J♂ + 2B♀ 2E♀ P1w♀	H1w♂ Kw♂ *J1w♂ 2E♀ P1w♀ R1w♀	H1w♂ Kw♂ '1Jy♂ 2E♀ P1w♀ R1w♀ 4Ub
Southern	Aw♂ 2K♂ Ey♂ By♀ * 2N♀	Aw♂ Ey♂ By♀ S1w♀	Aw♂ Ey♂ By♀ S1w♀ 1Pw♂ 1Nw♀	Aw♂ Ey♂ By♀ S1w♀ 1Pw♂ 1Nw♀ Vw 2Ub
Northern	Ay♂ Tw♂ Pw♀ Bw♀	* Ay♂ Tw♂ Pw♀ Bw♀	Ew♂ Tw♂ Pw♀ Bw♀ 1Bw♂ L1w♀ +1Xw♂	Ew♂ Tw♂ Pw♀ Bw♀ 1Bw♂ L1w♀ 2Ub

Table 25 continued

TERRITORY	SEASON			
	-1970	1970-71	1971-72	1972-73
Western	Ry♂ 1Ay♂ Ty♀ Ub♀	Ry♂ 1Ay♂ Ty♀ Ub♀ Sy♀	Ry♂ *1Ay♂ * Ty♀ Ub♀ Sy♀	* Ry♂ * Ub♂ + Ub♀ Vy♀
Peninsular	-	-	M1w♂ Qw♀ *L1y♂ *N1w♀	M1w♂ * Qw♀ 1Tw♂ Q1w♂ 1Ww♂ 1Zw♂ Zw♀ *1Fy♂ *1Cy♀
Trap	-	-	-	T1y♂ Ub♂ 1Ky♀

* Bird left during the year　　+ Accidentally killed

' Expelled during season　　Ub Unbanded

Chicks of the year are underlined.
Adults are arranged in hierarchical sequence.
Season is taken from August to August.

Figure 38 Breeding Territories at Linton


3
4
2
5
1
Linton
50m

Figure 39 Breeding Territories at Pukepuke 1970-1971

W.T. = Western Territory
N.T. = Northern Territory
S.T. = Southern Territory
H.T. = Hide Territory
I.T. = Inlet Territory

Wider spaced dotting of boundary encloses the area of greatest use after laying.

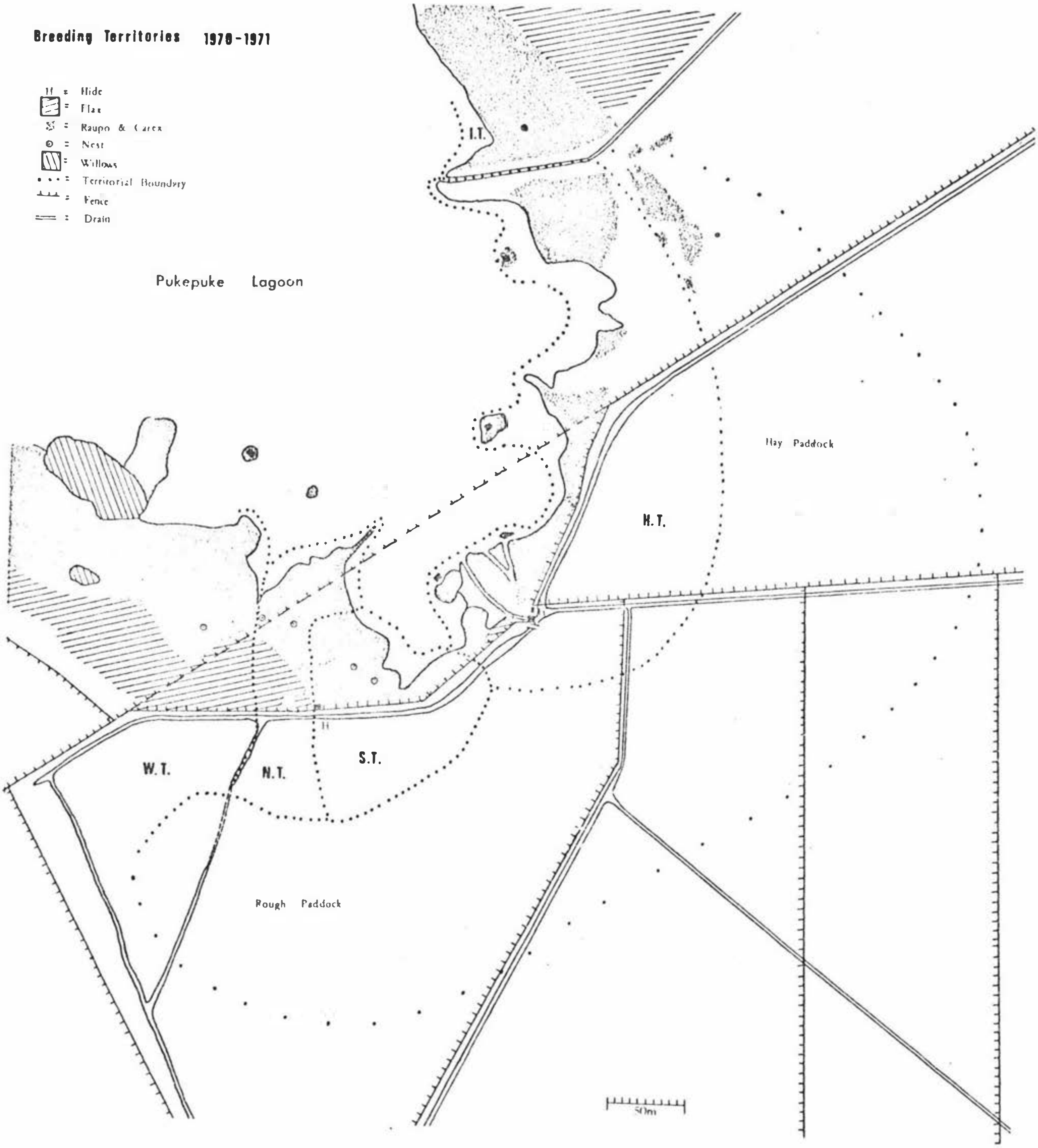

Breeding Territories 1970-1971
H = Hide
= Flax
= Raupo & Carex
= Nest
= Willows
= Territorial Boundary
= Fence
= Drain
Pukepuke Lagoon
I.T.
Hay Paddock
N.T.
W.T.
N.T.
S.T.
H
Rough Paddock
50m

Figure 40 Breeding Territories at Pukepuke 1971-1972

Wl.T. = Willow Territory
P.T. = Peninsular Territory
R.P.T. = Rough Paddock Territory

Wider spaced dotting of boundary encloses the area of greatest use after laying.

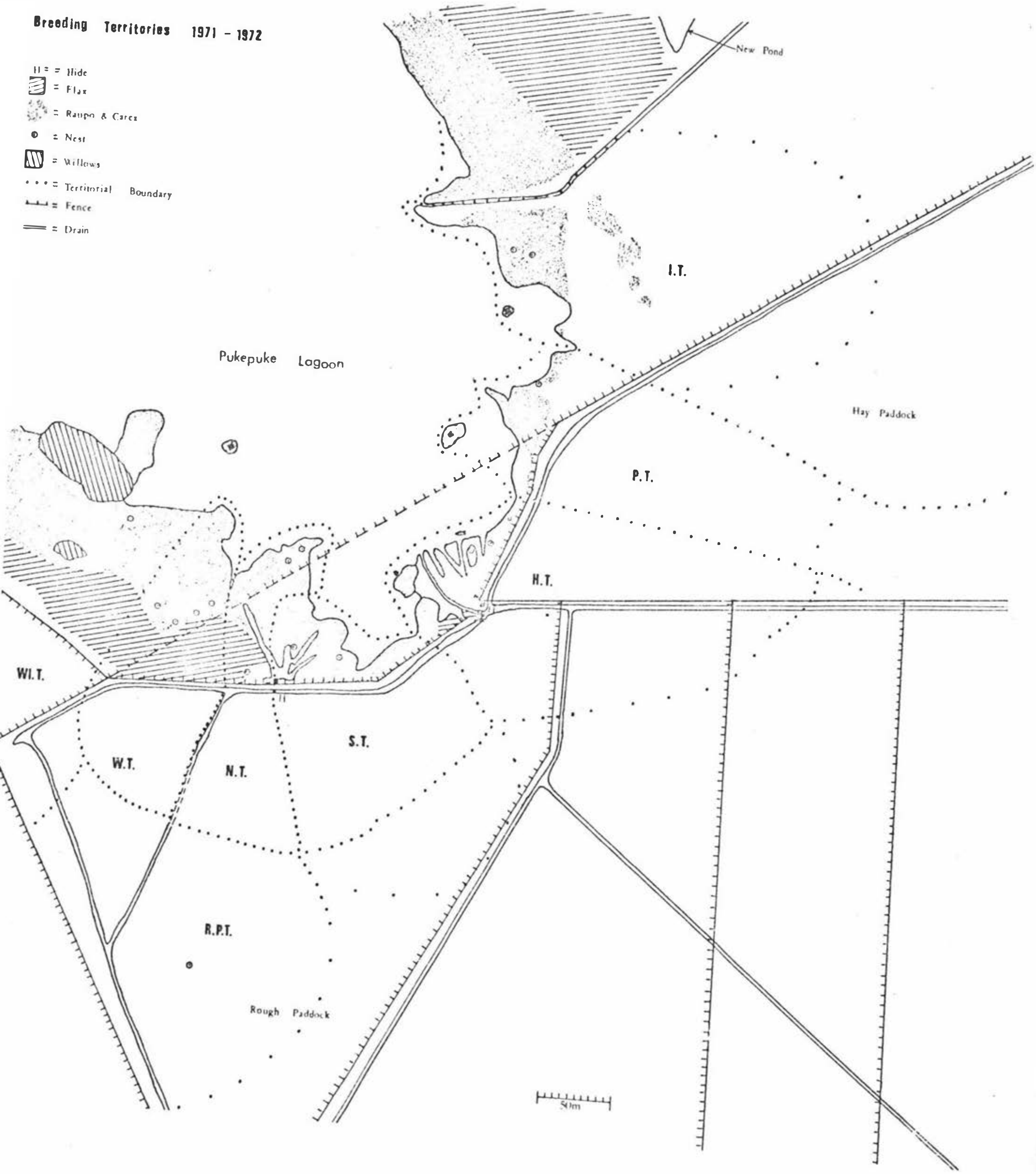
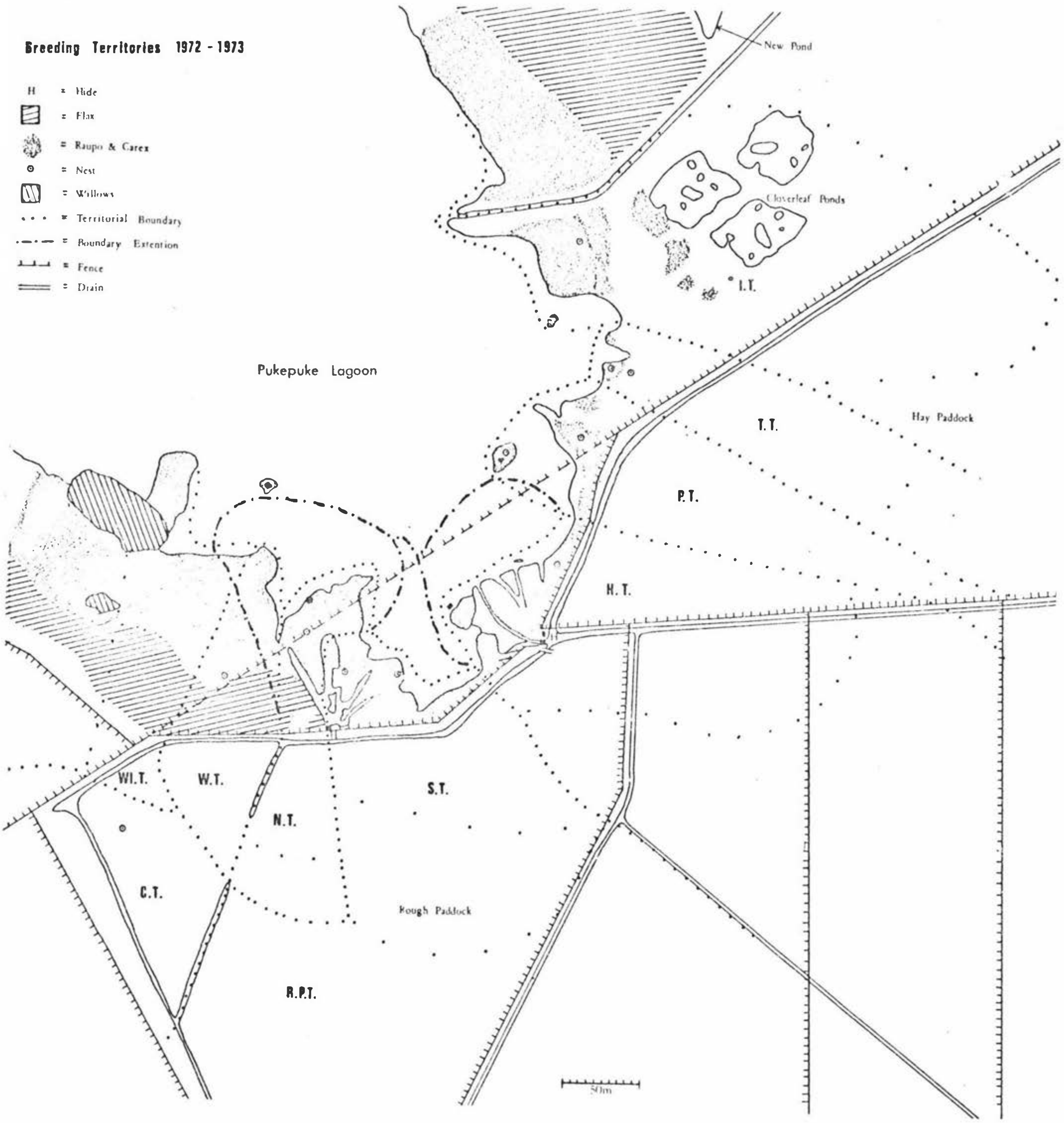

Breeding Territories 1971 - 1972
H = Hide
= Flax
= Raupo & Carex
= Nest
= Willows
= Territorial Boundary
= Fence
= Drain
New Pond
I.T.
Pukepuke Lagoon
Hay Paddock
P.T.
H.T.
WI.T.
H
W.T.
N.T.
S.T.
R.P.T.
Rough Paddock
50m

Figure 41 Breeding Territories at Pukepuke 1972-1973

C.T. = Corner Territory
T.T. = Trap Territory

Wider spaced dotting of boundary encloses the area of greatest use after laying.


Breeding Territories 1972 - 1973

(term is Gullion's, 1952). The remaining study territories (Northern and Southern) were more similar to Linton in that the breeding territory was defended all year. There was, however, a temporal pattern of use in 1971 in that both territories were actively defended during the daylight, but from dusk till immediately before dawn they were used for roosting by flock pukeko.

Membership of the four main Pukepuke territories was relatively constant (Table 25) although some birds disappeared and were replaced, and one bird, *Ew*, changed territories. Major membership changes did occur in the Western Territory in 1971-72, when consistent nesting failure (see Appendix 6) caused *Ty* and *Sy* to vacate the territory. In 1972-73, when the dominant female died in the territory, the two males deserted, the remaining female rejoined the flock (see p. 25) and the territory was absorbed by neighbouring territories (Fig. 41).

5.2 Behaviour Associated with Territory

The behaviour associated with territorial defence has already been used to analyse pukeko displays (Chapter 3). Territorial disputes fall into two categories:

(a) defence against known neighbours,

(b) expulsion of itinerant trespassers.

In the latter case, behaviour was relatively simple: the territory member either Charged or Splattered the intruder causing its retreat. The territorial bird usually had wings and tail Fully Down in contrast to the elevated wings and tail of the intruder. The attacking bird frequently concluded with a Wing Clap and call and often used a Long Call as well. Wing Claps and calls were frequently used by birds within their territory and appeared to proclaim ownership.

Defence of territory against a known neighbour was usually protracted. The boundary appeared to be known by all individuals and if a bird of a neighbouring territory trespassed, it was treated like any other intruder except that the attacking resident usually had elevated wings and tail, the degree of elevation increasing as it approached the boundary. Usually the neighbouring bird needed to be within only a few metres of the boundary to elicit a response from the resident. In this situation, if one bird attacked or adopted an aggressive display, the other replied in an agonistic posture: the more equal their distances from the boundary, the more similar their displays. This is shown by the high frequency with which two disputing birds were seen in the same display ('Aggressive' Uprights, Horizontal Forwards and Depressed Forwards - Table 8).

Usually in a boundary dispute one bird was the closer to the boundary, adopting a posture of high escape content (Table 8) before Moving Away. This retreating bird frequently moved only one to three metres, then turned and stood in an aggressive display which normally resulted in the second bird retreating and the first advancing once more thereby producing a number of zig-zag encounters. When neither bird retreated a fight resulted.

While the above describes the general nature of territorial encounters the majority were much more complicated. Most territories were held by a group (see p. 20) and so boundary disputes usually involved more than two birds. For instance, when one bird was attacked, its fellows aided it or more than one bird attacked simultaneously (Fig. 5). Multiple territorial defence also occurred in pair territories when young over three months of age joined in.

Trespassing by birds of neighbouring territories was common and much went undetected although few birds trespassed more than a few metres. Dominant males patrolled the boundaries periodically throughout the day and when traps were set near the boundaries these frequently caught the patrolling male from the adjacent territory. This applied to ***Hlw*** and ***Ew*** especially.

Weather conditions prevented birds from discovering all intrusions into their territory. The Linton valley ran approximately east-west and was, therefore, strongly affected by the prevailing westerly winds. Birds faced into a strong wind when feeding which meant that trespass was frequently undetected on such days even though the trespasser would have been detected if the territory owner had faced in the opposite direction.

Mistaken identity was apparently another cause of trespass. For example, on 20 June 1972 *INw* (Southern Territory) and *Tw* (Northern Territory) both fed at the same part of the boundary and *IBw* (Northern Territory) even walked out past *INw* and fed. When identity was finally established, *INw* dashed back to its own territory.

Another interesting case of trespass occurred after *Ew* left the Hide Territory and established himself as the dominant male in the Northern Territory. Within the following month, *Ew* returned to the Hide Territory three times, on one occasion giving a Long Call and Wing Clap on its return, and on another helping in a territorial dispute. On all occasions it was still treated as the dominant male of the Hide Territory by the other members. Thus for approximately one month *Ew* enjoyed dominant status in two territories simultaneously.

5.3 Effects of Status, Sex and Age on Frequency of Defence

In 1972, between March and December, the boundary between the Southern and Northern Territories at Pukepuke (Fig. 42) was studied in detail and all territorial interactions were recorded (Table 26). In both territories, adult males accounted for approximately 74% of the defence in the nine months, excluding the May shooting season. Proportions of defence attributable to females and juveniles in both territories was also similar, being 19% and 6.7% respectively.

Among the males there was inconsistent division of defence according to status. In Northern Territory, the dominant male, *Ew*, did 48% of the defence and the β male, *Tw*, only 25%. The converse applied in the Southern Territory where *Aw*, the dominant male, accounted for 25% of

Figure 42

Boundary zone between the Northern (left) and Southern Territories. Note the pegs at metre intervals (every third one has a numbered disk), and the screen. Three birds are out from each territory.

Table 26

PROPORTION AND FREQUENCY OF DEFENCE ATTRIBUTABLE TO INDIVIDUAL MEMBERS OF GROUP TERRITORIES

A single defence action was scored when a bird was observed to attack or display at a member(s) of the other territory regardless of actions of other members of the same territory. Birds are in order of status.

	Northern Territory							Southern Territory						
Month	♂ Ew	♂ Tw	♀ Pw	♀ Bw	J♂ 1Bw	J♀ L1w	Total	♂ Aw	♂ Ey	♀ By	♀ S1w	J♂ 1Dw	♀ 1Nw	Total
March	114 55.1%	33 16.0%	19 9.2%	28 13.6%	9 4.4%	4 2.0%	207	66 32.6%	78 38.5%	34 16.8%	15 7.4%	2 1.0%	8 4.0%	203
April	217 51.3%	94 22.3%	69 16.4%	31 7.4%	9 2.2%	3 0.7%	423	54 14.1%	226 59.0%	61 16.0%	25 6.6%	9 2.4%	8 2.1%	383
June July	41 25.8%	80 50.4%	21 13.2%	2 1.3%	12 7.6%	3 1.9%	159	42 30.9%	67 49.3%	14 10.3%	6 4.5%	4 3.0%	3 2.2%	136
August Sept Oct	66 60.6%	24 22.1%	10 9.2%	- -	8 7.4%	1 1.0%	109	17 26.6%	34 53.2%	2 3.2%	- -	10 15.7%	1 1.6%	64
Nov Dec	92 47.7%	42 21.8%	24 12.5%	3 1.6%	23 12.0%	9 4.7%	193	64 40.8%	55 35.1%	7 4.5%	15 9.6%	2 1.3%	14 9.0%	157
Total	530 48.6%	273 25.1%	143 13.1%	64 5.9%	61 5.6%	20 1.9%	1091	243 25.8%	460 48.8%	118 12.6%	61 6.5%	27 2.9%	34 3.6%	943

J = juvenile

the defence while the β male, Ey, did 48%. Correlation of defence with status was more evident in the adult females, as in both territories the dominant female did 13%, the β female only 6%. Defence by juveniles was variable: in the Northern Territory, the male, IBw, did more than the juvenile female, LIw, while the opposite occurred in the Southern Territory. Proportion of defence by all juveniles was similar. The complete absence of defence by the female of both territories in August-September-October was due to the fact that all watches during this time were from dawn and this coincided with the incubation shift of the female.

Monthly results reflect observation hours (Appendix 1) and the number of feed days rather than a natural distribution of territorial encounters. There was, however, a trend towards decreased defence by females and an increase in defence by juveniles during the breeding season.

Scores of territorial disputes in a pair territory (Linton 2) are given in Table 27. Complementary results for Linton 1 are not given because not all of the birds were banded. Unlike the group territories at Pukepuke, juveniles in Linton 2 took a major part in territorial defence, the two older juvenile males (Oy and 10w) accounting for 50% of the encounters. The adult male, 03, did a further 27.5%, thus in total, 84.4% of territorial defence was attributable to males. The adult female, 00, did more defence than any of the juvenile females but the difference is not great. There was no evidence of any relationship between status, independent of sex, and the proportions of defence.

5.4 Territorial Boundaries

5.4.1 Position

Boundaries generally followed geographical features, especially drains, fences, and lake edge. This reduced the length of boundary along which physical defence was necessary, although pukeko still displayed on either side of the

Table 27

PROPORTIONS OF TERRITORIAL DEFENCE ATTRIBUTABLE TO INDIVIDUAL MEMBERS OF A PAIR TERRITORY

(Linton 2)

(A single defence action was scored when a bird was observed to attack or display at a member(s) of an adjacent territory regardless of actions of other members of the same territory.)

	MONTH											Total	%
	Jan	Feb	Mar	Apr	May	June	July	Aug	Sept	Oct	Nov		
03	3	10	6	11	2	13	3	-	3	2	-	53	27.6
00	1	2	-	3	-	1	-	-	-	4	2	13	13
0y	-	3	3	13	1	4	3	7	3	*		37	19.8
10w	-	4	6	7	4	18	2	4	6	5	*	56	30.0
11y	-	-	-	2	-	1	-	1	3	-	*	7	3.8
6w	-	2	+									2	1.1
21w	-	-	-	-	-	4	-	3	-	4	*	11	5.9
17w	-	-	-	+	2	1	-	-	2	-	*	6	3.2
14w	-	-	-	-	1	1	-	-	-	-	*	2	1.1

187

\+ killed

* left territory

barrier. In a boundary dispute, the retreating bird frequently walked at an angle to the boundary moving gradually rather than directly away from it. It was thought that this might have affected the position of a boundary where a physical barrier did not exist. To test this idea a wire screen was placed at right angles to the boundary between Northern and Southern Territories (Fig. 42) to see if it would alter the position of the boundary. The screen forced displaying birds to retreat directly away from each other. Results for the males (Table 28) show that although the boundary did, as predicted, shift towards the Southern Territory while the screen was in place, the shift had started before the screen was erected and was not accelerated by it.

Table 28

CHANGE IN THE SOUTHERN-NORTHERN TERRITORY BOUNDARY, WITH TIME

Screen from 15.0 to 17.8 introduced 4 August 1972
removed 27 October 1972

(Units are 0.5 m taken from an arbitrary zero point)

	March	April	June/July	Aug/Sept/Oct	Nov/Dec
Boundary Position of $E_w - E_y$	14.5	16.5	17.6	17.9	17.5

The boundary did eventually shift past the end of the screen and then back again when it was removed, but at no time was the boundary far enough into the Southern Territory for the Northern Territory birds to walk around the end of the screen.

5.4.2 Size of Boundaries

Boundary lengths varied greatly from one territory to another. At Linton (Fig. 38) the boundary between territories 1 and 2 was never greater than 40 metres: all other Linton territories were separated by physical boundaries.

At Pukepuke all study territories (Figs 39, 40 and 41) were bounded by others on at least two sides; thus the defensible boundaries were large and in all cases were longer than those at Linton. Furthermore, most territories had a poorly defined boundary on at least one side (e.g. open paddock or lake) but these were still defended against itinerant birds. Pukeko spent little time in the open paddocks during the breeding season and the most commonly defended boundaries were those between the lake edge and the adjacent paddocks. The smallest of these were on either side of the Hide Territory and were less than four metres in length.

5.4.3 Stability of Boundaries

The position of boundaries at Pukepuke changed little during the study, but boundaries were 'elastic' in that when a neighbouring territory broke down or when gross changes in habitat occurred, e.g. the lake drying up and making more area available, boundaries were extended to take in part of these new areas. In February, 1972, the Peninsular Territory contained a breeding pair, and a male and a female chick. The neighbouring Hide Territory contained five adults and one juvenile who slowly encroached on the Peninsular Territory. At the same time, intensive duck trapping attempted at the end of the Peninsula attracted birds from all territories nearby (Hide, Peninsular and Trap), as well as the first flock birds. The 'Maimai Island' in the Peninsular Territory (Fig. 40) was lost to the Hide Territory and the end of the Peninsula to the Inlet Territory. By mid-March, the Peninsular Territory had become overrun with flock birds and it completely broke down.

In the 1972-73 breeding season, the Western Territory broke down after the dominant female died and the two males disappeared. At the same time, the lake began drying up. The Northern Territory expanded its boundaries (Fig. 41) to incorporate part of the Western Territory and part of the old lake bed which gave the birds continuing access to water. Drying of the lake also produced a change in the boundary between the Southern Territory and the Hide Territory that presumably ensured a water supply for the former. In contrast, the boundary between the Northern and Southern Territories was very stable and varied only 1.5 metres (Table 28).

At Linton, the territorial boundary underwent continual change (Fig. 43) with the boundary of the dominant males varying over 150 metres. This change appeared to be closely related to breeding, as both Linton 1 and Linton 2 were pair territories (except the former in 1970-71) and when a pair was nesting, most time was spent incubating or feeding and little time was spent maintaining the boundary. Thus, birds lost ground when breeding. When the chicks were two and a half months old, they began helping in territorial defence and ground was regained, but because breeding at Linton was asynchronous, the territorial boundary zig-zagged to and from the central fence. The two other major positions where the boundary stabilized, were gaps in the raupo cover which allowed birds to move freely from one side of the valley to the other.

5.5 Territory Size

Territory size (Table 29) was calculated from photographs of known scale between defended boundaries, or where these were not clear, between lines enclosing areas frequently used by the birds of the territory. This did not, therefore, include all the area ranged by a group of pukeko but only the areas of frequent use.

The two main Linton territories were very similar in size when the fence was taken as the boundary. When the full variation in size is calculated, however, over half a hectare changed ownership. Thus in June/July 1971, Linton 1 was

Figure 43

Changes in the position of the boundary between Linton 1 and Linton 2 in relation to nesting.

Fluctuations of the Territorial Boundary at Linton

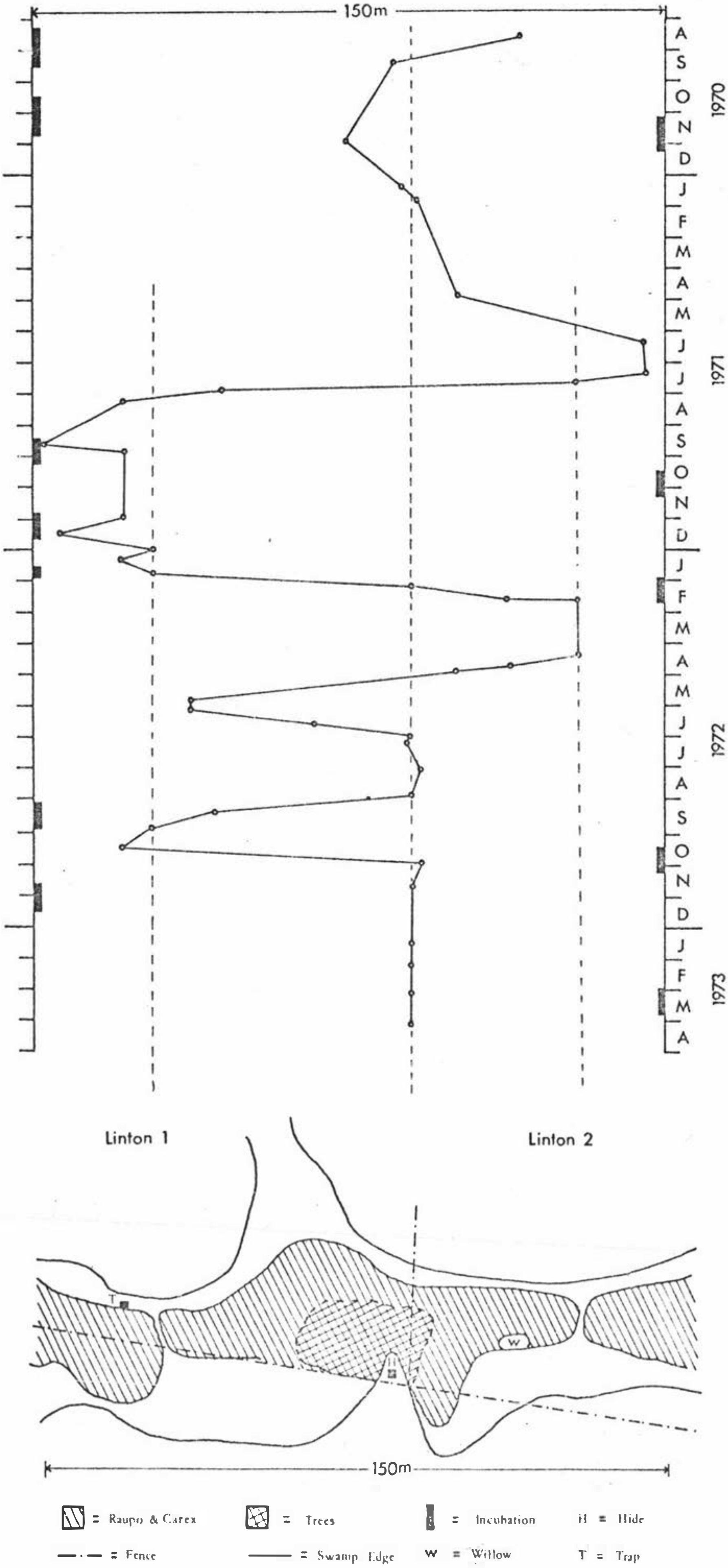


Table 29

MINIMUM AREA (ha) OF STUDY TERRITORIES

TERRITORY	1970-71	1971-72	1972-73
Pukepuke			
Hide	3.1 (6)	2.5 (6)	2.3 (6)
Southern	1.0 (4)	1.5 (4)	1.2 (6)
Northern	0.7 (4)	1.0 (4)	0.7 (6)
Western	-	1.2 (5)	0.9 (4)
Peninsular	-	2.0 (2)	1.6 (6)
Trap	-	-	1.0 (3)
Inlet	-	3.1 (5)	3.0 (6)
Corner	-	-	1.1 (4)
Rough Paddock	-	2.4 (5)	2.1 (5)
Mean	1.60	1.96 (4·4)	1.54 (5·1)
Linton			
Linton 1		0.79	
Linton 2		0.82	

The number of birds in each territory is given in brackets.

almost 1.0 ha and Linton 2 only 0.6 ha; while in October/November 1971, Linton 2 was more than 1.1 ha while Linton 1 was less than 0.5 ha.

Territory size at Pukepuke was extremely variable but between 1971-72 and 1972-73 there was a trend towards a decrease in size with an increase in the number of territories and birds in the area. The larger territories tended to have one or more undefined boundaries (Figs 39, 40 and 41) while the smaller territories were surrounded on almost all sides by other territories. There was no simple relationship between territory size and the number of birds per territory (Appendix 3) and territory size decreased in many cases even though the number of birds present in the territory was greater.

The large size of the Hide Territory in 1970-71 was associated with lack of cover caused by extensive grazing by cattle. When the cattle were excluded from the Reserve (see p. 6), the birds began nesting and the territory shrank markedly in size (Fig. 39).

5.6 Intergroup Hierarchy

So far, 'territorial boundary' has implied a distinct line, but in 1971 it became obvious that different pukeko from each territory defended different boundaries against different members of the opposing territory. To investigate this complicated situation, a number of boundary areas were marked with numbered pegs at metre intervals, and small amounts of food were put out at irregular intervals to increase the number of interactions. The birds rapidly associated my presence with the provision of food so that even on days when food was not put out, they went to the boundary searching for food and interacted. All interactions were recorded, including the places where the attacking bird began and ended its advance, and the places where the retreating bird started and finished its escape. Frequently two birds advanced towards each other and this double advance was scored separately as was the location of fights.

The presence of more than one member of a territory in the boundary zone at one time made interpretation of the interactions difficult. Thus when a juvenile of territory A was out alone, the male from territory B would charge to a certain point (X), but when the dominant male of territory A was out with the juvenile and the neighbouring male charged, the juvenile usually ran to the shelter of the dominant male not back to (X). Also low ranking birds tended to advance further when accompanied by more dominant birds than when they were alone. Hence the position of the boundary for any bird with the partial exception of α males was dependent on the status of other birds with it. Extracts from my field notes demonstrate the complexity of such situations (Note: The measurements were 50 cm intervals with the zero point marking the furthest point a bird from the Southern Territory advanced into the Northern Territory):

(i) 1 April 1972

0700 hrs 1Bw, L1w at 13, Ey 17 charged to 15. 1Bw ran back to 9 W & TFU (Wings and Tail Fully Up) and L1w to 8 W & TFU. 1Nw at 19. Pw at 3. Ey feeding at 15. 1Bw and L1w still 8. 1Nw moved to 16. 1Pw at 19 and S1w at 21. By came out to 17. Pw walked in 'Aggressive' Upright W & TFU to 9. Ey W & TFU went back to 16 and By back to 18. Pw went to 11 and fed. 1Pw at 18 and Pw in an 'Aggressive' Upright at it and it dashed back to 20 TFU. Ey in an 'Aggressive' Upright at Pw who turned and Ey charged to 14. Pw W & TFU dashed away and Ey charged to 9. W & TEU (Exaggerated Up) back to 7. Pw turned and a full fight with Ey at 9. Bw in an 'Aggressive' Upright W & TFU at 7. Ey went back to 12 W & TFU and Pw to 10 W & TFU. Pw then went back to 4 and preened and Ey to 15 and fed.

(ii) 6 October 1972

1Pw at 20, Ey at 21 and Ew at 16 in an 'Aggressive' Upright. 1Pw W & TFU back to 21.5 and fed immediately behind Ey.

(iii) 25 March 1972

Ew at 16 and 1Bw feeding immediately behind it. Ey at 18. Ew head under water pulling at raupo shoot. Ey charged to 16 at 1Bw who dashed back W & TEU to 9. Ew pulled shoot up and into an 'Aggressive' Upright W & TFD and Ey W & TFU back to 19.

(iv) **Aw** at 18, **1Pw** at 19, **By** at 20 and **1Nw** at 205. **1Bw** charged W & TFU from 16 at 1Pw who dashed back W & TFU to 21 where it turned and had a full fight with 1Bw. 1Bw then dashed back to 16 W & TFU and 1Pw in an 'Aggressive' Upright W & TFU to 19. (Note that here 1Bw charged past three other members of the Southern Territory when fighting 1Pw).

Because of the influence of other birds, results were separated into 'guarded' and 'unguarded' depending on whether a bird was at the boundary area alone (or in the company of lower status birds) or whether it was accompanied by a bird of similar or higher status. Results for two different portions of the boundary between the Southern and Northern Territories were compared monthly (Appendix 5) but were added to give an overall result for the year (Table 30).

The boundary between any two birds was obtained by taking the overall (true) mean of all interactions involving those birds.

An estimate of the boundary was obtained from four different values, guarded and unguarded being treated separately.

(a) Mean fight locations.

(b) Where one bird advanced and the other retreated:

  (i) True mean of the mean maximum advance of bird A and the mean maximum retreat of bird B.

  (ii) True mean of the mean maximum advance of bird B and the mean maximum retreat of bird A.

(c) Where both birds advanced, the true mean of the mean maximum advance of both A and B.

For adult males, these four values were in close agreement but guarding masked the results in lower ranked birds. In many, the difference between guarded and unguarded interactions was substantial but only a few of these were significant (Appendix 5). The failure to demonstrate significance in other cases was due to the small number of

Table 30 RELATIVE TERRITORIAL BOUNDARY POSITIONS BETWEEN THE BIRDS OF THE SOUTHERN AND NORTHERN TERRITORIES

Boundaries are given in metres relative to the boundary of dominant males (0.00). Negative values indicate that boundary is on Southern Territory side of zero line. Actual numbers of encounters that the boundaries are calculated from are given in brackets. Birds are in order of intra-territorial status.

		Northern Territory Birds						
		Ew	Tw	Pw	Bw	1Bw	L1w	Correlation
Southern Territory Birds	Aw	0.00 (109)	0.13 (147)	2.24 (68)	1.57 (17)	1.84 (30)	3.01 (26)	+
	Ey	-0.16 (361)	-0.01 (124)	1.05 (71)	1.54 (34)	1.25 (49)	1.62 (30)	+
	By	-1.62 (35)	-0.85 (27)	-0.44 (32)	0.44 (43)	1.38 (17)	1.72 (28)	o
	S1w	-1.70 (35)	-1.35 (20)	-1.11 (14)	-0.04 (12)	1.32 (26)	1.13 (17)	*
	1Pw	-1.73 (69)	-0.91 (22)	-0.72 (16)	-2.15 (14)	-0.24 (34)	0.88 (12)	ns
	1Nw	-1.99 (48)	-0.76 (23)	-0.75 (26)	-0.26 (22)	-0.17 (27)	0.21 (21)	*
Correlation		+	ns	+	ns	+	*	

ns not significant
+ p 0.05
* p 0.01
o p 0.001

results. Where unguarded results are known, these were similar to fight locations but the difference between fight and guarded was large. Ideally only unguarded results should have been used for calculating boundaries but in many cases none were observed. Overall mean results (where known) for March to December 1972 are given in Figs 44 and 45.

Combined action of two birds also affected results. For example, on 8 April 1972, the two males of the Southern Territory (*Aw* and *Ey*) repeatedly combined to attack *Ew* and the joint effort managed to push *Ew* back a further four metres (Appendix 5).

In the overall results there is a positive link between intra-territorial and inter-territorial status where the latter is demonstrated by different boundary positions. This link shown by linear regression analysis (Table 30 and Fig. 46) is significant at the 5% level in all except three cases but this does not hold for all monthly results, some of which are definitely non-linear. However, it is assumed that inter-territorial status is established separately from intra-territorial status and is probably decided in first territorial encounters. But it is probable that a linear relationship between the two ranks would have been demonstrated in all months if sufficient unguarded results had been obtained. Despite this, there was considerable individual variation and birds tended to attack mostly birds of similar status and age in the opposing territory. Thus *Aw* reacted the most with *Ew* but less than *Ey* in respect of all other members of the Northern Territory (Figs 44 and 45). This trend is well illustrated by the fact that for any one bird, its boundary closest to the zero point was with the bird of similar status in the opposing territory.

The effects of breeding on boundary positions were obvious because the boundaries of females retreated in relation to those of the males during the breeding season. The boundaries, and hence the status, of the juveniles (especially males) advanced with increasing age.

The results (Appendix 5) also demonstrate the ritualization of behaviour to display and the resultant low

Figure 44 Inter-territorial Status as Demonstrated by Boundary Position.

The boundary positions of the Southern Territory pukeko are given in relation to each of the Northern Territory birds. Northern Territory birds are in order of intra-territorial status and the Southern Territory birds are represented numerically in order of rank (Aw, Ey, By, S1w, 1Pw, 1Nw).

Boundary position is relative, with that of the dominant males taken as the zero point. Positive values mean that the bird was able to drive birds further than the dominant male's boundary and negative values mean the converse.

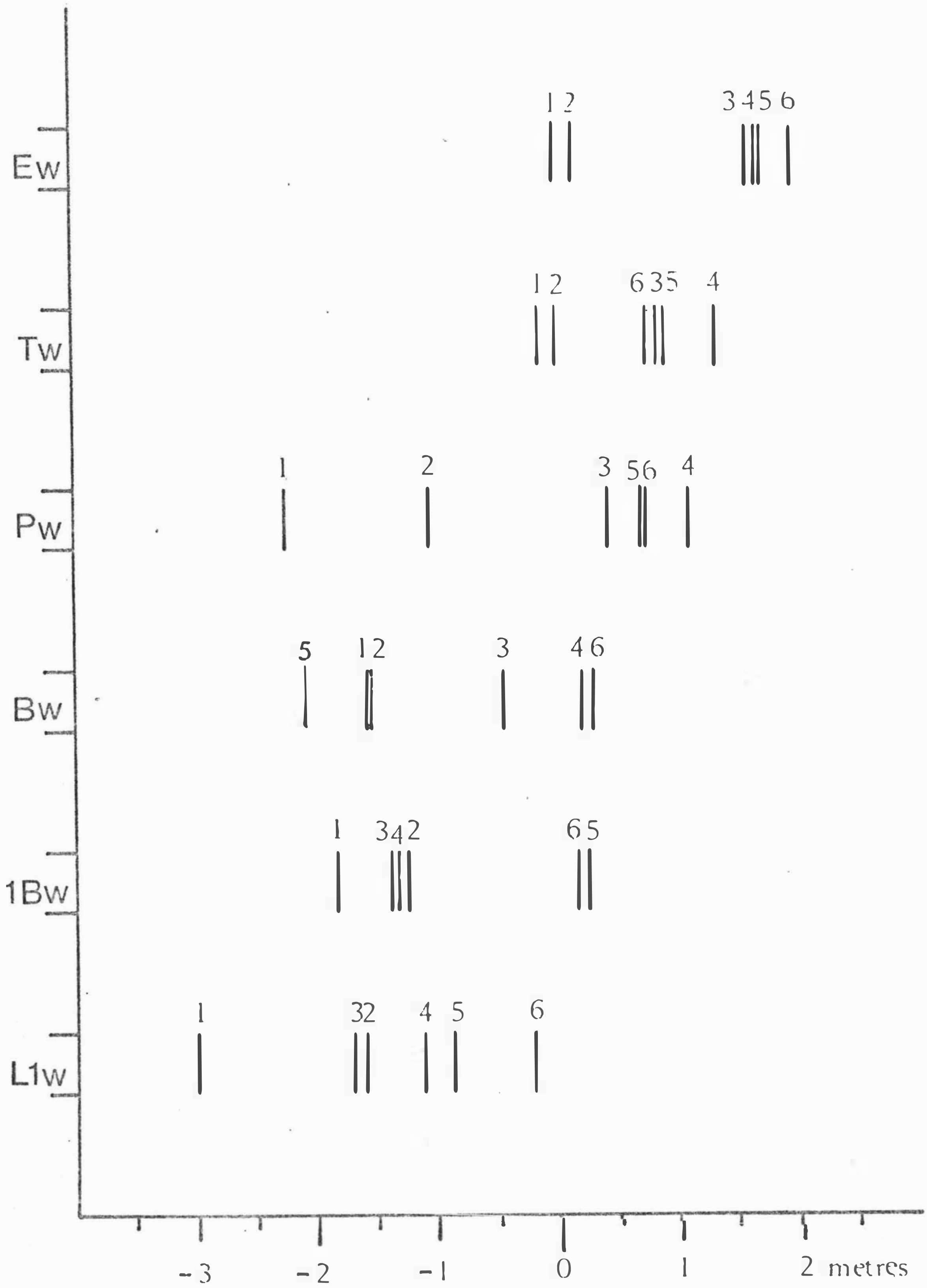

1 2
3 4 5 6
Ew
1 2
6 3 5
4
Tw
1
2
3
5 6
4
Pw
5
1 2
3
4 6
Bw
1
3 4 2
6 5
1Bw
1
3 2
4
5
6
L1w
-3
-2
-1
0
1
2 metres

Figure 45 Inter-territorial Status as Demonstrated by Boundary Position.

The boundary positions of the Northern Territory birds are given in relation to each of the Southern Territory birds. Southern Territory birds are given in order of intra-territorial status and the Northern Territory birds are represented numerically in order of rank (Bw, Tw, Pw, Bw, 1Bw, L1w).

Boundary position is relative, with that of the dominant males taken as the zero point. Positive values mean that the bird was able to drive birds further than the dominant male's boundary and negative values mean the converse.

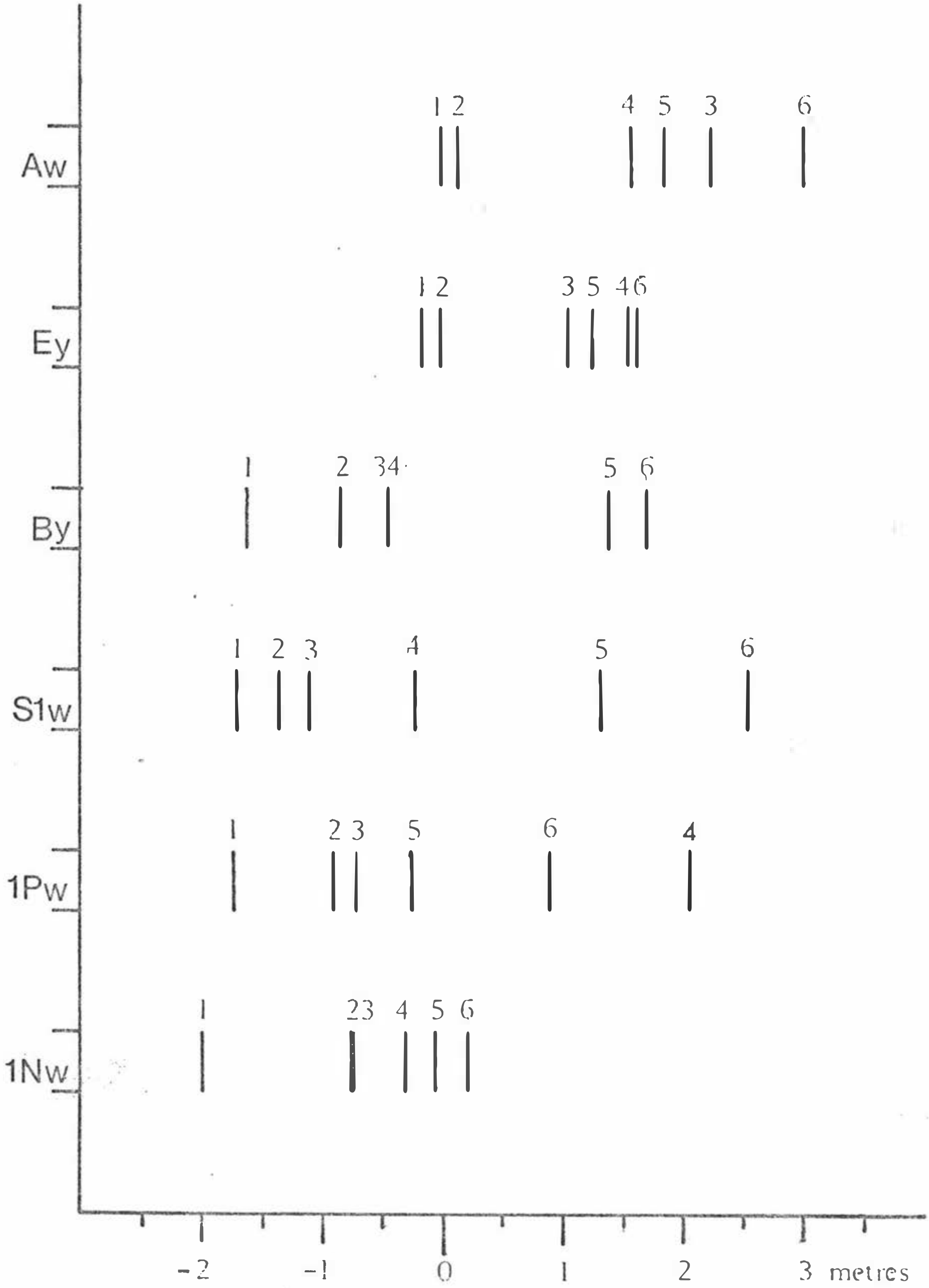
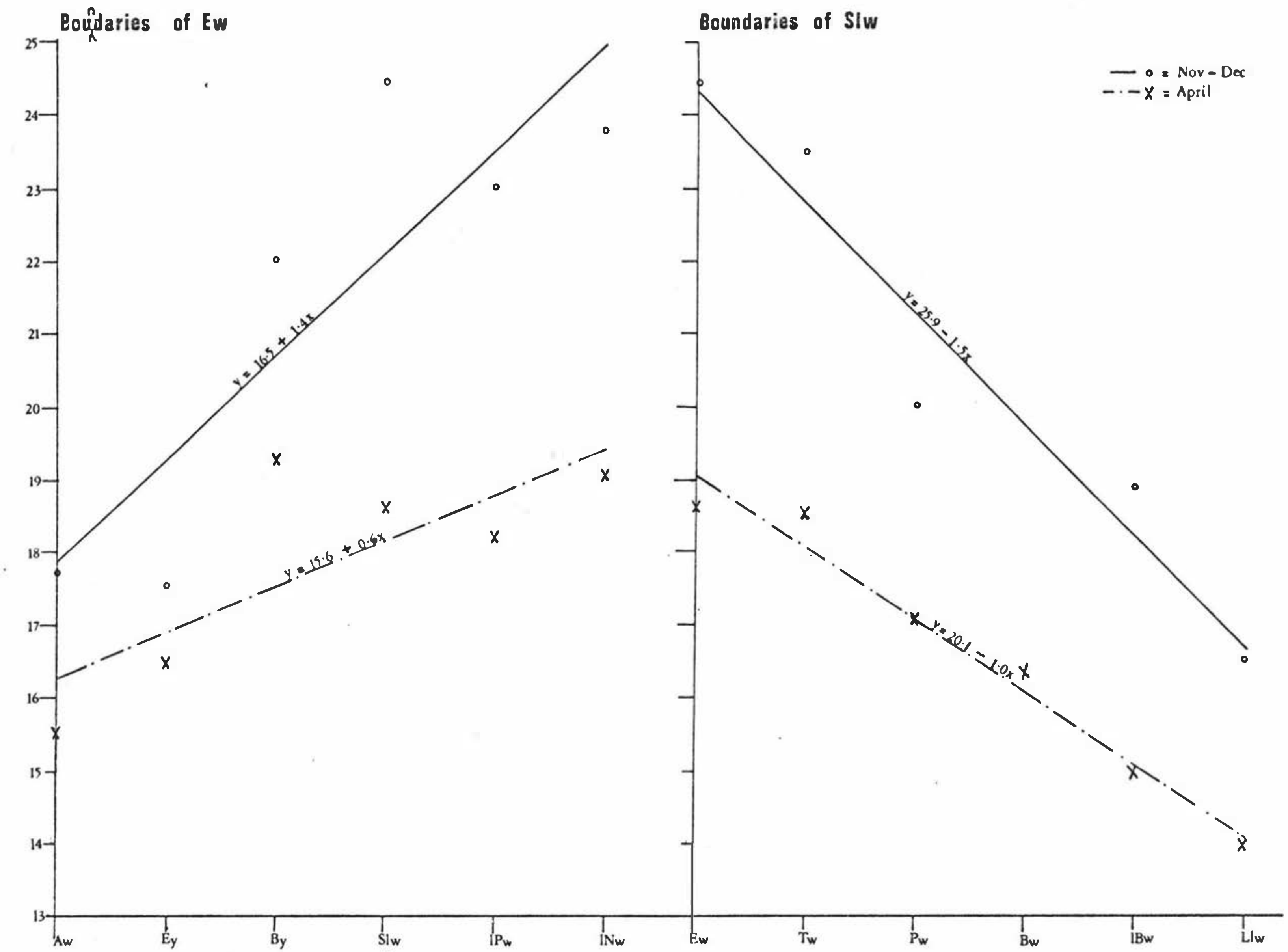

Aw
1 2 4 5 3 6
Ey
1 2 3 5 4 6
By
1 2 3 4 5 6
S1w
1 2 3 4 5 6
1Pw
1 2 3 5 6 4
1Nw
1 2 3 4 5 6
-2
-1
0
1
2
3 metres

Figure 46 Relationship Between Intra- and Inter-Territorial Status

The boundary positions of Ew and S1w in relation to the birds (given in order of intra-territorial status) of the opposing territory for April and November-December. Lines derived from linear regression analysis are shown to demonstrate variation of closeness of fit to a linear relation between intra- and inter-territorial status. Boundaries are measured in 0.25 m units from an arbitrary zero point.



Boundaries of Ew

Boundaries of Slw

frequency of overt aggression. Only 29 of 1758 interactions were fights (1.65%).

These findings of different boundary positions for different pairs of birds are pertinent to the previous discussion on boundaries where the 'boundary' referred to was that of the dominant males. Thus, although topographical features marked many boundary areas, the side of this barrier on which disputes occurred depended on the status of the interacting birds. Thus birds of similar status displayed on their respective sides of the barrier, e.g. a drain, but when there was disparity of status, the dispute occurred on one side of the drain.

5.7 Discussion

Pukeko pairs and groups were spatially distributed in localized defended areas during the breeding season. The seasonal existence of these territories was variable; some were defended throughout the year, defence of others was reduced to a 'core' area during the non-breeding season and a small number were temporary, breaking down completely outside the breeding season. The permanence of territory appeared to depend on the membership and the physical characteristics of the territory.

All territories that completely or partially broke down contained, or were adjacent to, main winter feeding areas, or were marginal areas. Those which broke down completely had been formed from flock birds, mainly in marginal areas. Death of a dominant member also caused dissolution of the territory. Gullion (1953) reports similar findings for the coot.

The stability of most territorial boundaries confirms the belief that pukeko are able to recognise a boundary. The extreme stability of the boundary between the Northern and Southern Territories is believed to be the result of stable membership and equal numbers of birds in the two territories. However, the zig-zag nature of defence suggests the recognition of a boundary zone rather than a distinct line in space, although it is possible that a sharp line is recognised with defence on such a fine scale an impossibility. The boundary consequently represented only the middle of this zone but as such it is a valid reference for defining spatial relationships of the birds.

The large proportion of territorial defence carried out by males is in accord with the divisions of labour common in most birds (Hinde, 1956, 1970; Welty, 1964). Defence was closely related to intra-group status in that higher ranking birds were responsible for more of it than lower ranked pukeko. The exception to this (*Ey* from the Southern Territory) may have been due to individual differences in aggressiveness and/or division of labour related to breeding (see p. 188).

Ridpath (1972) records the frequency of initiation of territorial disputes by male and female Tasmanian native hens and, as in the pukeko, males were responsible for a greater number than females. Ridpath (1972) also found a high proportion (33%) of disputes at territorial boundaries that were far in excess of the number found in my study. The very low number of fights observed in pukeko boundary disputes is in keeping with the theory (Lorenz, 1966) that aggressive behaviour is strongly ritualized, reducing overt aggression and thus preventing injury to the birds, but Ridpath's results appear to contradict this.

The close association of territorial boundaries and physical barriers has been recorded for many non-passerine species (Gullion, 1953; Welty, 1964), and is clearly advantageous in that it reduces the length of boundary requiring defence, and so allows more time for other activities.

The length of defended boundary in relation to the number of birds in a territory suggests a reason for the existence of pair and group territories. The boundary of all pair territories was small whereas that of group territories was large, suggesting that a pair may be incapable of maintaining large boundaries, especially in optimal areas where population density is high. The best evidence for this is gained from the continual shift of the Linton boundary. In these territories, expulsion of young was concomitant with the onset of nesting and hence in the breeding season not only were the juveniles no longer available for territorial defence but one adult was involved with incubation. Thus only one bird was able to defend the boundary and because the onset of breeding and the expulsion of young was out of phase between the territories, one territory always contained more birds available for defence than the other, and was increased in size. When the chicks were old enough, they began helping with defence and feeding later broods, and the territory increased in size. The asynchrony of breeding times and consequently in the ages of the young in the two Linton territories produced a continual change in the boundary. Gullion (1953) records similar changes in the boundary of coot territories where nesting of adjacent pairs was asynchronous.

Further evidence for the relationship between the number of birds in a territory and the size of the boundary can be taken from the Peninsular Territory in 1971-72. This territory was held by a pair who were unable to withstand the pressure of neighbouring territorial groups after these had finished breeding, and it was greatly reduced in size before the influx of non-territorial flock birds caused it to break down completely. The ability of the Peninsular pair initially to maintain their boundary may have been due partly to near synchrony of nesting with adjacent territories (see Appendix 6). But it was probably due largely to the more secretive behaviour of breeding birds which restricted them to cover and hence reduced the size of the defended boundary. This was especially marked with the Hide Territory-Peninsular Territory boundary which was reduced to about four metres.

The high frequency of defence by males would explain why the birds in Linton 1 in 1970-71 were unable to maintain a constant boundary even though three adults were involved. Because females accounted for such a small amount of territorial defence, the presence of an extra female in this territory would not help maintain the boundary. An extra male, however, would be highly advantageous in maintaining the territory and this would explain why the Trap Territory of two males and one female was maintained against large groups on either side. Similarly, the acceptance of the male 10y , into Linton 1 was accompanied by a significant gain in area.

Since birds fed exclusively within their territories, the lack of correlation between territory size and the number of birds within a territory, coupled with the fact that in many cases territory size decreased even though the number of birds present increased, suggests that food may have been unimportant in determining territory size in the study area. No estimate of available food was made however. The variation in size of the Hide Territory suggests a closer link between cover and territory size, and the increase in territory size when the lake dried up stresses the importance of water as well. These conclusions are in line with Tunnicliffe's (1965) findings that the presence of wet ground and emergent vegetation for cover were the most important characteristics of a pukeko territory. Parry (1968) and Ridpath (1972) have demonstrated a direct link between territory size and the number of birds in kookaburras and Tasmanian native hens respectively. Carrick (1963) found no direct correlation between territory size and the number of Australian magpies within a territory but suggested upper and lower limits of territory size were set by the number of birds in the territory. This is also likely for pukeko.

Tunnicliffe (1965) estimated pukeko territories to be from 0.12-0.24 ha but this is a considerably lower range than I obtained. In other rails the size of the territory varies greatly. Tasmanian native hens (Ridpath, 1972) had territories of 0.42-1.47 ha although only first year groups had a territory less than 1 ha. Gullion (1953) found American coot territories varied from 0.15-0.6 ha. Thus my territories were similar to those of Tasmanian native hens but it is difficult to make a useful comparison of territory sizes in different habitats for the same species, let alone for different species.

Ridpath (1972) found a decrease in territory size with increasing population density and similar findings have been reported for other species (Kendeigh, 1941; Condor, 1956; Watson, 1965; Pettingill, 1970). At Pukepuke, not only did territory size decrease with increasing population density, but the intra-territory density also increased. Further discussion of territory and its 'functions' will be reserved till breeding data have been presented (p. 193).

The observation that all birds from the same territory did not defend the same boundary demonstrates the existence of an inter-territorial hierarchy and shows that there must be individual recognition between members of adjacent territories. The link between intra- and inter-territorial status suggests that the characteristics used for determining rank must be similar in both cases. However, this link was not found in all cases and demonstrates that the two hierarchies were independent. These findings, along with the frequent observations of trespass and the hierarchical results in the flock (p. 113) demonstrate that the present concept of territory is inadequate to explain inter-group spacing in the pukeko. This will be discussed further in Chapter 7.

The sheltering of low ranked birds behind those of higher status in inter-group encounters is similar to the findings of Lawick-Goodall (1968) for intra-group encounters of chimpanzees. The combined attacks of *Aw* and *Ey* which won them a position in advance of what each could have achieved alone, is similar to interactions in Canada geese 'families' (Raveling, 1970) and turkey, Meleagris gallopave, sibling groups (Watts and Stokes, 1971), where status is dependent on group size, and birds separated from their groups are consistently defeated.

So far as is known, no comparable findings of inter-group interactions have been reported, but the frequently recorded observation in other birds (Snow, 1956; Gibb, 1956; Parry, 1968; Reid, pers. comm., and many others) that males fight males, and females fight females during territorial disputes can be explained by these findings. Thus, if inter-territorial status is applicable in these cases, then without sexual segregation, the two combats would occur at different points. It would be expected, therefore, that where both pairs were present in a territorial dispute, each fight would be sexually segregated.

6. BREEDING BIOLOGY

6.1 Introduction

The breeding system of pukeko varied from monogamy through polygamy to communal breeding, depending on the number of birds in the territory. (Communal breeding is defined as where two or more males and females breed and mate promiscuously, but as distinct from true promiscuity, a bond is formed between all individuals). The majority of pukeko in the study areas were already paired or grouped and defending a territory before the breeding season (ie. prior to courtship being observed). However, a small number of territories were formed immediately prior to the breeding season (see p. 24), but these latter territories usually broke down after nesting. No recognised pairing or grouping displays were observed and birds present in a territory at its inception usually remained together.

6.2 Courtship

Using the term in its broadest sense (Morris, 1970) and extended to allow homosexual interactions within groups, courtship in pukeko consisted of allopreening, courtship feeding and copulation. These have been described on pp. 57 and 59 and the last will be treated separately (p. 163).

Most courtship was seen between late July and early December, although isolated incidents of courtship preening were seen between March and July.

Both males and females preened each other and in group territories preening was not restricted to members of the opposite sex. Preening was usually initiated by one bird presenting in a Full Bow and holding this while the other bird approached. Where the approaching bird was dominant, it normally assumed an Upright whereas a subordinate advanced in a Bow. Dominants initiated courtship preening more frequently than subordinates (Table 31). Subordinates,

Table 31

INCIDENCE OF COURTSHIP ALLOPREENING AND FEEDING IN RELATION TO SEX AND STATUS

Allopreening

Bird Preening	Bird Preened	
	Male	Female
Male	14*	16
Female	26	11+

* Dominant preened subordinate 4 times

+ Dominant preened subordinate 5 times

Allopreening initiated by dominant 40 times; by subordinate 27 times

Courtship Feeding

Bird Offering 'Food'	Bird 'Fed'	
	Male	Female
Male	-	13
Female	4	4*

* In all 4 cases, the dominant fed the subordinate

however, preened dominants more frequently than the converse.

On many occasions, a dominant approached a bowing subordinate, presented its head for preening, but the subordinate did not preen. Each time the dominant opened its eyes and lifted its head, the subordinate Faced Away but when the dominant presented again, the subordinate put its head beside the dominant's but did not preen. Once *1Pw* refused to preen *Ey* for almost three minutes, and *Ey* eventually pecked *1Pw* before walking off.

Courtship feeding was more infrequent (Table 31) and was only once observed in a pair territory. The 'Food' exchanged was usually only Lemna leaves but pieces of raupo shoot were occasionally given. In contrast to courtship preening, courtship feeding from dominant to subordinate was more frequent and both birds kept their eyes open.

Females preened males more than the reverse, and males preened males more often than females preened females. In contrast, males courtship-fed females more often than the reverse and males were never observed to feed another male.

6.3 Copulation

6.3.1 General

Copulations were more localized in time than courtship feeding and preening, most being observed between August and November, although the initiation of many second clutches after November suggests that copulations did occur but were not seen. More than 90 complete copulations were observed.

Initiation of copulation was difficult to determine. Mostly, the male approached the female in a 'Sexual' Upright and began giving the Humming Call, whereupon the female typically raised her tail and began walking in front of the male. Actions were very stiff-legged and the birds appeared to strut, often both in step. If the female continued to strut in front of the male, he adopted the 'Sexual' Forward. Eventually, the female began to assume the Precopulatory

Hunch and finally the Precopulatory Position. The male then mounted and copulated (see pp. 59 and 61). After cloacal contact, the male dismounted over the front of the female assuming a Wings and Tail Fully or Exaggerated Up (see Fig. 31) and then walked away; the female usually preened after copulation. Less than one third of the observed attempted copulations went to completion, with either bird terminating the attempt, and the female most commonly doing so by Head Flicking.

Occasionally the female appeared to initiate copulation. It was suspected that she used a call because frequently two or more males ran to her at the same time and, in these cases, the female immediately assumed a Precopulatory Position.

Copulation attempts were not restricted to two birds nor did males mount only females. The Humming Call was audible at long distances and in group territories one bird attempting to copulate with another usually attracted other members of the territory (Fig. 47). Occasionally members of adjacent territories were drawn by a copulation to the boundary. Extra birds (from the same territory) either participated or watched the copulation. Multiple participation in a copulation attempt took various forms but mostly the extra birds joined in line and strutted behind the first two (Fig. 47a). Lines of up to five individuals were not uncommon and frequently culminated in two pairs of birds copulating. Another common variation of multiple participation in copulation was one in which a female ran ahead of a male apparently attempting to avoid copulation and a second bird joined the chase. The two pursuing birds ran on either side and behind the female, both attempting to mount whenever she slowed down. This was especially common in the Peninsular Territory in 1972 and at times all five males were seen running behind *Qw* or *Zw*. In this territory, up to three birds attempted to mount at the same time - irrespective of orientation. Another variation consisted of a second female attempting to get under the first, and pecking at her breast and neck (Fig. 47a). In all cases, the extra female was a yearling raised within the territory.

Figure 47 MULTIPLE PARTICIPATION IN COPULATION by Birds of a Group Territory

(a) Two males approaching a female for copulation. Right hand male in a Sexual Upright and male (second from left) is dropping to a Sexual Forward. The bird partially obscured is a yearling female who is Facing Away after the adult female turned and pecked her as she had been attempting to get between the legs of the front female.

(b) The same birds with the dominant male copulating with the dominant female while the other two feed in close proximity.

This was first observed in 1971 when *P/w* consistently attempted to get under *2E* whenever *2E* was involved in a copulation attempt. *R/w* reacted similarly to *P/w* in 1972 and *L/w* and */Nw* were seen to do likewise to *Pw* and *By* respectively. This action by the juvenile female mainly resulted in the adult female pecking it or one of the males mounting, although this latter alternative was observed only in respect of *P/w*. Interruptive behaviour by yearling females resembled juvenile food begging. On one occasion a yearling male, */Pw*, interrupted a copulation attempt between *Aw* and *By*, by food begging but did not attempt to get under the female.

Table 32 NUMBER OF BIRDS INVOLVED IN COPULATIONS AND ATTEMPTED COPULATIONS

No. of Birds in Territory	Territory	No.of Birds involved in Copulations and Attempts					No. of Complete Copulations	No. of Complete Copulations involving Two Birds
		2	3	4	5	Tot		
4	Northern 1971-72	14	6	-	-	20	7 (35%)	6 (86%)
	Southern 1971-72	7	-	-	-	7	5 (71%)	5 (100%)
5	Hide 1971-72	24	17	6	-	47	18 (38%)	14 (78%)
6	Hide 1972-73	16	17	10	-	43	10 (23%)	8 (80%)
	Northern 1972-73	12	1	-	-	13	4 (31%)	3 (75%)
	Southern 1972-73	11	9	1	-	21	10 (48%)	7 (70%)
7*	Peninsular 1972-73	15	46	93	28	182	19 (10%)	7 (37%)
Total							73 (41%)	50 (69%)

* By definition (see p. 21) there were only six birds in this territory but initially seven birds were involved in copulations.

In the main group territories a large number of copulation attempts involved more than two birds (Table 32), and multiple participation tended to increase with the number of birds in the territory. However, a high proportion of complete copulations involved only two birds. The majority of copulations and attempts were between a male and a female with the former mounting the latter.

Twenty three copulations were homosexual; 18 between females and the remainder between males of the Peninsular Territory in 1972. One female-male copulation was observed - between *Tw* and *Bw* on 27 September 1972 - and immediately followed a copulation between *Bw* and *Tw*. While these birds were copulating, the dominant male (*Ew*) ran over and stood in an 'Aggressive' Upright beside them. *Tw* dismounted over the front of *Bw*, to a spot immediately in front of the other two birds, and instead of assuming the post-copulatory Wings and Tail Fully Up, *Tw* went into an Erect Hunch and *Bw* mounted.

It is interesting to note that after one homosexual copulation between *Plw* and *2E*, *Plw* went into a pre-copulatory position in front of *2E* on dismounting and *2E* then mounted *Plw* but immediately dismounted, giving a superficial resemblance to an incomplete female-male copulation.

6.3.2 In Relation to Status

All attempted and full copulations according to status and sex are given in Table 33. The dominant male had more copulation attempts in the Southern and the Northern Territories but this trend did not hold in the Hide and Peninsular Territories. Yearling males were involved in few attempted copulations and none achieved a mount. The proportion of attempts that were successful was variable but α males tended to be more successful than β males.

Correlation between frequency of copulation attempts and status in females was also variable. Dominant females were involved in copulations more often than β females in five out of seven territories, but the number that was

TABLE 33

COPULATIONS IN RELATION TO STATUS AND SEX
Birds in Order of Status

(i) 1971-72 Hide Territory

Mounting Bird

bird mounted

	Hlw ♂	Kw ♂	2E ♀	Plw ♀	Total
Hlw					
Kw					
2E	${}^{6}_{8}16^{2}$	${}^{4}_{5}14^{5}$		${}^{2}3^{1}$	33^{8}
Plw	${}^{2}2$	9^{9}	${}^{2}3^{1}$		14^{10}
Total	18^{2}	23^{14}	3^{1}	3^{1}	47^{18}

1972-73

Mounting Bird

bird mounted

	Hlw	Kw	Plw	2E	1Jy ♂	Total
Hlw						
Kw						
Plw	${}_{2}4^{2}$	${}^{3}_{3}10^{4}$		${}^{2}_{1}3$	${}^{2}2$	19^{6}
2E	${}^{4}_{4}9^{1}$	${}^{3}_{2}5$	${}^{2}_{3}7^{2}$		${}_{2}3^{1}$	24^{4}
1Jy						
Total	13^{3}	15^{4}	7^{2}	3	5^{1}	43^{10}

(ii) Southern Territory, 1971-72

	Aw ♂	Ey ♂	By ♀	Slw ♀	Total
Aw					
Ey					
By	${}^{1}4^{3}$	1^{1}			5^{4}
Slw	${}^{1}2^{1}$				2^{1}
Total	6^{4}	1^{1}	-	-	7^{5}

1972-73

	Aw	Ey	By	Slw	1Pw ♂	Total
Aw						
Ey						
By	${}_{2}4^{2}$	${}^{1}_{1}5^{3}$			${}_{3}3$	12^{5}
Slw	${}_{3}8^{5}$	${}_{1}1$				9^{5}
1Pw						
Total	12^{7}	6^{3}	-	-	3	21^{10}

(iii) Northern Territory, 1971-72

	Ew ♂	Tw ♂	Pw ♀	Bw ♀	Total
Ew					
Tw				${}^{1}1$	1
Pw	${}_{2}4^{2}$	${}^{1}_{1}3^{1}$			7^{3}
Bw	${}^{2}_{2}7^{3}$	${}^{3}_{2}6^{1}$	1		13^{4}
Total	11^{5}	9^{2}	1^{1}	1	20^{7}

1972-73

	Ew	Tw	Pw	Bw	Total
Ew					
Tw					
Pw	${}_{3}4^{1}$	${}_{2}3^{1}$			7^{2}
Bw	${}^{1}_{2}3$	2^{2}	${}^{1}1$		6^{2}
Total	7^{1}	5^{3}	1		13^{4}

Key:

$${}^{b}_{a}T^{c}$$

a = attempted copulation (including all behaviour short of a full mount)
b = mount
c = full copulation
T = Total

TABLE 33 contd COPULATION IN RELATION TO STATUS AND SEX

(iv) Peninsula Territory 1972-73

(a) Attempted copulations

Bird Mounting

Bird Mounted	M1w	1Tw	Q1w	1Ww	1Zw	Qw	Zw	Total
M1w								
1Tw								
Q1w								
1Ww								
1Zw								
Qw♀	${}^{1}1$	${}^{5}6^{1}$	${}^{5}6^{1}$	${}^{12}14^{2}$	${}^{10}11^{1}$			38
Zw♀	${}^{13}14^{1}$	${}^{3}3$	${}^{17}17$	${}^{9}12^{3}$	${}^{12}13^{1}$			59
Total	15	9	23	26	24			97

a b
T

a = attempted copulation

b = attempted copulation with pecks

(b) Mounts and Full Copulations

Bird Mounting

Bird Mounted	M1w	1Tw	Q1w	1Ww	1Zw	Qw	Zw	Total
M1w								
1Tw	1^{1}							1
Q1w		1^{1}						1
1Ww	${}^{1}_{1}2$	${}^{1}1$						3
1Zw				${}^{1}1$				1
Qw		3^{2}	${}^{1}_{1}2$	${}^{3}_{3}7^{1}$	${}^{4}_{4}9^{1}$			21
Zw	${}^{4}6^{2}$	${}^{3}5^{2}$	${}^{6}_{6}14^{2}$	${}^{5}_{1}11^{5}$	${}^{9}_{1}15^{5}$	${}_{1}1$		52
Total	9	10	16	19	24	1		79

b c
T
a

a = full copulation

b = mount

c = mount with pecks

Proportion of copulations involving Qw before October = 90.5%
(n = 64)

successful was similar for all females. One factor that could account for the low success of dominant males and females, especially in the Hide Territory was frequent interruption of copulation; ie. the action of *Plw* disrupted most attempts of *Hlw* to mount *2E*.

On eight occasions dominant males actively prevented a subordinate male from copulating, but this behaviour was inconsistent. For example, on 2 October 1971, *Hlw* prevented *Kw* copulating with *2E* but allowed it to copulate with *Plw* less than ten minutes later. Occasionally dominant birds interrupted their own copulation to drive a subordinate away.

The Peninsular Territory, 1972, was atypical in the large number of copulation attempts observed (Table 33) and this was possibly a reflection of the skewed sex ratio within the group (see p. 20). Effects of individual status were more evident among the females of this territory. Up till the end of September, *Qw* was involved in 58 attempts whereas *Zw* was involved in only six. *Qw* was observed once to attack *Zw* when the latter was copulating. After *Qw* left the territory in mid-October, *Zw* became the only female and thus the focus of copulations.

The males in the Peninsular Territory attempted to copulate with a female almost every five minutes the birds were in view. For example - condensed extracts from my notes on 18 September 1972:

0720 1Zw and 1Ww attempted to mount Qw.

0722 1Zw - 1Ww and Q1w chasing after Qw. 1Zw mounted and 1Ww one foot up.

0724 1Ww after Qw, mounted but Qw pecked it.

0740 1Zw and 1Ww behind Qw who stopped and both males tried to mount. Qw resumed running and both males ran after her. Three ran past Zw and the two males ran after Zw. Both 1Zw and 1Ww returned and mounted Qw. Q1w ran over and Qw collapsed.

1750 1Zw and 1Ww walking after Qw in a 'Sexual' Upright and Zw is immediately in front of Qw. 1Ww eventually mounted and had a full copulation with Qw.

Male homosexual mountings were also observed in the Peninsular Territory. In all five of these, the dominant mounted the subordinate after four or five males had been attempting to mount the same female and one had done so successfully.

Aggression was seen in many of the copulation attempts in the Peninsular Territory. The males frequently pecked the female when she would not allow them to mount or would not raise her tail to make cloacal contact possible. On six occasions (Table 33), *Qw* pecked males attempting to mount her.

In pair territories (Table 34) copulation was rarely seen but almost half of the attempts were complete, and although juvenile males attempted to copulate with their mothers and sibling females, none succeeded in mounting.

It should be noted that only one attempted copulation involving a juvenile female was observed except in the Hide Territory where adult females had died and the juvenile females bred. Thus, although pukeko are capable of breeding in their first year as evidenced by *2E* and *Plw*, no juvenile did so while in its natal territory, unless it was replacing an adult.

6.4 Nests

Pukeko built large numbers of nesting structures. About a month before laying a number of 'trial' nests (following Williams, 1960) were built in the territory. Many of these were roughly constructed and lacked a definite bowl, but some were well-shaped, and, as laying approached, more well formed bowls were completed with usually two or three made ready for laying. Early nests and trial nests were frequently used as roosts and were soiled with faeces. Normally, one nest was chosen for laying but in Linton 2 (1971) two nests, 3 m apart, were laid in but only one was incubated.

Trial and egg nests were constructed mainly in two

Table 34

COPULATORY BEHAVIOUR IN RELATION TO AGE AND SEX IN PAIR TERRITORIES

(Yearlings are underlined)

Linton 1 1972-73

		Mounting Bird	
		Ubo♂	71y♂
Mounted Bird	41y♀	${}^{1}_{3}8^{4}$	${}_{3}3$
	81y♀	-	${}_{2}2$

Linton 2

1971-72

	03♂
00♀	${}^{1}_{1}3^{1}$

1972-73

		Mounting Bird	
		03♂	10w♂
Mounted Bird	00♀	${}^{1}_{3}8^{4}$	${}_{3}3$
	11y♀	-	${}_{1}1$

$\boxed{{}^{b}_{a}T^{c}}$

a = Attempted copulation including all behaviour short of a mount.

b = Mount

c = Full copulation

places in a Carex or Mariscus tussock, or between raupo shoots, while other nests were found in grass clumps or in rushes, (Juncus spp). A typical raupo nest comprised dry and fresh raupo leaves between the bases of 3-8 raupo shoots with some of the support shoot leaves interlaced above and into the nest. Raupo nests were usually about 20 cm above water level. Carex and Mariscus nests were constructed either in the crown of the clump or on one side of it with the bowl made of Carex and raupo leaves and usually 60 cm above water level. Most Carex nests were in the crown of a clump that was itself sheltered by an adjacent overhanging Carex or by raupo. An exception was the Western Territory where nests were almost always in the crown of a single Carex and were very open.

All nest bowls were approached by one or two ramps made of raupo and were 0.2-1 m long, although the Mariscus nest used by the Hide Territory in 1971 had a ramp almost three metres long. Most nests also had a 'landing pad' in nearby raupo. This was constructed by interlacing the leaves of a number of shoots and provided a firm landing platform for incoming birds about 1-2 m above water level.

The chosen nest site was consistent in most territories (Table 35) with three exceptions: the Southern Territory nested once in Carex and once in raupo every year; the Hide Territory changed from raupo to Carex in 1971, while the Northern Territory changed from Carex to raupo.

Nest material was occasionally carried long distances, and one nest in 1970 in grass beside the drain to Kaikokopu had a bowl made of raupo leaves, the nearest source of which was at least 300 m distant. Material was added throughout incubation and the bowl enlarged to take the number of eggs laid.

All nests in the study areas were single-bowled and with one exception were used for a single clutch. In the Peninsular Territory in 1972, the first replacement clutch was laid in the same nest as the original clutch. One nest outside the study area (Awahuri) was used successively by

Table 35

NEST SITES IN STUDY TERRITORIES

Territory	Season		
	1970-71	1971-72	1972-73
Linton 1	C,C	C,G,G'	C,C
Linton 2	C*,C	C',C,C	M,M
Hide	R	C,R'	C
Peninsular	-	C	G*,G*,R
Trap	-	-	G*,C
Inlet	C	C	C
Southern	R,C	C,R	C,R
Northern	C,C	R+,M,R	R,R
Western	C	C*,C,C*,C	C
Corner	-	-	J*
Rough Paddock	-	M	-

C = _Carex_ (28), R = Raupo (10), G = Grass (5)

J = _Juncus_ (1), M = _Mariscus_ (4)

+ flooded ' deserted

* destroyed by predator

three females from the same territory. Initially a clutch of three eggs was laid and five days before these hatched, a second clutch of four of a different colour was added and ten days before the second clutch hatched, another three eggs of yet another colour were added.

After the eggs hatched, brood nests were constructed for brooding young at night. Many of the raupo egg nests were used as brood nests but Carex nests never were. Brood nests were frequently abandoned and new ones built usually closer to regular feeding areas, were extremely bulky, and initially had a shallow bowl, but the bowl increased in depth as the chicks grew older. Nests were kept free of faeces except for chick droppings in brood nests, but heaps of faeces were frequently found close to a nest.

Nest construction was rarely observed but on the few occasions it was, only males including yearlings were building.

6.5 Eggs

6.5.1 General

In most cases eggs were laid daily just after dawn, although single rest days were common. The exceptions to this were group territories where more than one female laid in the same nest. Evidence for this was as follows:

(a) Eggs of two different colours in the same nest (Fig. 48). The colour difference was very obvious and in many cases was as distinct as brown and white domestic hen eggs. As well as a difference in colour, there was a regular difference in size between eggs of different colours as illustrated by the Reichenow index of egg shape (Romanoff and Romanoff, 1949) (Table 36). Egg size (Table 36) and colour in pair territories was consistent, and egg shells from most territories, kept for comparison, showed that colour within a territory was also consistent from year to year. Colour

Figure 48

Two hen clutch with six brown and three white eggs.

Table 36 EGG SIZE IN RELATION TO COLOUR

Northern Territory

Season	Clutch	Colour	Egg Size	*Reichenow Index
1970-71	1	Brown	57.06 x 35.41	62.18
			54.28 x 36.22	66.73
			57.94 x 35.92	62.00
			54.38 x 35.26	64.84
	2	Brown	52.48 x 36.68	69.89
			50.56 x 35.02	69.26
			53.42 x 35.10	65.71
			57.12 x 33.66	58.93
1971-72	1	Brown	51.22 x 36.68	71.61
			52.16 x 36.26	69.52
			51.22 x 34.68	67.71
	2	White	57.52 x 35.80	62.24
			56.12 x 35.92	64.01
			54.28 x 35.88	66.10
		Brown	50.82 x 34.58	68.04
			51.42 x 35.38	68.81
			53.01 x 33.06	66.13
			51.18 x 35.78	69.91
	3	White	53.18 x 36.24	68.15
			56.04 x 36.02	64.28
			57.14 x 36.00	63.00
			57.06 x 36.92	64.70
1972-73	1	White	53.44 x 36.34	68.00
			60.34 x 34.46	57.11
		Brown	52.56 x 35.58	67.69
			54.32 x 36.94	68.00
			53.35 x 37.16	69.65
			51.48 x 34.70	67.40
	2	Brown	53.90 x 36.28	67.31
			52.16 x 35.88	68.79
			52.45 x 37.78	72.03
			53.94 x 36.32	67.33
		White	52.52 x 35.48	67.56
			54.12 x 35.66	65.89
			58.42 x 35.16	60.18

Table 36 cont. Southern Territory

Season	Clutch	Colour	Egg Size	*Reichenow Index
1970-71	1	White	50.62 x 35.98	71.08
			54.44 x 36.66	67.34
			52.24 x 36.48	69.83
			50.96 x 37.52	73.63
	2	White	52.14 x 35.30	67.70
			54.82 x 36.26	66.14
			52.42 x 35.84	68.37
		Brown	50.56 x 35.08	69.38
			49.06 x 36.74	74.89
			49.86 x 36.28	72.76
			49.98 x 37.16	74.35
1971-72	1	White	55.22 x 35.64	64.54
			53.24 x 36.40	68.37
			52.02 x 36.62	70.40
			55.52 x 35.76	64.41
			52.84 x 36.46	69.00
		Brown	47.94 x 34.52	72.01
			47.48 x 34.86	73.42
	2	Brown	44.50 x 34.32	77.12
			46.64 x 35.54	76.20
			49.26 x 36.38	73.85
			49.82 x 36.68	73.63
		White	53.64 x 35.80	66.74
			53.00 x 35.92	67.77
			55.28 x 37.10	67.11
			55.70 x 35.62	63.95
1972-73	1	White	53.48 x 36.66	68.55
			56.48 x 36.56	64.73
			55.94 x 37.66	67.32
			56.62 x 37.04	65.42
	2	Brown	51.70 x 36.28	70.17
			47.26 x 34.92	73.89
			50.28 x 36.22	72.04
			48.34 x 36.96	76.46
			49.74 x 36.28	72.94
			50.52 x 36.42	72.09
			49.82 x 35.58	71.42
		White	54.66 x 35.84	65.57
			55.22 x 36.92	66.86
			53.84 x 36.50	67.79
			55.10 x 36.52	66.28
			54.92 x 37.16	67.66

Table 36 continued

Hide Territory

Season	Clutch	Colour	Egg Size	*Reichenow Index
1970-71	1	Brown	49.20 x 36.26	73.70
			50.84 x 35.40	69.63
			50.04 x 35.06	70.06
			51.46 x 35.00	68.01
		Lighter Brown	49.00 x 34.22	69.84
1971-72	1	Brown	49.90 x 37.56	75.27
			49.36 x 37.10	75.16
			50.24 x 36.94	73.53
			50.92 x 35.84	70.38
			49.30 x 35.74	72.49
			52.88 x 36.98	69.93
		Lighter Brown	48.36 x 37.80	78.16
	2	3 Light Brown 5 Brown		
Eggs destroyed by predator before measured				
1972-73	1	White	48.74 x 36.56	75.01
			48.54 x 37.52	77.30
			49.48 x 37.16	75.10
		Brown	51.38 x 36.58	71.20
			51.28 x 36.74	71.65
			52.02 x 35.96	69.13
			52.86 x 36.48	69.01
			50.08 x 36.88	73.64

Table 36 continued

Western Territory

Season	Clutch	Colour	Egg Size	*Reichenow Index
1972-73	1	Brown	50.94 x 35.62	69.93
			49.74 x 36.04	72.46
			53.08 x 34.82	65.60
			51.16 x 34.96	68.33
			52.18 x 35.22	67.50
			48.78 x 35.24	72.24
		Grey	48.98 x 35.80	73.09

Linton 1

Season	Clutch	Colour	Egg Size	*Reichenow Index
1972-73	1		55.40 x 38.35	69.22
			55.35 x 37.80	68.29
			53.40 x 38.40	71.91
			54.65 x 38.25	68.99
			53.15 x 37.80	71.12
	2		52.36 x 38.24	73.03
			52.78 x 38.50	72.94
			53.66 x 38.12	71.04
			53.38 x 38.08	71.34
			54.06 x 37.72	69.77
			54.94 x 36.96	67.27

* Romanoff & Romanoff (1949)

differences were less obvious in the Hide Territory where females were related (mother and daughter) in all years, but size differences were obvious (Table 36).

(b) Two eggs appearing in a nest in one day. These eggs were always of different colours. For example:

(i) Southern Territory

Date	Hour	No.of Eggs	Colours	
20 Dec 71	1200	2	2 brown	
22 Dec 71	1430	6	4 brown	2 white
1 Nov 72	1100	4	1 brown	3 white
3 Nov 72	1710	7	2 brown	5 white

(ii) Hide Territory

7 Oct 72	1030	4	3 brown	1 white
8 Oct 72	1120	6	4 brown	2 white

(c) A gap of more than two days in a laying cycle. In all cases the eggs produced after the gap were of a different colour and size from those produced prior to the gap. For example:

(i) Southern Territory

Date	No.of Eggs	Colours	
25 Oct 71	5	5 white	
27 Oct 71	5	5 white	
29 Oct 71	6	5 white	1 brown
30 Oct 71	7	5 white	2 brown

(ii) Western Territory

10 Oct 72	6	6 brown	
13 Oct 72	6	6 brown	
18 Oct 72	7	6 brown	1 white

(iii) The previously discussed nest at Awahuri (see p. 175).

Laying was frequently initiated at the same time in adjacent territories (see Appendix 6) and on two occasions, the Northern and Southern Territories initiated nests on the same day.

6.5.2 Clutch Size

Clutch size is taken as the maximum number of eggs in a nest (Davis, 1955). Overall clutch size was constant in 1971-72 and 1972-73 at 6.2 (n = 34) but varied greatly between territories and also varied directly with the number of birds in the territory (Table 37). In pair territories, first clutches were larger than later ones, while in all group territories, first clutches were smaller than subsequent ones. Clutch size in 1970-71 was lower than in other years but the history of the birds was unknown in that year.

6.5.3 Clutch Size in Relation to Status

In nests with eggs of more than one colour, the colours were never equal in numbers and attempts were made to ascertain which female laid the greater number of eggs. The egg colour of each female was determined by:

(a) Observing which female was on the nest when an egg was laid. To pinpoint exact arrival time of eggs, nests were checked immediately before dawn and again after the female left the nest. The presence of a female on the nest was deduced by direct observation or, where this was not possible, from the fact that all other territory members were in view.

(b) Comparing egg colours between years when previously only one of the females had been present. This was useful in the Hide Territory only.

(c) Experiment: In 1972, the Northern Territory females were trapped as regularly as possible

Table 37

CLUTCH SIZE

Year	Number of Birds in Territory				
	2	3	4	5	6
1970-71	6,3	4,6	4,7 4,8 4,4 9	5	
Mean*	4.5	5	5.7	5	
Overall Mean	5.3 n = 12 s.d. = 1.88				
1971-72	7,5,5 6,3 6		4,5 7,9 7,4	8,8 6,7,10,7 4	
Mean^{o}	5.3		6.0	7.1	
Overall Mean	6.2 n = 19 s.d. = 1.84				
1972-73	5,6 6,5 4	4	7 4		8 5 5,12 6,8 8
Mean^{+}	5.2	4	5.5		7.4
Overall Mean	6.2 n = 15 s.d. = 2.145				
Overall Mean for All Years = 6.0 n = 46 s.d. = 1.95					
Overall Mean of first and subsequent clutches	6.0,4.5		5.0,6.2	7.0,7.5	5.5,9.5
Overall Means^{o}	5.2	4.7	5.8	6.9	7.4
s.d.	1.21	1.15	1.97	1.89	2.44

* No significant linear correlation

+ Linear correlation significant $p<0.05$

^{o} Linear correlation significant $p<0.01$

and force-fed with gelatine capsules of lipid dyes of different colours. The dyes used were Sudan III, Sudan Black, and Sudan Blue which all stain the yolk. Rhodamine B, which is recorded to stain egg shell (Romanoff and Romanoff, 1949) was also fed to the bird given Sudan III. On 11 September 1972, *Pw* was fed one capsule of Sudan III and one of Rhodamine B. The following morning, a pink streaked white egg appeared in the nest. *Bw* had been fed Sudan Black two weeks previously and one brown egg was later removed from the nest and boiled but the yolk was normal. This may have been due to the large gap (20 days) between feeding the dye and laying. The experiment did, however, confirm that *Pw* laid the white egg, a fact that had been deduced from (a) above.

Based on these criteria, the number of eggs laid by the females of the study territories is given in Table 38. Generally, dominant females laid more eggs than the subordinate females but this was complicated by age. In the Northern Territory in all years, and in the Hide Territory in 1972, the older female laid more eggs than the younger dominant. The older female in all territories laid the greater proportion of the first clutch. It is interesting to note that in the group territories the average number of eggs laid by each female was much smaller than that laid by a female in a monogamous territory (Table 37).

6.6 Incubation

6.6.1 General

Incubation rarely started with the first egg but usually began mid-clutch. Eggs were initially cold to touch but were warm after incubation began. A thermistor (McConkey, 1972) was put in an egg which was substituted in Nest 1, Northern Territory, 1971-72. Due to calibration

Table 38

CLUTCH SIZE OF INDIVIDUAL FEMALES IN GROUP TERRITORIES

Season	Territory							
	Northern		Southern		Hide		Western	
	Pw(W)	Bw(B)	By(W)	S1w(B)	2E(B)	P1w(W)	Ub♀(B)	Vy(W)
1970-71	4B 4B		4W 3W	4B	-		-	
1971-72	3W 4W	3B 4B	5W 4W	2B 4B	7B 5B	1W 3W	-	
1972-73	4B 5B	2W 3W	4W 5W	7B	5B	3W	6B	1W

Overall mean clutch size of single female = 3.9 (n = 28)
s.d. = 1.474

Females in order of status

( ) Egg colour

Note: 2E and P1w reversed dominance in 1972 (see p.107) errors, actual temperatures could not be calculated but the thermistor did show that incubation was irregular at first as the eggs were left for periods of up to ten hours before incubation began in earnest. All birds from a territory were frequently observed feeding together when the clutch was incomplete but while eggs were occasionally left unattended during later stages of incubation, these spells were short, usually from two to fifteen minutes.

Incubation was followed by direct observation where possible, but most nests were not visible from the hides; so an automatic camera recorder was devised (Craig & Craig - in press, and Appendix 2). Initially no time scale was included and results in 1971 gave only order and frequency of incubation shifts. An electric clock was placed in the field of view but led to desertion of the nest (Nest 1, Western Territory). Early in the 1972-73 season, a small mechanical clock, suitably camouflaged, was used successfully and later an automatic time scale was included. Film also gave records of behaviour at the nest.

Incubation time averaged 24.8 days (range 23-27), (n = 12). This calculation does not include early eggs which could take up to 29 days to hatch.

6.6.2 Behaviour

Birds at the nest behaved in accord with their status. Low ranking birds were usually in a Bow, Wings and Tail Fully Up when entering the nest and normally had Wings and Tail Fully Up when relieved by a more dominant. Subordinates frequently left the nest before the dominant arrived and by the ramp on the opposite side of the nest from which the dominant approached. When the subordinate left by the same ramp as the dominant approached, it was in a Bow and was occasionally pecked. Rarely birds fought on the ramp or in the nest but this behaviour was seen mainly in the territories formed from the flock. This was suspected to be the cause of some egg damage and ejections.

In most instances, the sitting bird left when the relief arrive, but if it did not and was a subordinate, the dominant sat with it, pushed it off the nest, or pecked it. Where the two birds sat together, it was always beak to tail. Birds frequently brought nest material to the nest when relieving especially when a dominant relieved a subordinate (Table 39). Allopreening was also common during the change over. Sometimes a bird left a nest before another arrived and on all occasions, this bird then gave a Wing Clap and call which immediately brought another bird which usually took over. After relief, a bird frequently returned to the nest with building material (Table 39) but this behaviour did not appear to be clearly related to rank or sex.

Table 39 INCIDENCE OF BUILDING TRIPS TO NEST BEFORE AND AFTER INCUBATION

Figures represent the number of times a bird was observed to carry material to the nest.

Before Incubating

Southern Territory
1972-73

Relieving

Sitting	Aw	Ey	By	S1w
Aw		1	-	-
Ey	2		-	-
By	1	4		-
S1w	2	2	8	

Peninsular Territory
1972-73

Relieving

	Dominant	Subordinate	
	♂	♂	♀
Dom.♂		5	-
Subord. (♂	20		-
Subord. (♀	8	-	

After Incubating

Peninsular Territory
1972-73

M1w	1Tw	Q1w	1Ww	1Zw	Zw
3	8	12	-	1	11

The Peninsular Territory, 1972-73, was the most disorganised and disputes were common on the ramp when more than one bird arrived for relief. The female, *Zw*, was regularly pecked when relieving and departing, and normally reverted to Head Flagging. Non-breeding yearlings in their natal territories did not incubate but occasionally visited the nest.

6.6.3 In Relation to Status and Sex .

Dominant males and females tended to carry out proportionately more of the incubation. Individually, dominant birds did more of the observed incubation shifts and also did longer shifts than the subordinates in most of the study territories (Table 40).

The Southern Territory in all years, the Peninsular Territory in 1972-73 and the Hide Territory, 1970-71, were exceptions and the β male did more incubation than the dominant male. *2E* was also an exception among the females as she did more than *2B* in 1970-71 and approximately the same as *Plw* in 1972-73.

In pair territories, incubation regularly alternated between the male and the female with day shifts of approximately three hours duration. In all territories, males sat at dusk and were relieved immediately before dawn by a female. The dominant male sat at night in all known cases and was usually relieved by the dominant female who was in turn relieved by the β female. Times involved in night and dawn shifts are not included in Table 40 but would further accentuate the greater proportion of incubation attributable to the dominant pair. Non-breeding yearlings were not observed to incubate but frequently visited the nest.

6.7 Chick Care

Pukeko chicks are nidifugous, requiring to be fed (Fig. 49), led, brooded, and protected from predators. Hatching

Southern Territory 1972-73 (Nest 1)

	Aw♂	Ey♂	By♀	S1w♀	n
Number	8(1)	19(2)*	38($\underline{9}$)	27(6)*	92
Frequency %	8.7	20.7	41.3	29.4	

Southern Territory 1972-73 (Nest 2)

	Aw♂	Ey♂	By♀	S1w♀	n
Number	13(2)	15(2)*	18($\underline{7}$)	18(3)*	64
Frequency %	20.3	23.4	28.1	28.1	

Peninsular Territory 1972-73

	M1w♂	1Tw♂	Q1w♂	1Ww♂	1Zw♂	Zw♀
Number	36(5)($\underline{1}$)	58($\underline{1}$)	30	32	31	37(3)
Frequency %	16.1	25.9	13.4	14.3	13.8	16.5
Mean Time (mins)	33.70	49.45	29.24	32.15	28.74	27.46
Frequency %	15.4	36.3	11.1	13.0	11.3	12.9

( ) = number of dusk shifts
(_) = number of first dawn shifts
( )*= number of second dawn shifts

Figure 49

An adult male (Tw) and a yearling female feeding two chicks in the Northern Territory. Note the difference in the size of the two chicks.


T

was asynchronous and spread over three to six days. During this period one parent continued to sit on the eggs and newly hatched chicks while other members of the territory brought food giving it either to the sitting bird who then fed the chicks, or directly to the chicks. Within the first three days after hatching, chicks were led from the nest and fed in its vicinity, often on platforms built on the water out of large numbers of Carex and raupo leaves. As the chicks grew, they were led further from the nest.

Chick loss was high in the first two months, especially in the first few days, and when a few chicks hatched well in advance of the majority of the clutch, they frequently died in the nest - presumably of starvation. Less frequently the last eggs were abandoned and the hatched chicks were led to food: in one nest, Linton 4, 1970-71, the last egg was pipped and the chick visible when deserted. Dead chicks were frequently found in territories within the first fortnight of hatching and continued to disappear till two months of age.

Chicks began to feed themselves from about two days but still received the majority of their food from the adults until they were two months old. By this age, chicks spent much time alone but the adults rushed to them whenever harriers were overhead. In their turn, the chicks kept close to cover in their first two months. At Pukepuke in early 1973, adults were progressively forced by the drying up of the lake to feed further from cover; thus the chicks of second broods were left alone for long periods of time and none survived.

In pair territories both adults fed the chicks until re-nesting when the non-incubating bird alone cared for the chicks. Chicks were thus forced to become independent relatively earlier in pair territories, and when the second clutch hatched, older chicks did most of the caring for the younger ones.

Care of chicks was unequally distributed among the birds (Table 41). In the study territories in 1971-72, the

Table 41

CHICK CARE IN RELATION TO STATUS, SEX AND AGE

The figures show the number of times birds were seen with chicks. Birds are in order of status and yearlings are underlined.

1971-72 1972-73

Hide Territory

	H1w♂	Kw♂	2E♀	P1w♀		H1w	Kw	P1w	2E	R1w♀
Dec	7	5	3	3	Nov	2	3	1	3	1
Jan	14	3	5	4	Dec	2	6	4	8	4
Feb	1	3	1	1						
Mar	1	-	3	10						
Total	23	11	12	18	Total	4	9	5	11	5
Freq.%	35.9	17.2	18.8	28.1	Freq.%	11.8	26.5	14.7	32.4	14.7

Southern Territory

	Aw♂	Ey♂	By♀	S1w♀		Aw♂	Ey♂	By♀	S1w♀	1Nw♀	1Pw♂
Dec	12	1	7	4	Oct	3		3	3	2	1
Jan	7	1	4	16	Nov	18	2	3	8	16	31
Feb	4	1	4	3	Dec	7	5	8	6	3	12
Mar	14	5	5	7							
Total	37	8	20	30	Total	28	7	14	17	20	45
Freq.%	38.9	8.4	21.1	31.6	Freq.%	21.4	10.7	5.3	13.0	15.3	34.4

Northern Territory

	Ew♂	Tw♂	Pw♀	Bw♀	1Bw♂	L1w♀
Dec	12	18	26	22	Juv	Juv
Jan	6	12	2	1		
Feb	20	5	2	7		
Mar	36	2	4	6	5	11
Apr	14	5	10	11	6	7
Total	88	42	44	47	11	18
Freq.%	35.2	16.8	17.6	18.8	4.4	7.2

	Ew	Tw	Pw	Bw	1Bw	L1w
Nov	-	7	1	2	2	6
Dec	5	5	8	-	4	1
Total	5	12	9	2	6	7
Freq.%	12.2	29.3	22.0	4.9	14.6	17.1

dominant male cared for the chicks substantially more than any other member of the territory. The subordinate female was next and the β male scored poorly. This pattern was not so obvious in 1972-73 when yearlings were present in all territories, as they accounted for a large proportion of the chick care. In the Southern Territory, the dominant male still cared more for the chicks than any other adult but this was not so in the Hide and Northern Territories although there are few results in these cases.

6.8 Reproductive Success

Hatching success and survival rate varied markedly between territories and also from year to year (Table 42 and Appendix 6). Survival rates were very low at Pukepuke. In 1970-71 only two chicks survived from all broods, and in all years survival was low for second and subsequent broods, possibly because of low water levels (see p. 22). Survival rates at Linton were high in all years.

Overall breeding success was inversely related to the number of birds in the territory; pairs being more successful than groups in all except the 1970-71 season. It is probably unrealistic however, to compare the stable pair territories at Linton with the groups at Pukepuke, many of which were unstable having been formed from flock birds. When the results of stable groups are compared with stable pairs, groups have a significantly lower breeding success in terms of surviving offspring, but have a higher hatching rate although this is not significant. This trend of lower success of groups also appears when pairs are compared with groups at Linton, but the results are again not significant possibly because of the smaller numbers involved. Only one pair was found at Pukepuke which is insufficient for a meaningful comparison to be made between pairs and groups at this area.

When survival rates for individual territories are examined they appear to be closely related to water depth

Table 42

REPRODUCTIVE OUTPUT OF PAIRS AND GROUPS

	1970-71				1971-72					1972-73			Totals												Overall Total
	Linton		Pukepuke		Linton		Pukepuke			Linton	Pukepuke		Linton		Pukepuke			All	All	Stable				Flock Unstable Pukepuke	
	Prs	Gps	Gps		Prs	Gps	Prs	Gps		Prs	Gps		Prs	Gps	Prs	Gps		Prs	Gps	Linton	Puke	Prs	Gps		
			3&4	5&6				4	5		3&4	6				3&4	5&6								
No. of Territories	1	3	3	1	2	2	1	2	4	3	3	4	6	5	1	8	9	7	22	9	10	6	13	4	29
No. of Nests	2	5	5	1	6	3	1	5	8	5	4	8	13	8	1	14	17	14	39	19	18	13	24	8	53
No. of Eggs	10	24	29	5	28	15	6	30	47	26	18	47	64	39	6	77	99	70	215	94	119	64	149	30	285
No. Hatched	5	20	28	5	16	15	6	23	26	21	7	35	42	35	6	58	66	48	159	70	92	42	120	17	207
													ns*		ns*			ns*		ns*		ns*			
Hatching Success	50%	83%	97%	100%	57%	100%	100%	77%	55%	81%	39%	74%	66%	90%	100%	75%	67%	69%	74%	74%	77%	66%	81%	57%	73%
No. of Chicks Surviving to 4 months	2	8	1	2	11	3	2	5	3	11	0	9	24	11	2	6	14	26	31	36	18	27	28	0	57
													ns*		ns*			$p<0.01$*		$p<0.01$*		$p<0.05$*			
Breeding Success	20%	33%	3%	40%	39%	20%	33%	17%	6%	42%	0%	19%	38%	28%	33%	8%	14%	37%	14%	38%	15%	42%	19%	0%	20%
Mean No. of Chicks Surviving/ Territory	2.0	2.7	0.3	2	5.5	1.5	2	2.5	0.75	3.7	0	2.3	4	2.2	2	0.8	1.6	3.7	1.4	4	1.8	4.5	2.2	0	2.0
Mean No. of Chicks Surviving/ Bird	1.0	0.8	0.9	0.4	2.8	0.4	1.0	0.6	0.2	1.8	0	0.4	2.0	0.5	1.0	0.2	0.3	1.9	0.3	1.6	0.4	2.3	0.2	0	0.5

* Using X^2 contingency test

Note: Where it is suspected that not all nests were found, the results of that territory are not included.

and the area of cover vegetation available (Table 43). Territories with large areas of cover had higher survival rates than those with little cover, with the exception of the Western Territory. The low success in the Western Territory was possibly due to the very high proportion of Carex in the vegetation and the birds' failure to provide cover for their nests from aerial predators (see p. 173). Although there was little Carex or raupo cover in Linton 4, rank grass clumps provided sufficient protection and aerial predators were rarely seen. Chick survival also appeared to be directly related to constancy of water levels although Linton 4 was again an exception. The high mortality of eggs and chicks in the Inlet, Peninsular, Corner, Rough Paddock and Trap Territories was partly caused by the small area of cover vegetation but more by the low water levels, nest sites, and mustelid predation. Mustelids were suspected to have taken eggs because nests were well covered but many were at ground level and mustelids were seen in the territories in early summer. Tracks used by me to these nests were always retraced and crossed in an attempt to provide a confused trail for ground predators. Egg loss for all territories is detailed in Table 44. Predation was the greatest source of egg loss but desertion and ejection were also common.

6.9 Discussion

Courtship and other sexual behaviour was strongly affected by individual status. Courtship involved adoption of the frontal posture with the lowest aggressive content. The observation that dominants initiated courtship more frequently than subordinates is in keeping with the expectation that subordinates would tend to avoid contact with dominants. The frequently observed failure of subordinates to preen a presenting dominant suggests that inhibition of contact is high especially where disparity of rank was great. The red colour of the iris was similar to the colour of the bill which is the aggressive weapon and

Table 43

BREEDING SUCCESS IN INDIVIDUAL TERRITORIES IN RELATION TO COVER AND WATER LEVEL

Territory	No. of Eggs Laid	No. of Eggs Hatched	Chicks Surviving	Area of Raupo and *Carex*	Water Level
Western	40*	27	1 (2.5%)	0.32 ha	>60 cm
Northern	32*	28	5 (15.6%)	0.23 ha	>60 cm
Southern	45	39	5 (11.2%)	0.28 ha	>60 cm
Hide	29	16	7 (24.2%)	0.23 ha	>30 cm
Peninsular	6 8	6 5	2 (33%) 0	0.08 ha 0.06 ha	>30 cm >30 cm
Trap	7	2	0	0.02 ha	<30 cm
Corner	4	0	0	0.01 ha	-
Rough Paddock	4	3	0	0.01 ha	-
Linton 1	39	24	15 (40%)	0.4 ha	60 cm+
Linton 2	31	23	13 (42%)	0.4 ha	60 cm+
Linton 4	24	23	8 (33%)	0.06 ha	-

* Eggs believed lost by my interference not included.
\+ Constant water level

Table 44

CAUSES OF EGG LOSS

Cause	Number Lost	Total
Predation - Harrier	25+	
Mustelid	6	
Man	4'	35
Deserted		20
Ejected - cracked	12	
not cracked	3	15
Addled		8
Died in hatching		2
Infertile*		1
Unknown		10

+ Loss of six believed to be due to automatic camera.

' One removed in an experiment.

* Judged infertile because no decomposition had occurred after full incubation (Roderick, pers. comm.).

this may explain why dominants closed their eyes during allopreening.

Courtship feeding appears to be completely ritualized and no longer serves any function of increasing nutrient intake of the female. This ritualization has been suggested in many other species (Welty, 1964) although Tinbergen (1959) suggests courtship feeding has a nutritive function in gulls where significant quantities of food are given.

The observation that courtship occurred between all members of a group territory is probably related to the fact that all birds in a territory participate in most breeding activities and so aggression among all birds must be reduced to promote co-operation for nesting. Courtship between all members probably also helped synchronize sexual cycles and so ensure that all birds were ready for nesting at the same time. Gullion (1954) records allopreening between members of winter flocks of coots regardless of sex but found that it became increasingly restricted to between males and females.

The similarity of the Sexual Upright and Forward and the 'Aggressive' Upright and Forward suggests a high aggressive element in the sexual displays of the male (mounting bird). This is further demonstrated by the frequency of copulations and attempts involving pecking, especially in the Peninsular Territory (Table 33).

The frequently observed copulations between females of the same group territory are also believed to help synchronize the cycles of the females so that they can lay in the same nest at the same time. Synchronized laying would not only reduce the likelihood of predation by reducing the number of nests, but would also reduce the length of vulnerable time spent on the nest. It would also effect more synchronous hatching which, in turn, would reduce the time when labour was necessary for incubation and chick care simultaneously.

The frequency with which females copulated with females especially in the Hide Territory, the link between status and frequency of mounting, and the apparent completeness of many female homosexual matings casts severe doubt on sexing by copulations alone. This was especially so in regard to *Plw* which was obviously a female by measurement and was also sexed internally but which regularly copulated with *2E*, the other female. Ridpath (1972) relied solely on observed copulation for sexing Tasmanian native hens and commented (pers. comm.) that homosexual and reverse mountings were far outnumbered by normal heterosexual copulations, but he gave no figures. Ridpath further stated (pers. comm.) that female-male mountings were always incomplete. However, in pukeko, (as noted on p. 167) *Plw* fully copulated with *2E* on one occasion (both females) and then *2E* mounted *Plw* but immediately dismounted giving superficial resemblance to an incomplete female-male mounting. No female-male copulations are recorded for monogamous rails (Howard, 1940; Gullion, 1954; Kornowski, 1957; Reid, 1967 and pers. comm.).

The participation of more than two birds in most copulation attempts appears superficially maladaptive in that it prevented many copulations from going to completion but it is suggested that multiple participation is important in synchronizing the sexual cycles of all birds in the territory. In addition to this social stimulation within the territory, there appears to have been stimulation between territories as evidenced by synchrony of nests in adjacent territories (Appendix 6). Social stimulation synchronizing nesting has been recorded in many other species (e.g. Patterson, 1965) and it is suggested that this is advantageous in relation to predation by condensing vulnerable nesting time to a minimum.

The repeated rape attempts in the Peninsular Territory appeared to be a direct outcome of the skewed sex ratio and must have been partly maladaptive as they significantly reduced feeding by the female at a time when she needed extra nourishment for egg production.

The observation that yearlings, retained in natal territories where all adult birds were still in residence, rarely or never participated in copulations is in agreement with previous observations that these birds must continually show juvenile behaviour and supress adult behaviour patterns to be able to remain in the territory. This would also explain the begging-type behaviour of yearling females when the adults were copulating. The participation in breeding by 2E and Plw show that yearlings are elevated to reproductive status when a breeding adult is lost.

The highly elevated wing and tail positions of males when dismounting after copulation is probably due to loss of status when immediately in front of another bird, (see p. 121). The adoption of a Pre-copulatory Position when dismounting, perhaps similarly explained, was seen twice only: once when a dominant female mounted a subordinate in a homosexual mating, and once when a β male had mounted a female in the presence of a dominant male. In the latter case, it is believed that the β male was reacting to the other male rather than the female even though she mounted. A male Post-copulatory Position similar to the female Pre-copulatory Position has been recorded in moorhens (Howard, 1940), and Tribonyx (Ridpath, 1972). Takahe frequently adopt this posture in front of the female after unsuccessful attempts to mount (pers. observ.).

Apart from the Peninsular Territory, there appeared to be no relationship between status and frequency of copulations in females but dominant males attempted to copulate more frequently than subordinate males and prevented the latter from mounting on a number of occasions. There was, however, no link between full copulation and status, and it is doubtful if the dominant male had any reproductive advantage in relation to the number of eggs fertilized. Guhl, Collias, and Allee (1945) investigated mating behaviour of domestic fowls and found negative correlations between:

(1) Social position and frequency of mating.

(2) Social position and frequency of being courted.

(3) Social position and frequency of inviting the cock to mate.

Thus higher ranked hens mated less frequently than those lower in the scale but laid more eggs. If sub-flocking occurred so that all higher ranking hens were together in the absence of most subordinates, they mated more often than when no sub-flocking occurred (Guhl, 1950). Therefore, the habit of dominating interferes with mating in hens. However, mating was sufficient for fertilization and consequently higher ranked hens produce more offspring.

The site of egg nests in each territory was consistently in the same vegetation. The exceptions to this suggest that the dominant male was responsible for nest site selection. The change from Carex to raupo in the Northern Territory and the reverse change in the Hide Territory coincided with the shift of *Ew* from the latter territory to the former. The regular change in the Southern Territory suggests that both *Aw* and *Ey* chose different nest sites and is further evidence of the high status of *Ey*. It is suspected therefore that choice of nest site may be learned behaviour with males building in the same nest types as they were reared in. This should be a subject of future investigation.

The construction of multiple nests prior to laying may be related to the platforms made by more aquatic rails and used for copulation (e.g. Howard, 1940; Gullion, 1954; Kornowski, 1957). Trial nests have also been recorded for pukeko by Tunnicliffe (1965), for Tribonyx (Ridpath, 1972) and Notornis (Williams, 1960). Tunnicliffe (1965), Guthrie-Smith (1927), Oliver (1955) and Morrison (pers. comm.) record multiple nests for pukeko where two or three nests were constructed close together and all were used for laying and incubation. No such nests were found at Pukepuke and all communal nests were single-bowled. It is suggested that this may be an anti-predator device in that it reduces the size of the nest area and hence decreases the likelihood of it being found by an aerial predator. The multiple nests recorded by Tunnicliffe (1965) and Morrison (pers. comm.) were all in very open areas where each nest regardless of its size was obvious to predators, and it was also always in view of the pukeko. Thus because the nest and the incubating bird were so exposed, reduction of nest size to a single bowl would not have made the nest less obvious to aerial predators.

In many species there is consistent variation in the colour of eggs from different individuals (Romanoff and Romanoff, 1949), but in some species colour can be extremely variable especially in those species that lay two eggs (Welty, 1964). Notornis females lay eggs which usually vary markedly in colour (pers. observ.). Egg shape is reported to be regular but can also vary within a laying cycle (Romanoff and Romanoff, 1949). Despite this, pukeko egg colour in monogamous nests was consistently the same but where two different egg colours appeared in a nest, eggs of each of the two colour types were consistently similar, even from year to year and were consistently dissimilar from the other type, both in colour and size. Taken with the evidence of deposition time, egg colour is believed to be a very reliable guide to the number of hens laying in a nest in pukeko. Egg colour is genetically determined (Romanoff and Romanoff, 1949) and this would explain the similarity of egg colour in nests where the females were related.

Tunnicliffe (1965) also used egg colour, egg size and the deposition of more than one egg a day to determine if more than one hen was laying in a nest. Moreover, he categorized nests with more than eight eggs as communal, but many communal nests at Pukepuke contained fewer than nine eggs, hence egg number is a poor criterion for communal nests. Co-partnership or communal nests have been recorded for wekas (Guthrie-Smith, 1927) and promiscuous laying has been recorded in coots (Alley & Boyd, 1947; Fredrickson, 1970). Ridpath (1972) did not comment on more than one female Tasmanian native hen laying in the same nest but gave only one plate of a nest, which contained six eggs of two distinct colour types.

Other authors give varying estimates of pukeko clutch size. McLean (1902) gives 3-14; Oliver (1955) 5-7; Falla *et al* (1966) 4-7; and Tunnicliffe (1965) 3-8 for monogamous and 9-18 for co-partnership nests. Morrison (pers. comm.) gives a mean clutch size of 4-7 for monogamous nests and 5-18 when co-partnership nests are included.

The larger clutch size in my group territories in comparison with pairs was caused by more than one female laying in the nest and not to an increase in the number of eggs laid by a female in a group territory. In fact, individual clutch sizes are lower for communal females than monogamous hens. Morrison (pers. comm.) found that the clutch size of individual females in a group nest was 4.75, slightly higher than for monogamous females, but results were taken from three nests only.

The significant correlation between clutch size and the number of birds in group territories with more than four individuals is believed to be due to the increasing age of the females and not to more females laying. Parry (1968) recorded an increased clutch size of kookaburras in group territories, but this was not significant. Ridpath (1972) showed that the Tasmanian native hen yearlings had smaller clutches, and he recorded a significant increase in clutch size between group and pair territories with birds of similar ages. This, he suggested, was 'presumably connected in some way with having more males'. However, there is considerable evidence from pukeko (see pp. 27, 122, and 199) to question Ridpath's sexing. It is likely, therefore, that this increase in the clutch size of *Tribonyx* trios arose from more than one female laying in some of his territories, and this conclusion is backed up by the only photograph of a nest which contains what appears to be a two hen clutch.

The dominant female in most territories laid more eggs than the subordinate. This may have been a reflection of age in that the older female (who was also dominant in most territories) laid the greatest number of eggs in every territory. In general, the older (and dominant) hen was responsible for most of the first clutch. Older birds are recorded as laying earlier in many species (refs in Davis, 1955; Coulson & White, 1958). As discussed above, egg production is directly related to status in domestic hens (Guhl et al, 1945) but the hens in question were of similar age.

As in other rails (Gullion, 1954; Ridpath, 1972) incubation by pukeko did not start with the first egg, so that the time between laying and hatching varied between 23 and 29 days, with most taking 24-25 days. Incubation in other rails is also variable (review in Gullion, 1954), varying from 16-27 days. Incubation in pukeko was shared by both sexes as in most monogamous species (Lack, 1968) and depended on status with the dominant pair being mainly responsible, but again, E_y was an exception. As with all interactions between birds, behaviour at the nest was strongly influenced by status, and because birds were in very close contact, appeasement and aggressive behaviour was common. Subordinates exaggerated postures and used Facing Away and Head Flagging as expected in a close contact situation (see p. 119). Fights were observed, however, and were probably the cause of cracking and ejection of eggs. The habit of the dominant taking nesting material to the nest when relieving a subordinate was possibly to cause a change of motivation of the subordinates from escape behaviour into nest building and so bring about a non-violent change over. Morrison (pers. comm.) has also recorded agonistic behaviour at a change over and the presentation of nest material.

Previous workers have suggested that the male is responsible for the majority of incubation (Guthrie-Smith, 1927; Tunnicliffe, 1965) and this has been accepted by others (e.g. Oliver, 1955; Falla et al, 1966), while McLean (1902) reports the female was responsible for incubation. My results show that the incubation is shared between the sexes and the high incidence of incubation attributed to the male by other workers is probably due to the fact that the dominant male usually returns to the nest after a disturbance. Gullion (1954) recorded that male coots, like pukeko, did night incubation shifts.

Even though pukeko chicks are precocial and nidifugous, they are dependent on their parents until at least one month of age and mortality was high during this time. Captive chicks can be taught to feed themselves completely from about four days (Reid, Roderick, and Kelly, pers. comm.). As with other activities, chick care by adults varied with status. Females initially tended chicks more than did males, but dominant males subsequently took on an increasing amount of chick care. Where yearlings were present these assumed the major role in chick care and if a second brood survived past two weeks, chicks of the first brood were responsible for most of their feeding. This was especially obvious in pair territories.

The presence of extra helpers in chick care has been recorded in many species (Skutch, 1961; Harrison, 1969; Dow, 1970). Many of these extra helpers were young of an earlier brood or young of the previous year (Skutch, 1961; Rowley, 1965; Parry, 1968; Dow, 1970; Fry, 1972). Howard (1940) demonstrated young of an earlier brood helping feed a subsequent moorhen brood and Ridpath (1972) also recorded this in Tasmanian native hens. A full discussion of the phenomenon of helpers at a nest will be given in the next chapter.

Reproductive success was low (20%) but egg loss also was comparatively low, whereas chick mortality was high especially in the first month. Tunnicliffe (1965 and pers. comm.) attributed low reproductive success at Ellesmere to egg losses caused by flooding, but he gave no figures. Reproductive success of other rails is very similar to my results but the hatching rate of rails is more variable.

Reproductive success in individual territories appears closely related to shelter from predators. For successful rearing of chicks, a minimum area of cover appears necessary in relation to aerial predators and a minimum water depth of about 30 cm appears necessary perhaps to eliminate ground predators.

Table 45 BREEDING SUCCESS OF OTHER RAILS

Species	Source	Hatching Rate/Clutch	Survival Rate/Clutch
Coot	Alley & Boyd (1947)	34.7%	23.1%
	Gullion (1954)	48%	26%
	Sage (1970)	33.8%	20.6%
Moorhens	Anderson (in Dunnet, 1965)	70%	-
Tribonyx	Ridpath (1972)	89%	39-64%
Notornis	Williams (1960)	57%	-

The lower reproductive success, measured by the proportion of young surviving to four months to the number of eggs laid, of group territories in comparison with pairs is one of the more unexpected results of the study. Hatching success was higher (although not significantly so) in group territories presumably because more birds were available for incubation but overall success was lower for groups. There was, however, a higher reproductive success of birds at Linton in comparison with those at Pukepuke and as all except one of the pairs followed was at Linton and most of the groups were at Pukepuke, the difference between pairs and groups may have been due mainly to habitat. Comparison of pairs with groups at Linton also shows a trend of lower reproductive success of the latter but results are too few and the difference is not significant ($X^2 = 0.23$). As Linton groups were found mainly in areas with variable water levels while most of the pairs had constant water levels in their territories, this difference may also be due to habitat. Fluctuating water levels were also believed to have been an important factor in the lower reproductive success of groups at Pukepuke. Most territories dried up at the time of the hatching of late first and second clutches from which no chicks survived with the exception of the

Northern Territory 1971-72. This high mortality is thought to have been caused by a depletion in the supply of animal food so necessary for chick growth. As physical characteristics of a territory appear to determine the number of birds in the territory, it is hard to separate the effects of habitat from that of the number of birds in the territory and reproductive success is probably the result of a complex interplay of both.

Dominant females were more likely to leave surviving offspring because they laid a greater proportion of the more successful first clutches. No such relationship can be assumed for the males.

Increased reproductive success with an increase in the number of birds per territory has been described in other species, e.g. kookaburras (Parry, 1968) and Tasmanian native hens (Ridpath, 1972). Both authors suggest that this was due to the increased care afforded by the extra birds. However, Ridpath (1972) did not give sufficient data to allow for reworking his results and also bases his comparison between pairs and groups of clutch size, percentage survival per clutch, and the mean number of young surviving in December on different sample sizes. Moreover, he measured survival of chicks to December, and in his words - 'to four months of age'. These terms are not synonymous as the second clutches (which accounted for much of the increased success of his group) did not hatch till December and thus were only days old when counted. If similar criteria were used for calculating pukeko reproductive success, groups would definitely have a greater success than pairs due to their larger second clutches. However, I have used the age of four months (when birds were capable of independence) and not a calender month as the cut-off time for survival. The high mortality of chicks in both this study and that of Ridpath makes any estimate of survival taken under one month of age unrealistic. Further evidence for the validity of the cut-off age can be gained from the fact that only three of the 57 chicks alive at four months died before eight months of age.

A full discussion of the implications of reproductive success will be given in the next chapter.

7. FINAL DISCUSSION

7.1 Use of Space

7.1.1 General

An animal's use of space is governed by its social organization which in turn is closely linked to and determined by habitat type especially in relation to food (Crook, 1965; Brown & Orians, 1970; Brereton, 1971). Social organization has two distinct aspects - it produces a non-random distribution of individuals which is believed to reduce competition and predation, but maximize utilization of resources (Kikkawa & Thorne, 1971), while also bringing members of the opposite sex together for breeding. The social organization of a species is, therefore, a compromise between these two aspects and must result from natural selection. Various workers have attempted to classify dispersion patterns and explain their evolution but only a few (Wynne-Edwards, 1962; Brown & Orians, 1970; Brereton, 1971) have attempted to link all known forms of dispersion and then propose a general selective theory which is applicable to all species.

One of the problems in classifying an animal into a particular type of dispersion is that many species have a different spatial organization at different times of the year or they have different social phases (McBride, 1971). Brereton (1971) has suggested classification by breeding phase organization and suggests three basic types:

(i) Gregarious - amorphous flocks with no recognisable internal organization.

(ii) Interspersing - interacting flocks with definite organization such as a hierarchy.

(iii) Territorial - pairs or groups having exclusive use of resources in both time and space.

Brereton did not consider these as separate entities but more as a continuum of social organization related to habitat, with social organization tending towards (i) with increasing aridity and uneven distribution of resources. Before the results of previous chapters are taken together to classify the social organization of pukeko, it is relevant to review the two main spacing concepts - social hierarchy and territory.

7.1.2 Social Hierarchy

The concept of social hierarchy is usually first associated with Schjelderup-Ebbe (1922, 1935 from Guhl & Allee, 1944) who first demonstrated a ranking order in a flock of domestic chickens. The ranking order was termed a 'peck order' as it was measured by unidirectional pecking at a food tray. Since then, a large number of studies have been undertaken but mainly on captive birds or primates (Brown, 1963; Bernstein, 1970).

Early evidence suggested the existence of two different forms of peck order (Masure & Allee, 1934). The simple, usually linear, despotic organization reported by Schjelderup-Ebbe was termed 'peck right', where the dominant or alpha (α) bird could peck all those lower in rank, the second or Beta (β) bird could peck all except α which could however peck β, and the bottom or omega (ω) bird could be pecked by all but peck none in return. In large flocks this linear organization was frequently complicated by triangular relationships e.g. $\alpha > \beta > \gamma > \alpha$ (Allee, 1950; Wood-Gush, 1955).

Investigation of pigeons (Masure & Allee, 1934) produced a more complicated peck order where all birds were pecked but also pecked in return and dominance became a relative measure of pecks given to pecks received. This is termed 'peck dominance'. In the pigeon (Masure & Allee, 1934; Ritchey, 1951) dominance was found to be related to the site of the encounter in that even subordinate birds were able to defeat more dominant birds within their own 'territory' but were still not entirely free from being pecked. It should be noted that 'territory' used in this sense is not the classical 'defended area' but more closely resembles the home range system. Peck-dominance is usually associated with crowded populations. However, Marler (1955) associates peck-dominance with territories in the chaffinch.

Later work has demonstrated the existence of dominance ranks in many animal groups (c.f. refs in Allee, 1950; Wynne-Edwards, 1962) making the term 'peck order' redundant and it is now referred to as 'social hierarchy'. Furthermore, emphasis has shifted from scoring solely aggressive criteria, such as pecking and fighting, as indices of dominance and rank, to avoidance by subordinates and allowed priority of access to incentives for dominants (Bernstein, 1970). Willis (1967) emphasized the importance of both aggression and submission in hierarchies. Thus hierarchies establish sequences of precedence according to rank in competitive situations within a group.

For a hierarchy of any form to exist, members of the group must be able to recognize every other individual (Collias, 1952). Schjelderup-Ebbe (from Collias, 1952) noted this and by altering head characteristics was able to change the status of some members. Hediger (1950) and Collias (1952) state that a hierarchy means that members not only recognize each other but also form appropriate habits of interaction with each other member of the group. The interactions between dominant and subordinate individuals reinforce these habits and subordinates adopt more submissive postures and thus offer weaker stimuli for aggression. Consequently, intensity of aggression and avoidance become reduced and behaviour patterns become more symbolic (ritualized) such as threat. For example, avoidance may be reduced to simple facing away of the head (Hafez, 1950; Tinbergen, 1959). Thus tolerance develops within the group and this social inertia promotes social stability. Sabine (1959) also demonstrated ritualization of pecking and stressed the use of avoidance rather than pecking as a criterion for assessing rank. Dixon (1965) criticized the investigation of hierarchies at a single feeding station as this can lead to an erroneous interpretation that a 'peck-right' order exists whereas that population may in reality have a 'peck-dominance' hierarchy with status dependent on site.

These criticisms were recognized in the present study. As a result, both aggression and avoidance were used as criteria, and hierarchies were investigated at a number of sites. Both criteria gave the same results and at any single point, a linear hierarchy devoid of triangular relationships was demonstrated. This linear grouping was stable among members of a territory for all parts of the territory but status was found to be site dependent (peck-dominance) among birds of the flock.

7.1.3 Territory

The concept of territory is usually attributed to Howard (1920) although prior references do occur (cf. Nice, 1941; Lack, 1944). Early work on territory involved considerable controversy over its definition, although Noble's (1939) definition of 'any defended area' is the most accepted (Hinde, 1956). However, because of its simplicity, it is not without criticism. Nice (1941) and Armstrong (1956) argue that the definition does not state against whom the territory is defended. Armstrong argued that defence against competitors of the same species is the essential feature, while Nice's definition (accepted by Welty, 1964) takes it further to embody defence against members of the same sex. However, Nice's definition is too specific, being readily applicable only to the male defended territories of some passerines, and the existence of interspecific territories (Lanyon, 1956; Orians & Wilson, 1964; and other references in Hinde, 1956) tends to negate Armstrong's objection.

Using Noble's definition of territory, all pukeko pairs and groups in the study areas were territorial during the breeding season although a small number of individual birds were non-territorial and did not breed. Outside the breeding season, the degree of defence of breeding territories varied from complete defence at Linton and some Pukepuke territories to total breakdown of defence of those territories invaded by the flock. Thus the standard definition of territory did not fit all groups outside the breeding phase.

Following the review of territory summarized by Hinde (1956), Emlen (1957) immediately criticized the accepted definition of 'any defended area'. Emlen emphasized the danger of fitting observations into an accepted pattern through the use of approved terms and phrases instead of reporting observations directly and he further doubted that the area was the <u>object</u> of the aggressive behaviour. He defined territory more loosely as 'an area of space in which a particular bird is aggressive and largely, if not supremely, dominant with respect to certain categories of intruders'. Emlen's objection is upheld when many of the papers summarized by Hinde (1956) are considered.

Young (1956) recorded extensive trespass in the American robin, <u>Turdus migratorius</u>, and commented that the concept of territory as 'a defended area' did not completely fit the situation. Snow (1956) recorded that territorial blackbirds, <u>Turdus merula</u>, were more tolerant of trespass in winter. Swanberg (1956) noted frequent tolerance of intruders in the nutcracker, <u>Nucifraga caryocatactes</u>, and that birds were driven from the stored food supply but not from the territory, while Blank & Ash (1956) described overlapping territories in the partridge, <u>Perdix perdix perdix</u>.

Tinbergen (1957) similarly linked dominance and territory. He considered geographical fixation irrelevant but, where it did occur, it was the result of two distinct tendencies: (a) site attachment
(b) hostility.

Each of these tendencies could, however, occur without the other. Patterson (1965) has shown that hostility related to distance from aggressor is the most important aspect in dispersion patterns such as territory and that boundaries are only secondary due to site attachment and learning.

Pitelka (1959) also criticized the accepted definition of territory despite the fact that his study species, the pectoral sandpiper, Erolia melanotus, defended its breeding range.

Pitelka criticized the use of the word 'defended' and considered that 'the fundamental importance of territory lies not in the mechanism (overt defence or any other action) by which the territory becomes identified with the occupant, but in the degree to which it is in fact used exclusively by its occupant'. Pitelka preferred the definition 'an exclusive area'. However, while this removes the focus from defence it still fails to allow for trespass or overlap. Young (1970) used Pitelka's definition.

Davis (1958) from his work with caged house mice, added further to Emlen's and Tinbergen's idea of dominance in territory by postulating a link between social hierarchy and territory. He found that with mice 'the area defended decreases as density increases until none is held'. He advanced the hypothesis that "territorialism and social rank are two poles of a continuum of behaviour that is dependent on density. At all densities the individuals arranged themselves in a rank, but at low density the groups tend to be smaller so that at the lowest density, each 'group' consists of one animal who has a territory and who is naturally dominant". In other words the territory owner is dominant within his own territory. This has been substantiated by Kinsey (1971) in wood rats, Neotoma fuscipes.

It should be noted however that the idea of dominance of the territory owner is not new but had been included in Nice's (1941) definition of territory where she described the territorial male as being 'supremely dominant' within his own territory. Gibb (1956) in discussing territory in the rock pipit, Anthus spinoletta, also stated 'owners are always dominant over the rock pipits in their territories'. However, unlike Emlen (1957) and Davis (1958) these works still emphasized defence of trespass rather than domination of trespasser. It should also be noted that the switch from social hierarchy to territory with decreasing density was previously noted by Greenberg (1947) in captive green sunfish, Lepomis cyanellus.

Davis (1959) further extended his idea with his work on starlings, Sturnus vulgaris, to include the concept of territorial rank. He found that starlings did not have territories but the male dominated a nest hole and drove other birds away. This is similar to the nest hole territory of the pied flycatcher, Muscicapa hypoleuca (Haartman, 1956). Davis (1959) postulated that 'territory is really a special case of social rank' in that subordinate birds can flee in the wild but not in captivity. He therefore concluded that 'the starling has social rank in the wild but the subordinate individuals are present only temporarily and thus we have superficial resemblance to territorial behaviour'.

Further evidence for the concept of social hierarchy and territory being two poles of a continuum is given in Brown's (1963) work on stellar jays, Cyanocitta stelleri, where social rank was strongly dependent on area - in this case distance from nest site. Brown considered this intermediate between social hierarchy independent of site (peck right) and the conventional defended territory. Similarly, Willis (1967) found that bicoloured antbirds, Gymnopithys bicolor, were always dominant on their own nesting area. Unlike Brown's (1963) work where feeding was at artificial food sources, bicoloured antbirds naturally crowd over swarms of ants, forming stable hierarchies in which the pair on its own nesting area was dominant. Thus in both species there was overlap of feeding areas but non-overlap of nesting areas producing a spatially related dominance reversal where birds were dominant in their own territories but subordinate in nesting areas of other. Willis (1967) criticized the classical definition of territory because it 'merely expresses one factor space - which can determine dominance in an encounter between animals'. He concluded that consistent reversals of dominance with difference in space should be made the criterion for territoriality and defined territory as 'a space in which one animal (or group) generally dominates others which become dominant elsewhere'.

It has already been noted that if this definition of

Willis's is used for pukeko, then most of the study pukeko can be said to have been territorial all the year round, because even where territorial defence broke down partially or completely (cf. Western, Hide, Peninsular and Trap territories) the dominant birds within the territory were still dominant over all birds (trespassers and other members alike) when in their old breeding territory area.

Correlation between rank and distance from nesting area has also been shown in Carolina chickadee, *Parus carolineuis*, (Dixon, 1963), and many other species of tits (refs in Willis, 1967). Sabine (1959) and Kikkawa (1961) also showed an interrelation of territory and social hierarchy in the juncos, *Junco* spp., and white-eye, *Zosterops lateralis*, respectively, where conventional territories held during the breeding season gave way to site dependent hierarchy ('peck right') and eventually to a simple hierarchy with increase in flock size. These all add further to the idea of a continuum between hierarchy and territory and Willis (1967) considered exclusion as seen in classical territory only as a special case of dominance.

Perhaps the strongest case for territory being an extension of social hierarchy comes from the work of McBride *et al* (1969) on the feral domestic fowl. The feral fowl has two seasonal phases to its social system, and during all phases hierarchies exist between males and between females of the flocks. During the breeding phase (season) six categories of males were recognized forming a scale from territorial to hierarchical with variations in the degree to which dominance was expressed in the exclusive control of space. None of the females was territorial but usually joined flocks associated with territorial males. During the winter phase, territories broke down and males adopted a system of overlapping home ranges with a hierarchy between alpha males. Throughout both phases, hierarchies among the females were absolute (Leyhausen, 1971) being independent of locality. Because of this, McBride *et al* (1969) concluded that the term territoriality was a gross over-simplification but that the concept of dominance providing control over fixed or portable space clarified the situation and that dominance had little meaning unless some distance was included.

The finding of a hierarchy between pukeko territorial groups further emphasizes the inadequacy of territory when viewed as an isolated phenomenon; but can be explained in a spatially related dominance system.

The idea of dominance in territory, like Emlen's (1957) critique, reduces the emphasis on defence and aggression and makes avoidance as important a criterion. Other authors have also noted the importance of avoidance and escape in both classical territory and hierarchy (e.g. Lack, 1954; Etkin, 1964; Willis, 1967; Tinbergen, 1968; Hornocker, 1969). Many mammals restrict activities to a particular locality and defence or dominance of the area may not be observed. But because avoidance as well as defence or dominance gives exclusive use, it is often difficult to distinguish between home range and territory no matter how the latter is defined. Thus Etkin (1964) defined territoriality as 'any behaviour on the part of an animal which tends to confine the movements of the animal to a particular locality'. This tends to merge the broad concept of home range with territory.

All previous discussion on territory has considered it as a mechanism of spatial dispersion, but Hornocker (1969) extended the concept of territory to be solely temporal in exclusiveness. He found that mountain lions, Felis concolor, had overlapping ranges but avoidance gave exclusive use of resources in time though not necessarily in space.

The complete defence of the Northern and Southern Territories against flock birds in 1972 during the day, with trespass for roosting being tolerated at night, emphasizes the importance of both time and space in the social organization of pukeko.

Leyhausen (1971) further discussed the concept of time and space in both territory and hierarchy and derived both from individual distance. He suggested that if an animal is equipped with structural and behavioural prerequisites for fighting, then fighting is employed to maintain individual distance. The outcome is that more aggressive and stronger animals maintain greater distances around them (cf. Patterson, 1965). Thus one gets what Leyhausen terms 'an individual distance differential' and space becomes a symbol of social status (cf. McBride et al, 1969). However, the motivational state of an animal varies with circadian and seasonal rhythms as well as other factors and consequently individual distance and status also vary with time. Ranking order that is observed by all individuals at all times and in all places is an absolute social hierarchy (Leyhausen, 1971). This applies only to the hierarchy observed between members of the same 'territorial' group of pukeko.

Similarly territory can be derived from individual distance by localization to make it a topographically defined area. When discussing territory in mammals, Leyhausen used the concept of a 'time-space fabricated straight-jacket' in that mammals form a network of pathways and a time-schedule by which this network is used. He emphasized that a territory is not just an area inside a fixed boundary but a network of paths and places to visit and use, (cf. Emlen, 1957) on which the animal moves and has its activity (cf. Etkin, 1964). In many cases a boundary does not exist for mammals, but in areas of overlap there is a kind of traffic regulation where animals making use of, for example, a communal water hole or border path, do so at different times (cf. Hornocker, 1969). The question of who has right of way is solved during territorial fights but this ranking is site fixed.

Thus Leyhausen (1971) called ranking related to time and/or space a relative social hierarchy. Consequently, classical territory is only an extreme case of relative social hierarchy. The finding of the hierarchy between territorial groups of pukeko at the boundary area with status dependent on site supports this theory.

Leyhausen further agreed with the statement of Davis (1958) that the effect of crowding on the balance between the two hierarchies (Relative and Absolute) is a growing preponderance of the latter, which eventually becomes despotism and tyranny.

Kaufman (1971) also questioned whether territory is definable and, like Leyhausen (1971), commented on the lack of a single common factor in the many examples of territory. He gave examples of what he termed 'purely functional territories' (cf. Pitelka, 1959). For example, Coatis, Nasua rarica, and Australian quokkas, Setonix brachyurus, have overlapping home ranges but non-overlapping 'core' areas within which they have exclusive use of resources. Kaufman suggested that no conflict need exist between concepts of territory and relative social hierarchy if it is agreed that priority of access to resources, e.g. food, water, shelter, space, receptive females, etc., is the important issue. Exclusive use (cf. Pitelka, 1959) is not necessary if intruders defer to the residents in economic matters and so defence is no longer necessary. Also exclusive use or priority of access is a phenomenon of time and space. Kaufman concluded that 'no simplified definition or explanation of territory yet advanced can cover all of the related kinds of behaviour known, and perhaps it is naive to look for one'.

However, an indefinable term is meaningless and so it is probably better to use a new term such as Leyhausen's (1971) relative social hierarchy and restrict the use of territory to the original concept of 'a defended area'. At the same time it should be realized that territory represents an extreme pole of a continuum of behaviour, which is directly related to distribution of resources (Brown & Orians, 1970 - see page 222).

As noted, the present study on pukeko adds further to the theory of a link between territory and hierarchy. All breeding groups held defended territories but outside the breeding season, the degree of defence varied. At Linton in all years, and in the Southern and Northern Territories in 1970-71 and 1972-73, territories were defended all year round at all times of the day. In the Hide and Western

Territories, defence was restricted to a 'core' area of raupo and Carex adjacent to the lake and trespass was tolerated in other areas outside the breeding season. But in those areas of the breeding territory where trespass was allowed, the dominant male and female were dominant over all other birds of the same sex and the male dominated all birds. Similarly, in the Peninsular and Trap Territories where defence completely broke down during the autumn and winter, the dominant birds from the territories dominated all other birds. Thus using Willis's (1967) definition for territory involving dominance reversals, all territories can be said to have been permanent.

The Southern and Northern Territories in 1971-72 were a special case in that while they were defended all year round, trespass occurred at night for roosting. Therefore trespass was temporally and seasonally regulated in these territories while in some others it was seasonally restricted only.

Outside the breeding season, part of the pukeko population formed into flocks which were believed to have been formed from non-breeding itinerants, yearlings and juveniles expelled from breeding territories; and also from breeding groups which held seasonal territories in sub-optimal areas. (Sub-optimal is here taken as areas lacking one or more of the attributes believed necessary in a territory - food, water or cover). Tunnicliffe (1965 & pers. comm.) reported total breakdown of his study territories outside the breeding season. Further research is needed to determine the requisites of a permanent territory as distinct from temporary territories.

Within territories and within the flock, a hierarchy existed. Between territorial members and between non-resident members of the flock, this was absolute (cf. Leyhausen, 1971) but between these two groups of birds, the hierarchy was relative with status related to distance from nest site. Furthermore, between members of adjacent territories a hierarchy existed but was manifested at the boundary area only. Thus a varied and complex territorial-hierarchical organization existed in the study population and dispersion was the result of the complex interplay of both spacing mechanisms. This provides strong evidence that territory and hierarchy are part of a continuum, and the temporal variations in the defence of the Northern and Southern Territories emphasize the inadequacy of present concepts of social organization based on spatial distribution only.

Applying Leyhausen's (1971) extension of Davis's density hypothesis of a shift from relative to absolute social hierarchy with an increase in density, the distribution within a group represented high density, while that between groups in relation to one another represented a low density. Therefore an absolute social hierarchy is found within groups (territories and flocks) and a relative social hierarchy between groups. The existence of a hierarchy between groups suggests the density of groups was high, relative to more strictly territorial species. Struhsaker (1971) has suggested similar conclusions for vervet monkeys, Cercopithecus aithiops, which also hold group territories.

7.2 Evolution of Social Organization

Once the spatial and temporal organization of a species has been delineated, it is desirable to postulate its selective advantages and hence its evolution. Previously this has been looked at more in terms of 'functions' of a particular organization, but as Brown (1964, 1969) has stressed, function is not synonymous with selective advantage but more readily equated with consequence.

Several theories have been advanced to explain the existence of social organization, especially spacing mechanisms, although most authors have treated the different mechanisms as distinct entities rather than part of a continuum. Wynne-Edwards (1962) has postulated that all forms of social organization and dispersion have evolved by inter-population (group) selection for the prevention of over-exploitation of resources by a species. Many workers have criticized Wynne-Edwards for the use of group selection (Smith, 1964; Lack, 1966; Chitty, 1967), and Brown (1969), Brown & Orians (1970), and Williams (1970) have shown that it is possible to explain the existence of the different forms of organization by natural selection alone. Lack (1954, 1966) postulated that individuals of a species tend to distribute themselves in suitable habitats according to the availability of food and other resources required for survival and reproduction and that territory is primarily an aid for attracting and keeping a mate, acting only secondarily in dispersion. Crook (1965) and Brereton (1971) linked social organization with overall habitat type although Crook also stressed predation. Brown (1969), Brown & Orians (1970) and Brereton (1971) provided a concise theory embodying the idea of spacing mechanisms being a continuum related to environmental resources.

Brown (1969) noted that some resources are distributed in time and space in such a way that they are economically defensible while others are not. Brown & Orians (1970) postulated that resources (taken to include food, water, cover, nest site, mates, etc.) will be defended where they are economically defensible (in terms of individual survival and reproductive output). Thus by a cost-benefit analysis it is possible to predict and explain the existence of the social organization of any animal. Zahavi (1972) has investigated this experimentally. Where territories do exist, it is possible to determine which resources are defensible from the type of territory (feeding, nesting, general, etc.) the animal holds. This theory can be used to explain the spatial organization of pukeko.

Pukeko live in swampy areas which are highly productive (Fiala & Kvet, 1971; and J. Ogden, pers. comm.) and hence food is seasonally available in large quantities in a small area. Small areas of continuous nest cover (raupo and <u>Carex</u>) are available and, in the study areas were adjacent to large areas of year-round food (pasture). Thus on the basis of Brown's theory it would be expected that where seasonally highly productive and protective swamp is adjacent to year-round food in the form of pasture, permanent territories will result. Where year-round food is spatially separated from the swamp areas which provide large quantities of vegetable and animal food during the breeding season, cover from aerial predators, and isolation of nest site and vulnerable young from ground predators, territories will be seasonal and birds will flock to winter feeding areas. Thus year-round territories could be expected on the basis of Brown's theory, and were found. The partial breakdown of some territories adjacent to areas of superior winter feed was also expected because defence of such a large area against large numbers of non-territorial birds would require the expenditure of uneconomical amounts of energy when the same outcome, viz. priority over resources, can be obtained by dominance.

The existence of both pair and group territories is believed to be related to the length of defensible boundary. Thus in areas such as Pukepuke, where long boundaries must be maintained, it may be impossible for two pukeko to defend a territory adequately and thus group territories may be advantageous. Whereas at such areas as Linton where natural boundaries delimit most territories and population density is low, pairs are capable of defending territories. This will be discussed further (see p. 231).

To summarize, the social organization of pukeko is a complex interaction of both relative and absolute social hierarchies with the extreme of the former, namely territory, being found in the breeding season for all groups and pairs. Outside the breeding season, there is a shift from the territorial end of the continuum towards a site-dependent hierarchy except at Linton where classical defence occurred at all times of the year. The situation at Linton is believed to be related to low population density and defensibility of resources.

7.3 Co-operative Breeding and Group Territory

Only recently (cf. Carrick, 1963; Rowley, 1965, 1968; Parry, 1968; Brown, 1969; Brereton, 1971; Fry, 1972; Ridpath, 1972) has work been done on communal breeding or group territory. Most previous work had been confined to monogamous passerines or marine species (refs in Wynne-Edwards, 1962; Lack, 1966, 1968), although references to 'helpers' at nests have been recorded (Skutch, 1961; Harrison, 1969). Dow (1970) preferred the term 'visitors' unless the birds were actually observed helping in nesting activities. Parry (1968, 1973) prefers the term auxiliary as it implies more than a casual relationship.

Lack (1968) defined co-operative or communal breeding as: 'where more than one pair share in building a nest, laying the clutch, helping with incubation or rearing the brood'. Lack preferred to exclude species where nest building is co-operative but the monogamous pairs still defend their own nests and raise young unaided as in some African weavers (Proceinae) (Crook, 1964; other references in Lack, 1968). Other cases such as some ratites (rhea, Rhea spp.; ostrich, Struthio camelus - refs in Crook, 1965) where several females lay in the nest of a male, but where all incubation and care of the young is done by the male are also excluded. Polygamy where one male is mated to two or more females but where the females lay in separate nests either

(i) within a larger male territory (e.g. lyrebirds, Menura novaehollandiae, Kenyon, 1972; wren, Troglodytes troglodytes, Armstrong, 1956)
or
(ii) in separate territories maintained by the same male (e.g. pied flycatcher, Haartman, 1956), is also excluded from discussion.

Many isolated cases of 'helpers' at the nest have been reported for many usually monogamous birds (Skutch, 1961). However, because these are uncommon, Lack (1968) suggested that such behaviour 'is evidently selected against and the extra helpers probably have no ecological significance'. Similarly, reports of more than one female laying in the same nest in a typically monogamous species (e.g. blackbird, Turdus merula; Newland, 1970) can be considered unusual and are excluded from discussion.

In many of the early reports of helpers at the nest (Skutch, 1961), the helpers were thought to be juveniles or yearlings and in many cases were suspected to be males. Some recent papers are as inconclusive (e.g. Dow, 1970) because individually marked populations were not used. More recent studies of banded birds (Carrick, 1963; Rowley, 1965; Parry, 1968; Fry, 1972) have demonstrated that in most cases the helpers were either young of an earlier brood or young of the previous year. Howard (1940) also demonstrated that young of an earlier brood help feed those of a subsequent brood in the moorhen. A similar report for captive pukeko has already been mentioned (p. 2).

Rowley (1965), Fry (1972), and Ridpath (1972) have shown that helpers tend to be males more often than females and that there is an overall unbalanced sex ratio favouring males. In Tribonyx, Ridpath (1972) reported that most of the trios (12 out of 13) involved sibling males or parent and male offspring although Ridpath's method of sexing is questioned. Parry (1968) recorded auxiliaries of both sexes and an even sex ratio in kookaburras Dacelo gigas. Similar to kookaburras, pukeko helpers were of either sex despite an apparent unequal sex ratio in favour of males.

The studies by Rowley, Parry and Ridpath have also demonstrated greater reproductive success, measured by more offspring per nest, for pairs with helpers in comparison with pairs without. The converse was found in the present study. In superb blue wrens, pairs with helpers raised more fledgings per adult than pairs without. In addition to helping raise more young per nest, extra helpers frequently took complete charge of the brood once it had left the nest and hence allowed the pair to raise a second brood (Rowley, 1965). A similar situation is found in pukeko pair territories where chicks of the first brood took over much of the rearing of later broods. Also in group territories with non-reproductive yearlings, these took over a large proportion of the chick care but this situation still did not lead to higher breeding success compared with pairs.

Like the pukeko, Australian magpies, *Gymnorhina tibicen* (Carrick, 1963), kookaburras (Parry, 1968) and Tasmanian native hens (Ridpath, 1972) are fully communal species in that all birds participated with all reproductive activities (in some cases even copulations, although these were rare in magpie and kookaburra) and groups remained together for life. In some cases (Rowley, 1963; Ridpath, 1972) more than one female laid in the same nest. In the few well documented cases of true communal species as in pukeko, a hierarchy was demonstrated between the members of the breeding group (Carrick, 1963; Parry, 1968). Ridpath (1972) reported a partial hierarchy where more than one bird held the same status, but this has been criticized as resulting from experimental method (see p. 122). Carrick (1963), Rowley (1965), Parry (1968), and Fry (1972) reported that the dominant members of the group normally prevented the more submissive individuals from breeding. This was not so in pukeko although dominants occasionally prevented subordinates from copulating. Similarly all birds copulated and bred in *Tribonyx* groups (Ridpath, 1972).

As with pukeko, territorial defence in most recorded co-operative and communal groups was done by all members of the group, with individuals aiding others when attacked, (Carrick, 1963; Rowley, 1965; Parry, 1968; Fry, 1972; and other refs in Lack, 1968). Communal defence of colonies of monogamous pairs has also been recorded (Crook, 1965; Young, 1972 and pers. comm.; Fry, 1972; other refs in Lack, 1968; and Brown, 1969).

Territory size appears to be directly related to the number of birds per group in Tasmanian native hens (Ridpath, 1972), kookaburras (Parry, 1968) and bee-eaters (Fry, 1972) although all authors report age as a complicating factor. Carrick (1963) considered the relation of food reserves to group size as the most important factor determining territory size in Australian magpies, but Parry (1968) considered ability to defend an area as the most important factor determining territory size in the kookaburra. Similarly it is believed that ability to defend boundaries in relation to population density is the most important factor regulating territory size in pukeko.

The evolution of co-operative breeding and communal territories can be explained by natural selection (Lack, 1968; Brown, 1969) and need not involve the postulation of group selection as Wynne-Edwards (1962) and Fry (1972) have done. According to the theory of group selection, communal nesting and communal territories have arisen as altruistic behaviour favouring the population by acting as a form of population regulation and 'providing a reserve of experienced birds for recruitment into the breeding population to make good its annual loss through death and emigration' (Fry, 1972). However, Lack (1968) and Brown (1969) have shown that evolution of communal breeding and group territory can be explained by individual and kin selection. (It should be noted that unlike group selection where individuals in the population need not be related, kin selection has a sound theoretical basis (Birch, 1960; Hamilton, 1963; Smith, 1964; and other refs in Brown, 1969). Brown (1969) suggested that the system of helpers at the nest is the first step towards, and a pre-adaptation for, the evolution of group territories.

In the case of helpers, this can be favoured by natural selection in that the pairs with helpers tend to produce more offspring than pairs without helpers, and so will be favoured by selection. Also if the helper is an offspring or sibling, as was the case for many of the pukeko, then they also will be selected because they help leave more individuals of a genotype similar to their own (kin-selection).

Ridpath and Maynard-Smith (1972) have shown that kin-selection can partially explain the existence of groups with related males in *Tribonyx*. They demonstrated that a male is almost as likely to leave as many genes when in a group with a brother as when in a pair, and hence is not at a selective disadvantage. But they failed to demonstrate a selective advantage for groups, and other factors must be investigated to explain fully the existence of groups.

Brown (1969) suggested that by attaching themselves to experienced breeders, helpers will have breeding 'practice' which may help them raise more young in subsequent years. Although there is no direct evidence to support this view, such a situation might arise in a population with a surplus of potential breeders that are prevented from establishing territories and breeding, particularly in long-lived species. Banding records (see p. 31) show that pukeko can live for at least seven years. Brown (1969) considered that communal territories could have evolved from the helper situation where family groups tend to remain together during the non-breeding season, as pukeko do. Again, this is only likely if part of the population is prevented from breeding (see p.243 for evidence for pukeko), and survival of young is enhanced by their remaining with parents. Also with increasing density that prevent part of the population from breeding, territorial birds would have to spend more time and energy in defence. This added cost might be offset by allowing subordinates that would normally be excluded to participate in territorial defence and other family affairs. Brown (1969) excluded copulating from permitted subordinate activities, but Rowley (1965), Parry (1968), Ridpath (1972) and Fry (1972) report birds other than the dominant pair participating in mating, although in some cases this was rare. Participation in copulation is taken as the criterion to distinguish communal breeding from co-operative breeding where copulation is not allowed.

If the population surplus is large and persistent enough, the probability of the individual eventually gaining the opportunity to breed successfully may be greater if it remains within the family group and awaits the death of elders (Brown, 1969; Harrison, 1969). Also at high densities, there will be intense competition and thus the group that can defend the necessary territorial area without detriment to breeding will be the most successful in terms of gene frequencies in the population. Brown's (1969) hypothesis is that 'in a species pre-adapted by the occasional participation of young birds in the care of subsequent broods, kin selection for this and related traits within the family become intensified through the persistent presence of a large surplus of potential breeders and the environmental conditions which lead to this surplus. This would act to increase the role of the young in the family, to lengthen their stay with their parents, and to increase the tolerance of parents for such a relationship'.

For 'extra' birds to be tolerated, there must be a decrease in aggression by the dominant birds and this may explain why subordinates in sexually dimorphic communal species have a delayed adoption of, or failure to adopt full male plumage (Rowley, 1965; Harrison, 1969). Subordinate males in relatively inconspicuous plumage are less likely to arouse aggression in the dominant male. This argument would suggest a higher probability of finding communal breeding in monomorphic species such as the pukeko.

Lack (1968) stressed that communal breeding is likely to arise only where young can remain with parents during the non-breeding seasons and consequently he excluded it in migratory species. He therefore suggested that it will be more common in warmer regions. Similarly, Fry (1972) emphasized the occurrence of co-operative and communal breeding in tropical, subtropical and Australian areas. Skutch (1961) listed 135 species in which helpers have been recorded. Discounting captive situations this leaves 65 species, of which 50 involve adult helpers, although many of these are young of previous years. Of these 50, 31 are tropical, subtropical, or Australian (Fry, 1972) and subsequent work has doubled this number (Rowley, 1968; Harrison, 1969; Fry, 1972). Emphasizing the overwhelming occurrence of this habit in more 'even' climates, Fry (1972) suggested that communal and co-operative breeding is unfavourable in temperate regions where migration, high mortality, and the short breeding season often allow only a single brood to be raised, necessitating the recruitment of nearly all sexually mature individuals into the population. However, there is evidence that many temperate species have a substantial non-breeding population (cf. Wynne-Edwards, 1962; Watson, 1967; Watson & Moss, 1971; Krebs, 1971).

Brereton (1971) has also linked social organization with ecological parameters such as habitat type especially in relation to food distribution, while Crook (1965) relied heavily on the enhanced food finding ability of groups as their main selective advantage. Brown (1969) countered this by stressing that in some species the extra helpers do not carry food to young or participate significantly in feeding young (Rowley, 1965; other refs in Brown, 1969). Parry (1968) has shown that young in group territories are not fed more as nestlings. Fry (1972) stressed that because of the occurrence of communal breeding in many different groups, with diverse ecological requirements, 'the possibility of one single variable inducing the evolution of co-operative breeding must be rejected'.

However, it is obvious that habitat type (Brereton, 1971), climatic conditions (making migration unnecessary - Lack, 1969 - but also allowing lower post-natal mortality with resultant high population density - Brown, 1969 -), and both temporarily and spatially scattered food resources (Brereton, 1971) are the most likely selective factors for groups and probably act together in many cases. Wynne-Edwards (1962) and Fry (1972) have suggested group territory evolved as a means of population control and Brown (1969) listed it with polygamy, delayed sexual maturation, and lower clutch size, as adaptations to population surplus in larger longer-lived species. This possible role of population regulation will be discussed fully, see page 239 to 248.

The group territories of pukeko are distinct from the helper situation in that all adults in the group participated in all reproductive activities, but the persistence of the previous year's young in the territory (Western, Northern, Southern and Hide) and the fact that these yearlings helped only with feeding young suggest that the group territory of pukeko could have evolved from a helper situation. When an adult died or left the territory (e.g. Hide Territory 1970-71 and 1971-72) these extra yearlings were promoted to full reproductive status. Unlike many of the studies mentioned above, helpers were of either sex but were more often female than male despite an apparently unbalanced sex ratio favouring males for the total population. The reason for this is not known.

Pukeko fit many of the suggested conditions necessary for group territories to have evolved:

(1) Young were able to remain with parents in the non-breeding season.

(2) There was a large portion of the population prevented from breeding (see p. 200), hence

(3) Young may have a better chance of breeding by remaining with their parents and by kin-selection certainly have a greater chance of leaving their genes by helping raise relatives of similar genotype.

(4) Pukeko are monomorphic, and related to this is the retention of juvenile behaviour patterns by 'extra' non-reproducing birds. Both of these factors are believed to help reduce aggression in group situations.

(5) The most important single factor, indicated by this study, is that with high population density, the time and energy expenditure on territorial defence is reduced by allowing subordinates to remain in the territory and help. The reasons for suggesting this are:

   (i) Pair and group territories were found in different habitats. Only one pair territory (Peninsular Territory 1971-72) was formed at

Pukepuke where population density was high and this territory was unable to withstand encroachment from neighbouring group territories. The fact that the pair did nest successfully is believed to have been due solely to synchrony of nesting with the adjacent territories and to the small size of the boundaries. In contrast, pair territories existed in all years at Linton which had low population density and the defended boundary between territories was small. Even though the boundary between the territories was small, neither pair was able to maintain it throughout the year because of asynchronous nesting.

(ii) Birds within a territory were not necessarily related. Relationships between birds in territories were unknown except in the Hide Territory where the breeding females were related in all years but the males were not, and in the Western Territory 1972-73, where the females were not related.

(iii) Reproductive success of groups was lower than that for pairs and even when kin-selection is invoked, survival was still insufficient to demonstrate a selective advantage for groups. However, this may have been a reflection of habitat.

It is suggested that if the Linton territories had been surrounded by other territories as was found at Pukepuke, they would have been unable to maintain boundaries and hence unable to breed successfully. Therefore while groups had lower reproductive success, it is predicted that pairs in the same habitat would be unsuccessful in maintaining their boundaries and hence unsuccessful in raising any young. Thus birds in groups would leave more offspring than if they had nested in pairs. Using Brown & Orians (1970) model, resources were economically defensible by pairs at Linton but only by groups at Pukepuke where natural boundaries were few.

As mentioned above, Ridpath and Maynard-Smith (1972) were unable to demonstrate a reproductive selective advantage of groups over pairs but Ridpath noted (pers. comm.) that pairs were more frequent in areas of lower population density. Thus a theory similar to that proposed for pukeko may hold for Tribonyx.

Group territories in pukeko are believed to have evolved from the extended family situation as suggested by the fact that young of the first brood frequently fed subsequent broods, and that yearlings were tolerated in some territories. However, the formation of groups is believed to be fully emancipated from the family situation in that group formation is no longer dependent on retention of related birds, but occurred among unrelated birds. The type of territory held is determined by habitat.

7.4 Ecological Consequences of Social Organization

7.4.1 General

Social systems are generally considered to be spacing mechanisms whereby conspecifics are organized spatially in accordance with economic or reproductive parameters (McBride, 1971). Many early references attributed varied functions to different social systems in different species. However, as Hinde (1956) pointed out, the observed functions of territory, especially apparent advantages, may not be the selective factor producing the territorial behaviour. In other words, attributed functions of social organization may be apparent rather than real, being only a consequence of the behaviour rather than the reason for its existence. Brown (1969) and Krebs (1971) also emphasize this difference between functions in the evolutionary sense, and consequences.

7.4.2 Social Hierarchy

As noted on page 209, this is primarily a spacing mechanism and serves to co-ordinate group activities and reduce aggression, allowing more dominant individuals priority to incentives but affording membership rights and hence protection from predators to all members. Guhl & Allee (1944) investigated the effects of social hierarchy in domestic hens. They compared a control sub-flock where a stable hierarchy was formed, with an experimental sub-flock where membership was continually altered and no stable order resulted. The experimental flock had higher levels of aggression, as measured by peck rates; they consumed less food and consequently lost weight; laid fewer eggs and had smaller combs. Guhl & Allee concluded that the decrease in intra-flock fighting and the greater consumption of food has immediate survival value for all members of such flocks. However, they also concluded that this 'stable peck order type of social organization in flocks of hens, may serve to build a co-operative social unit better fitted to compete or to co-operate with other flocks at the group level than are socially unorganized groups'. This argument is similar to 'group selection' (advocated by Wynne-Edwards, 1962) which as previously stated has a doubtful theoretical basis and need not be invoked as the behaviour can be explained by natural selection. The situation reported by Guhl & Allee is also artificial.

'Functions' of social hierarchy benefiting dominant members are easily found. Dominant individuals have priority to incentives such as food, water, sexual partners, etc. (Guhl, 1964). Because measurement of status is frequently associated with assessing priority to food and water (see p.102) these two incentives will not be discussed further.

Guhl _et al_ (1945) investigated mating behaviour in domestic fowls and found that high ranked hens mated less frequently than those lower in the scale but laid more eggs. No such correlation of mating frequency was found in pukeko. Although dominants tended to lay more eggs, they rarely prevented subordinates from mating.

In the male fowls, the converse was observed where dominant males mated more than subordinates and social 'castration' occurred in lower males (Guhl *et al*, 1945). Similar results have been obtained for captive birds (e.g. Burmese red junglefowl, *Gallus gallus spadiceus*, - Lill, 1966 -) and in the wild (e.g. grouse, *Lagopus spp.*, - Scott, 1942; and other refs in Collias, 1950 -). Thus dominant males have the opportunity to sire more offspring. No correlation between status of male pukeko and frequency of full copulation was found although dominants tended to attempt copulation more frequently.

Dominant individuals frequently have larger territories, (e.g. red grouse, *Lagopus lagopus*, Watson, 1967; and numerous other species, Wynne-Edwards, 1962) and subordinates may be prevented from holding territory, (Wynne-Edwards, 1962; McBride *et al*, 1969; Watson & Moss, 1970). The movement of *Ew* from the large Hide Territory to the smaller Northern Territory suggests that, in pukeko, the quality of territory is more important than size.

While the above discussion suggests possible selective advantages for dominant members of the flock at all times and for all members of the flock when food and water are limiting, the observed death of subordinates in times of food shortage (cf. refs in Wynne-Edwards, 1962) suggests the necessity to invoke 'group selection' to explain the existence of social hierarchies and the seemingly altruistic behaviour of the lower class birds. However, Murton (1967) has shown that subordinate pigeons are continuously 'uneasy', search for food at a lower rate and have a lower intake of food which may lead to death in times of food shortage. Solitary pigeons, however, have an even lower rate of food intake because they were even more 'uneasy' due to lack of protection against predators previously afforded by the flock. These solitary birds may actually starve 'while in the midst of plenty'. Murton concluded that 'on average it is safer for a bird to risk being dominated in a social hierarchy than to risk being caught napping by a predator'. Consequently, rather than showing altruistic behaviour for the survival of the group, subordinate birds are ensuring their own survival, and the evolution of social hierarchy may be explained solely by natural selection.

The role of social hierarchy in population regulation will be discussed separately (see p. 239).

In the pukeko, hierarchy appeared to reduce antagonism in that overt aggression was rarely seen in groups with established hierarchies but was common in the early stages of flock formation before a stable hierarchy was established. Groups with a stable hierarchy were highly co-ordinated and co-operated in breeding and territorial activities.

Dominant members had priority to incentives such as food, water and to a certain extent also to sexual partners. Dominant females did not copulate less frequently (cf. Guhl _et al_, 1945) but did lay more eggs especially in the more successful earlier clutches, although age was a complicating factor. Dominant males did tend to copulate more frequently than subordinates but this was not universal. There is, however, no evidence to suggest that the dominant males were more likely to leave more offspring than the β male, although 'social castration' (Guhl _et al_, 1945) of the lowest ranking birds (yearlings) did occur. Other reproductive activities, such as nest-building, incubation and chick care, were shared among all reproductive members of the group although the dominant pair tended to do more than the others. Non-reproductive yearlings participated only in chick care and often did more of this than the other birds.

Benefits for subordinate members were obvious. Some subordinates were able to breed which would have been less likely if they had attempted to breed alone (see p. 231). In the case of the subordinate yearlings which were prevented from breeding (except where an adult died), these did perpetuate their genes by helping to raise relatives of similar genotype. The advantage of protection from predators is probably also applicable to subordinate pukeko especially in the flock. The grouping behaviour of pukeko in response to harriers suggests that only solitary birds are vulnerable, that this protection is afforded all members of the group or flock and that all birds can feed in relative safety.

7.4.3 Territory (Relative Social Hierarchy)

Many early authors classified territories according to apparent function (e.g. Nice, 1941; Armstrong, 1947; Hinde, 1956). As Hinde stressed, however, these were intended only as 'an aid to discussion as the diversity of nature can never be fitted into a system of pigeon-holes'. Hinde (1956) and Carpenter (1965) gave long lists of apparent functions attributed to territory. Some of these were: regulating the population, facilitating pair formation, maintenance of pair bond, reduction of interference with reproductive activities, defence of nest and nest site, provision of adequate food supply, reduction of predatory losses, prevention of disease, range extension, and reduction of time spent in aggression. Various authors have attributed different functions to the territories of different species although Wynne-Edwards (1962) considered regulation of the population to be the basic function of territory in all species.

Any suggestion of function or consequence must be from circumstantial evidence but this is not without pitfalls as Hinde (1956) pointed out. For example, if the selective force depends on only one effect, say that of food supply, for the evolution of territoriality, then this could not lead to defence of an area larger than that necessary to guarantee supply. Defence of a larger area would entail disadvantageous consequences without compensatory reward. Also, feeding exclusively in a territory does not show *ipso facto* that provision of food is a significant or advantageous consequence (cf. Lack, 1954, 1966). Nor can it be argued that territory has no significance in relation to food if most or some of the food is collected outside the territory.

Despite this, it is obvious that many of the abovementioned functions of territory are at least advantageous consequences and in many cases may be selective functions of territory. Many of the functions of territory have been evaluated (cf. Lack, 1954, 1966, 1968; Wynne-Edwards, 1962; Hinde, 1956; Carpenter, 1965 and other refs given by same authors), but, as Watson and Moss (1971) have stressed, too little is known about most species, too few studies have involved individually marked birds and too few have involved experiments testing null hypotheses. Hence functions have been attributed to territory on too little evidence.

Consequently discussion for or against all the attributed functions of territory would be lengthy, inconclusive and in general of little relevance to the present study. Also it is obvious that function (and consequence) of territory must vary with the different types of territory and with the species.

Despite this, possible consequences of a relative social hierarchy (territory) in pukeko are:

(1) Priority of access to incentives such as food, cover, and nest sites. All feeding was done within the defended area (or area of dominance) except where large artificial concentrations of food were provided immediately outside this area. Pukeko territories in the study areas were multipurpose (Nice, 1941) and provided all requirements throughout the year.

(2) Reduction of interference with nesting activities. Nest sites were generally distant from defended boundaries.

(3) Reduction of predation. Territorialism spaced out groups and therefore also nests and possibly reduced predation as suggested by Tinbergen (1952) and Crook (1965), and demonstrated by Tinbergen *et al* (1967). The laying by several females in the same nest is also believed to help this.

(4) Regulation of population size. This will be discussed separately.

There is no evidence that territory was important in pair (group) formation as has been postulated for other species (e.g. Lack, 1954, 1966) because most pairs and groups were established prior to defending a territory. Some of the above consequences are possibly selectively advantageous but are probably secondary to the effects of habitat already discussed (p. 231).

7.5 Role of Social Organization in Regulation of Population Size

The fact that animal populations fluctuate numerically between rather restricted limits and that animals rarely deplete their food supplies (except in cases of human interference) has led to postulations that populations are regulated. Different workers have suggested conflicting mechanisms and considerable controversy has resulted, leading to three main theories:

(1) Populations are limited by density-independent factors affecting availability of resources, e.g. weather (Andrewartha & Birch, 1954).

(2) Populations are regulated by density-dependent mortality, and mortality rates balance reproductive rates (Lack, 1954, 1966).

(3) Populations are regulated by density-dependent natality with reproductive rates balancing mortality rates (Wynne-Edwards, 1962).

However, it is possible to subscribe to both density-dependent and density-independent theories depending on which part of the range of an animal is studied (Whittaker, 1971). Thus at the edge of a species' range in suboptimal conditions, density is low and density-independent factors limit the population, whereas in optimal areas of a species' range, density is high, feedback occurs and thus density-dependent factors limit the population.

Both Lack and Wynne-Edwards believe food limits most, if not all, populations but Lack believed food to be the proximate factor directly determining animal spacing while Wynne-Edwards has postulated that food is the ultimate factor controlling animal spacing acting through social behaviour as the proximate factor. Thus, in Wynne-Edwards' view social behaviour is the result of group selection whereby populations able to prevent over-exploitation of their environment are selected for, in contrast to populations with no internal control. This control is effected by adjusted reproductive rates, controlled recruitment to the breeding population, and socially induced mortality of surplus individuals (Wynne-Edwards, 1962, 1963). The types of behaviour related to population control involve the establishment of dominance by some animals over others by means of aggression, thus affecting the pattern of animal spacing. This results in an unequal division of resources such as food, nest sites, etc., according to the status of the individual. Both absolute and relative (including territory) social hierarchies are involved.

Much controversy wages over Lack's and Wynne-Edwards' postulated means of population control, especially in relation to territory. But as has already been stressed (p. 238) too few studies involving individually marked birds over long periods have been undertaken. Despite this, both Lack and Wynne-Edwards have amassed exhaustive evidence to support their a priori hypotheses. However, much of the evidence used is circumstantial and incomplete and many of the arguments are circular and semantic.

Lack (1966) claimed that food is the proximate controlling factor in many resident species holding only breeding territories and acts mainly through winter starvation. There is little direct evidence of winter starvation, however (MacArthur, 1971; Haartman, 1971). And if food was limiting in winter and exercised its greatest control at this time, then breeding distribution would be less likely to be related to food as also claimed by Lack, but would be more closely related to predation and preparing young for winter food searching (MacArthur, 1971). Evidence that breeding success is correlated with population density in the following spring tends to refute the role of winter starvation (Lack, 1966; Watson & Moss, 1970; Cody, 1971) as does Krebs' (1971) study where extra winter food was provided but failed to increase breeding density. In some species increased food reduced territory size (Stenger, 1958; Watson & Moss, 1970, 1971) and improved hatching success and early survival (Jenkins, Watson & Miller, 1963).

The main criticism of Wynne-Edwards' theory is his use of 'group selection' to explain the evolution of social behaviour as the control mechanism (Smith, 1964; Lack, 1966; Chitty, 1967) and also see page 222. However, even if it is possible to disprove group selection, this need not negate a role of social behaviour in population regulation. As Murton (1967) pointed out, social behaviour may act in population regulation but only fortuitously, having evolved for other reasons.

Much of the argument surrounding the regulating effect of social behaviour stems from the distinction between limiting the population as a whole and limiting only the breeding population. Brown (1969) made an extensive review of literature to evaluate the former, viz. limitation of the whole population. He suggested the necessity to differentiate between three critical population densities:

Level 1: The lowest level where territory size should not be limited by competition and all individuals obtain territories in optimum habitat. At this level marginal habitats need not be occupied and territorial behaviour can have no significant limiting effect on the reproduction of the population. In fact at such low densities territoriality may ensure maximum breeding performance. Brown doubted the existence of this level in many species in the wild, and it was not reached in either of the pukeko study areas.

Level 2: Some individuals are prevented from breeding in preferred (optimum) habitat by aggressive competition for territories and these birds are forced to breed in marginal or less productive habitats. This is frequently referred to as the 'buffer effect' and can occur only where birds have a choice of habitats within the small region where the individual is likely to seek a territory. At this level the reproductive rate (defined as output per bird) of the population is lower (due to the reduced breeding success of those pairs in marginal habitat) but there is still an increase in total production. The pukeko at Pukepuke in 1970-71 were at this level in that birds in the Hide Territory were forced into a sub-optimal area (poor cover due to cattle) but none was prevented from nesting. Because of the complicating factor of group territories, however, it may be said that some birds were prevented from breeding since only one female laid in each of the Southern and Northern Territories in 1970-71, although all birds copulated.

The best documented case of a level 2 population is that demonstrated by Krebs (1971) in the Great Tit, Parus major L. Great tits nest in mixed wood and surrounding hedgerows. Hedgerow pairs had lower clutch size and fledgling success than those in the wood. Krebs then removed territorial pairs from the wood resulting in:

(i) Territorial pairs in the wood moving to new territories, and/or expanding their territory size, and

(ii) Hedgerow pairs moving into vacated areas in the wood while their old territories remained unoccupied.

The pairs moving to the wood had increased clutch size and fledging success. This, correlated with the fact that territories in the centre of the wood were smaller than those at the edge, suggests that there was competition for territories in preferred habitat forcing some birds to occupy marginal areas because of territorial aggression (cf. Patterson, 1965). Other examples are given in Wynne-Edwards (1962), Brown (1969), and Watson & Moss (1970).

Level 3: All habitats, both optimal and marginal, are fully occupied by territorial individuals and a surplus of potential breeders exists as non-breeding floaters - the reserve population. At this level total production is still greater than level 2 but the reproductive rate is lower than either of the previous levels. Brown (1969) states that this is the level at which classical limiting effects occur. However, it should be noted that no account is taken of other density-dependent effects.

Level 3 is best demonstrated by removal experiments with rapid replacement of removed birds and also demonstration that floaters do occur. Proof of the latter is frequently difficult because of the inconspicuous behaviour of transient birds. Pukeko at Pukepuke were at this level in 1971-72 and 1972-73 in that a small number of non-breeding floaters (e.g. *Vy* , *Fly*) were observed, and it is suspected that many more were forced to emigrate. As well as this, all territories in 1972-73 contained a number of non-breeding yearlings. All optimal or sub-optimal areas were used for breeding (sub-optimal habitat is taken as that with an area of cover less than 0.2 ha and a water depth less than 30 cm - see page 196). Reproductive success in all territories in sub-optimal areas (e.g. Rough Paddock, Corner, Trap) was low and in most cases zero (Table 43).

Lack (1954, 1966) and Hinde (1956) provide examples of birds failing to set up territories and Wynne-Edwards (1962) records removal experiments. However, Brown (1969), reviewing past removal experiments (e.g. those of Hensley & Cope), criticized most because of the failure to demonstrate replacement of females. It is also necessary to show that it is the territorial behaviour that is preventing the birds from breeding and that the surplus does exist for some other reason - for example, shortage of nest sites (cf. Haartman, 1971).

The best examples of level 3 population are those of red grouse, (Watson & Moss, 1970) and magpies (Carrick, 1963). Other studies such as Zwickel (1972) and Bendell, King & Mossop (1972) on blue grouse, *Dendragapus obscurus*, suggest results similar to those of Watson & Moss but the experiments are at an earlier stage. Red grouse are territorial, and non-territorial birds took territories and bred only after vacancies were provided by shooting or removal of owners (Watson & Jenkins, 1968). Most non-territorial birds died in winter. Australian magpies show a slightly different organization with territorial groups in preferred and marginal habitats as well as large non-breeding flocks. Successful breeding was virtually restricted to dominant members of the group territories in the preferred habitat, (Carrick, 1963). In comparison, while successful breeding in pukeko was restricted to optimal habitat, only the bottom birds in the hierarchy (yearlings) were prevented from breeding. Other less conclusive evidence is reviewed in Wynne-Edwards (1962) and Brown (1969).

In no case above has it been shown that territorial behaviour has any direct regulatory effect on the number of floaters. Most studies have shown that predation, starvation and disease are the main controlling factors directly regulating numbers of floater (Watson & Moss, 1970; Carrick, 1963; Gullion, 1970). Thus it can be concluded that territorial behaviour may regulate the breeding density in some species (those at level 3) and may limit the breeding rate of species at levels 2 and 3, but in none can it be considered the proximate factor regulating the population as a whole. However, because the high level of predation and starvation among floaters is related at least partially to their exclusion (by territory and/or hierarchy) from the optimum habitats, territory could be considered as an ultimate control of population size in some species. Carrick's (1963) study is one of the few demonstrating the effect of hierarchy on breeding rate.

The above discussion was concerned with the effect of social behaviour on regulation of population numbers which is not the same thing as regulation of the breeding population as discussed by Watson and Moss (1970). In the latter, breeding success is de-emphasized and the emphasis is on control of recruitment to the breeding population and so only occurs at Brown's level 3.

In an attempt to assess accurately the role of social behaviour (via socially induced mortality and depression of recruitment) in regulating the breeding population, Watson and Moss (1970) drew up a rigorous set of criteria. They assumed that social behaviour may play a significant role in regulating the breeding population if it can be shown that:

(a) 'A substantial part of the population does not breed, either because animals die, or because they attempt to breed but they and/or their young all die, or because they are inhibited from breeding even although they may survive, and may breed in later years.

(b) Such non-breeders are physiologically capable of breeding if the more dominant or territorial (i.e. breeding) animals are removed.

(c) The breeding animals are not using up some resources completely, such as food, space, or nest sites. If they are, the resource is limiting.'

Watson and Moss (1970) gave two more conditions. The first by their own admission is relatively impossible to demonstrate in the wild. The final condition relates to a change in numbers following changes in food and demonstrates both food and social behaviour to be limiting. They also stressed the importance of assessing conditions over a number of years to demonstrate long term regulation of the breeding population.

Many experimental studies have investigated the effects of behaviour when resources such as food are not limiting. By providing excess of food, water, shelter and nest sites various authors have shown that subordinate and non-territorial animals have lower breeding success or are prevented from breeding by dominant and/or territorial individuals who were still able to breed successfully (e.g. Zahavi, 1972, for white wagtails; Myers & Poole, 1963, for rabbits; Calhoun, 1963, for rats; and other references in Wynne-Edwards, 1962; Watson & Moss, 1970). Few studies have attempted this in the wild.

Many studies have demonstrated lower breeding success of birds and mammals at high population densities (Kluyver, 1951, from Wynne-Edwards, 1962; Myers & Poole, 1961, other references in Wynne-Edwards, 1962). But factors which limit the breeding rate need not be the same as those limiting the breeding population because the critical factor is recruitment of young into the breeding population and not the number produced. Carrick (1963) and Watson & Moss (1970) have demonstrated that subordinate and non-territorial individuals have access to food but all work in the wild is hampered by problems of measuring quality and quantity of available food. No attempt was made to assess this in relation to pukeko.

Much previous work can be criticized (cf. Brown, 1964, 1969; Orians, 1971) in that workers have tended to seek functions for isolated behaviour patterns, especially territoriality, rather than to look at the overall responses of birds to space and to recognize that the patterns are only part of a continuum of behaviour. Wynne-Edwards (1962) is possibly closest to this approach, but his theory fails acceptance by the unnecessary implementation of group selection which does not account for the behaviour arising in the first population (Brown, 1964).

In conclusion, many of the arguments regarding population regulation are circular and semantic. The literature on the subject is voluminous and most of the studies lack sufficient demographic information and contain too many variables to state conclusively whether food or behaviour is the proximate or the ultimate factor, or only one of the factors. As Chitty (1967) points out: 'among these conflicting claims the answer probably lies'. He suggested that ecologists should perhaps doubt the truth of everything so far written if they are to find the answer.

It is unlikely that the same factors control every species in the same way and it is likewise totally unrealistic to postulate a single mechanism for population regulation. Also if the problem is tackled from the view of habitat selection, (cf. Haartman, 1971; Orians, 1971), the argument of proximate and ultimate factors becomes unnecessary when it is realized that control is the result of complex interactions between individuals and their environments.

Pukeko at Pukepuke were at Brown's (1969) level 2 in

1970-71 but at level 3 in 1971-72 and 1972-73. In the last two seasons, both optimal and marginal habitat was used, and a number of birds were prevented from breeding. These included both non-territorial floaters and lower ranked territorial birds. Reproductive success in sub-optimal areas was zero (Watson & Moss, 1970 - condition a). There is also evidence to suggest that those birds prevented from breeding were physiologically capable of doing so. In the case of the non-breeding territorial yearlings, it is assumed that these were capable of breeding as *2E* and *Plw* did so in the Hide Territory (see p. 200). Also *Vy* did not breed as a transient yearling in 1971-72 but joined the Western Territory in 1972-73 and laid.

No evidence can be offered regarding depletion of food supplies but the fact that territories continued to support more birds while decreasing in size, suggests that food was not limiting. Future work might well concentrate on this question.

Thus territoriality or relative social hierarchy could be said to limit the breeding population of pukeko at Pukepuke by preventing some birds from holding areas suitable for breeding and forcing others to breed in marginal areas. The absolute social hierarchy within the territorial groups prevented yearlings from breeding (cf. Carrick, 1963). Supernumerary males (e.g. *Jlw* , *lJy*) low in the hierarchy were also prevented from breeding. These birds were 'socially castrated' (Guhl et al, 1945). Similarly, pukeko numbers at Linton were presumed to be regulated in that the permanent territorial behaviour of the resident pairs forced all other birds, including offspring, to leave the area.

Thus the social organization of pukeko, consisting of both relative and absolute social hierarchy, appeared to regulate the breeding population by preventing some birds from breeding and forcing others to do so in marginal areas. This is believed to be a consequence of social organization, and not a selective advantage as proposed by Wynne-Edwards (1962), and can be explained by natural selection. Thus birds predisposed to, and capable of, holding territories leave more surviving offspring and are favoured. However, in areas where food, nest sites and cover are concentrated with few natural boundaries (Pukepuke), birds capable of tolerating others in the formation of a group territory have an advantage. As little is known regarding the survival of non-breeders and those forced to emigrate, the factors that regulate the total population remain uncertain.

Appendix 1

NUMBER OF HOURS SPENT OBSERVING PUKEKO FROM HIDES

	LINTON				PUKEPUKE				
Month	1970	1971	1972	1973	1970	1971	1972	1973	
Jan		14	17	2		17	29	5	
Feb		4	18	2		11	37	4	
Mar		11	11	2		18	40	5	
Apr		13	10			22	37	2	
May*	-	-	-		3	2	3	2	
June	2	20	8		-	18	10		
July	3	10	2		26	29	17		
Aug	13	9	9		18	18	29		
Sept	28	15	7		50	26	26		
Oct	31	4	11		35	30	32		
Nov	16	8	10		24	45	34		
Dec	16	11	5		42	39	33		
Total	109	119	108	6	198	275	327	18	1160

* Duck shooting season

Appendix 2

AN AUTOMATIC NEST RECORDER

Graham H. Craig and John L. Craig

Abstract

An inexpensive, reliable, automatic camera control for the observation of wildlife activities is described. The device will record a preset number of frames on 8 mm movie film either at preset time intervals up to 30 minutes, when triggered by a switch, or a combination of these. The timer automatically stops during darkness.

Introduction

An investigation is being made by one of us (J.L.C.) of the social organization of the pukeko, Porphyrio porphyrio melanotus. Pukeko hold both communal and pair territories and both sexes incubate. Most territories studied are communal containing three to eight adults, some of these being offspring of previous years. One or more females lay in the same nest. Research has revealed a linear hierarchy within groups and it was decided to investigate a possible correlation between status, age, and sex with incubation, as well as look at incubation behaviour in general. However, because nesting in the study areas occurs in two metre Typha stands, direct observation is impossible and so an automatic recording device was required.

Mechanical (e.g. Gurr, 1955) and telemetry (Barwick, pers. comm.) recording methods were tried but found inadequate. Telemetry is both expensive and necessitated capturing all the birds within the territory immediately prior to nesting - this proved impossible. It was decided that an automatic camera device would provide the fullest information. Systems used previously (e.g. Gysel & Davis, 1956; Dodge & Snyder, 1960; Weller & Derkson, 1972; Temple, 1972) were not considered suitable for this study, were costly and had high power demands requiring frequent replacement of large batteries. It was decided, therefore, to design an electronic switching device that would fulfill the following requirements:

(1) Record every nest change showing the identity and behaviour of all birds involved.

(2) Provide a time reference.

(3) Be readily adaptable to any 8 mm camera and be able to work off the camera's internal power supply if necessary. (An 8 mm camera was chosen because it provided automatic exposure control, zoom lens, and cassette film).

(4) Be small, reliable, economical in operation, and not costly to construct.

The unit described below was designed and constructed (by G.H.C.) to meet all these requirements. The camera (in this study a Canon 518) and circuitry (5 x 6 x 2.5 cm) were contained together in a waterproof metal case, (scarcely bigger than the camera itself) which was bolted to a pole driven into the swamp. Two suitably camouflaged foot pads with microswitches, were placed in the ramps leading to the nest under observation and were connected in parallel to the circuit. Depression of the foot pad(s) exposed a preset length of film and a built-in timer provided a time reference. All birds in the study territories were banded with coloured leg bands and patagial tags.

Circuit Description

The circuit (Fig. 1) can conveniently be divided into four parts to explain its operation.

1. Timer: Provides a positive pulse to turn on the control switch at a preset interval of between 5 and 25 minutes.
2. Control Switch A: Activated by the timer to turn the camera switch on for a varying duration (for 0-20 frames) to provide a time reference.

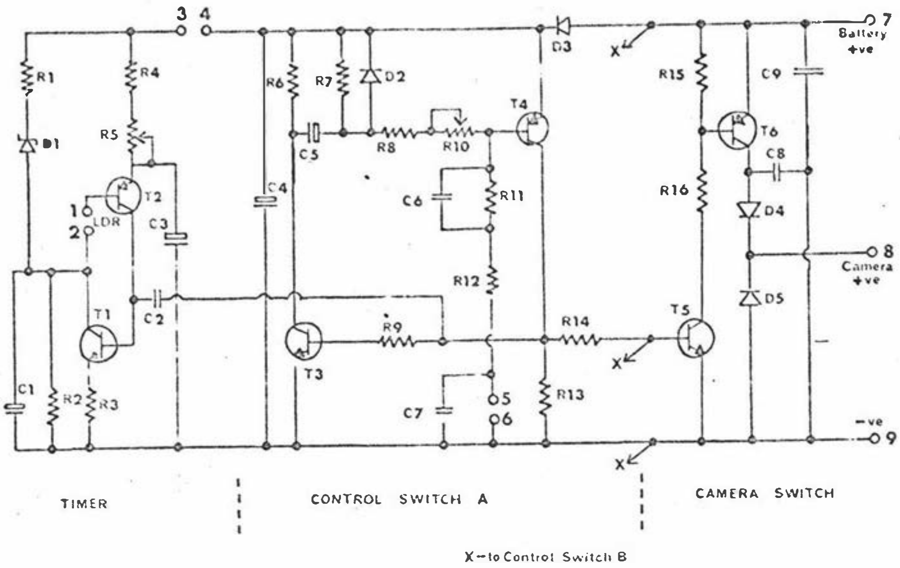


Figure 1 Camera Control Circuit

Resistors (all ¼ watt)

R1	1 k ohm
R2	3.3 M ohm
R3	100 ohm
R4	470 k ohm
R5	1 M ohm preset potentiometer (see text)
R6	1 k ohm
R7	100 k ohm
R8	100 ohm
R9	15 k ohm
R10	6.8 k ohm preset potentiometer (see text)
R11	3.3 M ohm
R12	1 k ohm
R13	1 k ohm
R14	15 k ohm
R15	10 k ohm
R16	390 ohm

Capacitors

C1	3.3 uF	10v	electrolytic
C2	0.1 uF	25v	polyester
C3	470 uF	16v	electrolytic (see text)
C4	100 uF	10v	electrolytic (see text)
C5	22 uF	16v	electrolytic (see text)
C6	0.01 uF	50v	Disc Ceramic
C7	0.001uF	50v	Disc Ceramic
C8	0.001uF	50v	Disc Ceramic
C9	0.01 uF	50v	Disc Ceramic

Semiconductors etc.

D1	4.3v 400mW zener diode (see text)
D2) D3)	small general purpose, silicon diode (e.g. AN2003)
D4) D5)	0.5A general purpose, silicon power diode (e.g. IN4001)
T1, 3, and 5	small signal, general purpose, npn silicon transistor (e.g. 25c371, BC108, BC148)
T2 and 4	small, signal, general purpose pnp silicon transistor
T6	pnp silicon power transistor (e.g. 25D434, 25A671, see text)
L.D.R.	see text

3. Control Switch B: (not shown in Fig. 1). Turns the camera switch on for a preset run (1-25 frames) when activated by a microswitch.

4. The Camera Switch: Provides power to the camera when switched on by one of the control switches.

Two control switches were needed to conserve film. One (B) was required to record the identity and behaviour of birds entering and leaving the nest on approximately 15 frames of film and a second (A) exposed a small number of frames for a time reference. Either of these control switches could be used separately or deleted. Control switch B is connected in parallel with control switch A at the points marked X in Fig. 1, and is identical to A except that C5 and R8 in B are 47 mfd 6.3 volts and 1 k ohms respectively. Each control switch is basically a monostable multivibrator that uses one npn and one pnp transistor, as this configuration gives zero current drain in its stable state. The microswitches are connected between pins 5 and 6 (of control switch B) by a length of thin twin cable and when a bird depresses a footpad, control switch B is activated and turns on the camera switch. Pins 5 and 6 on control switch A were unused in this project but were included on the design to make the device more versatile. If the microswitch is connected to control switch A rather than B then the timer and the switch both result in the exposure of the same number of frames of film and when the device is triggered by the microswitch, the timer automatically resets.

The timer also uses one npn and one pnp transistor but these are connected together to form the equivalent of a programmable unijunction transistor (P.V.T.). D1 is a zener diode which is used to form a voltage reference (of about two volts) but because of the very low current through the device, a 4.3 volt zener was required. This value, however, is not critical. The zener was used as it allows a high current to flow during the ON state but permits a very small current under OFF conditions, giving good battery economy. Pins 3 and 4 are provided so that the timer can be turned off when not required as this is the only part of the circuit that draws any standby current, although it is typically less than 4uA. Pins 3 and 4 are shorted together for normal operation of the timer. Pins 1 and 2 are also shorted together for normal operation but if a light dependent resistor (L.D.R.) is wired between these pins instead the device automatically turns off at night, preventing film wastage. The L.D.R. used had a resistance of about 100 ohms under bright light and about 50 M ohms under complete darkness. These values are not critical. The values of R4 and R5 shown give a time interval (variable by changing H5) anywhere from about 5-20 minutes. C3 should be a capacitor with low leakage current such as a tantalum electrolytic but a 470 mfd 16 volt standard aluminium electrolytic capacitor was found suitable provided that it was preformed by placing a 10 volt power supply across it for a few minutes.

The camera switch also contains one npn and one pnp transistor and these are connected so that when either control switch turns on, the battery voltage is applied to the camera (through D4 in the case of a 6 volt supply). The whole device was designed to work from either 4.5 volts (the camera's internal batteries) or 6 volts from an external supply. To use the camera's internal batteries, a small piece (about 5 mm across) of double-sided printed circuit board with a wire soldered to each copper side was inserted in series with the positive side of the batteries. The wire connected to the battery positive was soldered to pin 7 of the camera switch and the other wire to pin 8. A lead from the negative side of the batteries was connected to pin 9 to complete the supply to the board. D4 is shorted with a 4.5 volt supply. The camera batteries are normally good for about six films but with this unit in use, the voltage supplied to the camera is slightly lower than when supplied directly and hence the effective battery life is less. To compensate for this, a small battery holder containing four pen-light cells was added. Diode, D4 is required with the six volt supply to drop the voltage supplied to the camera.

Transistor, T6, is an epoxy case power transistor (Pc is 25W at 25°C) and this was used to provide a very low saturation voltage (less than 0.2 volts) across the transistor at the high current levels of the camera. A Toshiba 28B434 was used as it is small in size and is possible to mount in a small space on a printed circuit board by standing it on its three leads; but other similar types would have been as suitable.

Results and Conclusions

Excellent results were obtained from the device and included full sequences for most nest changes. Nest building, egg shell and dead chick removal, courtship, chick feeding, and identity of predators in the case of predated nests was also recorded. Batteries lasted for the full season, exposing eleven films. The authors feel that this system is readily adaptable to any situation where automatic recording of wildlife activity is required. No provision was made for night recording as it was not needed in this study, but this could be overcome by the exclusion of the L.D.R. and the inclusion of a flash unit and extra power supply. The devices main advantages were its versatility, reliability, low cost ($2-$8 excluding camera), and economical operation.

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Appendix 3

NUMBERS AND PROPORTION OF SEXES
IN
STUDY TERRITORIES

Territory	1970-71			1971-72			1972-73		
	No. of Birds	Sex M	F	No. of Birds	Sex M	F	No. of Birds	Sex M	F
Linton 1	3	1	2	2	1	1	2	1	1
Linton 2	2	1	1	2	1	1	2	1	1
Linton 3	3			-			-		
Linton 4	4	2	2	4	2	2	2	1	1
Linton 5	-			5			-		
Linton 0	-			4			3		
Western	4	2	2	5	2	3	4	2	2
Northern	4	2	2	4	2	2	6	3	3
Southern	4	2	2	4	2	2	6	3	3
Hide	5	3	2	5	3	3	6	3	3
Peninsular	-			2	1	1	6	5	1
Trap	-			-			3	2	1
Inlet	-			5			6		
Rough Paddock	-			5			-		
Corner	-			-			4		
TOTAL	29	13:13		48	14:15		50	21:16	

APPENDIX 4a

FLOCK HIERARCHY MARCH 1972

WINNER

LOSER

	Hlw	Kw	Rlw	Plw	2E	Tly	1Tw	Qw	Lly	Vly	1Cy	1Hy	1Jw	Vy	Zw	Nlw
Hlw																
Kw	${}^{1}3^{2}$															
Rlw						1^{1}										
Plw	${}^{6}13^{7}$	${}^{1}3^{2}$			${}^{2}4^{2}$											
2E	${}^{5}10^{5}$	${}^{2}5^{3}$	${}^{1}1$	${}^{2}2$												
Tly			${}^{3}6^{3}$	1^{1}	${}^{2}4^{2}$											
1Tw	${}^{2}2$				${}^{6}7^{1}$											
Qw	${}^{1}1$				${}^{7}7$						${}^{1}1$					
Lly				${}^{1}1$												
Vly	${}^{2}5^{3}$		1^{1}		${}^{7}10^{3}$	${}^{1}3^{2}$	${}^{2}4^{2}$	1^{1}								
1Cy	${}^{1}1$		${}^{2}4^{2}$		${}^{4}5^{1}$	${}^{2}2$	${}^{1}2^{1}$			${}^{2}2$						
1Hy	${}^{1}1$															
1Jw	${}^{3}5^{2}$				${}^{7}9^{2}$		${}^{4}5^{1}$	${}^{2}2$		${}^{4}4$						
Vy	${}^{3}4^{1}$	${}^{2}2$	${}^{4}4$		${}^{12}13^{1}$		${}^{1}1$			${}^{1}1$						
Zw			${}^{3}6^{3}$		${}^{2}3^{1}$											
Nlw			${}^{1}1$			${}^{1}2^{1}$				${}^{2}5^{3}$						

Food in Hide

Territory

a = Aggression

$\begin{array}{cc} a & b \\ \multicolumn{2}{c}{T} \end{array}$ **b = Avoidance**

T = Total

APPENDIX 4b

FLOCK HIERARCHY MARCH 1972

Food in Peninsular Territory.

WINNER

LOSER	Mlw	Hlw	Tly	lTw	Qw	2E	Plw	lFy	lEy	lHy	Vly	Lly	Vy	Rlw	lCy	Zw	lNw
Mlw																	
Hlw																	
Tly	$^{1}1$			$^{1}1$													
lTw																	
Qw	$^{1}1$		$^{3}5^{2}$														
2E					$^{1}1$												
Plw					$^{1}1$												
lFy	$^{4}4$		$^{1}1$		$^{2}2$												
lEy	$^{3}3$		$^{1}1$		$^{3}3$					$^{1}3^{2}$							
lHy	$^{2}2$		$^{2}5^{3}$		$^{2}2$				$^{3}5^{2}$								
Vly	$^{1}1$		3^{3}		$^{7}10^{3}$				$^{3}6^{3}$	$^{3}3$							
Lly					$^{1}1$			$^{2}2$	$^{7}10^{3}$					1^{1}		1^{1}	
Vy	$^{1}1$		2^{2}						3^{3}	$^{3}3$							
Rlw					$^{2}2$								$^{2}2$				
lCy	$^{3}3$		1^{1}		$^{7}8^{1}$				$^{4}8^{4}$	$^{3}4^{1}$	$^{10}13^{3}$	$^{3}4^{1}$		1^{1}			
Zw	$^{2}2$		$^{8}11^{3}$	$^{2}2$	$^{5}5$				$^{2}5^{3}$	$^{6}8^{2}$	$^{8}12^{4}$			1^{1}	$^{8}15^{7}$		
Nlw	1^{1}		$^{2}2$	$^{1}1$	1^{1}	$^{4}4$		$^{1}3^{2}$	$^{1}2^{1}$	$^{2}3^{1}$	$^{15}17^{2}$			$^{1}3^{2}$	2^{2}	7^{7}	

a = Aggression

$^{a}\underset{T}{ }^{b}$ b = Avoidance

T = Total

APPENDIX 4c

FLOCK HIERARCHY APRIL 1972

Food in Hide Territory.

WINNER

LOSER

	Hlw	Ow	Kw	1Ly	2E	Plw	Tly	1Tw	Rlw	1Zw	Qw	Lly	1Fy	1Ey	1Lw	Vly	1Vw	Vy	1Cy	Zw	Nlw	Iy
Hlw																						
Ow	$^{2}2$							$^{1}1$						$^{1}1$								
Kw	$^{3}5^{2}$																					
1Ly	$^{8}10^{2}$		$^{3}5^{2}$																			
2E	$^{6}9^{3}$		$^{2}2$	$^{3}3$		$^{4}5^{1}$																
Plw	$^{1}1$	1^{1}	$^{3}6^{3}$	$^{9}14^{5}$	$^{2}7^{5}$		$^{2}3^{1}$	$^{1}2^{1}$		$^{1}2$			$^{1}1$									
Tly	$^{1}2^{1}$	$^{2}2$	$^{1}1$	$^{1}2^{1}$	$^{6}6$	$^{4}4$			$^{1}1$													
1Tw	$^{2}4^{2}$	$^{6}8^{2}$	$^{1}1$		$^{11}12^{1}$	$^{9}10^{1}$	$^{14}14$															
Rlw	$^{2}4^{2}$		$^{2}3^{1}$	$^{7}10^{3}$	$^{2}7^{5}$	$^{6}8^{2}$	$^{1}1$	$^{1}1$			$^{2}2$											
1Zw	$^{4}6^{2}$	$^{3}5^{2}$	$^{7}9^{2}$	$^{1}1$	$^{14}16^{2}$	$^{7}6^{1}$	$^{5}7^{2}$	$^{4}5^{1}$			$^{1}3^{2}$			1^{1}								
Qw	$^{2}4^{2}$	$^{6}8^{2}$	$^{5}7^{2}$	$^{1}1$	$^{11}11$	$^{5}5$	$^{5}7^{2}$	$^{3}6^{3}$	$^{3}3$	$^{2}3^{1}$												
Lly	$^{3}5^{2}$	$^{3}4^{1}$	$^{6}6$	$^{2}2$	$^{15}15$	$^{7}7$	$^{7}9^{2}$	$^{10}12^{2}$		$^{1}1$	$^{3}4^{1}$			1^{1}		$^{1}1$						
1Fy	$^{3}4^{1}$	$^{2}3^{1}$	$^{4}5^{1}$	$^{7}8^{1}$	$^{18}20^{2}$	$^{11}12^{1}$	$^{5}8^{3}$	$^{4}5^{1}$	$^{3}3$	$^{1}2^{1}$	$^{6}7^{1}$	$^{4}4$		$^{1}1$								
1Ey	$^{3}5^{2}$	$^{1}5^{4}$	$^{1}4$	$^{1}1$	$^{19}20^{1}$	$^{7}7$	$^{15}16^{1}$	$^{6}9^{3}$	$^{4}4$	2^{2}	$^{3}5^{2}$	$^{3}4^{1}$	$^{7}7$									
1Lw					$^{2}2$	$^{1}1$		$^{2}2$														
Vly	$^{3}8^{4}$	$^{2}3^{1}$	$^{5}6^{1}$	$^{2}2$	$^{17}19^{2}$	$^{6}6$	$^{6}13^{7}$	$^{1}3^{2}$		$^{1}2^{1}$	$^{5}7^{2}$	$^{1}1$	$^{6}7^{1}$	1^{1}	$^{1}1$							
1Vw		$^{3}3$	$^{1}1$		$^{2}2$	$^{5}5$		$^{1}1$		$^{1}1$	$^{1}1$					1^{1}						
Vy	$^{2}5^{3}$	$^{1}2^{1}$	$^{3}3$	$^{1}3^{2}$	$^{12}14^{2}$	$^{5}6^{1}$	$^{4}5^{1}$		$^{4}5^{1}$	$^{1}2^{1}$	$^{5}6^{1}$	$^{3}3$	$^{2}2$			$^{6}7^{1}$						
1Cy	$^{5}10^{5}$	$^{4}4$	$^{4}5^{1}$	$^{6}12^{6}$	$^{23}27^{4}$	$^{11}13^{2}$	$^{1}5^{4}$	$^{4}5^{1}$	$^{4}6^{2}$	$^{1}1$		$^{1}1$	$^{4}5^{1}$			$^{3}3$		$^{2}2$				
Zw	$^{1}3^{2}$	2^{2}	$^{5}5$	$^{3}6^{3}$	$^{13}13$	$^{5}6^{1}$	$^{2}2$	1^{1}	$^{1}2^{1}$		1^{1}		$^{3}3$			$^{1}1$	1^{1}		$^{2}2$			
Nlw	$^{5}7^{2}$	$^{1}2^{1}$	$^{3}4^{1}$	$^{2}2$	$^{15}16^{1}$	$^{7}7$	7^{7}	$^{1}3^{2}$	1^{1}	$^{1}1$	3^{3}	$^{3}5^{2}$	$^{5}7^{2}$	$^{5}7^{2}$		$^{1}1$		$^{1}3^{2}$	$^{2}3^{1}$	$^{2}2$		
Iy	1^{1}			$^{3}3$	$^{7}7$	$^{1}1$	$^{1}1$				$^{4}4$	$^{1}1$				$^{1}1$		$^{2}2$	$^{2}2$		$^{2}2$	

$^{a\,b}_{\;T}$

a = Aggression

b = Avoidance

T = Total

APPENDIX 4d

FLOCK HIERARCHY APRIL 1972

LOSER \ WINNER	Hlw	Kw	Tly	lTw	Ky	Plw	2E	lZw	Qw	Lly	lFy	Vly	lEy	Rlw	Vy	Zw	lCy	Nlw	Iy
Hlw																			
Kw	$^{4}4$																		
Tly	$^{1}1$	$^{1}2^{1}$																	
lTw			$^{5}6^{1}$																
lLy		1^{1}	$^{1}1$			$^{1}1$													
Plw	$^{9}11^{2}$	$^{1}2^{1}$	$^{1}1$		$^{4}5^{1}$														
2E	$^{2}2$	$^{3}3$	$^{4}6^{2}$		1^{1}	$^{1}1$		$^{1}1$	$^{3}4^{1}$	2^{2}	$^{1}1$	$^{1}2^{1}$	$^{1}1$				$^{1}1$		
lZw	$^{3}3$	$^{2}3^{1}$	$^{14}15^{1}$	$^{2}5^{3}$		$^{4}4$	$^{5}5$												
Qw	$^{2}2$		$^{3}3$			$^{1}1$	$^{1}1$	$^{1}1$											
Lly	$^{6}8^{2}$	$^{4}4$	$^{11}24^{13}$	$^{7}7$	1^{1}	$^{5}5$	$^{2}2$	$^{2}17^{15}$	$^{1}1$		$^{1}1$	$^{1}1$	$^{1}1$						
lFy	$^{6}8^{2}$	$^{2}2$	$^{10}20^{10}$	$^{1}4^{3}$	$^{1}2^{1}$	$^{5}5$	$^{2}3^{1}$	$^{6}12^{6}$		$^{11}17^{6}$		$^{1}1$	1^{1}	$^{2}2$			$^{1}1$		
Vly	$^{4}9^{5}$	$^{4}5^{1}$	$^{11}17^{6}$	$^{1}1$	$^{1}3^{2}$	$^{6}9^{3}$	$^{5}6^{1}$	$^{2}15^{13}$		$^{17}23^{6}$	$^{8}8$				$^{1}1$				
lEy	$^{4}7^{3}$	$^{3}4^{1}$	$^{7}13^{6}$	$^{1}1$		$^{9}9$	$^{3}3$	$^{11}19^{8}$	$^{2}2$	$^{23}25^{2}$	$^{7}8^{1}$	$^{2}2$		$^{1}1$					
Rlw	$^{7}11^{4}$	$^{1}2^{1}$	$^{5}9^{4}$	$^{2}2$	$^{1}2^{1}$	$^{1}1$	$^{6}8^{2}$	$^{4}5^{1}$	$^{2}3^{1}$	4^{4}	$^{2}4^{2}$	$^{4}6^{2}$	1^{1}						
Vy	$^{6}7^{1}$		$^{3}8^{5}$			$^{4}4$	$^{2}2$	3^{3}		$^{9}11^{2}$	$^{6}7^{1}$	$^{2}3^{1}$	$^{2}4^{2}$	$^{4}4$					
Zw	$^{1}1$						$^{1}1$			$^{2}2$					$^{1}1$		$^{1}1$		
lCy	$^{5}6^{1}$		$^{7}10^{3}$			$^{2}2$	$^{1}1$	$^{4}6^{2}$		$^{5}6^{1}$	$^{11}11$	$^{8}8$	$^{3}3$			$^{2}2$			
Nlw	$^{2}2$		5^{5}		$^{1}2^{1}$	$^{3}3$	$^{1}2^{1}$	$^{1}5^{4}$	1^{1}	2^{2}	$^{4}4$		1^{1}	1^{1}			$^{1}5^{4}$		
Iy	$^{1}1$	$^{1}1$				$^{1}1$	$^{2}2$				$^{1}1$			$^{2}2$					

Food on Hide Territory -

Peninsular Territory Boundary

$^{a}T^{b}$

a = Aggression

b = Avoidance

T = Total

APPENDIX 4e

FLOCK HIERARCHY JUNE 1972

Food in Peninsula Territory

WINNER

LOSER	Hlw	Mlw	Kw	Ow	Tly	1Tw	Qlw	1Zw	Qw	Plw	1Ww	Lly	1Fy	1Ey	Iy	2E	Vly	Rlw	Zw	Nlw	1Cy
Hlw		2^{2}																			
Mlw	$^{3}4^{1}$																				
Kw	$^{4}6^{2}$								$^{2}2$												
Ow	$^{8}10^{2}$	$^{2}3^{1}$	1^{1}				$^{1}1$														
Tly	$^{4}8^{4}$	$^{3}3$	1^{1}	$^{2}3^{1}$				$^{1}1$			$^{1}1$										
1Tw	$^{7}10^{3}$	1^{1}		1^{1}	$^{2}2$		1^{1}														
Qlw	$^{5}8^{3}$	$^{4}5^{1}$		$^{1}2^{1}$	1^{1}			$^{1}2^{1}$													
1Zw	$^{9}14^{5}$	1^{1}	2^{2}	$^{3}5^{2}$	$^{4}7^{3}$		$^{1}3^{2}$		$^{1}1$									$^{1}1$			
Qw	$^{5}9^{4}$	$^{7}9^{2}$	$^{1}2^{1}$	$^{3}4^{1}$	$^{1}4^{3}$		$^{7}10^{3}$	$^{1}4^{3}$					$^{1}1$								
Plw	$^{6}10^{4}$		1^{1}		1^{1}				$^{4}4$				$^{1}1$								
1Ww	$^{5}8^{3}$		1^{1}	$^{2}3^{1}$		$^{3}4^{1}$	$^{2}3^{1}$	$^{2}3^{1}$	$^{1}2^{1}$	$^{1}1$											
Lly	$^{6}10^{4}$	$^{3}3$	1^{1}	$^{3}6^{3}$	$^{2}3^{1}$	$^{4}5^{1}$	$^{1}2^{1}$	$^{3}5^{2}$	$^{1}2^{1}$	$^{3}3$											
1Fy	$^{6}11^{5}$	$^{4}4$	1^{1}	$^{1}4^{3}$	$^{5}8^{3}$		$^{2}3^{1}$	$^{2}5^{3}$	$^{1}1$	$^{1}1$	$^{1}2^{1}$	$^{2}6^{4}$									
1Ey	$^{4}8^{4}$	$^{7}11^{4}$	1^{1}	$^{1}2^{1}$	$^{10}12^{2}$	$^{1}1$	$^{4}7^{3}$	$^{3}7^{3}$	6		$^{1}2^{1}$	1^{1}	$^{3}4^{1}$								
Iy	$^{6}11^{5}$	1^{1}	$^{2}3^{1}$	$^{3}4^{1}$	8^{8}	$^{2}3^{1}$		$^{2}7^{5}$	$^{1}2^{1}$		$^{2}2$	$^{6}14^{8}$	$^{8}17^{9}$	$^{6}8^{2}$		$^{1}1$				$^{1}2$	
2E	$^{2}6^{4}$						$^{1}1$		$^{1}1$		$^{2}2$		$^{3}3$		$^{1}1$						
Vly	$^{5}10^{5}$			$^{2}4^{2}$	1^{1}	1^{1}	$^{1}2^{1}$	$^{1}2^{1}$	$^{1}2^{1}$			$^{2}5^{3}$	$^{3}3$	$^{5}5$	$^{4}5^{1}$						
Rlw	$^{8}14^{6}$				$^{1}1$	1^{1}	1^{1}	$^{1}2^{1}$			$^{1}2^{1}$	$^{1}2^{1}$	$^{3}4^{1}$	$^{1}2^{1}$	1^{1}		1^{1}				
Zw	$^{3}8^{5}$	$^{1}2^{1}$		$^{1}2^{1}$	$^{3}7^{4}$	$^{1}2^{1}$	$^{1}2^{1}$	$^{2}4^{2}$	$^{4}4$		$^{2}2$	$^{1}7^{6}$	$^{6}9^{3}$	$^{2}4^{2}$	$^{2}2$		$^{5}5$	$^{1}1$			
Nlw	$^{3}6^{3}$			$^{1}4^{3}$	2^{2}	1^{1}	$^{1}4^{3}$	4^{4}	$^{4}5^{1}$		$^{1}2^{1}$	$^{3}7^{4}$	$^{3}7^{4}$	1^{1}	$^{1}3^{2}$		$^{2}5^{3}$		4^{4}		
1Cy	$^{2}5^{3}$			$^{1}1$			$^{1}1$								$^{1}1$						

Food in Peninsular Territory

a b
T

a = Aggression

b = Avoidance

T = Total

APPENDIX 4f

FLOCK HIERARCHY JULY 1972

Food in Hide Territory.

WINNER

LOSER	Hlw	Mlw	Kw	Jy	Plw	2E	Ow	Tly	1Tw	Qlw	1Zw	1Ww	Qw	Rlw	Lly	1Fy	1Ey	Vly	Zw	Nlw	Iy	1Cy
Hlw																						
Mlw																						
Kw	${}^{5}20^{15}$																					
Jy	${}^{15}22^{7}$		${}^{8}20^{12}$		${}^{2}3^{1}$	${}^{1}1$				${}^{3}3$		${}^{3}3$										
Plw	${}^{8}17^{9}$		${}^{7}14^{7}$	${}^{2}7^{5}$						${}^{1}2^{1}$		${}^{1}2^{1}$	${}^{1}2^{1}$									
2E	${}^{10}18^{8}$		${}^{3}9^{6}$	${}^{3}5^{2}$	${}^{3}7^{4}$						${}^{5}5$											
Ow	${}^{2}4^{2}$			${}^{2}2$	${}^{1}1$	${}^{7}7$																
Tly	${}^{1}1$	${}^{1}2^{1}$	1^{1}	${}^{2}2$		${}^{2}2$	${}^{3}10^{7}$															
1Tw	${}^{1}2^{1}$	2^{2}	1^{1}	${}^{4}4$	${}^{1}1$	${}^{2}2$	${}^{4}16^{12}$	${}^{1}2^{1}$						${}^{1}1$								
Qlw	${}^{1}3^{2}$	${}^{1}2^{1}$	${}^{1}4^{3}$	${}^{1}1$	${}^{2}3^{1}$		${}^{2}8^{6}$	1^{1}	${}^{3}4^{1}$		${}^{2}2$											
1Zw	${}^{5}8^{3}$	${}^{1}2^{1}$	${}^{3}4^{1}$	${}^{12}14^{2}$	${}^{2}3^{1}$	${}^{17}20^{3}$	${}^{2}5^{3}$	${}^{1}2^{1}$	${}^{2}2$	2^{2}		${}^{1}1$		${}^{1}1$								
1Ww	${}^{2}4^{2}$		${}^{2}5^{3}$	1^{1}	${}^{2}2$	${}^{12}13^{1}$	${}^{5}14^{9}$	${}^{2}4^{2}$	${}^{2}9^{7}$	${}^{2}3^{1}$	${}^{2}2$		${}^{1}1$	${}^{1}1$								
Qw	${}^{5}10^{5}$	1^{1}	${}^{1}3^{2}$	1^{1}	${}^{2}3^{1}$	${}^{2}2$	${}^{3}18^{15}$	${}^{1}4^{3}$	${}^{5}14^{9}$	${}^{1}2^{1}$	4^{4}	${}^{5}8^{3}$			1^{1}							
Rlw	${}^{8}24^{16}$		${}^{8}17^{9}$	${}^{6}9^{3}$	${}^{11}13^{2}$	${}^{4}7^{3}$				${}^{2}2$	${}^{5}5$	${}^{1}1$										
Lly	${}^{2}4^{2}$		${}^{1}4^{3}$	${}^{2}2$	1^{1}	${}^{4}4$	${}^{3}10^{7}$	${}^{4}4$	${}^{2}6^{4}$	${}^{4}4$	${}^{5}6^{1}$	${}^{4}8^{4}$	${}^{2}5^{3}$	${}^{2}2$								
1Fy	${}^{3}5^{2}$		2^{2}	${}^{3}5^{2}$		${}^{3}4^{1}$	${}^{2}6^{4}$	${}^{1}3^{2}$	5^{5}	${}^{3}7^{4}$	${}^{1}1$	${}^{3}5^{2}$	${}^{2}3^{1}$		${}^{3}7^{4}$							
1Ey	${}^{4}5^{1}$		${}^{1}1$	${}^{11}18^{7}$	${}^{1}2^{1}$	${}^{2}2$	${}^{1}4^{3}$	1^{1}	${}^{3}3$	${}^{5}8^{3}$	${}^{4}6^{2}$		${}^{17}20^{3}$	${}^{1}1$	${}^{3}8^{5}$	${}^{4}4$						
Vly			1^{1}	${}^{1}1$	${}^{2}2$	${}^{8}8$	${}^{3}11^{8}$	${}^{2}4^{2}$	${}^{2}6^{4}$	${}^{1}1$	2^{2}	2^{2}	${}^{1}4^{3}$	${}^{1}1$	${}^{3}8^{5}$	${}^{1}2^{1}$	${}^{2}2$					
Zw	${}^{2}4^{2}$	1^{1}	1^{1}	${}^{1}1$		${}^{5}5$	${}^{3}11^{8}$	${}^{1}1$	5^{5}	1^{1}	${}^{2}2$	2^{2}	${}^{1}5^{4}$	${}^{2}2$	${}^{3}9^{6}$	1^{1}	${}^{1}1$				${}^{1}1$	
Nlw	${}^{2}2$			${}^{1}1$		${}^{1}1$	${}^{1}7^{6}$		${}^{2}7^{5}$	${}^{1}5^{4}$	${}^{2}5^{3}$	4^{4}	${}^{2}12^{10}$		${}^{2}11^{9}$	${}^{3}4^{1}$	${}^{1}4^{3}$	${}^{1}1$			1^{1}	
Iy	${}^{1}2^{1}$		1^{1}	${}^{1}1$		${}^{5}5$	${}^{2}7^{5}$	1^{1}	${}^{1}5^{4}$	${}^{3}10^{7}$	3^{3}	${}^{4}5^{1}$	${}^{1}9^{8}$		${}^{4}11^{7}$	${}^{1}1$			${}^{1}1$	${}^{3}3$		
1Cy	${}^{3}7^{4}$		${}^{1}3^{2}$	${}^{5}12^{7}$	${}^{2}4^{2}$	${}^{6}6$	${}^{2}5^{3}$	${}^{1}3^{2}$	${}^{4}6^{2}$		${}^{3}6^{3}$	${}^{1}4^{3}$	${}^{2}6^{4}$	${}^{5}5$	${}^{2}3^{1}$	1^{1}	${}^{3}5^{2}$	1^{1}	${}^{1}1$	${}^{1}1$	${}^{2}2$	

Hlw has bill blackened

a = Aggression

${}^{a}T^{b}$ b = Avoidance

T = Total

APPENDIX 4g

FLOCK HIERARCHY, 14th JULY 1972

Food in Peninsula Territory (On the day Hlw's bill was blackened)

WINNER

LOSER	Mlw	Ow	Kw	Tly	1Jy	1Tw	Plw	Qlw	1Zw	Qw	1Ww	Lly	1Fy	1Ey	Iy	Vly	Nlw	Zw	1Cy
Mlw																			
Ow	$^{7}14^{7}$																		
Kw	$^{2}2$							$^{1}1$	$^{2}2$										
Tly	$^{9}15^{6}$	$^{4}5^{1}$						$^{1}2^{1}$											
1Jy	$^{1}1$	$^{1}1$								$^{2}2$	$^{2}2$								
1Tw	$^{7}10^{3}$	$^{9}17^{8}$	$^{1}1$	$^{7}12^{5}$	$^{1}1$					$^{2}2$									
Plw	$^{1}1$							$^{1}1$											
Qlw	$^{3}3$	3^{3}	$^{1}1$	$^{2}2$	$^{1}1$	$^{5}5$	$^{2}2$		$^{3}3$			$^{1}1$							
1Zw	1^{1}	$^{1}5^{4}$	$^{2}2$	$^{4}9^{5}$	$^{1}1$	5^{5}	$^{1}1$	$^{2}4^{2}$		2^{2}									
Qw	$^{1}10^{9}$	$^{5}13^{8}$	$^{1}1$	3^{3}	$^{1}1$	$^{1}8^{7}$	$^{2}2$	$^{1}3^{2}$	$^{4}7^{3}$		2^{2}	$^{4}4$	$^{2}2$						
1Ww	$^{7}12^{5}$	$^{5}8^{3}$	$^{1}4^{3}$	$^{6}6$		$^{3}9^{6}$		$^{3}4^{1}$	$^{5}6^{11}$	$^{1}4^{3}$		$^{1}1$	$^{1}2^{1}$						
Lly	$^{3}7^{4}$	$^{1}5^{4}$	$^{1}1$	$^{10}13^{3}$	$^{1}1$	$^{3}9^{6}$		$^{2}5^{3}$	$^{2}2$	$^{2}8^{6}$	$^{8}10^{2}$		$^{1}1$	$^{3}3$					
1Fy	$^{1}2^{1}$	1^{1}	$^{1}1$	$^{5}7^{2}$		$^{1}5^{4}$		$^{1}4^{3}$	$^{1}3^{2}$	$^{2}6^{4}$	$^{2}2$	$^{8}8$		$^{1}1$					
1Ey	$^{2}5^{3}$	$^{1}4^{3}$	$^{1}1$	3^{3}		$^{4}8^{4}$		$^{4}5^{1}$	$^{1}2^{1}$	$^{4}8^{4}$	$^{4}4$	$^{7}8^{1}$	$^{5}5$						
Iy	$^{4}10^{6}$	$^{3}9^{6}$	$^{2}2$	$^{7}11^{4}$		6^{6}		$^{4}7^{3}$	$^{2}6^{4}$	$^{6}9^{3}$	$^{5}7^{2}$	$^{5}6^{1}$	$^{3}5^{2}$	$^{5}8^{3}$		$^{1}1$			
Vly		$^{2}7^{5}$	$^{1}8^{7}$	$^{1}5^{4}$		$^{1}4^{3}$		$^{1}3^{2}$	2^{2}	$^{4}8^{4}$	$^{1}1$	$^{2}5^{3}$	$^{2}2$	1^{1}	$^{1}1$				
Nlw		4^{4}		$^{1}3^{2}$		2^{2}		2^{2}	1^{1}	1^{1}	$^{1}1$		$^{1}1$		$^{1}1$				
Zw	1^{1}	$^{1}5^{4}$	$^{1}1$	2^{2}		$^{3}4^{1}$		1^{1}	2^{2}	2^{2}		$^{1}1$			$^{1}1$		$^{1}1$		
1Cy	$^{2}7^{5}$	5^{5}	$^{1}1$	$^{1}6^{5}$		6^{6}		2^{2}	$^{1}5^{4}$	6^{6}	$^{1}3^{2}$	$^{5}10^{5}$	$^{1}2^{1}$	$^{2}8^{6}$	$^{5}7^{2}$	$^{1}3^{2}$			

$^{a}T^{b}$

a = Aggression

b = Avoidance

T = Total

APPENDIX 4h

FLOCK HIERARCHY JULY 1972

WINNER

LOSER	Hlw	Mlw	Kw	Ow	Tly	1Tw	Qlw	1Zw	1Ww	Plw	2E	Jy	Qw	Lly	1Fy	Rlw	1Ey	Vly	Vy	Zw	Nlw	Iy	1Cy
Hlw						${}_{1}1$	${}_{1}1$	${}_{2}2$	${}_{1}1$					${}_{1}1$	${}_{1}1$								
Mlw	1_{1}										${}_{1}1$												
Kw	${}^{5}_{1}12^{4}_{2}$	${}_{1}1$																					
Ow	${}^{6}_{2}17^{4}_{5}$	${}_{8}10_{2}$	${}^{1}_{1}2$						${}^{1}1$	${}_{1}1$		${}_{1}1$											
Tly	${}^{7}8^{1}$		${}_{1}1$	${}^{6}_{1}14^{7}$						${}_{1}1$													
1Tw	${}^{7}_{2}15^{5}_{1}$	${}_{4}5_{1}$	${}_{1}2_{1}$	${}^{9}_{2}18^{6}_{1}$	${}^{5}6^{1}$		1^{1}																
Qlw	${}^{12}_{6}20^{1}_{1}$	${}_{1}2_{1}$		${}^{8}_{2}16^{4}_{2}$	${}^{4}4$	${}^{3}4_{1}$		${}_{1}4_{3}$				${}_{1}1$											
1Zw	${}^{14}_{3}27^{8}_{2}$	${}_{2}3_{1}$	1^{1}	${}^{7}17^{6}_{4}$	${}^{1}3^{2}$	${}_{2}5_{3}$	${}^{2}5^{3}$			1^{1}	1^{1}	${}^{1}2^{1}$											
1Ww	${}_{1}1$	${}_{2}3_{1}$	${}_{2}3_{1}$	${}_{3}4_{1}$	${}_{1}1$	${}_{1}2_{1}$					1_{1}												
Plw	${}_{4}7^{1}_{2}$	1_{1}	${}^{1}_{2}4^{1}$	1_{1}		${}^{1}_{2}3$	${}_{3}3$	${}^{1}1$	${}_{1}2_{1}$				${}^{4}_{1}6_{1}$	${}_{2}2$	${}_{2}2$								
2E	${}^{2}_{4}7$	1_{1}	1_{1}				${}_{1}1$			${}_{1}1$			1_{1}										
Jy	${}^{10}_{1}17^{5}_{1}$	${}_{1}1$	${}^{5}_{1}9^{2}_{1}$		${}_{1}1$	${}^{1}1$	${}_{2}2$	${}^{2}2$	${}_{1}2^{1}$	${}_{1}2^{1}$	1_{1}		${}^{1}_{1}3_{1}$	${}^{3}_{1}4$			${}^{1}1$					${}_{1}1$	
Qw	${}^{7}12^{5}$	${}_{2}4_{2}$	${}^{3}_{1}7$[illegible]	${}^{4}_{2}16^{3}_{2}$	${}^{1}5^{3}_{1}$	${}^{1}_{1}2$	${}^{3}_{1}5^{1}$		${}_{1}1$	${}^{4}_{2}10^{3}_{1}$	2^{2}	${}^{1}4^{3}$		${}^{1}1$	${}^{1}_{1}2$	1^{1}							
Lly	${}^{7}_{2}20^{10}_{1}$	${}_{4}6_{2}$	${}^{5}_{1}10^{3}_{1}$	${}^{3}_{3}10^{2}_{2}$	${}^{2}_{1}10^{6}_{1}$	${}^{1}3_{2}$	${}^{2}_{1}7^{3}_{1}$	${}^{1}2^{1}$		${}^{1}_{1}4^{2}$	${}_{1}3^{1}_{1}$	${}^{5}9^{4}$	${}^{3}_{1}6^{1}_{1}$		${}_{1}1$	${}^{1}2^{1}$	${}_{1}1$						
1Fy	${}^{8}_{2}14^{3}_{1}$	${}_{1}2_{1}$	${}_{2}3_{1}$	${}^{7}12^{1}_{4}$	${}^{3}10^{5}_{2}$	${}^{1}_{1}3_{1}$	${}^{4}8^{1}_{3}$	${}^{1}_{1}6^{3}_{1}$	1_{1}	${}^{1}_{1}3^{1}$	${}_{1}1$		${}^{1}_{1}3^{1}$	${}^{2}_{1}3$									
Rlw	${}^{1}_{1}6^{1}_{3}$	2_{2}	${}^{1}_{1}4^{1}_{1}$						${}_{1}1$	${}^{1}_{2}5^{1}_{1}$	${}_{1}2_{1}$		${}^{2}_{2}6_{2}$	${}_{1}1$	${}_{1}1$								
1Ey	${}^{10}_{1}22^{18}_{1}$	${}_{1}5$[illegible]	${}^{5}5$	${}^{5}7_{2}$	${}^{3}6^{3}$		${}_{1}3^{1}_{1}$	${}^{2}3^{1}$		4^{4}	${}_{1}4^{3}$	${}^{1}_{1}12^{9}_{1}$	${}^{2}_{20}25^{2}_{1}$	${}^{2}3^{1}$	${}^{1}1$	2^{2}							
Vly	${}^{7}9^{2}$	${}_{1}1$		${}^{3}_{1}9^{1}_{4}$	${}^{1}2^{1}$	${}_{1}1$	5^{2}_{3}	${}^{1}3^{1}_{1}$	1_{1}		1_{1}		${}_{2}3^{1}$	${}^{1}2^{1}$									
Vy	${}^{1}1$					1^{1}		${}^{1}2^{1}$															
Zw	${}^{1}1$					${}^{1}1$			${}_{1}1$														
Nlw	${}^{2}4^{2}$			${}^{2}5^{3}$	2^{2}	1^{1}	${}^{2}_{2}6^{2}$	${}_{1}2^{1}$					${}^{1}2^{1}$	1^{1}	1^{1}		1^{1}						
Iy	${}^{19}_{3}33^{7}_{4}$	${}_{1}2_{1}$	${}^{1}_{1}6^{2}_{2}$	${}^{9}_{1}19^{4}_{5}$	${}^{5}13^{6}_{2}$	5^{1}_{4}	${}^{1}_{5}18^{3}_{6}$	${}^{1}_{1}8^{1}_{5}$	${}_{1}1$	${}_{3}4^{1}$	${}^{2}4^{1}_{1}$	${}^{2}11^{9}$	${}^{1}_{1}4$[illegible]		${}_{2}2$	1^{1}	${}^{6}_{2}9^{1}$	${}_{1}1$			${}^{1}1$		
1Cy	${}^{2}_{1}4_{1}$	${}_{2}4_{2}$	${}_{1}5^{3}_{1}$	${}^{1}2_{1}$			${}_{1}3^{1}_{1}$	${}^{1}2_{1}$	${}_{1}2_{1}$				${}^{2}2$	${}^{1}_{2}3$	${}^{2}3^{1}$		${}^{2}4^{2}$			${}^{1}1$		${}^{1}_{1}5^{3}$	

Food in Peninsular Territory.

Hlw Bill Non-Black top row.

Hlw Bill Blackened bottom row.

a = Aggressio

a b
${}_{a}T_{b}$ b = Avoidance

T = Total

APPENDIX 41

FLOCK HIERARCHY AUGUST 1972

WINNER (columns) / LOSER (rows)

	Mlw	Hlw	Ow	Tly	1Tw	Qlw	2E	1Zw	Qw	1Ww	Lly	1Jy	Plw	1Fy	1Ey	Vly	Zw	Nlw	Iy	1Cy	Rlw	1Vw
Mlw																						
Hlw	$^{1}1$					$^{1}1$					$^{1}1$											
Ow	$^{2}5^{3}$	$^{3}6^{3}$																				
Tly	$^{3}3$		$^{1}1$																			
1Tw	$^{4}5^{1}$	$^{1}1$	$^{4}7^{3}$	2^{2}																		
Qlw	$^{8}13^{5}$		$^{1}1$	$^{1}1$	$^{2}2$					$^{1}1$												
2E		$^{3}4^{1}$				$^{1}1$																
1Zw	$^{1}2^{1}$	$^{2}7^{5}$	$^{3}6^{3}$	$^{2}2$	$^{3}6^{3}$	$^{1}1$			$^{1}2^{1}$	$^{1}1$												
Qw	$^{9}14^{5}$	$^{4}7^{3}$	$^{3}5^{2}$	$^{2}2$	$^{2}6^{4}$	$^{7}9^{2}$	$^{2}2$	$^{4}4$		$^{1}1$				$^{1}1$	$^{1}1$							
1Ww	$^{6}6$	$^{1}1$	$^{2}2$	$^{6}7^{1}$	$^{2}2$	$^{6}9^{3}$		$^{1}3^{2}$	$^{1}2^{1}$													
Lly	$^{10}15^{5}$	$^{2}3^{1}$	$^{3}9^{6}$	$^{4}5^{1}$	$^{4}5^{1}$	$^{10}16^{6}$	$^{1}1$	$^{3}7^{4}$	$^{3}5^{2}$	$^{7}7$			$^{1}1$									
1Jy		$^{2}3^{1}$	$^{1}1$						$^{2}2$		$^{1}1$											
Plw	$^{1}1$	$^{3}5^{2}$			$^{1}1$				$^{1}1$		$^{2}2$											
1Fy	$^{5}12^{7}$	$^{3}3$	$^{3}12^{9}$	1^{1}	$^{1}3^{2}$	$^{2}4^{2}$		$^{1}4^{3}$		$^{4}4$	$^{9}13^{4}$		$^{1}1$									
1Ey	$^{1}1$	$^{1}3^{2}$	$^{1}1$	1^{1}	$^{5}8^{3}$	$^{1}1$		$^{1}2^{1}$		$^{1}2^{1}$			$^{5}5$	$^{3}3$								
Vly	$^{2}6^{4}$		3^{3}		3^{3}	4^{4}		1^{1}	2^{2}		$^{1}4^{3}$			$^{1}3^{2}$								
Zw		$^{1}1$	$^{1}3^{2}$		$^{1}2^{1}$			$^{1}2^{1}$							1^{1}							
Nlw	1^{1}	$^{1}2^{1}$	$^{1}3^{2}$	1^{1}	$^{2}4^{2}$	1^{1}		$^{1}5^{4}$	1^{1}	1^{1}	1^{1}			$^{2}2$	2^{2}		$^{1}1$					
Iy	$^{1}6^{5}$	$^{5}8^{3}$	$^{6}12^{6}$	$^{2}2$	$^{5}9^{4}$	$^{4}7^{3}$		5^{5}	1^{1}	$^{2}5^{3}$	$^{7}11^{4}$	$^{1}1$		$^{4}6^{2}$	$^{3}4^{1}$	$^{2}2$	1^{1}	$^{1}1$				
1Cy	3^{3}	$^{2}2$	$^{2}2$	$^{1}1$	$^{1}2^{1}$	$^{4}6^{2}$	$^{1}1$	$^{1}3^{2}$	2^{2}	$^{3}3$	$^{4}7^{3}$		1^{1}	$^{1}2^{1}$		$^{2}3^{1}$	$^{1}1$		$^{1}1$			
Rlw		$^{1}5^{4}$	$^{1}1$			$^{1}1$			$^{1}2^{1}$			$^{1}1$										
1Vw			1^{1}																			

Food in Peninsular

Territory

$^{a}\,^{b}$
T

a = Aggression

b = Avoidance

T = Total

APPENDIX 4j

FLOCK HIERARCHY AUGUST 1972

WINNER

LOSER	Mlw	Ow	Tly	1Tw	Qlw	1Ww	1Zw	Qw	Lly	1Fy	Zw	Vly	Nlw	Iy	1Cy	Vy
Mlw																
Ow	$^{4}6^{2}$															
Tly	$^{2}3^{1}$	$^{3}5^{2}$														
1Tw	$^{4}6^{2}$	$^{1}6^{5}$	$^{5}9^{4}$					3^{3}								
Qlw	$^{1}3^{2}$	$^{1}2^{1}$	$^{4}5^{1}$	$^{9}18^{9}$												
1Ww	$^{1}6^{5}$	$^{5}9^{4}$	$^{3}8^{5}$	$^{1}3^{2}$	$^{4}7^{3}$		$^{1}1$									
1Zw	2^{2}	$^{2}6^{4}$	$^{3}6^{3}$	$^{9}17^{8}$	$^{4}6^{2}$	$^{1}3^{2}$		1^{1}								
Qw		$^{1}3^{2}$	$^{1}2^{1}$	$^{1}9^{8}$	$^{3}3$		$^{1}2^{1}$			$^{1}1$						
Lly	$^{1}4^{3}$	$^{1}5^{4}$	$^{2}10^{8}$	$^{5}11^{6}$	$^{2}5^{3}$	$^{7}10^{3}$	$^{1}3^{2}$	1^{1}		1^{1}						
1Fy	$^{1}2^{1}$	$^{3}8^{5}$	$^{1}3^{2}$	$^{1}2^{1}$	$^{4}4$	$^{3}6^{3}$	$^{2}3^{1}$	1^{1}	$^{3}5^{2}$							
Zw		$^{1}1$	2^{1}	4^{4}	$^{1}3^{2}$	$^{1}5^{4}$	2^{2}	3^{3}	$^{1}7^{6}$	2^{2}		1^{1}				
Vly	$^{1}3^{2}$	$^{2}5^{3}$	$^{1}5^{4}$	$^{1}12^{11}$	$^{4}10^{6}$	$^{1}5^{4}$	5^{5}	4^{4}	$^{1}3^{2}$	$^{2}2$	$^{2}2$					
Nlw			1^{1}	1^{1}	$^{1}1$											
Iy	$^{1}5^{4}$	4^{4}	$^{3}8^{5}$	$^{5}12^{7}$	$^{5}8^{3}$	5^{5}	$^{1}3^{2}$	$^{2}10^{8}$	$^{1}4^{3}$	$^{2}3^{1}$	$^{1}1$	$^{2}2$				
1Cy	5^{5}	$^{1}4^{3}$	$^{2}5^{3}$	$^{1}10^{9}$	3^{3}	4^{4}	$^{2}3^{1}$	$^{2}7^{5}$	$^{3}7^{4}$	$^{2}3^{1}$	$^{2}2$			$^{5}5$		
Vy	1^{1}	1^{1}		1^{1}	1^{1}	1^{1}	1^{1}	1^{1}								

Food on Peninsula
Territory and Hide
Territory Boundary

a b
T

a = Aggression

b = Avoidance

T = Total

Appendix 5

TERRITORIAL BOUNDARY POSITIONS OF PAIRS OF OPPOSING NORTHERN AND SOUTHERN TERRITORY BIRDS

Results are divided into three categories:

(i) Where one bird advanced and the other retreated, the figure given representing the true mean of the mean maximum advance of one bird and the mean maximum retreat of the other. Unguarded results, i.e. where no bird of higher status was present are given first.

(ii) Where both birds advanced towards each other, the figures represent the true mean of the mean maximum advance of both birds. Unguarded results are again given first.

(iii) Mean fight location.

The units used are 0.5 m measured from an arbitrary zero point at the Northern Territory edge of the boundary zone except for March A where results were taken from a different part of the boundary and the zero point was at the Southern Territory edge of the zone.

March A

	Bw	Aw	Bw	Ey
(i)	15.00 (1)	15.00 (4)	–	15.31 (8)
(ii)	16.00 (1)		–	
	Boundary = 15.17 (6)		Boundary = 15.31 (8)	

March A continued

	Bw	By	Bw	S1w
(i)	- 12.00 (2)	15.50 (1) 14.25 (4)	- 13.40 (2)	- 14.00 (1)
(ii)	- 15.25 (1)		- -	
	Boundary = 13.97 (8)		Boundary = 13.90 (3)	
	Bw	1Nw	Bw	1Pw
(i)	- 12.08 (6)	- 12.75 (1)	- 12.00 (1)	- -
	Boundary = 12.18 (7)		Boundary = 12.00 (1)	
	Ew	Aw	Ew	Ey
(i)	13.13 (8) -	13.36 (7) -	13.00 (1) 13.63 (13)	- 13.58 (6)
(ii)	13.167 (1) -		13.50 (2) 13.13 (2)	
(iii)			13.50 (1)	
	Boundary = 13.23 (16)		Boundary = 13.54 (25)	
	Ew	By	Ew	S1w
(i)	- 12.50 (1)	- -	10.00 (1) 12.67 (3)	- -
	Boundary = 12.50 (1)		Boundary = 12.00 (4)	
	Ew	1Nw		
(i)	- 11.80 (4)	- -		
	Boundary = 11.80 (4)			
	Pw	Aw	Pw	Ey
(i)	- -	19.00 (1) 15.17 (3)	- 18.00 (1)	- 15.60 (2)
	Boundary = 16.13 (4)		Boundary = 16.40 (3)	

March A continued

	Pw	By	Pw	S1w
(i)	- 12.00 (1)	- 13.90 (2)	- 11.00 (2)	- 12.00 (1)
(ii)	- 14.50 (1)		- -	
	Boundary = 13.57 (4)		Boundary = 11.33 (3)	
	Pw	1Nw	Pw	1Pw
(i)	- 13.10 (4)	- -	- 13.75 (2)	- -
	Tw	Aw	Tw	Ey
(i)	12.75 (1) 12.75 (1)	13.25 (2) -	- 12.50 (3)	- 13.75 (1)
(ii)	- -		- 11.75 (2)	
	Boundary = 13.00 (4)		Boundary = 12.46 (6)	
	L1w	Aw	L1w	S1w
(i)	- -	- 13.25 (1)	- -	- 11.50 (1)
	L1w	1Nw	L1w	1Pw
(i)	- 11.00 (1)	12.50 (1) -	- 15.50 (1)	- -
(ii)	- 14.25 (1)			
	Boundary = 12.58 (3)			
	1Bw	Ey	1Bw	1Nw
(i)	- 14.25 (2)	- -	- 13.50 (3)	13.00 (1) -
			Boundary = 13.38 (4)	

March B

	Bw	Aw	Bw	Ey
(i)	- -	9.00 (2) 11.50 (4)	- 12.00 (1)	11.00 (1) 11.33 (3)
	Boundary = 10.67		Boundary = 11.40	
	Bw	By	Bw	S1w
(i)	- 11.00 (1)	- 10.33 (3)	- 11.00 (1)	- -
(ii)	- 13.50 (1)		- -	
	Boundary = 11.10 (5)			
	Ew	Aw	Ew	Ey
(i)	15.46 (7) -	15.00 (4) -	*16.00 (11) 14.47 (15)	14.55 (5) 13.50 (9)
(ii)	13.89 (7) -		15.63 (4) 14.11 (16)	
(iii)	13.00 (1)		13.67 (3)	
	Boundary = 14.66 (19)		Boundary = 14.55 (63)	
	Ew	By	Ew	S1w
(i)	19.00 (1) 15.83 (3)	18.75 (1) -	- 14.13 (4)	- -
	Boundary = 17.05 (5)			
	Ew	1Nw	Ew	1Pw
(i)	18.50 (1) 19.00 (1)	- -	- 18.33 (3)	- -
	Boundary = 18.75 (2)			

March B continued

	Pw	Aw	Pw	Ey
(i)	– –	– 10.50 (1)	– 10.25 (4)	13.00 (1) 9.50 (1)
(ii)	– 11.50 (1)		– –	
	Boundary = 11.00 (2)		Boundary = 10.58 (6)	
	Pw	By		
(i)	– 9.75 (2)	– –		
	Tw	Aw	Tw	Ey
(i)	– 13.33 (9)	– 12.71 (6)	– 12.88 (2)	– 12.25 (1)
(ii)	– 12.82 (7)		– 13.50 (1)	
(iii)	12.25 (2)		13.50 (1)	
	Boundary = 12.94 (24)		Boundary = 13.00	
	Tw	By	Tw	S1w
(i)	– 11.90 (2)	– –	– 15.10 (2)	– –
	L1w	Aw	L1w	Ey
(i)	– –	6.00 (1) 13.50 (4)	– –	8.00 (1) 7.08 (3)
	Boundary = 12.00 (5)		Boundary = 7.31 (4)	
	L1w	By	L1w	S1w
(i)	– –	7.50 (2) 12.86 (7)	– –	5.75 (2) 11.00 (1)
	Boundary = 11.67 (9)		Boundary = 7.50 (3)	

March B continued

	L1w	1Nw	L1w	1Pw
(i)	- 16.00 (1)	- 14.38 (4)	- -	- 12.00 (1)
	Boundary = 14.70 (5)			
	1Bw	Aw	1Bw	Ey
(i)	- -	- 9.50 (3)	- -	- 12.50 (3)
	1Bw	By	1Bw	S1w
(i)	- -	8.50 (2) 11.88 (4)	- 13.00 (2)	6.83 (3)* 10.58 (3)
(ii)	- 13.50 (1)		- -	
	Boundary = 11.14		Boundary = 9.78 (8)	
	1Bw	1Nw	1Bw	1Pw
(i)	- 15.50 (1)	- -	- -	- 12.50 (1)
	1Xw	Aw	1Xw	Ey
(i)	- -	- 10.20 (3)	- -	- 6.50 (1)
	1Xw	By	1Xw	S1w
(i)	- -	- 11.25 (4)	- -	- 6.20 (3)

April

	Bw	Aw	Bw	Ey
(i)	- -	- 13.25 (2)	- 9.50 (1)	- 11.84 (16)
			Boundary = 11.71 (17)	
	Bw	By	Bw	S1w
(i)	19.00 (2) 16.17 (3)	14.75 (5) 15.01 (12)	20.00 (1) 17.83 (3)	- 14.31 (4)
(ii)	17.88 (2) 20.00 (1)			
(iii)	19.00 (1)			
	Boundary = 15.97 (26)		Boundary = 16.34 (8)	
	Bw	1Nw	Bw	1Pw
(i)	27.50 (1) 18.92 (6)	- -	*27.75 (2) 19.25 (8)	21.50 (1) -
	Boundary = 21.14 (7)		Boundary = 21.00 (11)	
	Ew	Aw	Ew	Ey
(i)	17.50 (1) 17.63 (2)	16.19 (4) 17.33 (6)	16.94 (54) 16.96 (7)	16.57 (34) 16.58 (3)
(ii)	- 14.07 (7)		16.77 (43) 12.87 (13)	
(iii)			16.5 (3)	
	Boundary = 15.51 (25)		Boundary = 16.46	
	Aw and Ey combined		Aw and Ey combined	
(i)	13.00 (4)	11.50 (1)	13.28 (8)	12.64 (7)
	Boundary = 12.70 (5)		Boundary = 12.98	

April continued

	Ew	By	Ew	S1w
(i)	19.90 (5) 18.91 (8)	- -	- 18.54 (17)	20.00 (1) -
	Boundary = 19.29 (13)		Boundary = 18.63 (18)	
	Ew	1Nw	Ew	1Pw
(i)	19.75 (2) 18.98 (12)	- -	19.13 (2) 19.22 (22)	16.50 (1) -
	Boundary = 19.09 (14)		Boundary = 18.22 (25)	
	Pw	Aw	Pw	Ey
(i)	- 15.40 (5)	14.13 (2) 15.54 (7)$^{+}$	13.81 (4) 15.50 (8)	12.22 (9) 14.84 (14)
(ii)	14.00 (3) 13.88 (2)		12.13 (4) 15.20 (5)	
(iii)			12.00 (3)	
	Boundary = 14.93 (19)		Boundary = 13.73 (47)	
	Pw	By	Pw	S1w
(i)	- 17.36 (9)	- 16.83 (6)	- 17.96 (7)	- 15.00 (3)
(ii)	- 18.31 (4)			
	Boundary = 17.39 (19)		Boundary = 17.07 (10)	
	Pw	1Nw	Pw	1Pw
(i)	- 16.89 (9)	- -	- 16.80 (5)	- -
(ii)	- 15.00 (1)			
	Boundary = 16.70 (10)			

April continued

	Tw	Aw	Tw	Ey
(i)	17.08 (3) 17.39 (7)	15.75 (2) 17.83 (6)	16.36 (9) 16.98 (10)	15.28 (8) 16.17 (6)
(ii)	17.00 (1) 18.25 (2)		15.70 (10) 17.25 (14)	
(iii)			15.5 (2)	
	Boundary = 17.38 (21)		Boundary = 16.19 (49)	
	Tw	By	Tw	S1w
(i)	19.00 (3) 17.00 (8)	17.50 (1) 18.50 (4)	*20.00 (1) 18.38 (10)	- -
(ii)	17.50 (2) 17.67 (3)		- 18.5 (1)	
	Boundary = 17.74 (21)		Boundary = 18.52 (12)	
	Tw	1Nw	Tw	1Pw
(i)	- 18.03 (8)	- -	- 18.31 (9)	- -
(ii)	- -		- 19.5 (1)	
			Boundary = 18.43 (10)	
	L1w	Aw	L1w	Ey
(i)	- -	11.00 (1) 12.75 (3)	- -	10.75 (2) 13.78 (15)
	Boundary = 12.31 (4)		Boundary = 13.43 (17)	
	L1w	By	L1w	S1w
(i)	- -	- 13.48 (12)	- -	- 13.97 (8)

April continued

(i)	L1w	1Nw	L1w	1Pw
	- 16.50 (2)	- 12.50 (4)	- 18.25 (1)	- 15.00 (3)
	Boundary = 13.83 (6)		Boundary = 15.81 (4)	
(i)	1Bw	Aw	1Bw	Ey
	- -	- 13.43 (7)	- -	9.94 (4) 13.39 (20)$^{+}$
			Boundary = 12.81 (24)	
(i)	1Bw	By	1Bw	S1w
	- -	- 13.00 (5)	- 18.00 (1)	- 14.35 (5)
			Boundary = 14.96 (6)	
(i)	1Bw	1Nw	1Bw	1Pw
	- 15.67 (3)	- 15.75 (1)	25.00 (1) 18.13 (4)	- 15.83 (3)
	Boundary = 15.69 (4)		Boundary = 18.13 (8)	
(i)	1Xw	Aw	1Xw	Ey
	- -	9.00 (1) 13.10 (4)	- -	- 14.57 (7)
	Boundary = 12.28 (5)			
(i)	1Xw	By	1Xw	S1w
	- -	- 12.70 (3)	- -	- 15.60 (2)
(i)	1Xw	1Nw		
	- -	- 14.25 (2)		

June/July

	Bw	Aw	Bw	Ey
(i)	-	-	-	-
	-	14.25 (2)	-	17.00 (2)
	Bw	By	Bw	1 Nw
(i)	-	-	17.50 (1)	-
	15.50 (1)	15.83 (3)	12.50 (1)	11.00 (2)
	Boundary = 15.75 (4)		Boundary = 13.00 (4)	
	Bw	1 Pw		
(i)	-	-		
	17.50 (1)	-		
	Ew	Aw	Ew	Ey
(i)	16.67 (3)	15.00 (1)	17.88 (4)	-
	17.25 (7)	16.67 (3)	18.92 (3)	16.88 (2)
(ii)	16.25 (2)		17.00 (5)	
	17.19 (4)		17.50 (5)	
	Boundary = 16.85 (20)		Boundary = 17.61 (19)	
	Ew	By	Ew	1 Nw
(i)	18.50 (1)	-	-	-
	17.75 (2)	-	18.06 (4)	-
	Boundary = 18.00 (3)			
	Ew	1 Pw	Pw	Aw
(i)	-	-	15.94 (4)	15.50 (1)
	20.50 (1)	-	16.50 (1)	15.67 (3)
(ii)			14.00 (1)	
			16.25 (1)	
			Boundary = 15.73 (11)	

June/July continued

	Pw	By	Pw	1Nw
(i)	19.00 (1)	18.50 (2)	22.00 (2)	-
	17.00 (2)	15.50 (1)	18.50 (2)	-
	Boundary = 17.58 (6)		Boundary = 20.25 (4)	
	Pw	1Pw		
(i)	21.50 (1)	-		
	19.25 (3)	-		
	Boundary = 19.81 (4)			
	Tw	Aw	Tw	Ey
(i)	17.31 (4)	17.25 (1)	17.31 (4)	-
	17.48 (13)	16.41 (8)	17.43 (11)	16.55 (5)
(ii)	16.67 (6)		17.25 (1)	
	17.19 (12)		17.08 (9)	
(iii)	16.00 (3)		16.00 (1)	
	Boundary = 17.01 (47)		Boundary = 17.12 (31)	
	Tw	By	Tw	S1w
(i)	-	-	19.25 (2)	-
	17.83 (3)	-	18.50 (2)	-
			Boundary = 18.88 (4)	
	Tw	1Nw	Tw	1Pw
(i)	-	-	-	-
	18.10 (5)	-	17.88 (4)	-
	L1w	Aw	L1w	Ey
(i)	-	10.75 (2)*	-	-
	-	15.33 (3)	-	14.20 (3)
	Boundary = 13.50 (5)			

June/July continued

	L1w	By	L1w	S1w
(i)	- -	- 16.10 (3)	- -	- 15.50 (1)
	L1w	1Nw	L1w	1Pw
(i)	- 18.75 (2)	- -	23.50 (1) -	- -
	1Bw	Aw	1Bw	Ey
(i)	- -	- 16.00 (3)	- -	8.00 (1) 15.46 (6) +
	1Bw	By	1Bw	S1w
(i)	- -	- 14.90 (5)	- -	1.50 (1) 13.31 (4) +
			Boundary = 10 95 (5)	
	1Bw	1Nw	1Bw	1Pw
(i)	23.00 (1) 18.33 (3)	- 19.50 (1)	21.00 (1) 17.90 (5)	18.50 (2) -
(iii)			19.75 (2)	
	Boundary = 19.50 (5)		Boundary = 18.69 (10)	

August/September/October

	Ew	Aw	Ew	Ey
(i)	19.00 (1) 19.75 (7)	17.00 (1) 17.75 (2)	18.21 (12) 17.95 (10)	17.44 (8) 17.31 (4)
(ii)	- 18.13 (2)		18.38 (4) 17.94 (4)	
	Boundary = 18.92 (13)		Boundary = 17.90 (42)	

August/September/October continued

	Ew	By	Ew	1Nw
(i)	23.88 (2)	-	-	-
	21.13 (2)	20.75 (2)	21.04 (6)	-
	Boundary = 21.92 (6)			
	Ew	1Pw	Pw	Aw
(i)	-	-	15.75 (1)	11.50 (2)
	20.48 (16)	-	-	-
(ii)			-	
			11.00 (1)	
			Boundary = 12.44 (4)	
	Pw	1Nw	Pw	1Pw
(i)	22.00 (2)	-	21.50 (1)	-
	18.50 (2)	-	*19.25 (3)	-
	Boundary = 20.25 (4)		Boundary = 19.81 (4)	
	Tw	Aw	Tw	Ey
(i)	16.63 (2)	-	17.71 (7)	16.55 (5)
	16.50 (1)	17.20 (5)	17.38 (2)	16.00 (3)
(ii)			17.13 (2)	
			-	
	Boundary = 16.97 (8)		Boundary = 17.04 (19)	
	Tw	By	Tw	S1w
(i)	-	-	-	-
	20.50 (1)	-	22.00 (1)	-
	Tw	1Nw	Tw	1Pw
(i)	-	-	-	-
	19.25 (4)	-	18.56 (4)	17.00 (1)
			Boundary = 18.25 (5)	

August/September/October continued

(i)	L1w	Aw	L1w	Ey
	-	1.00 (1)	-	-
	-	15.25 (2) +	-	14.00 (2)
	Boundary = 10.50 (3)			
(i)	L1w	1Nw	L1w	1Pw
	-	-	-	10.50 (2)
	20.50 (1)	18.00 (1)	-	13.50 (2)
	Boundary = 19.25 (2)		Boundary = 12.00 (4)	
(i)	1Bw	Aw	1Bw	Ey
	-	-	-	-
	-	15.00 (1)	-	14.50 (2)
(i)	1Bw	1Nw	1Bw	1Pw
	-	-	-	-
	21.75 (1)	-	17.75 (5)	16.00 (3)
(ii)	-		-	
	-		16.25 (2)	
			Boundary = 16.93 (10)	

November/December

(i)	Bw	Aw	Bw	Ey
	-	-	-	-
	-	9.50 (1)	-	14.00 (2)
(i)	Bw	1Nw	Bw	1Pw
	-	-	-	-
	17.50 (1)	14.00 (2)	18.00 (1)	-
(ii)	-			
	18.40 (1)			
	Boundary = 16.41 (4)			

November/December continued

	Ew	Aw	Ew	Ey
(i)	17.75 (2) 17.75 (4)	18.08 (3) 16.83 (3)	17.77 (11) 17.61 (7)	16.84 (8) 17.81 (4)
(ii)	19.00 (2) 17.25 (3)		17.83 (6) 17.63 (4)	
	Boundary = 17.71 (17)		Boundary = 17.54 (40)	
	Ew	By	Ew	S1w
(i)	22.38 (4) -	21.00 (1) -	30.25 (2) 23.08 (6)	- 20.75 (1)
(ii)	21.88 (2) -			
	Boundary = 22.04 (7)		Boundary = 24.42 (9)	
	Ew	1Nw	Ew	1Pw
(i)	28.67 (3) 21.63 (12)	29.50 (1) -	23.86 (7) 20.38 (8)	26.00 (1) 20.25 (1)
(ii)	26.75 (2) -		25.31 (4) -	
(iii)			25.17 (3)	
	Boundary = 23.81 (18)		Boundary = 23.04 (24)	
	Pw	Aw	Pw	Ey
(i)	* 9.32 (7) 13.75 (1)	6.22 (8) 14.75 (4)+	- 14.00 (1)	13.25 (2) 14.88 (4)
(ii)	7.80 (5) 17.25 (1)		- 16.00 (1)	
(iii)	8.00 (2)			
	Boundary = 9.29 (28)		Boundary = 14.50 (8)	
	Pw	By	Pw	S1w
(i)	- -	- -	- -	- 20.00 (1)
(ii)	17.00 (1)			

November/December continued

	Pw	1Nw	Pw	1Pw
(i)	- 19.63 (4)	- -	- 20.00 (1)	- -
	Tw	Aw	Tw	Ey
(i)	*17.55 (11) 18.44 (4)	16.48 (14) 17.31 (4)	- 18.63 (4)	- 17.38 (6)
(ii)	- 16.69 (9)		- 17.67 (4)	
(iii)	17.00 (1)		-	
	Boundary = 17.07 (43)		Boundary = 17.82 (14)	
	Tw	S1w	Tw	1Pw
(i)	- 23.50 (1)	- -	- 21.00 (3)	- -
	Tw	1Nw	L1w	Aw
(i)	23.00 (1) 17,75 (4)	- -	8.50 (3) 10.00 (1)	1.00 (3)* 15.00 (1)
(ii)	- 19.50 (1)			
	Boundary = 18.92 (6)		Boundary = 6.69 (8)	
	L1w	Ey	L1w	By
(i)	- -	9.50 (1) 15.67 (3)	7.50 (1) -	4.00 (2) 12.50 (1)
	Boundary = 14.13 (4)		Boundary = 7.00 (4)	
	L1w	S1w	L1w	1Nw
(i)	18.25 (1) 17.00 (1)	12.25 (1) 18.50 (1)	17.00 (1) -	- 15.63 (2)
	Boundary = 16.50 (4)		Boundary = 16.09 (3)	

November/December continued

	1Bw	Aw	1Bw	Ey
(i)	- 13.60 (5)	3.50 (2) 14.50 (8)+	- 15.75 (1)	- 15.33 (9)
(ii)	- 16.25 (1)		- 18.00 (1)	
	Boundary = 13.08 (16)		Boundary = 15.61 (11)	
	L1w	1Pw	1Bw	S1w
(i)	- 21.00 (1)	- -	18.00 (1) 25.25 (4)	12.25 (1) 21.00 (1)
			Boundary = 18.89 (7)	
	1Bw	1Nw	1Bw	1Pw
(i)	18.88 (4) 19.00 (1)	10.67 (3) 20.08 (3)*	- 18.80 (3)	- 15.50 (1)
(ii)	18.00 (1) -		- 16.00 (1)	
	Boundary = 17.06 (12)		Boundary = 17.58 (5)	

Student 't' test used to test differences between guarded and unguarded results.

* $p < 0.05$ + $p < 0.01$

Appendix 6

BREEDING DATA OF STUDY TERRITORIES

Territory	Date of First Egg	Clutch Size	Number Hatched	No. Surviving at Age of 4 Months
Linton 1 (G)	20/8/70	4	4	1
	30/10/70	6	5	3
Linton 2 (P)	4/11/70	4	Robbed by predator and deserted	
	17/11/70	6	5	2
Linton 3	1/10/70	3	1	0
Linton 4 (G)	5/9/70	4	3	2
	2/11/70	7	7	2
Hide (G)	19/11/70	5	5	2
Southern (G)	8/10/70	4	3	0
	23/12/70	8	8	0
Northern (G)	8/10/70	4	4	0
	29/11/70	4	4	0
Western (G)	5/10/70	9	9	1
Inlet	16/10/70	4	Robbed by predator	
Linton 0 (G)	29/9/71	6	6	1
Linton 1 (P)	12/9/71	6	4	3
	23/11/71	7	4	3
	15/1/72	5	deserted	
Linton 2 (P)	16/10/71	1		
	18/10/71	6	6	5
	27/1/72	3	2	2
Linton 4 (G)	21/8/71	4	4	2
	25/10/71	5	5	0
Inlet	21/9/71	5	4	2
Peninsular (P)	19/10/71	6	6	2
Hide (G)	12/10/71	8	6	1
	27/12/71	8	deserted	
Southern (G)	20/10/71	7	7	2
	19/12/71	9	7	0
Northern (G)	28/9/71	3	deserted and flooded	
	23/10/71	7	7	2
	19/12/71	4	2	1
Western (G)	20/8/71	6	Robbed by predator	
	18/9/71	7	6	0
	8/11/71	10	Twice robbed by predator	
	14/12/71	7	7	0
Rough Paddock	18/11/71	4	3	0

Territory	Date of First Egg	Clutch Size	Number Hatched	No. Surviving at Age of 4 Months
Linton 1 (P)	1/9/72	5	4	3
	21/11/72	6	3	2
Linton 2 (P)	11/10/72	6	6	4
	24/2/73	5	4	0
Linton 4 (P)	25/8/72	4	4	2
Trap (G)	30/9/72	3	Robbed by predator	
	26/10/72	4	2	0
Peninsular (G)	1/10/72	2	Robbed by predator	
	13/10/72	1	Robbed by predator	
	7/11/72	5	5	0
Inlet (G)	15/9/72	8	6	?
Southern (G)	23/8/72	5	4	3
	29/10/72	12	10	0
Northern (G)	11/9/72	6	4*	2
	4/11/72	8	7	0
Western (G)	3/10/72	7	5	0
Corner (G)	23/10/72	4	Robbed by predator	
Hide (G)	2/10/72	8	5	4

(G) = group

(P) = pair

* one egg removed in experiment

Synchronized nests are underlined

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