SEASONAL DISPERSION AND ACTIVITY OF THE PUKEKO *PORPHYRIO P. MELANOTUS* (RALLIDAE) IN SWAMP AND PASTURE

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SUMMARY: Numerical and spatial components of dispersion, and the activity of pukeko *(Porphyrio p. melanotus)* in swamp and pasture in coastal Manawatu, New Zealand, are described. Pukeko are concentrated in few locations during the autumn population peak, but are widely scattered in spring when the population size is minimum. Flocks are consistently larger in pasture than swamp; those of up to ten birds are more frequent in swamp. And those of 25 or more birds more frequent in pasture. In pasture, pukeko distribution and density declines outwards from the edge nearest to water. The suite of activities is similar in swamp and pasture but feeding is more frequent in pasture, and the main kinds of feeding employed vary in frequency between the habitats. Activity is labile, but feeding is interrupted less frequently than non-feeding behaviour. Use of swamp and pasture is discussed briefly. Pukeko grazing effects may be significant in autumn, but mainly in pasture close to water and cover.

KEYWORDS: behaviour; spacing behaviour; flocking; feeding; habitats; pukeko; *Porphyrio porphyrio melanotus*; Rallidae; Pukepuke Lagoon; Manawatu.

INTRODUCTION

In New Zealand, the pukeko *(Porphyrio p. melanotus)* (Rallidae) inhabits wet lowlands and breeds in swamps, but uses such habitats as pasture, crops, farm ponds, road verges and forest margins which collectively provide a more diverse environment and offer feeding opportunities unavailable before the large-scale lowland clearance and swamp drainage of the last 150 years. In Australia, it also ventures from still and moving water into open pastures to feed (Slater, 1970; Reader's Digest, 1976; Briggs, 1979) as does the Tasmanian native hen *(Gallinula mortierii)* (Ridpath, 1972). Changes in land use could be locally advantageous to pukeko, as claimed by Guthrie-Smith (1953), and affect population levels (Carroll, 1969) but by what process is not clear, although social parameters are responsive to habitat (Craig, 1979) and changes in grouping and activity could occur.

At Pukepuke Lagoon in Manawatu, swamp and adjacent pasture provide a natural interface across which pukeko interactions with habitat can be measured. Analyses of behaviour, breeding, and social organisation in relation to habitat at Pukepuke Lagoon have been provided by Craig (1977, 1979, 1980a, b). The habitat requirements of a species are complex, but the gamebird status of pukeko, and the damage to pasture and crops sometimes attributed to it suggests that assessing its use of different habitats, and suite of activities, could assist in appropriate management. This paper examines the dispersion and activity of pukeko in swamp and pasture in an attempt to answer the question-how are pukeko distributed spatially and numerically, particularly in pasture, and how do activity patterns differ between swamp and pastoral habitats?

STUDY AREA

Pukepuke Lagoon (400 20'S, 175º 16'E) comprises c. 82.2 ha of swamp-dominated reserve (M. Sell, pers. comm.) enclosing areas of open water, the largest being a shallow lake of c. 15 ha (Caithness and Pengelley, 1973) (Fig. 1). The history and climate of the locality are detailed by Ogden and Caithness (1982). Pukepuke Lagoon is slightly saline and enriched by nutrients entering via drains from surrounding flat pastures. The water level, controlled artificially by a sill (Gibbs, 1973) is low during summer when lagoon margins may become exposed, but high in winter and spring when drains carry water continuously.

The flora of the lagoon (Potts, 1976; Kelly, 1978; Craig, 1979; Ogden and Caithness, 1982) is dominated over c. 42.6 ha (M. Sell, pers. comm.) by thick

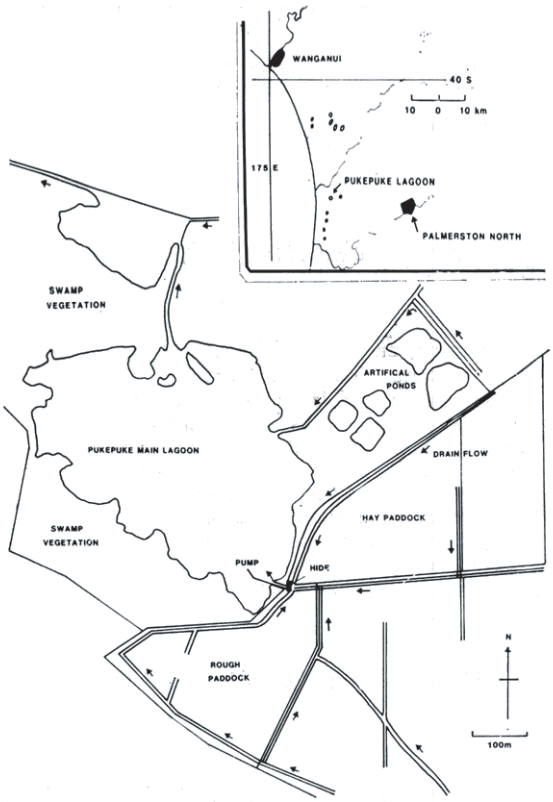

FIGURE 1. *Pukepuke Lagoon and adjoining paddocks to the east and south. Arrows indicate drain flow.*

stands of raupo *(Typha orientalis),* sedge *(Carex secta),* flax *(Phormium tenax),* cut grass *(Cyperus ustulatus)* and cabbage tree *(Cordyline australis).* Separated from the main lagoon by a low stop-bank and drains 2-3 m wide and about 1 m deep, are paddocks (Fig. 1) in which surface flooding and slow drainage have encouraged the invasion of wetland plants such as *luncus* sp., *Cyperus* sp., and *Ranunculus* sp. The 'Rough' paddock was partly-drained swamp comprising a wet lumpy turf, while the cultivated 'Hay' paddock held more grasses and legumes and fewer wetland species.

METHODS

Data were collected during afternoons before sunset between February, 1971 and May, 1974 with 8 x 40 binoculars and 15-60X telescope from an elevated hide (Fig. 1). Seasons and habitats were sampled evenly through 1971, but no observations were made during spring in 1972 or 1973. The distribution of individuals and groups in .swamp and pasture were noted every 15 minutes, and in the Hay paddock the numbers of birds in different zones were scored every five minutes. The zones, which began at the outer lip of the lagoon-side drain, were 12.5 m wide, and ran for 115 m parallel to the edge of the paddock next to the main lagoon. Zone boundaries were defined by lines of 1.5 m high markers. Because groups of pukeko formed and broke-up continually any individual or group more than 10 m (estimated from the elevated hide) from other pukeko was termed a flock. The activity of each pukeko, some of which were individually marked, was recorded at five-minute intervals on the assumption that this interval did not match any naturally periodic behaviour (Fordham, 1978).

RESULTS

Gross dispersion

The pukeko population at Pukepuke Lagoon changed seasonally from a low during nesting, from late winter through spring, to a peak in autumn, particularly April-May (Craig, 1979). The study population fluctuated with the movement of transients but the autumn peak was 60-80 birds over the study period. The numbers of pukeko seen in similar locations were accumulated from daily maps to indicate distributional foci (Fig. 2). Use of the area was localised in autumn when 13 locations were each used by a total of 21-100 birds, and three by 100-500 birds. The areas used most intensely were concentrated in a broad band of lagoon and pasture within 50 m of the dividing drain. Fewer pukeko used the same region in winter and gradually dispersed through the reserve prior to breeding. The spring pattern was one of numerous scattered locations used by only one to five birds, but during summer the distribution of birds became more concentrated. Through the year 68% (n = 148) of the locations used by one to five birds were in swamp, with the highest proportion in autumn (75%, n = 33) and the lowest in summer (58%, n = 24).

Aggregation and flock sizes

Individual pukeko foraged at different rates and frequently changed direction so the size of groups altered continually, although territorial cohorts sometimes retained a separate spatial identity. Flocks fluctuated in size from small in spring to large in autumn, when about 60 individuals were seen together (Fig. 3). In swamp and pasture the average flock size varied significantly between seasons (by t test, $p < 0.001$). Flocks were significantly smaller ($p < 0.001$) in swamp than pasture over each season, and in nearly all months. In autumn, when the difference between habitats was greatest, pasture flocks were, on average, about three times larger than swamp flocks. In swamp there were many small flocks (i.e.

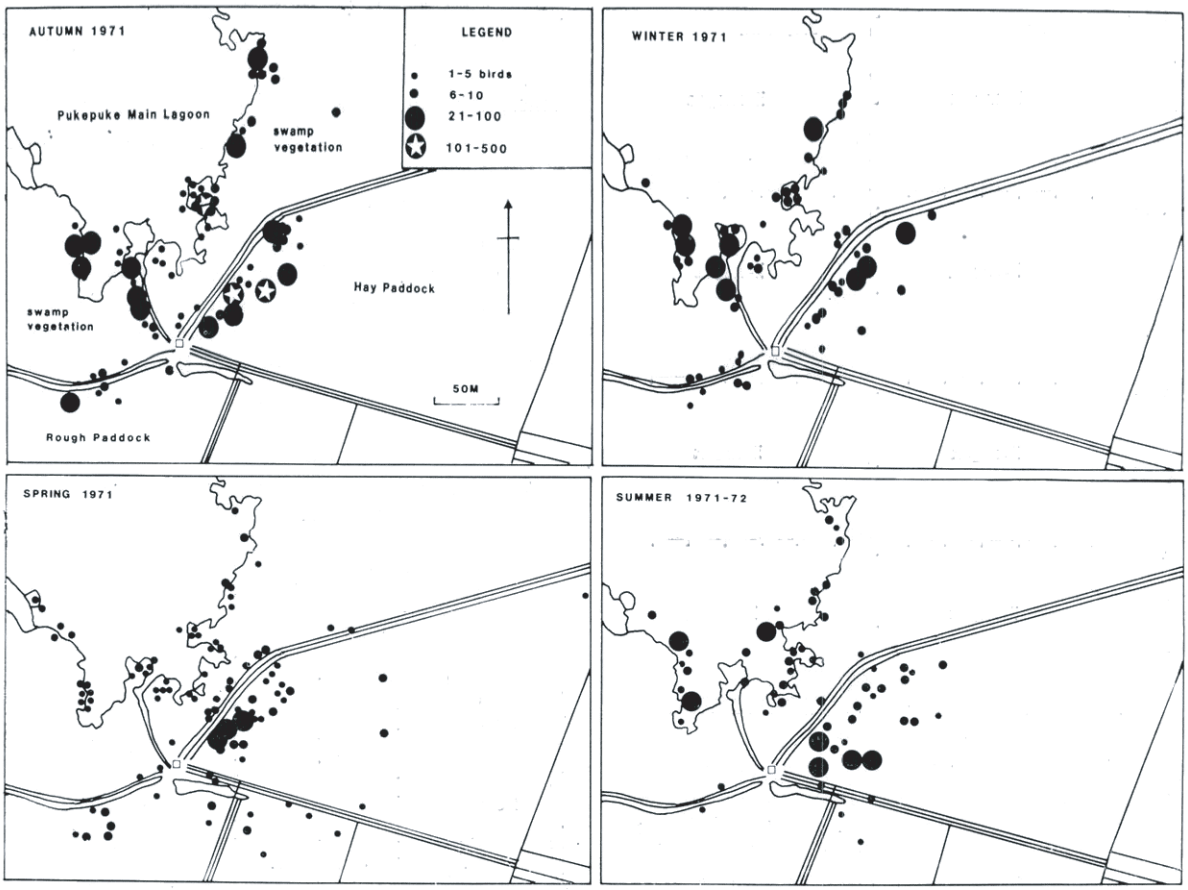

FIGURE 2. *Distributional foci of pukeko at Pukepuke Lagoon in autumn (March-May, 8 days); winter (June-August, 7 days); spring (September-November, 10 days); summer (December-February, 7 days). The solid line around the main lagoon marks the water edge.*

≤ 5) in each season (100%, n = 97, in spring) and few larger ones (Fig. 3). The patterns in pasture were different, excepting spring. In summer 75 % (n = 110) of flocks held up to five pukeko (cf. 92 %, n = 263, in swamp) and these were relatively more flocks with between six and 25 individuals. During autumn, pasture flocks grew sharply in size; only 41 % (n = 183) comprised one to five pukeko, medium-sized flocks were infrequent but very large ones became relatively abundant. During winter, flocks of 11-20 birds were proportionally more common than in autumn, but no larger flocks were ever seen.

The distribution of the population between flocks of differing size (Fig. 4) was identical in swamp and pasture in spring, when all birds were associated in. groups of one to five individuals, but differed strongly in other seasons. In summer, autumn, and winter 60-100% of pukeko in the swamp were associated with flocks composed of one to 10 individuals, compared with about 18-80% in pasture. The free aggregation of pukeko into large and medium-sized flocks (i.e. 11 or more birds) in summer, and especially autumn, in pasture, but not in swamp, was the main difference in dispersion between the two habitats.

Spatial distribution in pasture

Dispersion in the Hay paddock (Table 1) changed with season (X^2 = 443.4, d.f. = 12, $p < 0.001$), but divided broadly into one pattern for summer, and another for the remainder of the year, with an autumn transition. There was a year-round gradient across the paddock, with the zone nearest the lagoon (the first 12.5 m) being occupied most frequently, and the region beyond 50 m least. In zone 1 the birds

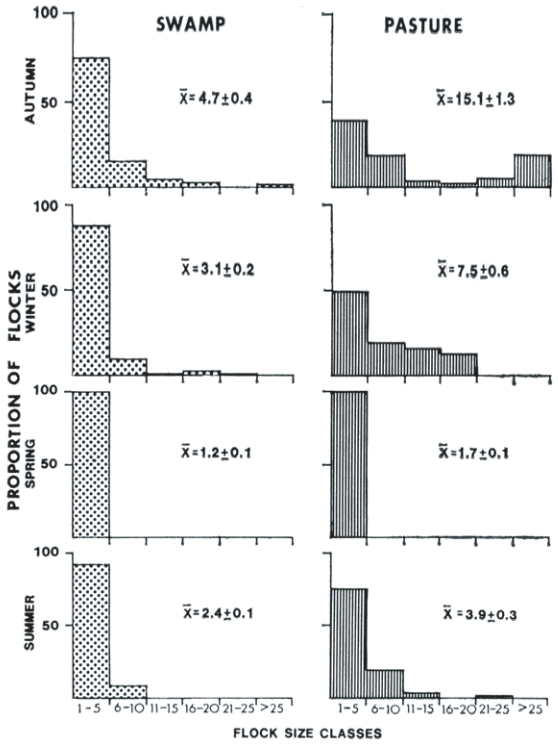

FIGURE 3. *Proportional frequency of flocks of different size in swamp and pasture at Pukepuke Lagoon, 1971-1974. Number of flocks and largest flock ( ): Swamp-autumn, 229 (52); winter, 226 (24); spring 97 (3); summer 263 (10). Pasture-autumn, 183 (62); winter, 106 (20); spring 154 (5); summer, 110 (22).*

frequently occupied the strip about 6 m wide next to the drain, and through the afternoon tended to move further out into the paddock. At dusk, the birds retreated rapidly together to the swamp. In summer, pukeko were scattered across the pasture; about one-third remained close to the lagoon while 20% ranged between 50 m and 100 m from the lagoon. In other seasons, particularly winter, they were concentrated near water. The broad patterns summarised in Table 1 may result from a mosaic of individual distributions. For instance, in spring 1971, 292 records of four marked pukeko from the Hide Territory (Craig, 1979) showed that each individual used pasture differently. The female foraged further from the lagoon than the three males, which respectively occupied zone 1 (nearest to the nest) 61 % (n = 146), 51 % (n = 67) and 41 % (n = 29) of the time, in direct relation to their status in the territorial hierarchy. Continuous observation of nine marked individuals for a total 31.5 h in 1971 showed free movement within and between zones during foraging. Most (84%, n = 119) zonal changes involved adjacent zones, and only 4 % were across three or more, which suggests that in pasture foraging paths are generally progressive.

Density in pasture

Because the Hay paddock (c. 9 ha in area) extended about 450 m from the lagoon (Fig. 1), the distance that pukeko intruded into pasture was trivial when viewed on a larger scale. Correspondingly, in most seasons their impact, measured in terms of numbers and area exploited, fell away steeply from the edge

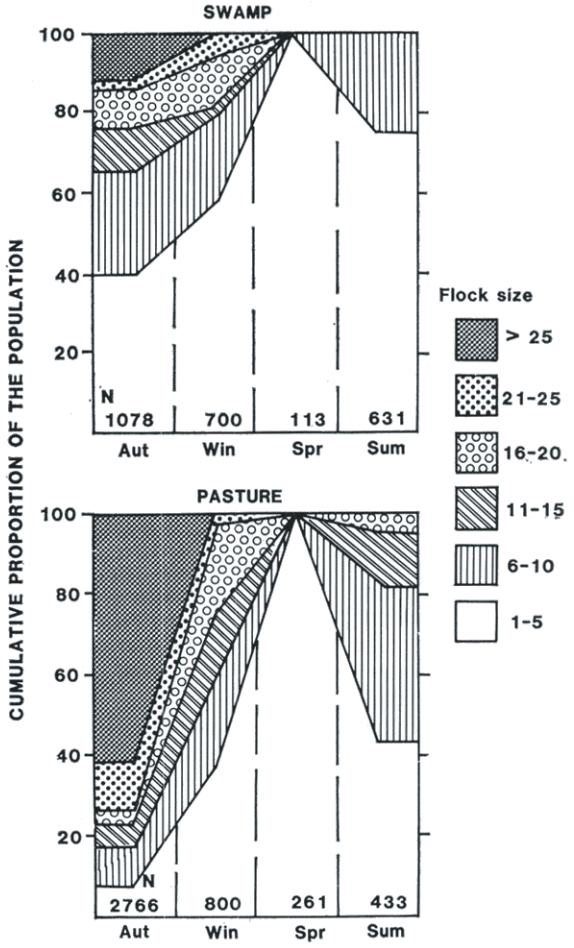

FIGURE 4. *Seasonal changes in the distribution of the population between flocks of different size at Pukepuke Lagoon 1971-1974.*

TABLE 1. *Seasonal distribution (%) of pukeko in the Hay paddock, Pukepuke Lagoon,* 1971-1974.

Zone:	1	2	3	4	5-8		
Distance (m) of outer zonal boundary from pasture edge.	12.5	25	37.5	50	62.5-100	No. of birds	n
Autumn (Mar-May)	43.9	29.9	15.5	6.0	4.7	3007	231
Winter (Jun-Aug)	55.9	18.1	10.6	10.3	5.1	1145	124
Spring (Sep-Nov)	50.7	28.2	8.8	6.9	5.4	535	216
Summer (Dec-Feb)	32.1	22.6	15.2	9.7	20.4	1143	252
Total	44.6	26.0	13.8	7.7	7.9	5830	823

TABLE 2. *The average density of pukeko per hectare of pasture in the Hay paddock, Pukepuke Lagoon,* 1971-1974. *Density estimates are derived from the average number of birds per zone (Table* 1), *and the area of each zone (0.14375 ha), and of the Hay paddock (c.9 ha). The zones are as in Table 1.*

	Zone					Total	Total	Total
	1	2	3	4	5-8	1-4	1-8	paddock
Autumn (Mar-May)	39.8	27.0	14.0	5.5	1.1	21.6	11.3	1.4
Winter (Jun-Aug)	35.9	11.6	6.8	6.6	0.8	15.2	8.0	1.0
Spring (Sep-Nov)	8.7	4.9	1.5	1.2	0.2	4.1	2.2	0.3
Summer (Dec-Feb)	10.1	7.1	4.8	3.1	1.6	6.3	3.9	0.5
Year	22.0	12.8	6.8	3.8	1.0	11.3	6.2	0.8

nearest the lagoon. Seasonal changes in pukeko density (Table 2) follow inevitably from the trends described in Figures 2-4. Characteristically the population changed from the pattern of widely scattered small groups in spring, to relatively concentrated large flocks, supplemented by immigrants in autumn. Autumn densities were 4-5 times higher than those in spring, and in all seasons densities dropped steadily with increasing distance from the lagoon. Beyond 50 m from the. lagoon densities were slight, summer being the highest, and over the year pukeko infrequently ventured further than 100 m from the lagoon. Over the whole paddock pukeko density was negligible.

Seasonal pattern of activity

A total of 8989 individual activities were recorded in swamp and pasture. There were strong similarities in the annual patterns of activity, and the composite seasonal frequencies are given in Table 3. The distribution of activities varied significantly between seasons in swamp (X^2 = 103, d.f. = 18, p< 0.001) and pasture (X^2 = 222, d.f. = 18, p < 0.001). In both habitats, feeding was significantly more frequent in autumn and winter combined, compared with spring and summer (Swamp, X^2 = 36.1, p < 0.001; pasture, X^2 = 36.7, p < 0.001), and was complemented by changes in look-at-ground behaviour. Except for agonistic encounters, which were more common in spring, other activities had variable seasonal frequencies in swamp and pasture. The same suite of activities occurred in swamp and pasture but the frequencies in the two habitats differed strongly in each season and over the year (X^2 in all tests> 100, d.f. = 6, p < 0.001).

Feeding was the dominant activity in swamp and pasture, occupying nearly 50 % and 73 % respectively of pukeko time overall (Table 3). In every season the birds spent relatively more of their time in pasture foraging, and this conclusion was supported by records of marked individuals. Birds fed from the water surface and sometimes plunged their heads

TABLE 3. *Seasonal and annual frequencies* (%) *of Pukeko activities* in *pasture* (P) *and swamp* (S) *at Pukepuke Lagoon, February* 1971 - *August* 1973.

	Autumn Mar-May		Winter June-Aug		Spring Sep-Nov		Summer Dec-Feb		Total P		Total S	
Activity	P	S	P	S	P	S	P	S	n	%	n	%
1. Feeding	76.6*	53.4	73.8*	55.3	69.3*	41.1	67.8*	44.9	4046	73.3*	1726	49.7
2. Look at ground	6.0	10.5*	9.5	11.9	11.8	14.0	12.1	18.3*	472	8.6	492	14.2*
3. Look about	7.4	20.1*	12.2	15.4*	9.1	17.2*	11.2	20.4 *	507	9.2	643	18.5*
4. Bodily care	4.8	9.4*	0.5	7.9*	2.0	12.5*	1.2	10.5*	165	3.0	334	9.6*
5. Agonism	1.4	2.7*	0.5	3.0*	4.3	5.6	3.1	2.0	110	2.0	97	2.8*
6. Courtship	0.1	-	-	0.4	0.9	0.6	-	0.1	10	0.2	8	0.2
7. Alarm	1.4	0.9	1.2	2.8*	2.0	4.7*	3.2	2.1	102	1.8	78	2.2
8. Other	2.3	3.0	2.3	3.3	-	4.3*	1.4	1.7	103	1.9	96	2.8
Total									5515	100.0	3474	100.0
n	2773	807	875	1055	647	321	1220	1291				

Significantly higher frequencies in pasture or swamp are indicated by *.

Observations in different years were: pasture - autumn 1971, 918; 1972, 746; 1973, 1109; winter 1971, 330; 1972,485; 1973, 60; summer 1971-72, 739; 1972-73,481. Swamp - autumn 1971, 534; 1972, 75; 1973, 198; winter 1971, 718; 1972, 61; 1973, 276; summer 1970-71, 72; 1971-72, 419; 1972-73, 800.

The pukeko has varied behaviour, and a wide range of agonistic and courtship displays (Craig, 1977). Here broad categories of related activities are recognised, and for most analyses agonistic and courtship frequencies are combined. Components included in categories are:

[1]Peck at food while standing or walking. Digging into the ground with the beak, other than in an agonistic context (Craig, 1977). Peck at food held by one foot on or off the ground.

[2]Look at ground with head and neck turned down while standing or walking. This activity nearly always preceded feeding.

[3]Look round in "relaxed" attitude while standing or walking.

[4]Preen, scratch, stretch, wash.

[5]Threat and appeasement (including escape), pecking and fighting (Craig, 1977).

[6]Displays leading to copulation, and post-copulation displays (Craig, 1977).

[7] Alert (Craig, 1977).

[8]Drink, sit, swim, fly. Nesting activities (e.g. building, incubating) were not recorded.

TABLE 4. *The frequency* (%) *with which the initially recorded activity of known pukeko was repeated at subsequent, consecutive five minute intervals.*

Initial category of activity	No. of episodes beginning with the initial activity.	Initial activity not repeated at the next interval	No. of subsequent intervals at which the initial activity was repeated. 1	2	3	4	5	Total
Feeding	822	77.0	16.8	4.4	1.0	0.7	0.1	100.0
Look at ground	186	92.5	7.5					100.0
Look about	226	97.0	2.6	0.4				100.0
Bodily care	65	89.2	10.8					100.0
Agonism	31	100.0						100.0
Courtship	11	100.0						100.0
Alarm	43	95.3	4.7					100.0
Other	29	100.0						100.0
Total	1414	84.5	11.8	2.6	0.6	0.4	0.1	100.0

below (d. Frost, 1975), plucked plant material, dug into the ground or the bases of raupo stems, and occasionally, in summer, stripped seed from grass stalks. Plant material shorn or pulled from the ground was frequently transferred to one foot before being chopped and swallowed.

The relative frequencies of the three main styles of feeding (pecking while standing or walking, and holding food in the foot) varied with season in pasture and swamp. In pasture, birds stood to peck most in autumn (58.5%, n = 2125) and least in spring (44.9%, n = 448), walked while pecking with increasing frequency from autumn (10.6%, n = 2125) through to spring (41.3 %, n = 448) and summer (40.1 %, n = 827), and employed feeding from plants held in the foot three times more often in autumn and winter (30.5%. n = 2771) than in spring and summer (10.4%, n = 1275).

In swamp, the seasonal patterns of pecking while standing or walking were generally similar to those in pasture, but the birds consistently stood still to peck more in swamp (69.4%, n = 1726) than in pasture (54.8%, n = 4046), and fed from items held

in the foot much less frequently (swamp, 10.3 %, n = 1726; pasture, 34.1 %, n = 4046), particularly in autumn (swamp, 7.0%, n = 431; pasture, 30.9%, n = 2125) and in winter (swamp, 12.7%, n = 583; pasture, 29.0%, n = 646).

Practically all non-feeding activities occurred more frequently in swamp than in pasture (Table 3), and those involving looking at the ground or looking about were approximately twice as common, while bodily care was three times more common in swamp.

Activity of individually marked pukeko

Scores were kept of the number of consecutive five-minute intervals at which a total of 63 known pukeko were engaged in the same activity as at the previous interval, and provided a measure of lability. Nearly 85% of all the activities noted at one interval were not recorded again at the succeeding one, indicating that the birds switched activity frequently (Table 4). Bodily care, alarm and other watchful behaviour were noted at one or two subsequent intervals, but only feeding ever spread over more than two, hence feeding episodes apparently lasted longer than non-feeding ones (X^2 = 89.3, d.f. = 2, P < 0.001), which agrees with the gross distribution of activities (Table 3).

DISCUSSION

Grouping

Two main components of diurnal dispersion can be recognised: group sizes, and their arrangement in space and time. For both components important differences exist between swamp and pastoral habitats. Grouping is numerically characterised by an annual cycle between a spring low, when with few exceptions (Craig, 1979) only territorial breeders were pre~ent and an autumn high, when residents plus young of the year were joined by immigrants. The origins of immigrants to Pukepuke Lagoon were not known, but there were many potential sources in Manawatu, from other lagoons, lakes, swamps and river estuaries. Population increases through summer and autumn have been noted by Craig (1979), and in autumn and winter at the estuary of the Manawatu River, by 1. Davies (pers. comm). Carroll (1969) also referred to seasonal flocking and to seasonal variation in flock size, which apparently does not occur in Australia (Reader's Digest, 1976).

Seasonal changes in group sizes followed similar trends in swamp and pasture. Average flock size was lowest in spring and highest in autumn when the largest flocks were seen. In swamp the peak sometimes fell in May rather than in April, as in pasture, probably because pukeko sought cover more actively during shooting in May. Moreover, this behaviour partly explains the lower reduction of flock sizes over winter in swamp. Competition among potential breeders for nesting territories probably also helped to sustain the size of flocks in the swamp.

On average small flocks were more frequent in swamp, and mean flock size was consistently less than that in pasture, especially in autumn. The clear differences in swamp and pasture in the way the population was distributed between flocks of varying size raises the question-what is the function of grouping in non-breeding months? Larger flocks in pasture might simply reflect individual reactions to more advantageous feeding there. In both habitats individuals fed independently, and with no clear evidence of synchronous foraging, grouping did not obviously confer benefits in feeding. Mutual protection from the harrier *(Circus approximans)* frequently occurred however. Grouping patterns might also reflect a trade-off between food needs and breeding right. Since flocks promote mixing, they could be a a mechanism by which places in the matrix of breeding territories are annually determined.

Distribution

The foci of pukeko distribution were mostly around the interface of swamp and pasture, but the spacing of birds was different in the two habitats, though less noticeably in spring. In swamp they spread over numerous, fairly scattered locations, but in pasture they were relatively localized into fewer areas sustaining heavy use.

The strong distribution gradient across the Hay paddock showed that the birds preferred areas of

pasture near the lagoon, especially in winter. Sheep and cattle had no lasting effects on this gross pattern, neither did the extension of some group breeding territories into the paddock, as these either collapsed or became greatly compressed in summer and autumn (Craig, *1979)*. The marked withdrawal in winter to zones near the lagoon, and the contemporary heavier usage of swamp compared with pasture reflected habituated cover-seeking caused by shooting, as well as the annual competition for territories. Only in the summer post-reproductive phase were areas more than 50 m from the lagoon-side drain used significantly. The gradual shift through the afternoon to areas further out in the paddock was probably a passive response to lack of disturbance.

Activity patterns

The gross seasonal pattern of activities was similar in pasture and swamp, but feeding occupied 18-28 % more time in pasture in every season. Nearly all other activities especially bodily care, look-about and look-at-ground were more frequent in swamp. In the swamp, activity frequencies recorded where birds were visible might have differed from those deep in the vegetation, and in both habitats frequencies could have been biased against transitory courtship and agonistic postures, but overall the pasture appeared to be primarily a place to feed.

The entire suite of activities was highly labile; the rails switched readily away from non-feeding activities because some were intrinsically brief (stretching, flying) or socially transient (courtship and agonism). In all seasons, however, feeding of any kind was relatively long-lasting. In pasture and swamp, feeding occurred more frequently in autumn and winter, and look-at-ground less frequently, than in other seasons. Pukeko switched continually between these two activities in a sequence of search, locate, and feed, suggesting both could be treated as feeding (cf. Fordham, 1978). With the frequencies of these activities combined, "feeding" was still 18 % more common in pasture, and seasonal variation was reduced more in pasture than in swamp.

Use of swamp and pasture

Seasonal use of habitats by pukeko and the main kind of feeding employed during foraging is possibly influenced by the annual cycles of local plants. For instance, through autumn and winter the above-ground parts of raupo, which are eaten by pukeko, become dry, while the persisting rhizomes are not readily available. New shoots erupting in late winter, can be taken by pukeko about one month later (J. Ogden, pers. comm.), so between about mid-autumn and early spring there is little raupo to eat. Secondly, in pasture the production of grass and clover declines in autumn and winter (Mitchell, 1960; Brougham, 1962) further reducing the gross supply of food. But the seasonal, diurnal, and spatial concentrations in plants of soluble carbohydrates and proteins (Johns, 1955; Lyttelton, 1973; Smith, 1973) could explain why pukeko fed longer in pasture in autumn and winter, and pecked more than in swamp at whole plants held in the foot in the way used by takahe (Williams *et al,* 1976). A correlation between use of a main winter food and its carbohydrate level was demonstrated for the takahe by Mills *et al* (1980).

In any season pukeko forage over distinct plant associations, and feed with different intensity in each (Wright, 1978), indicating that separate habitats are treated as complementary, not alternative, sources of food. The relative importance of swamp and pasture is difficult to assess however because events in one habitat influence events in the other, but an interesting question is what, if any. nutritional and demographic constraints are experienced by pukeko in swamps?

Synthesis

Estimates of peak autumn populations suggest that highest densities could have been reached in 1973, when about 80 pukeko were present. Assuming that all these birds entered the Hay paddock together and became distributed in the average autumn pattern (Table 1), the following per ha. densities would have obtained: zone 1, 244; zone 2, 166; zone 3, 86; zone 4, 33; zones 5-8, 7; total zones 1-4, 133; total zones 1-8, 70; total for the paddock, 9. If all the birds fed in zone 1, next to the lagoon, the density there would have risen to 557 per ha. These values are not maxima, but depend upon the peak size of the local autumn population (flocks of over 80 birds were seen elsewhere in Manawatu), synchronous entry to the paddock by all the birds, and probably also on the availability of protective cover about the pasture margins. Further, because the size of the autumn population is fluid it is likely that a very high density would be temporary.

The annual cycle of pukeko numbers and density means that grazing pressute on pasture is heaviest in autumn particularly April, and lightest in spring. Because the birds disperse differentially about the paddock, regions close to water absorb most of the imp'ict. A similar picture was painted for Tasmanian native hens by Ridpath and Meldrum (1968a, b). For pukeko one could predict that only in a year with an unusually high post-breeding population might pressures increase in more distant parts of the pasture. In pasture pukeko feed considerably more than they do in swamp, and feeding is interrupted less frequently than non-feeding behaviour. In pasture

the frequency of feeding is also high through the year, but highest in autumn. Use of pasture by pukeko would be relatively more important between midsummer and winter, when extremes of temperature and rainfall may reduce pasture production below stock requirements, and would be influenced by the height of the water table, availability of protective cover about the pasture, attractiveness of neighbouring crops, and seasonal farm management practices. In Manawatu a period of particular interest would be midsummer to early autumn, when the food demands of lactating cows are still high (Brougham, 1969, 1970) and breeding ewes require boosted rations prior to mating (J. W. M. Gardner, pers. comm.). Local measures to inhibit pukeko use of pasture might then become appropriate.

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