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THE TIME BUDGET AND FEEDING ECOLOGY OF THE PUKEKO

Porphyrio porphyrio melanotus

Temminck, 1820

A thesis presented in partial fulfilment of the  
requirements for the degree of Master  
of Science in Zoology at Massey University.

John D. Wright  
November, 1978

ABSTRACT

The annual and seasonal time budget and feeding ecology of pukeko Porphyrio porphyrio melanotus are described both as a composite day and diurnally. The study shows pukeko do not spend equal time in all activities in all habitats over the day, for each season or over the year. They spend by far the bulk of their time feeding (75-90%), and less time to attentiveness, bodily maintenance, and social encounters. However time allocated to all activities varies with habitat. By far most time is spent in dryland (pasture), and less in turn in rush margins, swamp and water. Bimodal activity patterns (dawn and dusk) are described for each season, whereas feeding effort is unimodal peaking in the mid to late afternoon. Direct sampling of an adjacent population indicates pukeko gradually increase the length of tiller taken and quantity of ingesta consumed over the day. Pukeko do not peck at the same rate or feed at the same intensity in all habitats, at all times of the day, for each season or over the year - feeding fastest and most intensely in rush margin and mud areas, and slower and less intensely in dryland, swamp and water. However considering use of habitats over the year pukeko feed most intensively and extensively in dryland, but less in rush margin, mud, swamp and water. Feeding in the latter three habitats is linked notably with seasonal availability (and/or quality) of forage. Evidence indicates pukeko are able to gauge seasonally the availability (and/or quality) of forage, and allocate their feeding effort appropriately.

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## 1. INTRODUCTION

The pukeko Porphyrio porphyrio melanotus (Temminck), is a non-endemic native, swamp or wet-land dwelling gallinule, found commonly throughout New Zealand. It belongs to the widely distributed genus Porphyrio which, according to Vielliard (1974) "ranges over the Old World in four basic types of colouration. The nominate form, entirely violet, is endemic to the western Mediterranean region; and the madagascariensis group of tropical Africa, Madagascar and Egypt has a green back contrasting with blue remiges and underbody. The poliocephalus group, from Turkey to Indo-China, is light blue with the head pale grey; this passes, in Malaysia, into the melanotus group of very pigmented forms, the head and back becoming almost black, across the Australasian region" - further the same subspecies is found in the south and east of Australia, New Guinea, New Caledonia, Norfolk Island, Lord Howe Island, and Tasmania (RAOU, 1926).

From evidence of sub-specific characters, between New Zealand's pukeko and Australia's Eastern Swamphen, Fleming (1962) regards the pukeko as a late arrival in New Zealand, around the late to middle Holocene period, i.e. 10-15,000 years ago, "showing, in European times, all the vigorous adaptability of a new immigrant, remarkably versatile in a rapidly-changing environment" (Falla, 1953).

Detailed knowledge of the seasonal, let alone diurnal, food habits of pukeko, as with all rails, is scarce, although Buller (1877) described the pukeko as "semi nocturnal in its habits, being most active after dusk." Muggeridge and Cottier (1931), working in conjunction with the Wildlife Service, Internal Affairs, Wellington, and local Acclimatisation Societies, investigated their food habits, by studying the gizzard contents of 63 birds. They were taken from Auckland, Wellington, North Canterbury, Southland and Otago, being ideally collected at a rate of two birds from the vicinity of crops, and from swamp land distant from crops,

i.e. in all 20 birds each month. However, local branches of the Acclimatisation Societies were unable to supply the appropriate number of birds. The time of day at which the birds were shot, as well as the habitat over which they were shot, were unrecorded. At that time, and to the present, Acclimatisation Societies and farmers appeared to be at a difference of opinion, concerning the effects of pukeko on crops and pasture. The farmers believed the birds were the source of great damage to crops and pasture, (see also Bell, 1955), and spread disease (e.g. Salmonella), while the Acclimatisation Societies, believing that pukeko were mainly insectivorous, contended that the good accruing from the number of injurious insects destroyed, outweighed any damage that might be done to the crops. Muggeridge and Cottier, however, concluded that pukeko were primarily vegetarian, and that insects did not form a staple part of their diet, even given that insect remains were rendered unidentifiable more readily, and did not persist as long as, the vegetative portion of the diet.

Tunncliffe (1965), following preliminary accounts by McLean (1902) and Guthrie-Smith (1927), studied the pukeko's general biology, presenting details of distribution, the laying season, breeding cycle, moult, measurements and weights of captured birds, and also behaviour. He did not study the feeding patterns of pukeko.

Carroll (1966), in an attempt to define the pukeko's food habits, to dispel old arguments that once again had arisen between farmers and Acclimatisation Societies, arranged for the collection of 298 pukeko gizzards, from throughout New Zealand, and at all times of the day. From analysis of gizzard contents, she attempted to determine the foraging habitat over which the birds were shot, and also to measure the relative importance of marginal habitats to the overall feeding effort of the birds. Shooters were asked to note the time of shooting (as either early morning, mid-day, or late afternoon), and to define the habitat over which the birds were shot (as either swamp, pasture, or a swamp/pasture mixture), and for these reasons definition

of habitat was largely subjective.

Her results confirmed Muggeridge and Cottier's, in that most gizzards contained plant remains and only a few had insects. Significantly also, a number of gizzards contained oats, barley and other cereals. The most abundant material, found in 70% of the gizzards, was the grasses, especially Poa spp. and less importantly Glyceria spp., Holcus and Anthoxanthum. "There appeared to be no preferential selection of grass seeds as items of food; instead, they were always associated with other parts of the plant. Most favoured portions were the tender stalk-bases, although often the whole plant was eaten, being snipped by the sharp beak of the pukeko into approximately quarter-inch sections, as if by a pair of scissors. Vegetative parts of sedges appeared in 56% of gizzards, not only were stalks, leaves, and rootstocks eaten, but the fleshy tubers, whole or fragmented, were often found to form the bulk of the meal. Sedge seeds frequently occurred in considerable quantities." Other species eaten included Eleocharis, Scirpus, Carex, Cladium, and Mariscus. Seeds of rushes, Juncus spp., occurred in 15% of all stomachs. Dicotyledonous leafy material found in gizzards was almost exclusively clover, occurring in 34% of the specimens. Other plants eaten included Polygonum spp. and Rumex spp., as well as Bidens, Stellaria, Ranunculus, Salvinia, Lemna, Zannichellia, Potamogeton, and Eloдея - the latter group being consumed infrequently.

Over the day, gradually less plant food (dry weight) was found in the digestive tract, but because the birds were not sampled consistently throughout the year the results are probably distorted.

Data on the utilisation of each habitat was inconsistent, as the bird's gizzards seldom held pasture or swamp plants exclusively. However Carroll concluded "pukeko forage at all times of the day, although perhaps less in the afternoon and evening ... and ... it appears the birds feed as they move about in a particular habitat, which normally includes swamp, damp pasture, and grassland. Seeds, predominantly those of sedges, rush, grass, sorrel, and dock are eaten in

season. Grasses, clover leaves and the more tender portions of swamp plants form their staple diet throughout the year."

McKenzie (1967), pointing out that raupo Typha and other "fringe" foods, such as blackberry Rubus spp., had not shown up in Carroll's analysis of stomach contents, quoted experiences of seeing pukeko taking carrion (see also - McLean, 1902; Oliver, 1930 and 1955; Bryant, 1940; Gorgas, 1968; Craig, 1974, and personal observation), and eggs (see also - Oliver, 1930 and 1955; Bryant, 1940; Fitzgerald, 1966; Fogarty, 1968; Gorgas, 1968; Barlow et al., 1972 and Craig, 1974) of waterfowl. He suggested a possible modification of the pukeko's diet since the times of Buller (1877) and Oliver (1930), which was probably paralleled by habitat modification, such as drainage of swamps, and establishment of highly productive pastures.

From 1971-1973, Fordham (unpub.) periodically observed pukeko occupying two areas, pasture and swamp, for two to three hours prior to sunset at Pukepuke Lagoon, Himatangi - a Game Management Reserve, under the control of the Wildlife Branch, Department of Internal Affairs. Data combined from all years, indicated the birds in pasture spent most time feeding in winter (83.3%; n=875 bird-observations), followed in turn by autumn (82.6%; n=2773 bird-observations), spring (69.3%; n=647 bird-observations) and summer (79.9%; n=1220 bird-observations), while in swamp they were seen feeding most frequently in winter (67.2%; n=1055 bird-observations), and least often in spring (55.1%; n=321 bird-observations). Throughout the year the birds spent more time feeding in pasture than in swamp. Rates of feeding in these and other marginal areas of the lagoon were not measured.

Caithness (1973), referring to Fordham's (unpub.) work, commented that "examination of faeces and direct observations show that pukeko mostly feed in the belt of pasture closest to the lake. Here pasture growth in enclosures, which deny entry to the birds, suggest that pukeko have a considerable influence."

Recently Craig (1974) investigated the year-round social organisation of the pukeko in two areas of differing habitat. Subsequent publications include Craig 1976 and 1977.

Special emphasis was given to assessing the interaction of social hierarchy and territory, and the role of communal breeding. He observed that "pukeko were mainly herbivorous, although quantities of animal food were taken in the breeding season, and fed mainly to chicks." He found 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.

Within New Zealand, the takahe Notornis mantelli is the pukeko's closest relative, sharing rather unusually, a similar ecto-parasitic mite spp. (Holloway, 1955; Pearce, 1976). Since its re-discovery in 1948 in the Murchison Mountain Range, Fiordland National Park, much time and effort has been devoted to gathering information on this bird's feeding habits, in an attempt to understand, and perhaps prevent further reduction of the remaining population.

Generally feeding activities pursued by this bird (Falla, 1949; Smith, 1952; Gorgas, 1968), are similar to those described for pukeko (see later). Gurr (1951) found that most remains in takahe chick faeces, were of insects whereas Falla (1949), Williams (1952, 1960), Secker (1953), Reid (1967), Gorgas (1968) and others, have found the adults are almost entirely vegetarian, - the rearing success of takahe chicks being related to the quality of food within a territory (Kean, 1956). Moreover, the quality of the bird's diet in relation to its daily energy requirements has been investigated (Reid, 1974).

Research was then directed towards determining the population dynamics of takahe, particularly the difference in mortality and recruitment rates that existed between habitats of varying quality of preferred food plant spp., (Mills and Lavers, 1974; Mills, 1975), and the possible effects of competition from red deer Cervus elaphus (Mills, 1976).

Most recently however, seasonal analysis of macronutrients of preferred sub-alpine food spp., and observations on the food preferences and feeding rate of takahe (Williams et al., 1976b; Mills and Mark, 1977), have shown the presence of a

food preference rank for snow tussock Chionochloa spp., which corresponded to the relative amounts of major nutrients (especially phosphorus) and sugars they contained. Selection between plants of the same species for the highest levels of phosphorus occurred in spring, early summer and autumn, while in winter, the birds switched from snow-covered sub-alpine plants to feed primarily on the summer-green fern Hypolepis millefolium found in the sub-alpine Mountain Beech Nothofagus solandri var. Cliffortioides forests.

Work on other closely related rails, e.g. Purple Gallinule Porphyryula martinica, indicates omnivory in adults (Meanley, 1963), while the chicks are primarily insectivorous (Trautman and Glines, 1964).

Carroll (1963) studied the food habits of 94 North Island Wekas, Gallirallus australis greyi, taken from Waimata Valley, East Coast district, North Island. Oliver (1955) wrote that the birds consumed large quantities of grass-grubs, and other noxious insects, rats and mice, as well as an assortment of vegetable material. Although primarily carnivorous, wekas were found to be omnivorous, eating especially grass leaves and stalks, fibrous material, small pieces of wood, clover leaves, and less frequently small leaves (e.g. manuka Leptospernum scoparium) and moss - a total percentage volume, excluding seeds, of 55.68 cm<sup>3</sup>, and percentage dry-weight of 46.17 gms. Monthly data indicated most vegetable matter was eaten in winter, while most animal matter and seeds were taken in spring and summer. Insects predominated in the animal food taken - the most important being beetles, wetas, and grass hoppers. Earthworms were also a major item of the diet, while insect eggs and millipedes were frequently found.

From preliminary work, the endangered Lord Howe Island Woodhen Gallirallus sylvestris appears to feed on almost any invertebrates found during foraging on the forest floor and in lower parts of the vegetation, and not to eat fruit from forest trees. They have also been observed eating eggs

and chicks of the Providence Petrel Pterodroma solandri, but the latter may be carrion-feeding and not predation (Fullagar and Disney, 1975).

Recent studies of Tasmanian native hen Tribonyx mortierii show adults, consuming mainly the short, young shoots of grass and low herbs, and seeds (Ridpath, 1964, 1972a), act as secondary grazers, and are dependent on other animals e.g. sheep and rabbits, for the primary mowing effect (Ridpath and Moreau, 1966; Ridpath, 1972b), while the young are insectivorous (Ridpath, 1972a). Concerning the effects of these birds on oat crops, Ridpath and Meldrum (1968) noted a reduction of weight of the yield at six-eight weeks after sowing, of 24-36% on the immediate edge of one margin of a paddock that bordered water. For the entire paddock the reduction in weight attributable to native hen feeding activities, was 8% - an estimate similar to that given to damage on the same crop caused by rabbits. Ridpath, (1972a) observed that native hens grazed steadily all day, within their territories, pecking at a rate of c. 100 pecks per minute which was considerably faster than that recorded for pukeko (c. 38 pecks/min.). However, no detailed seasonal or diurnal activity pattern, or feeding rate studies were carried out.

Fordham (1978) noted that while detailed descriptive work had been carried out on moorhen Gallinula chloropus behaviour, breeding biology, and sexual discrimination (references therein), feeding ecology had not attracted much attention. Feeding intensities of moorhen at dawn and dusk in late winter and spring were indexed by scoring activity frequencies, and combining the frequency of feeding with the rates at which birds pecked. Results indicated that both the frequency of feeding and pecking rates were higher before sunset, than after sunrise. The feeding intensity and time allocated to feeding during the central daily periods were not investigated.

Hence, knowledge of the seasonal and diurnal variation of time allocated to various activities for rails as a whole,

and pukeko in particular, is scarce. This study was intended to fill, at least a few of these gaps. The aims of my project were:

1. To determine for each season the diurnal changes in time allocated by pukeko to various activities, e.g. feeding, alertness, con-specific agonistic encounters, bodily maintenance, courting, and other activities.
2. To determine, seasonally and diurnally, the feeding intensity (following Fordham, 1978, - calculated from time spent eating and pecking rates) for an "average" bird of the flock feeding in any one of the five habitats recognised in the study area (i.e. dryland, rush margin, mud region, swamp and water).
3. To determine diurnally and seasonally, the relative importance of each habitat to an "average" feeding pukeko at Hamilton's Lagoon.
4. To determine, by direct sampling, diurnal food intake patterns of pukeko, as a check on the indirect measures of feeding intensity.

## 2. STUDY AREAS

Observations were made at two locations: Hamilton's Lagoon, where the bulk of the work was centered; and Fell's Lagoon, a swamp used exclusively for collecting pukeko specimens (Fig. 1). Identifications of grasses were made from Lambrechtsen (1972); aquatic plants from Mason (1964) and Mason and West (1965); and birds from Falla, Sibson, and Turbott (1966).

### 2.1 Hamilton's Lagoon

#### 2.1.1 General

"Hamilton's Lagoon" was the name given to an extensive lagoon, 800 m. x 60 m., running approximately southwest/northeast, located east of Hamilton's Line, Tiakitahuna, 7 km. southwest of Palmerston North, (see "New Zealand Topographical Map" number 148, Department of Lands and Survey, Wellington, at grid reference 994280, c. 40° 26' S. x 175° 29' E.). The lagoon is an old oxbow of the Manawatu River, and is fed directly by rain and farm run-off. In very wet seasons man-made drains carry excess water to the Manawatu River, some 1000 m. distant, however, during my study the lagoon never overflowed. Surrounding pasture had a predominantly ryegrass (Lolium spp.)/white clover (Trifolium repens) sward, although scotch (Onopordum sp.) and Californian (Cirsium sp.) thistles were common in spring and summer.

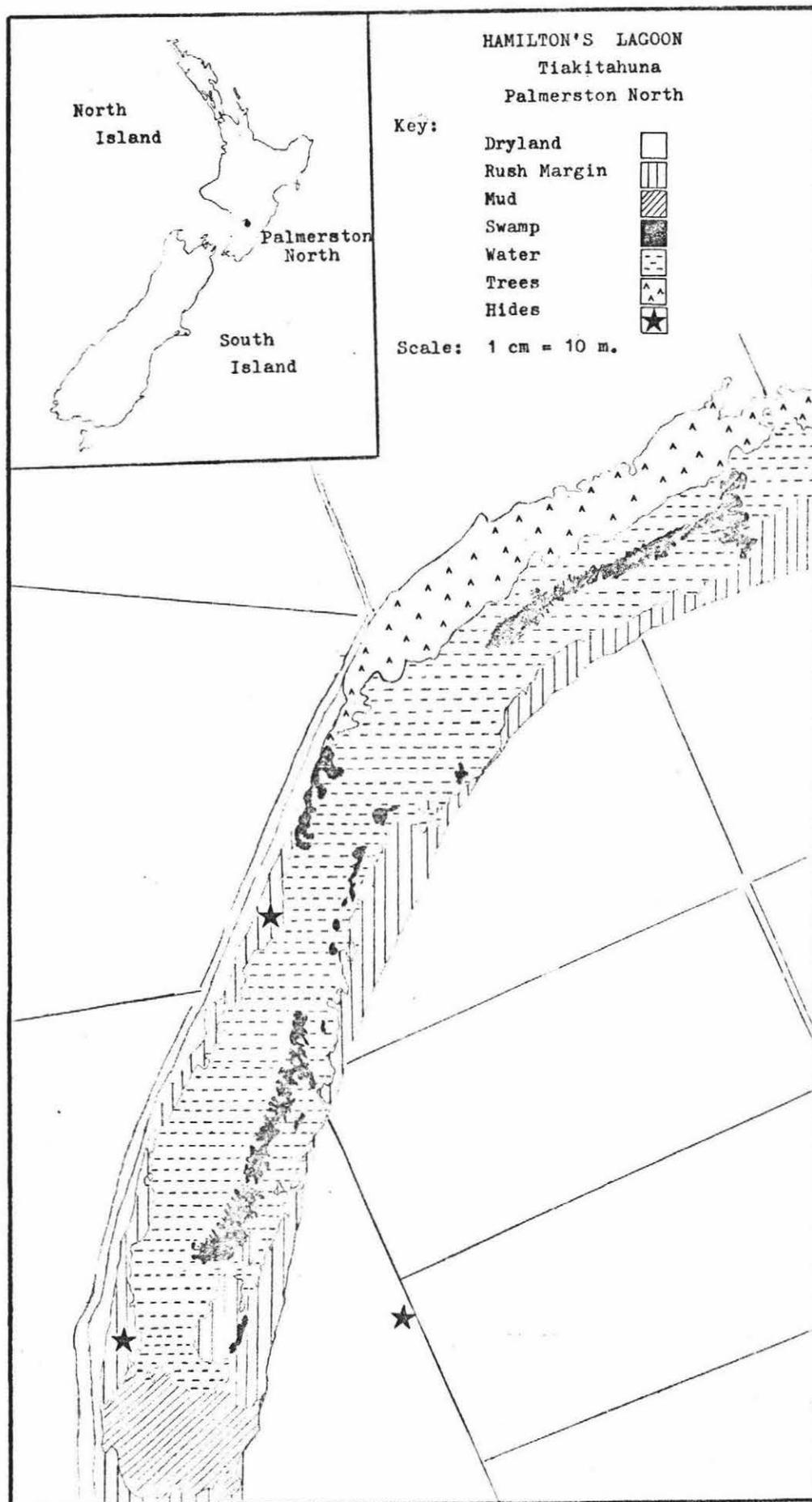
#### 2.1.2 Flora

The lagoon and surrounds were characterised by five floristic associations, which were treated as separate habitats, (Fig. 1).

##### 1. Dryland

This comprised the pasture surrounding the lagoon in which ryegrass and white clover were dominant. Other species present included plantain (Plantago spp.), the fescues - especially Festuca rubra, barley grass (Hordeum murinum), scotch and Californian thistles.

FIGURE 1



## 2. Rush Margin

This referred to the lagoon periphery, and included the transitional zone between water and dryland. Common plants included Ranunculus sceleratus (water buttercup), Polygonum decipiens, P. hydropiper (willow weed), Juncus articulatus, Carex secta (niggerhead), Glyceria fluitans (floating sweet grass), Rumex obtusifolius (broadleaved dock), Holcus lanatus (Yorkshire fog), and ryegrass.

## 3. Mud Region

The most variable of all the habitats in terms of species diversity, the mud region was a shallow area at the southern tip of the lagoon, which was covered by up to 70 cm of water in winter, but was dry in summer. Hence, the vegetation was transitory, and dominant species varied seasonally. In winter and spring water buttercup, which grew to a height of 1-1.5 m. co-dominated with Rorippa spp. (watercress), Myriophyllum propinquum (water milfoil), and floating sweet grass. Floating, non-rooted plants, such as Lemna minor and Azolla friliculoides were also present.

In summer when the substrate dried out completely, water milfoil and Azolla friliculoides persisted longest. Eventually they too died and the substrate reverted to dry dirt. When autumn rains came, pasture plants invaded this area and were heavily grazed by cattle, sheep and pukeko.

## 4. Swamp

This occupied the central lagoon area, dominated by Typha muelleri (raupo). Other species infrequently present included water buttercup and ryegrass.

## 5. Water

This region comprised the lagoon's surface. The plants consisted of submerged and emergent rooted species, submerged floating, and free floating aerial leaved plants. Submerged and emergent

rooted plants - Ranunculus fluitans (water crowfoot), watercress, Myriophyllum elatinoides (water milfoil), M. propinquum (water milfoil), Callitriche stagnalis (water starwort), Ottelia ovalifolia, Elodea canadensis (oxygen weed), Lagarosiphon major (oxygen weed), Egeria densa (oxygen weed), Aponogeton distachyus (Cape pondweed), Potamogeton crispus, and P. cheesemanii (pondweed).

Submerged floating plants (non-rooted) - Ceratophyllum demersum (hornwort) and Utricularia protrusa (bladderwort).

Free floating, aerial leaved plants - Azolla filiculoides, Lemna spp. (duck weed), and Spirodela oligorrhiza (duck weed).

### 2.1.3 Fauna

Birds noted at Hamilton's Lagoon during 1977/1978 included New Zealand Dabchick (Podiceps rufopectus). Black Shag (Phalacrocorax carbo), Pied Shag (P. varius), Little Shag (P. melanocleucus), White-faced Heron (Ardea novaehollandiae), Black Swan (Cygnus atratus), Paradise Shelduck (Tadorna variegata), Mallard (Anas platyrhynchos), Grey Duck (A. superciliosa), Grey Teal (A. gibberifrons), New Zealand Shoveller (A. rhynchotis), Australasian Harrier (Circus approximans), Pukeko (Porphyrio porphyrio melanotus), Banded Dottrel (Charadrius bicinctus), Pied Stilt (Himantopus himantopus), Dominican Gull (Larus dominicanus), New Zealand Kingfisher (Halcyon sancta), Skylark (Alauda arvensis), Welcome Swallow (Hirundo tahitica), Song Thrush (Turdus philomelus), Blackbird (T. merula), Yellow Hammer (Emberiza citrinella), Goldfinch (Carduelis carduelis), House Sparrow (Passer domesticus), Starling (Sturnus vulgaris), and White-backed Magpie (Gymnorhina tibicen hypoleuca).

Non-avian fauna included eels (Anguilla spp.), golden bell-frog (Litoria raniformis), Rattus sp. and domestic cattle and sheep. Invertebrates were not sampled extensively, but species important to pukeko included earthworms

(Lumbricus sp.) and the grass moth (Crambus flexuosellus).

## 2.2 Fell's Lagoon

### 2.2.1 General

On the property of Mr A. Fell, "Fell's Lagoon" is a willow (Salix spp.) covered swamp, 900 m. x 30 m., running approximately east/west, south of No. 1 Line, Tiakitahuna, and is 3.5 km north-east of Hamilton's Lagoon. (See "New Zealand Topographical Map" number 149, Department of Lands and Survey, Wellington, at grid reference 005310, approximately at 40° 23' 30" S. x 175° 30' E.). The lagoon is an oxbow of the Manawatu River, and may be older than Hamilton's Lagoon. Only pasture (dryland habitat) is discussed here, as the dense willow stand prevented observations of the central lagoon area.

### 2.2.2 Flora

The pasture was generally similar to that at Hamilton's Lagoon, being dominated by ryegrass and white clover, but an important difference between the two swards was the tiller length. At Fell's Lagoon pasture was grazed solely by horses and there always appeared to be food available for pukeko, even in late summer and early autumn 1978, when at Hamilton's Lagoon the drought and heavy grazing by sheep had greatly reduced the forage available for pukeko.

The central area of Fell's Lagoon consisted primarily of large Carex clumps and open water, which in spring was 1.8 - 2.0 m. deep around the margin, while the central area was deeper than 2.0 m. It was in the shallower water-saturated region that most of the willows grew, reaching a height of 10 - 15 m. and formed a dense canopy. Raupo was absent. A 2 m. wide strip adjacent to the water was dominated by rank pasture grasses including Anthoxanthum odoratum (sweet vernal), Bromus unioloides (prairie grass), Agrostis tenuis (brown top), A. stolonifera (creeping bent), chewings fescue and ryegrass.

A supplementary ration for horses, consisting primarily of crushed oats and barley, with additives of bran, hay and molasses, was fed twice daily between 08:15 - 09:15 and 15:30 - 16:30 hours. After the horses had eaten, pukeko would walk to the food bins, and feed. It is possible that individual pukeko learned to exploit this regularly appearing food, which probably influenced patterns of feeding.

### 2.2.3 Fauna

The species listed below are those seen during the twelve weeks spent at Fell's Lagoon: White-faced Heron, Mallard, N.Z. Shoveller, Australasian Harrier, Pukeko, Pied Fantail (Rhipidura flabellifera), Dominican Gull, N.Z. Kingfisher, Skylark, Welcome Swallow, Song Thrush, Blackbird, Silvereye (Zosterops lateralis), Goldfinch, House Sparrow, Starling, White-backed Magpie, Opossum (Trichosurus vulpecula), and Rats. Domestic stock included thoroughbred race horses, cattle and sheep. Invertebrates were not sampled.

### 3. METHODS

#### 3.1 Standard Observations

A total of 725 hours were spent observing pukeko from three permanent hides, elevated on 3.5 m. legs, between 21 March 1977 and 19 March 1978. Most birds observed were within 150 m. of the hides and often between 10 and 40 m. The year was divided into thirteen four-week periods (Fig. 2). Spring, summer, autumn and winter were defined as follows, from official sunrise and sunset data contained in "The Air Almanac", United States Government Printing Office (1976). Initially mid-summer and mid-winter solstices were determined, and from these dates, the spring and autumn equinoxes were established. The start of the season in question was then determined by the mid-points between the summer and winter solstices and the spring and autumn equinoxes.

Not all the seasons were of equal length (Fig. 2) - winter and spring being twelve weeks in duration while summer and autumn each totalled fourteen weeks. Spring consisted of Periods 1, 2, and 3; summer - 4, 5, 6, and 7/2; autumn - 7/2, 8, 9, and 10; and winter - 11, 12, and 13. Data from Period 7 were divided in half for amalgamation with either summer or autumn when seasons were being compared. Autumnal data were derived from observations recorded in both late autumn 1977, and early autumn 1978. However, as eight of the fourteen week's data were collected in 1977, results are presented for the autumn to summer year.

Standard observations consisted of four separate watches each week that collectively sampled the entire daylight period. Dense fog prevented observations on three occasions, and very strong winds, twice. No night watches were performed.

Hide watches provided data on the proportion of time spent by an "average" bird on a particular activity, and the intensity of feeding. Following Fordham (1978), the time spent by the birds on each activity was measured by recording, for every bird at five minute intervals, their

FIGURE 2

DIVISION OF YEAR

MONTH	APR	MAY	JUN	JUL	AUG	SEPT	OCT	NOV	DEC	JAN	FEB	MAR	
PERIOD	9	10	11	12	13	1	2	3	4	5	6	7	8
SEASON	AUTUMN		WINTER			SPRING			SUMMER			AUTUMN	

behaviour and surrounding habitat. Data collected at the end of each five minute interval was assumed to be directly representative of the proportion of time the birds allocated to a particular activity for that hour. Feeding rate was scored by noting the number of pecks delivered by a feeding bird in 30 seconds. This period was chosen after pilot observations indicated that few birds fed uninterrupted for longer than 30 seconds. In the analyses only those birds which fed throughout the entire 30-second interval were considered. Brief adoption during feeding of "Stand Look Round" or "Walk Look Round" (see Section 4.2) was ignored, and every effort was made to exclude unsuccessful pecks. Measurement of the number of paces taken per unit of time was not appropriate as the birds commonly paused to eat food held "parrot-like" in one foot.

An overall index of feeding "intensity" was obtained by combining both sets of data (Fig. 3). Feeding behaviour was separated into appetitive and consumatory feeding, and "other" activities, and the proportion of time spent by an "average" bird in consumatory feeding activities was converted to minutes of an hour for each habitat and season. From the mean number of pecks per 30-seconds, the number of pecks delivered by an "average" bird to any substrate per hour, was readily calculated.

For example:

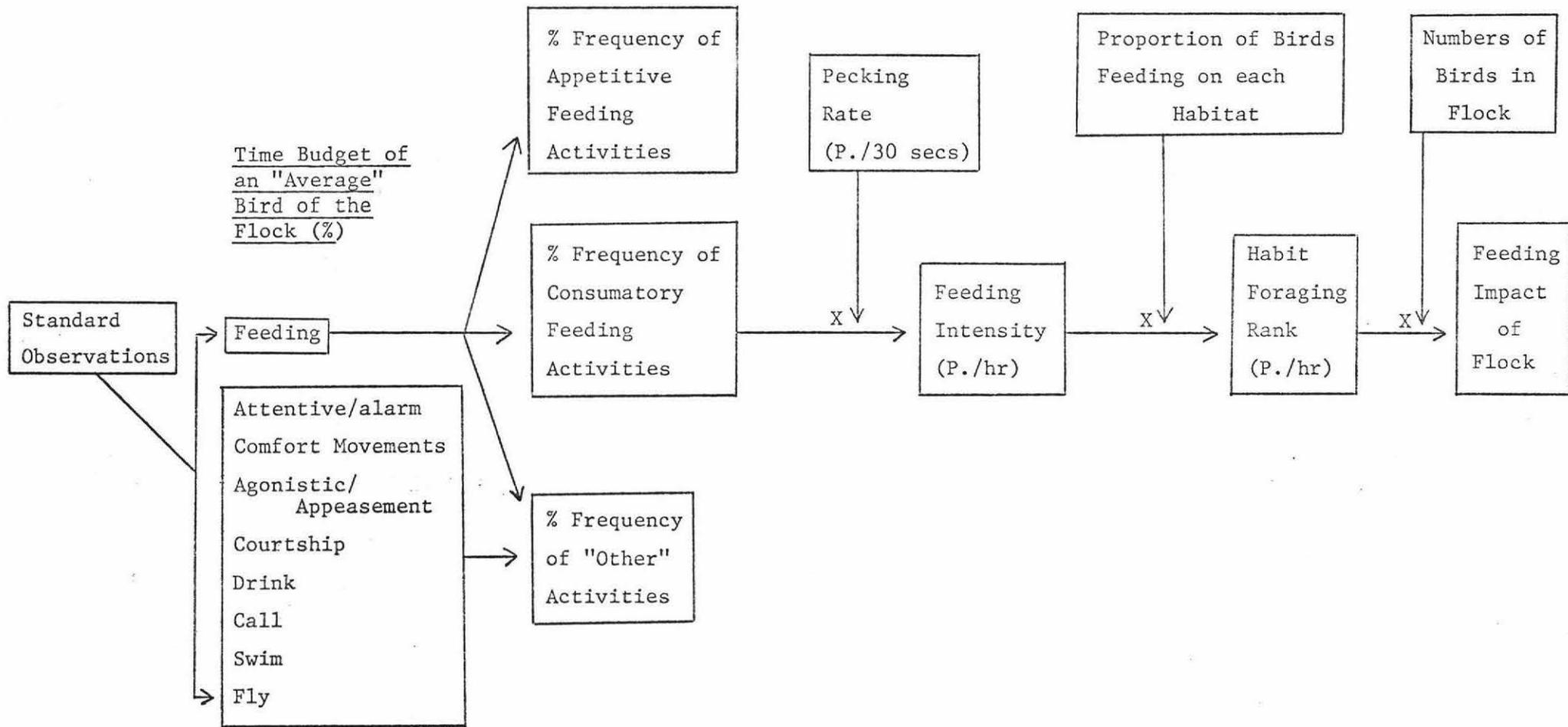
Season: spring  
 Period: first hour after sunrise  
 Habitat: dryland (pasture)

Category	n	Percent	
Feeding - consumatory	573	42.95	
- appetitive	557	41.75	
- other	3	0.23	"Other Activities"
Attentive/alarm	91	6.82	
Comfort Movements	60	4.50	
Agonistic/appeasement	33	2.47	
Courtship	13	0.98	
Drinking	0	0.00	
Calling	4	0.30	
Swimming	0	0.00	
Flying	0	0.00	
Total	<u>1334</u>	<u>100.00</u>	

$$\begin{aligned} \text{Mean pecks/30 secs.} &= \frac{964}{65} \\ &= \underline{14.83} \end{aligned}$$

$$\begin{aligned} \text{Therefore pecks/hour} &= \frac{42.95}{100.00} \times \frac{60}{1} \times \frac{2}{1} \times \frac{14.83}{1.00} \\ &= 764.34 \\ &= \underline{\underline{764}} \end{aligned}$$

FIG. 3 ANALYSIS OF DATA



Time allocated to various activities, seasonally and diurnally, in different habitats were compared by Chi-square, against the null hypothesis of equal distribution of activities over the day, season, or year. Calculated feeding intensities for different habitats, and "habitat foraging ranks" were compared also by Chi-square, against the null hypothesis of even distribution of total pecks, and use of available habitats for foraging over the day, season, or year. In all tests, significance was set at the five percent level (i.e.  $p > 0.05$ ).

Before each watch air temperature, cloud cover and presence/absence of dew, were recorded, and stock numbers in adjacent paddocks noted. After each watch, meteorological data taken included air temperature, rainfall, air maximum/minimum, and water maximum/minimum for the previous 24 hours, the water level of the lagoon, humidity (relative and absolute), and wind direction and velocity. Means for these data were calculated for each period and season (App. 1).

The species composition of the surrounding pasture was analysed monthly by a point analyser, and the state of the marginal vegetation and swamp was assessed visually and photographically. Above ground invertebrates inhabiting scotch and Californian thistles thickets were collected using a sweep net.

### 3.2 Gut Analysis

In September 1977 and again in March 1978, pukeko were collected on a permit from the New Zealand Wildlife Service from Fell's Lagoon, for analysis of stomach contents. For two weeks prior to September and March the activity and feeding rate of the Fell's Lagoon flock was monitored in the standard way established at Hamilton's Lagoon to test for comparable behaviour in the flocks. The birds were shot with a .22 rifle from a hide, or by stalking.

By spreading collections over several weeks, birds were sampled throughout the day, thereby providing a direct measure of diurnal changes in feeding intensity. Particular

care was taken to shoot birds near the end of each chosen feeding period (Tab. 1).

Immediately on being shot the bird's gut was injected with 15 ml of 10% formalin, to prevent further digestion of the contents. Usually within 12 hours, and never more than 20 hours after collection, the birds were weighed, dissected and sexed. Measurements taken, following Williams and Miers (1958), and Craig (1974), included the length of culmen plus shield, shield width, bill depth and the nares-to-tip length (Fig. 4 a&b ; App. 2).

Once removed the gut was divided into:

1. Oesophageal region - from mouth to inlet of proventriculus;
2. Gizzard region - including proventriculus and gizzard;
3. Gastric region - from the exit of the gizzard to the mid-point between the gizzard and the intestinal caecum;
4. Intestinal region - from the mid-point just mentioned to the anus.

The lengths of these regions were measured to the nearest 0.5 cm and then stored in 10% formalin. Later contents were washed from the gut onto a 1 mm mesh screen, where any grit was removed. On two occasions, when this method was unsuccessful, grit and fine plant remains were separated by the use of a sugar solution of 1.4 S.G. The residue was filtered through a millipore filter (gauge c. 1 mm) under a slight vacuum. Except for the gizzard, the residue was then dried to a constant weight at 80°C. for 24 hours.

Gizzard contents were weighed while wet and a sub-sample of one-tenth wet-weight taken, in which the lengths of separate plant pieces were measured in units of 2.5 mm under a stereomicroscope. These measurements indicated the length of pieces of plants taken at a peck. Well masticated vegetation was not measured. The whole gizzard sample was finally dried and weighed as above.

### 3.3 Moult

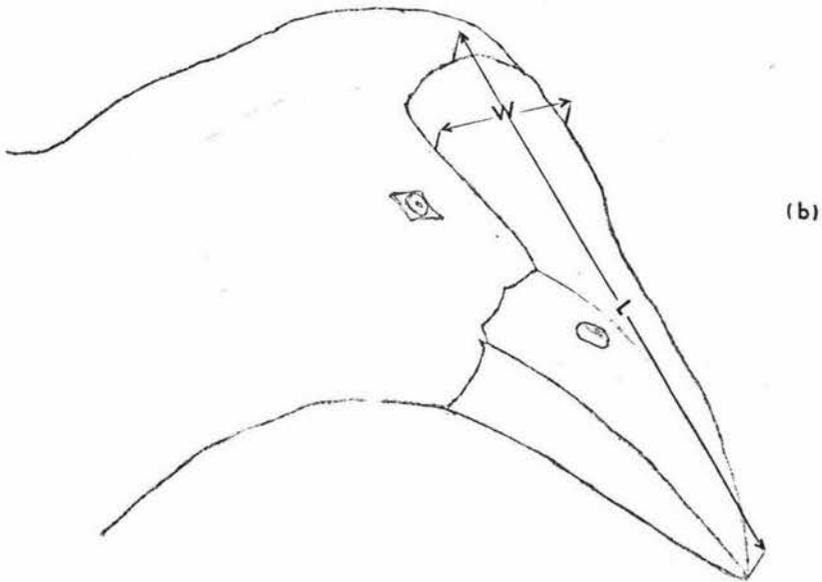
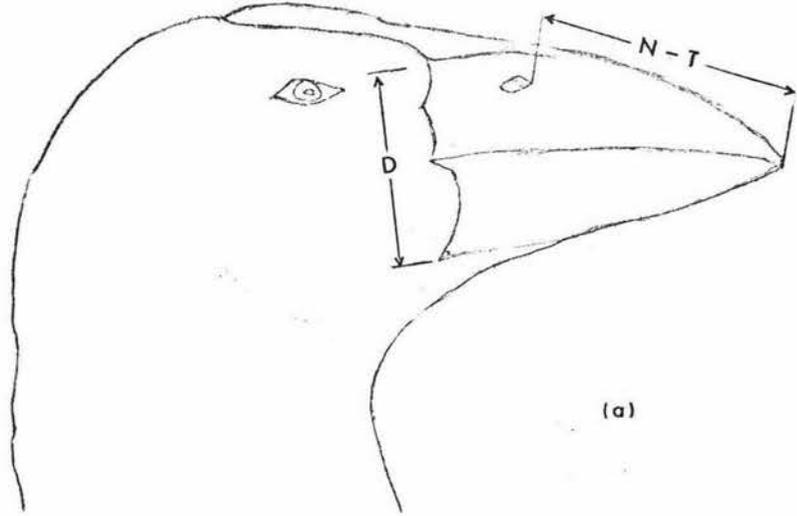
The moult season of pukeko was also investigated (App. 3).

TABLE 1

DIVISIONS OF THE "PUKEKO-DAY" FOR DIRECT SAMPLING

Divisions Periods	SR - +2	+2 - +4	+4 - Midday Midday - -4	-4 - -2	-2 - SS	Photoperiod
1/2 August/ September	06:45 - 08:45	08:45 - 10:45	10:45 - 12:19 12:19 - 13:53	13:53 - 15:53	15:53 - 17:53	11:08 hours
8 MARCH	06:31 - 08:31	08:31 - 10:31	10:31 - 12:23 12:23 - 14:14	14:14 - 16:14	16:14 - 18:14	11:43 hours

0 1 2 3 cm



#### 4. DESCRIPTION OF BEHAVIOUR

In total, over fifty separate activity patterns, arising from nine categories of behaviour, were recognised. Feeding was by far the most important category, followed by agonistic/appeasement, comfort movement and attentive/alarm categories, while the remaining categories, drinking, courtship, swimming, flying, and calling, either showed strong seasonal fluctuations and/or were of little importance in the overall time-budget of the birds. What follows is a description of the behavioural repertoire of the pukeko.

##### 4.1. Feeding

For the purpose of calculating feeding intensities (see p. 17) pukeko feeding activities were separated into appetitive, consumatory, and "other" components.

##### Appetitive or "Food Locating" Activities

###### 1. "Walk Look Down" - WLD

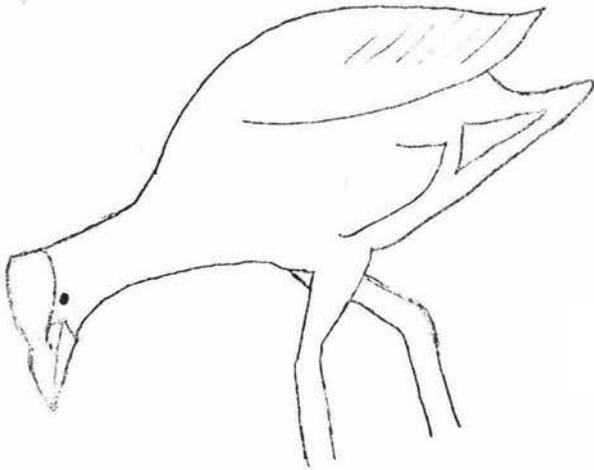
WLD and "Stand Peck" (see below) were the most commonly recorded activities. WLD was described as that behavioural pattern followed when a bird walked with its head held low and was "looking" at the ground. (Fig. 5a)

###### 2. "Stand Look Down" - SLD

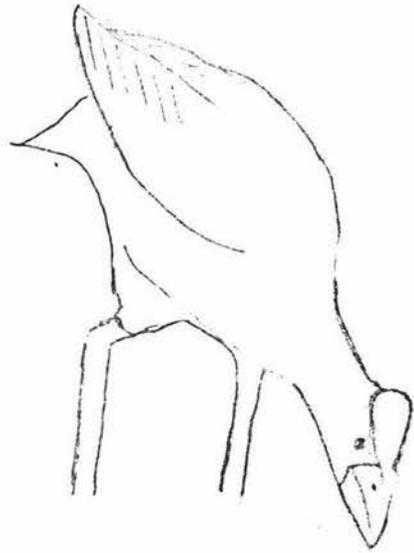
Although frequently pursued for only a short time, almost invariably prior to pecking, SLD contributed significantly to the overall time spent in appetitive activities. In this activity the stationary bird held its head close to the ground but did not feed.

###### 3. "Turn-over Cow Pad" - TOCP

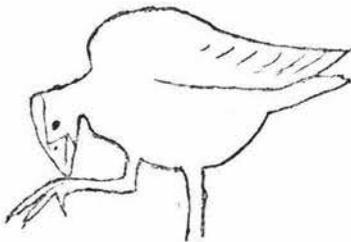
Seen almost exclusively in spring and winter this activity involved grasping "bills-full" of cow manure, and scattering it. When cow pads or sheep faeces were dry, birds simply flicked them over with the bill.



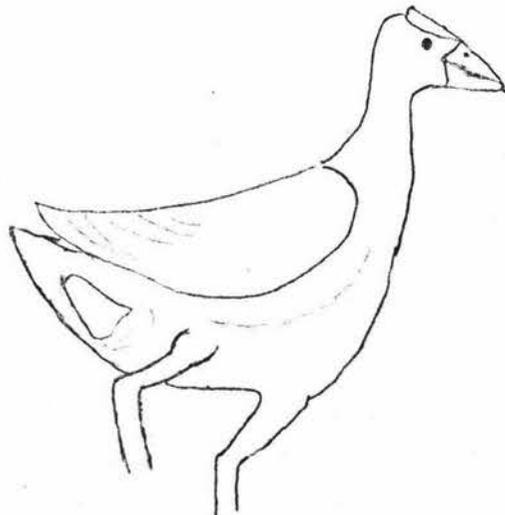
(a)



(b)



(c)



(d)

4. "Trot-food" - TF  
In this rarely seen activity the bird ran or "trotted" while looking down for food.
5. "Run After Food" - RAF  
RAF described the pursuit of an aerial invertebrate, usually over a short distance, (80 - 120 cm), and was seen occasionally during summer and autumn.

#### Consumatory Feeding Activities

1. "Stand Peck" - SP  
Accounting for the bulk of consumatory feeding activities, SP described a stationary bird pecking at the substrate. (Fig. 5b)
2. "Walk Peck" - WP  
In this posture the peck was delivered while the bird was walking rather than standing.
3. "Peck From Foot" - PFF  
Perhaps the most distinctive of all feeding postures for pukeko, this behaviour comprised pecking at plant food held "parrot fashion" in the foot. Food was held in either foot, on the pad between the three anteriorly-directed toes, and the single posteriorly-directed toe. Plants were held in the foot while still rooted, or pulled completely out of the ground, the birds pausing sometimes to pull the plant further through the foot before eating more. This activity was noted previously in pukeko by Hutton (1871), Buller (1877), Travers (1882), and Stubbs (1959) and in other species by Vielliard (1974) for purple gallinule, Williams (1960) for takahe, and Rowley (1968) for bald coot (Fulica atra). (Fig. 5c)
- 4a. "Tug"  
Usually associated with PFF, Tug was the posture in which pukeko grasped a plant that it intended to eat, with its bill, and pulled back vigorously. Birds sometimes fell over backwards during vigorous tugging efforts. Once pulled out, the plant was usually held in the foot, and eaten (PFF), but if

broken, the pieces were swallowed directly. In the field it was extremely difficult to distinguish between Tugs that were successful with fragmented plant material, and those that were totally unsuccessful.

4b. "Dabble"

Dabble, the aquatic equivalent of Tug, involved plunging the head and neck into the water, grasping some vegetation with the bill, and then jerking upwards. Once exposed the plants were usually held in the foot, as for PFF, and then eaten. Similar activities have also been described for purple gallinule (Frost, 1975), and bald coot (Anon., 1947).

5. "Stand Strip"

In this activity, a stationary pukeko ran its partially open bill up the stem of a grass seed head, stripping the seeds from the stem as it went. Plants eaten this way included ryegrass, Yorkshire fog, floating sweet grass, and dock.

6. "Rest-sit-peck" - RSP

RSP, was mostly seen about midday, when birds occasionally lay down on one wing, and proceeded to partially cover themselves with grass. Once covered, birds then switched between "Rest sit", "Sleep" (see later), and RSP - the latter activity involving plucking and eating grass within reach.

7. "Swim and Feed"

This activity consisted of swimming, with wings and tail held high above the water, and pecking at the leaves of submerged plants that approached the water's surface.

#### "Other" Feeding Activities

This category included activities that were neither appetitive nor consumatory. Collectively, however, none of the following contributed significantly to the overall feeding time-budget.

1. "Food Wetting" - FW  
FW consisted simply of placing food (e.g. grass or raupo) in water, from where it was taken up, held in the foot and eaten (PFF). The function of this rarely observed activity which has also been described for Buff-backed heron (Ardeola i ibis) (Goodwin, 1948), is unclear.
2. "Parent Feeds Chick" - PFC  
PFC described the sequence of activities involved in the presentation of food by an adult to a chick and the subsequent acceptance of the food.
3. "Allo-Feeding"  
In this activity, both birds faced each other in the "Bow" posture (see below). Food was passed backwards and forwards between the birds, for several minutes, until eaten. Craig (1974, 1977) described a similar activity and, believing it to be used in courtship termed it "Courtship Feeding".
4. "Carry Food"  
In this activity an adult carried food in the bill to water, a chick, or another adult.
5. "Pukeko Takes Duckling" - PTD  
Recorded only once during the breeding season of the Mallard duck, pukeko took ducklings on three other occasions, two of which ended with the death of the one- or two-day old ducklings.  
An edited extract from field notes on 18 October, 1977, describes the taking and disembowelling of a duckling:  
"...The duckling was alive. The pukeko carries the duckling in its bill by one leg. The parent duck makes repeated attempts (chases) to induce the pukeko to release the duckling - unsuccessful; she leaves helpless duckling and returns to her brood; pukeko returns to the water's edge; head region of duckling opened - decapitated and being fed to the three chicks of Sw<sub>1</sub> territory. ...Strips of meat are being taken off the duckling's breast, which is either eaten by the adult or passed onto the chicks; adult removes down from the duckling, by taking bills-full of it, and then washing out its

bill with water; the duckling is held in the foot and eaten by the parent ..."

On another occasion, an adult pukeko, carrying a duckling in its bill away from the water, was pursued in flight by the parent duck, which hit the fleeing pukeko in the back of the neck and tumbled it over. The duckling was released and slowly made its way back to the water, under the watchful guard of its parent - the pukeko remaining at some distance.

#### 4.2 Attentive/alarm

The activities "Walk Look Round"/"Stand Look Round" and "Fly-escape" represented the two extremes of a continuum, along which all other activities included in this category were placed. The activities are described in order of increasing escape tendency.

1. "Walk Look Round" - WLR

In this activity the bird assumed an upright posture with the neck vertical. Direct observations showed the bird was looking around while walking, in a state of general attentiveness. (Fig. 5d)

2. "Stand Look Round" - SLR

SLR was the same in context as WLR, only that the bird was stationary.

3. "Alert"

Pukeko exhibited this behaviour while either walking or standing still. Almost invariably anxiety was reflected by "tail-flicking" - the white under-tail coverts being briefly and repeatedly exhibited when the tail was lifted and then dropped. Body feathers were sleeked and the bird was very erect, and continually looked round. A short sharp call was sometimes emitted.

4. "Alarm"

This behaviour described active displays against all predators (except Man), in which pukeko congregated, usually as close to cover as possible, with wings slightly drooped, tail feathers splayed, body feathers ruffled, and giving loud calls. With

Harriers and sometimes Magpies, pukeko would group together, giving alarm calls, and if the Hawk swooped or came low enough, the pukeko would fly up and attack with feet and beak. Hawks behaved warily and actual contact was never observed.

5. "Run-escape"

This activity was seen most often in chicks and adult pukeko that were disturbed away from cover. Rapid tail-flicking occurred, body feathers were sleeked, and the birds ran for cover, with their neck and body parallel to the ground.

6. "Fly-escape"

In this activity, escaping pukeko flew directly for cover, usually as a response to the sudden appearance of aerial predators near the nest or young. During winter, whole flocks feeding far out in paddocks in late afternoon, sometimes escaped this way from swooping Magpies.

#### 4.3 Comfort Movements

The various activities described under comfort movements are readily recognisable and, with some exceptions, will not be detailed here.

1. "Preen"

Preen included sunbathing as well as other bodily maintenance.

2. "Stretch"

Stretch was recorded when the wing and/or legs were stretched posteriorly.

3. "Rest-stand"

This was an upright relaxed stationary, non-anxious state.

4. "Rest-sit"

This was a relaxed stationary, non-anxious bird lying down.

5. "Sleep"

Sleep was rarely observed, but took place in the Rest-sit position.

6. "Shake"

This involved the fluffing and ruffling of feathers.

## 7. "Bathe"

Bathe consisted of the usual bathing behaviour of anterior ducking and wing-rubbing movements.

## 8. "Bow and Nibble"

Previously described by Tunnicliffe (1965) and Craig (1974, 1977), and known as "Allo-preening" by the latter author, this behaviour was followed when one bird presented its head and neck, with eyes closed and accompanied by soft calls, to another bird. The first bird usually pursued a "Bow" posture (see below), to which the second bird responded by "nibbling", (i.e. preening) the neck and head region of the first bird.

## 9. "Skip and Fly"

In this activity a bird took a few steps with its wings out-stretched, jumped in the air and flapped its wings. While in the air it twisted and turned, flying first one way, then another. This sequence of activities was repeated a number of times. Its function is unclear.

4.4 Agonistic/appeasement

Some activities in this category ("Aggressive Upright", "Anxiety Upright", and "Bow"), are taken directly from Craig (1974, 1977), and will be described only briefly here.

## 1. "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. A bird in an Aggressive Upright nearly always faced its opponent and occasionally advanced towards it ..." Craig (1974, 1977).

## 2. "Anxiety Upright"

"...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. Orientation was variable ..." Craig (1974, 1977). Intermediates between these two extremes of behaviour described above were frequently observed.

3. "Bow"

"This posture was extremely variable, ...the important unifying feature was that the bill pointed vertically downwards at the ground...", Craig (1974, 1977).

Included under this broad heading are the "Head", "Full" and "Body" bows (recognised by Craig, 1974, 1977), which were seen as variations in the bill and body orientation, and also in the wing and tail postures.

4. "Fight"

Birds belonging to the same territory were not seen to Fight, however, skirmishes were common between birds of neighbouring territories. Usually encounters were short, although prolonged fighting between members of adjacent territories was sometimes observed. The birds would fly up face-to-face and try to force their opponent, by means of wing blows and ripping movements of the feet, into a position where it could not deliver a peck. Once, seven birds were observed fighting in the same territorial dispute.

5. "Chase"

This involved a dominant bird running after a subordinate after appeasement behaviour had failed or was not performed in time. Pukeko also chased a number of other birds, including N.Z. Dabchicks, Mallards, N.Z. Shovellers, Australasian Harriers, Pied Stilts, and small passerines (e.g. Goldfinches and House Sparrows). Usually assumption of the Aggressive Upright posture was sufficient to put most birds to flight, but sometimes a charge would

follow. Harriers were vigorously attacked by groups of two or more pukeko, particularly when close to the nest or young (see "Alarm").

6. "Flight"

Flight described the escape of pukeko to their territory, to avoid a pursuing neighbour.

7. "Splatter"

Both the pursued and the pursuer were seen splattering, which involved running and wing-flapping, in attempts to increase speed and also to retain balance.

#### 4.5 Courtship

Although Craig (1974, 1977) recognised seven distinct sexual postures, I recorded only three - "Courtship Chase" (known as Sexual Upright by Craig, 1974, 1977), "Precopulatory Position" and "Copulation", the latter two following Craig (1974, 1977). The "Courtship Chase" activity lasted, at the most one or two minutes, but more usually only five to fifteen seconds, while "Precopulatory Position" and "Copulation" were of only one to five seconds duration. The short duration of the entire courtship process may have prevented a more detailed recognition of the other postures. In addition to the above Craig (1974, 1977) identified four other postures - "Allo-preening", which appeared to be very similar to the activity described as "Bow and Nibble" (see above), and "Courtship Feeding" (here called "Allo-feeding", see above), were two such postures. Two other postures, "Sexual Forward" and "Precopulatory Hunch" (Craig, 1974, 1977), which momentarily precede "Precopulatory Position", were not observed.

1. "Courtship Chase"

A bird, usually a male, approached another from behind, and continually uttered a low monotonic call ("Humming Call" - Craig, 1974). If the front bird moved off then a short "chase" ensued, concluding with the leading bird in a hunched-over posture. In both birds the wings and tails were generally down.

2. "Precopulatory Position"

After the "Courtship Chase", the leading bird stood

with its head bent forwards between its legs, its wings slightly spread, and its scapulars raised. Meanwhile the pursuing bird continually called.

### 3. "Copulation"

Mounting the leading bird, which was in the "Pre-copulatory Position", the trailing bird treaded, copulated and then dismounted anteriorly, over the female. Immediately prior to cloacal contact, the male, who throughout the entire copulatory process uttered "Humming Calls" (Craig, 1974), balanced himself by flapping his wings.

#### 4.6 Drinking

Pukeko usually drank water from the lagoon, but sometimes collected water from grass tips, particularly after sunrise on cool mornings, or following heavy rain in late winter. In addition, they drank water droplets which had condensed on fence wire during fog.

#### 4.7 Calling

This category included all calls except those associated with alarm reactions and copulation.

#### 4.8 Swimming

Though lacking webbed feet, pukeko are apt swimmers, holding both wings and tail high above the water. Tunnickliffe (1965), reported that they will dive to escape predators, but this was not observed.

#### 4.9 Flying

This activity described all flying for feeding or dispersal, other than that clearly associated with escape.

## 5. TIME BUDGET AND FEEDING ECOLOGY - COMPOSITE DAY

### 5.1 Introduction

A total of 110,263 bird-observations were recorded over 725 hours spent in hide watches at Hamilton's Lagoon. The time pukeko allocated to each activity was calculated as a proportion of the total observations recorded, and from these data annual and seasonal time-budgets were constructed, for a composite day and diurnally.

### 5.2 Annual Time Allocation

Combination of data from all hourly intervals and seasons allows expression of the annual time-budget for an "average" bird of the flock (Tab. 2). From pooled observations of all habitats, pukeko spent 80.7% of their time feeding, 9.3% in attentive/alarm activities, 6.5% in comfort movement activities, and 1.6% in agonistic/appeasement encounters. Other activities contributed 2.0% to the overall time-budget - courtship 0.3%, drinking 0.2%, swimming 0.8%, calling 0.1%, and flying 0.6%.

Time spent feeding accounted for most observations in all habitats, except water, occupying more time in pasture, mud and rush margins, than in swamp, while that spent in attentive/alarm postures was similar in all habitats. Comfort movements took up most time in swamp, with rush margins, mud and dryland following, while agonistic/appeasement encounters were infrequently observed in all habitats. In rush margins and swamp, remaining time comprised drinking, calling and courtship activities, while for mud, drinking and courting made up the remainder. In dryland residual time was spent courting and calling, and in water birds recorded swimming made up the balance of observations. The null hypothesis that pukeko spent equal time in all activities in all habitats was rejected ( $p < 0.001$ ).

### 5.3 Annual Habitat Utilisation

Proportional use of each habitat by an "average" bird of the flock was determined by scoring the habitat within which each activity was observed. Data pooled by hour and season indicated the annual distribution of birds according



to habitat. When observations from all activities were combined, dryland was the habitat most frequently used, followed by rush margins, mud and swamp (Tab. 3). The remaining observations included birds recorded in water and in flight.

Dryland was used mostly for agonistic/appeasement encounters, feeding, attentive/alarm, courtship, and calling activities. Comfort movements were observed less frequently on dryland than in the rush margin, which was the second most frequently exploited habitat, where birds drank, called, courted, looked about, fed and interacted socially.

Comparatively few birds courted, fed or were engaged in bodily maintenance or attentive/alarm activities, in mud, while even fewer birds were seen drinking, calling or in agonistic/appeasement postures.

Swamp was used occasionally as indicated by the number of birds recorded in con-specific encounters, attentive/ alarm activities, feeding, courting or drinking, although the proportion of birds in swamp observed calling or engaged in bodily maintenance activities was appreciable.

Feeding in water was of little significance. Chi-square tests ( $p < 0.001$  in every case) indicated pukeko did not preen, feed, court, drink or call, nor were they equally attentive or aggressive in all habitats.

#### 5.4 Feeding

##### 5.4.1 Appetitive and Consumatory Feeding and "Other" Activities

From data pooled by hour, season, and habitat, pukeko spent 47.7% of their time in consumatory feeding, 32.5% in appetitive feeding, and 19.8% in "other" activities (Tab. 4). Analysis of each habitat indicated a similar allocation of time to eating in pasture and rush margins, while in mud, proportionally more time was spent consuming food. For swamp and water, the birds spent less time eating, while time spent looking for food was greatest in dryland, least in rush margins, with swamp and mud intermediate. The remaining time for all habitats was assigned to "other"

TABLE 4  
ANNUAL ALLOCATION OF TIME TO APPETITIVE  
AND CONSUMATORY FEEDING AND "OTHER" ACTIVITIES - COMPOSITE DAY

HABITAT \ ACTIVITY		APPETITIVE FEEDING	CONSUMATORY FEEDING	"OTHER"	TOTAL
DRYLAND	n	29,123	36,456	10,816	76,395
	%	38.1	47.7	14.2	100.0
RUSH MARGIN	n	4,338	10,813	6,623	21,774
	%	19.9	49.7	30.4	100.0
MUD REGION	n	1,201	3,416	1,076	5,693
	%	21.1	60.0	18.9	100.0
SWAMP	n	1,206	1,743	1,800	4,749
	%	25.4	36.7	37.9	100.0
WATER	n		205	860	1,065
	%		19.25	80.75	100.0
(FLY)	n			587	587
	%			100.0	100.0
ALL HABITATS COMBINED	n	35,868	52,633	21,762	110,263
	%	32.5	47.7	19.8	100.0

activities, occupying proportionally more time in water, swamp and rush margins, than in dryland and mud. Between the habitats unequal time was allocated to appetitive feeding ( $p < 0.001$ ) and consumatory feeding ( $p < 0.001$ ), and "other" ( $p < 0.001$ ) activities.

#### 5.4.2 Peck Rate - Feeding Intensity

Composite data for all seasons, habitats and hourly intervals resulted in an "average" pecking rate of 18.9 pecks per 30 seconds (Tab. 5). Pukeko pecked unequally in the habitats ( $p < 0.001$ ). Analysis by habitat showed birds in mud and rush margins pecked fastest, while those in pasture, water and swamp were slower.

Over the entire year feeding intensity was highest in mud and rush margins and lowest in water. With habitat data pooled the "average" number of pecks delivered per hour was 1085.

#### 5.4.3 Habitat Foraging Rank

The proportional contribution (or rank) of each habitat to the overall feeding strategy of an "average" bird of the flock at Hamilton's Lagoon, was calculated (Tab. 5) by multiplying the feeding intensity for a habitat by the proportion of the flock observed feeding there. Dryland and rush margins contributed most and were succeeded by mud region and swamp, while water was least important. The hypothesis that each habitat contributed equally to the overall feeding strategy was rejected ( $p < 0.001$ ). The proportional contribution of each habitat to the total number of pecks delivered per hour followed the rank described above (Tab. 5).

### 5.5 Discussion

The annual expression of data acts as a general introduction to the time budget and aspects of pukeko feeding ecology. Previous workers such as Buller (1877), McLean (1902), Oliver (1930), Muggeridge and Cottier (1932),

TABLE 5  
ANNUAL PECK RATE, FEEDING INTENSITY AND HABITAT  
FORAGING RANK - COMPOSITE DAY

HABITAT	PECK RATE (Pecks/30 secs)	FEEDING INTENSITY (Pecks/hour)	HABITAT FORAGING RANK	
			(Rel. no. pecks /hour)	(% of total pecks)
DRYLAND	n = 4,027 16.86	965	713.5	67.72
RUSH MARGIN	n = 1,636 22.99	1,370	235.7	22.37
MUD REGION	n = 562 25.82	1,549	81.3	7.72
SWAMP	n = 484 14.94	659	22.2	2.11
WATER	n = 71 15.65	369	0.9	0.08
ALL HABITATS COMBINED	n = 6,780 18.93	1,085	Tot. = 1,053.6	Tot. = 100.00

Tunnicliffe (1965), Carroll (1966), McKenzie (1967), and Craig (1974), recognised the pukeko primarily as a vegetarian. Annually for combined habitats and for each habitat except water, feeding activities occupied over 75% of the bird's time - an effort undoubtedly related to the pukeko's grazing mode of foraging, and to the quality of food ingested.

Excepting rush margins, the next greatest proportion of time was spent "looking round" (attentive/alarm) and in bodily maintenance. However of the remaining categories of behaviour, only agonistic/appeasement encounters were relatively frequently recorded, with other less important or less time demanding activities (e.g. drinking or courtship) making up the balance of time.

Birds rested most, and fed but little in swamp. Rush margins were used more than mud or dryland for loafing, but less for feeding. Birds appeared equally attentive in all habitats.

Over the year pasture was by far the most frequently used habitat during daylight hours, followed in turn, by rush margins, mud, swamp and water. This pattern of use applied to all activities, except comfort movements or drinking, when rush margins were most frequently used. Dryland was the most important foraging site, the area over which most con-specific disputes and calling birds were recorded, the most important courting substrate, the habitat on which fewest birds drank, and the habitat that afforded least protection as evidenced by the highest proportion of attentive birds, and by lowest occurrence of loafing and preening.

In all activities (except drinking) rush margin was intermediate to dryland on the one hand, and mud and swamp on the other. However, apart from being used more frequently than mud as a loafing area and for calling, swamp was used less frequently for all other activities. In water the birds mainly swam.

### Foraging

In all habitats except swamp and water, consumatory

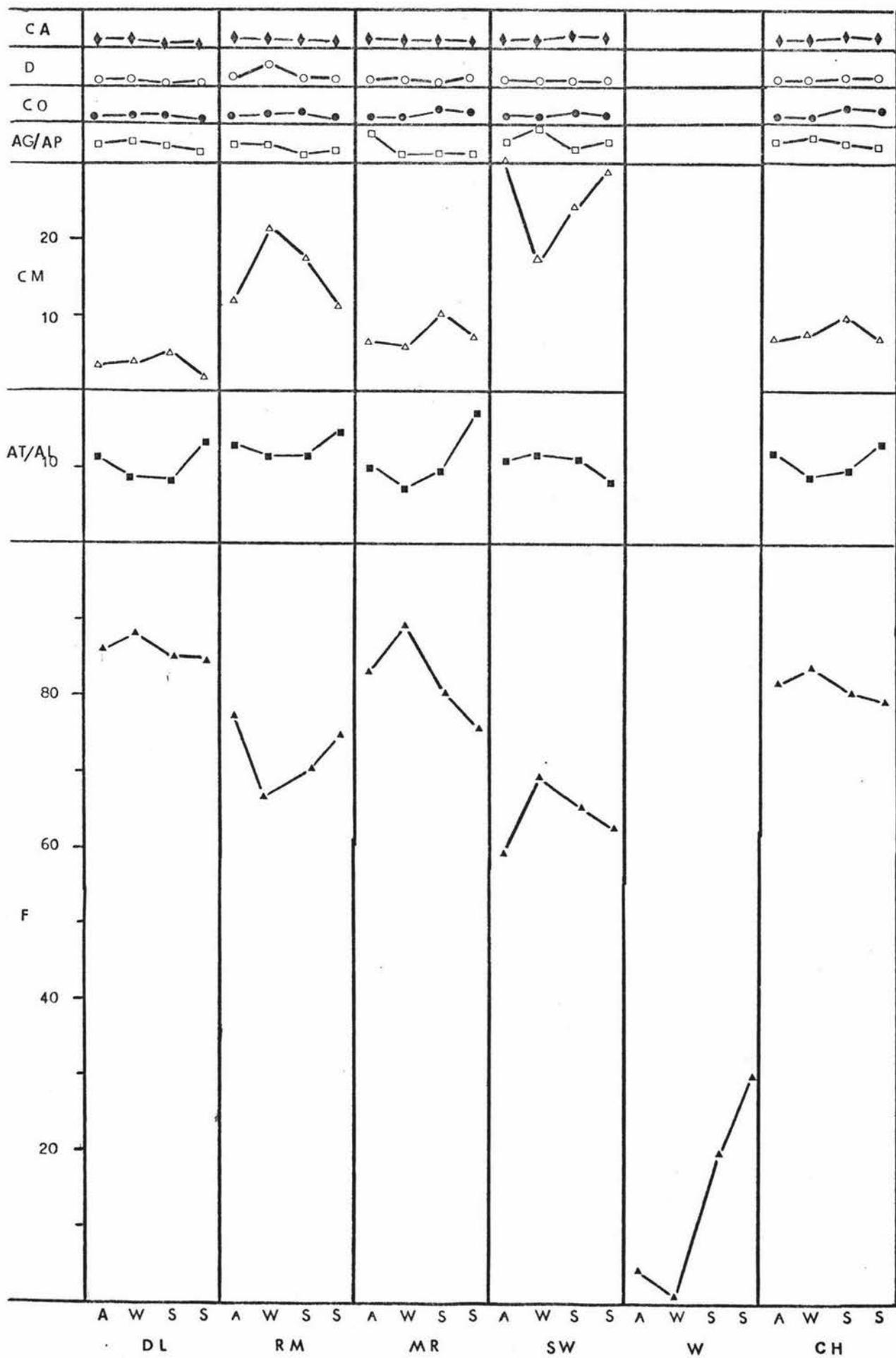
feeding was the most frequent activity, followed on dryland and mud by appetitive feeding, and in rush margins by "other" activities. This indicated that the birds searched more selectively for food in dryland and mud, and less selectively in rush margins, allocating more time to "other" activities here. Birds in swamp were recorded more frequently in "other" activities and eating, and less often in looking for food, indicating that food was apparently readily available, although perhaps less desirable than pasture or marginal vegetation. The greater availability of forage in swamp meant the birds could spend more time pursuing "other" activities here (e.g. comfort movements, courtship, etc.).

Birds pecked faster and more intensely in mud, rush margins and pasture than in swamp or water - the areas in which least time was spent eating. In general, annual peck rate, feeding intensity and habitat foraging rank data support the hypothesis that in terms of both the time spent eating, and the rate at which food was consumed, pukeko may have fed most in those habitats (e.g. pasture) where the availability and/or quality of food was greatest. Thus they may have capitalised on differences in the availability (quality) of forage between feeding areas, by feeding more keenly where food was apparently more available, or of a higher quality (i.e. in pasture, rush margins, and mud) than where food was less available or of a lower quality (i.e. in swamp and water).

#### 5.6 Seasonal Time Allocation

Seasonal variation in time allocated each day to various activities was analysed for all habitats combined and for each habitat separately (Fig. 6, Tab. 6).

Pooled habitat data showed most time was spent feeding, which occurred most frequently in winter, decreased in spring and summer, and increased again in autumn. Attentive/alarm activities were more frequently observed in summer and autumn, than in winter and spring, while time allocated to comfort movements, showed a reciprocal pattern. Over the



TAB. 6 SEASONAL TIME ALLOCATION (COMPOSITE DAY)

SEASON	ACT. HAB.		F.	AT/AL	CM	AG/AP	CO	D	CA	S	FLY	TOT.
	n	%										
AUTUMN	DL	n	11336	1376	344	227	4		1			13288
		%	85.31	10.35	2.59	1.71	0.03		0.01			100.00
	RM	n	2651	408	381	52		10	2			3504
		%	75.66	11.64	10.87	1.48		0.29	0.06			100.00
	MR	n	313	34	21	12						380
		%	82.37	8.95	5.52	3.16						100.00
SW	n	657	111	333	23			1			1125	
	%	58.40	9.87	29.60	2.04			0.09			100.00	
W/-	n	3							80	103	83/103	
	%	3.61							96.39	100.00	100.00	
CH.	n	14960	1929	1079	314	4	10	4	80	103	18483	
	%	80.94	10.44	5.84	1.70	0.02	0.05	0.02	0.43	0.56	100.00	
WINTER	DL	n	30021	2497	997	692	30	8	23			34268
		%	87.60	7.29	2.91	2.02	0.09	0.02	0.07			100.00
	RM	n	5061	797	1569	119	25	138	10			7719
		%	65.56	10.33	20.33	1.54	0.32	1.79	0.13			100.00
	MR	n	1423	101	78	3		2				1607
		%	88.55	6.29	4.85	0.19		0.12				100.00
SW	n	708	116	172	34		2	2			1034	
	%	68.47	11.22	16.64	3.29		0.19	0.19			100.00	
W/-	n								165	182	165/182	
	%								100.00	100.00	100.00	
CH.	n	37213	3511	2816	848	55	150	35	165	182	44975	
	%	82.74	7.81	6.26	1.89	0.12	0.33	0.08	0.37	0.40	100.00	
SPRING	DL	n	13343	1252	680	307	123		28			15733
		%	84.81	7.96	4.32	1.95	0.78		0.18			100.00
	RM	n	3964	611	961	33	47	27	17			5660
		%	70.04	10.79	16.98	0.58	0.83	0.48	0.30			100.00
	MR	n	2544	290	305	11	39	2	1			3192
		%	79.70	9.09	9.56	0.34	1.22	0.06	0.03			100.00
SW	n	673	108	244	9	5	1	5			1045	
	%	64.40	10.33	23.35	0.86	0.48	0.10	0.48			100.00	
W/-	n	65							281	106	346/106	
	%	18.79							81.21	100.00	100.00	
CH.	n	20589	2261	2190	360	214	30	51	281	106	20882	
	%	78.94	8.67	8.40	1.38	0.82	0.11	0.19	1.08	0.41	100.00	
SUMMER	DL	n	11057	1683	171	146	37		12			13106
		%	84.37	12.84	1.31	1.11	0.28		0.09			100.00
	RM	n	3621	688	506	37	8	22	9			4891
		%	74.03	14.07	10.35	0.76	0.16	0.45	0.18			100.00
	MR	n	387	84	34	1	4	3	1			514
		%	75.29	16.34	6.61	0.20	0.78	0.58	0.20			100.00
SW	n	963	111	429	31	2	1	8			1545	
	%	62.33	7.18	27.77	2.01	0.13	0.06	0.52			100.00	
W/-	n	137							334	196	471/196	
	%	29.09							70.91	100.00	100.00	
CH.	n	16165	2566	1140	215	51	26	30	334	196	20723	
	%	78.01	12.38	5.50	1.04	0.25	0.13	0.14	1.61	0.94	100.00	

four seasons fairly similar time was spent in agonistic/ appeasement encounters, being greater in winter and autumn, than in spring and summer. Courting birds were seen mostly in spring and at lower levels during summer and winter, while none were recorded during autumn. The remaining observations for each season were of birds drinking, swimming, flying or calling.

Taking the habitats separately, time allocated to feeding in pasture accounted for most observations in each season. Feeding occurred at similar levels throughout spring, summer and autumn, and at a slightly higher level in winter. The birds were most attentive during summer, being observed progressively less often during autumn, winter and spring, whereas time allocated to bodily maintenance increased progressively from summer, through autumn and winter, to peak in spring. Pukeko were observed in encounters more often in winter and spring, than in summer and autumn, and courted more often in spring, than in summer and winter, while this activity was absent in autumn. Birds observed calling in dryland in spring, summer and winter comprised the remaining time.

Birds in rush margins fed least during winter, and progressively more frequently during spring, summer and autumn. Time spent in attentive/alarm was greater in summer than in winter, with spring and autumn intermediate, while that allocated to bodily maintenance was greater during winter and spring, than during summer or autumn. Conflict encounters increased progressively from a spring minimum through summer, to autumn and winter maxima, whereas courtship activities peaked in spring, were absent in autumn and at low levels during summer and winter. Winter was the only season in which appreciable time was spent drinking and for all seasons the remaining time was spent calling.

In mud proportionally more time was spent feeding in winter than during either spring, autumn or summer, accounting for the bulk of observations in all seasons, while that

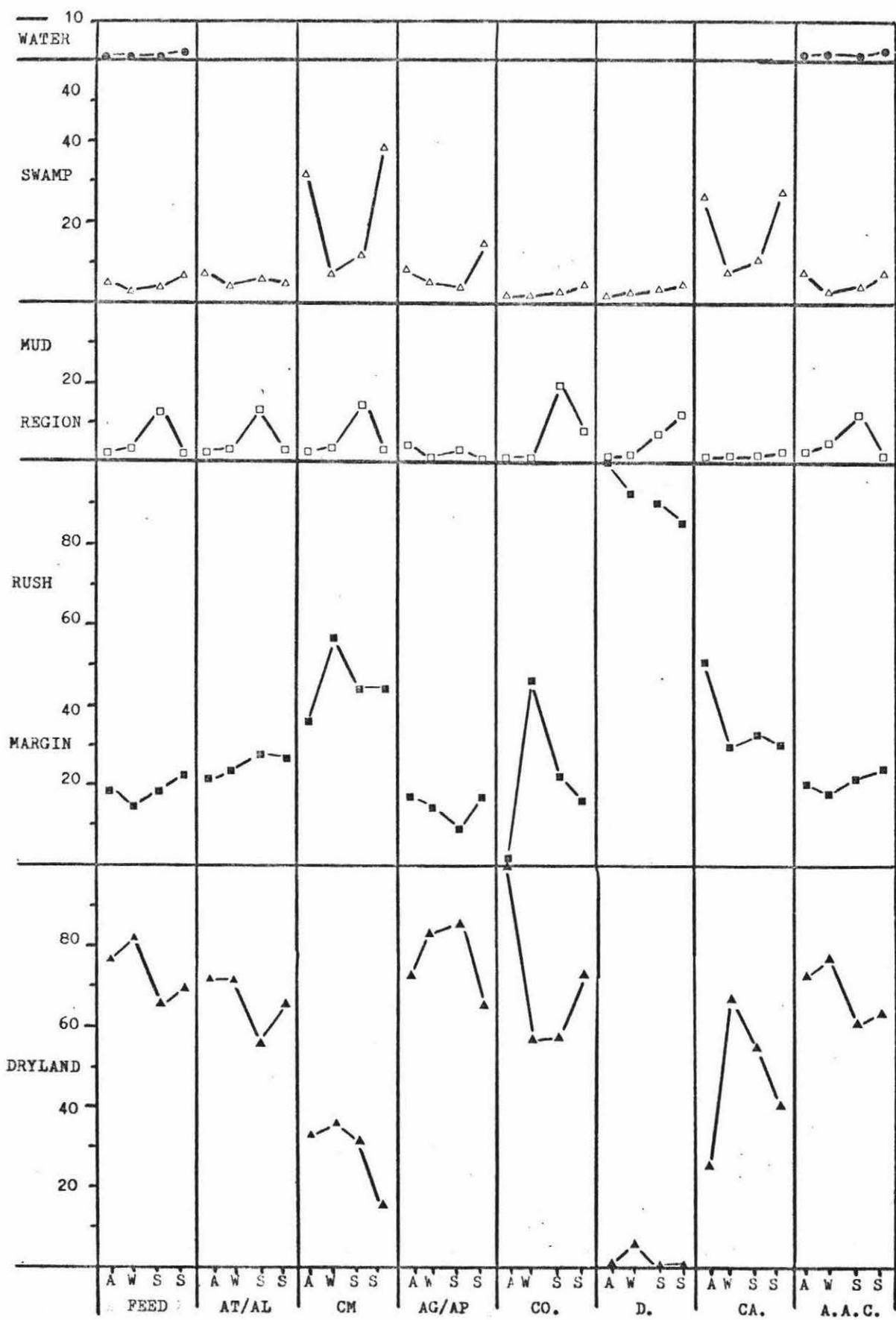
allocated to bodily maintenance decreased progressively from a spring maximum, through summer and autumn to a winter minimum. Birds were most wary in summer and least in winter, while conflict between them was proportionally greater in autumn, compared to the consistently lower levels observed for spring, summer and winter. They courted chiefly during spring, also during summer, but not at all in autumn or winter. Drinking, seen infrequently during spring, summer and winter, and calling recorded only in summer, comprised the remaining observations.

In swamp, time allocated to feeding peaked in winter, and decreased progressively during spring, summer and autumn, while comfort movements showed a reciprocal pattern. Attentive/alarm activities accounted for a similar proportion of the bird's time during winter, spring, and autumn, and were observed less frequently in summer, whereas encounters occupied least time in spring, and most in winter. In spring and summer the balance of time was spent drinking, courting, and calling, while calling accounted for the remaining time in autumn. In winter drinking and calling made up the remainder.

Pukeko fed in water more frequently in summer than during spring or autumn, and did not feed here in winter. Swimming was seen least in summer and most in winter. The hypothesis of equal time distribution in each habitat to each activity over the four seasons was tested and rejected, as time budgets recorded for each season were significantly different ( $p < 0.001$ ).

### 5.7 Seasonal Habitat Utilisation

Data combined from all activities indicated dryland was the most frequently used habitat, being used progressively more often from spring through to winter (Fig. 7; Tab. 7). In rush margins, the second most frequently exploited habitat, comparatively more birds were observed there during spring and summer than autumn and winter, whereas mud showed considerable seasonal variation, being used mostly during spring.



TAB. 7

SEASONAL HABITAT UTILISATION  
(COMPOSITE DAY)

SEASON	ACT HAB.	F	AT/AL	CM	AG/AP	CO	D	CA	S	FLY	AAC.
AUTUMN	DL	n 11336 % 75.78	1376 71.33	344 31.88	227 72.29	4 100.00		1 25.00			13288 71.89
	RM	n 2651 % 17.72	408 21.15	381 35.31	52 16.56		10 100.00	2 50.00			3504 18.96
	MR	n 313 % 2.09	34 1.76	21 1.95	12 3.82						380 2.05
	SW	n 657 % 4.39	111 5.76	333 30.86	23 7.33			1 25.00			1125 6.09
	W/-	n 3 % 0.02							80 100.00	103 100.00	23/103 0.45/0.56
	TOT.	n 14960 % 100.00	1929 100.00	1079 100.00	314 100.00	4 100.00	10 100.00	4 100.00	80 100.00	103 100.00	18483 100.00
WINTER	DL	n 30021 % 80.67	2497 71.12	997 35.40	692 81.60	30 54.55	8 5.34	23 65.72			34268 76.19
	RM	n 5061 % 13.60	797 22.70	1569 55.72	119 14.03	25 45.45	138 92.00	10 28.57			7719 17.16
	MR	n 1423 % 3.83	101 2.88	78 2.77	3 0.36		2 1.33				1607 3.57
	SW	n 708 % 1.90	116 3.30	172 6.11	34 4.01		2 1.33	2 5.71			1034 2.30
	W/-	n %							165 100.00	182 100.00	165/182 0.57/0.41
	TOT.	n 37213 % 100.00	3511 100.00	2816 100.00	848 100.00	55 100.00	150 100.00	35 100.00	165 100.00	182 100.00	44975 100.00
SPRING	DL	n 13343 % 64.81	1252 54.99	680 31.05	307 85.28	123 57.48		28 54.90			15733 60.32
	RM	n 3964 % 19.25	611 26.83	961 43.88	33 9.17	47 21.96	27 90.00	17 33.33			5660 21.70
	MR	n 2544 % 12.36	290 12.74	305 13.93	11 3.05	39 18.22	2 6.67	1 1.96			3192 12.24
	SW	n 673 % 3.27	108 4.74	244 11.14	9 2.50	5 2.34	1 3.33	5 9.81			1045 4.01
	W/-	n 65 % 0.31							281 100.00	106 100.00	346/106 1.33/0.40
	TOT.	n 20589 % 100.00	2261 100.00	2190 100.00	360 100.00	214 100.00	30 100.00	51 100.00	281 100.00	106 100.00	26082 100.00
SUMMER	DL	n 11057 % 68.40	1683 65.59	171 15.00	146 67.91	37 72.55		12 40.00			13106 63.24
	RM	n 3621 % 22.40	688 26.81	506 44.39	37 17.21	8 15.69	22 84.61	9 30.00			4891 23.60
	MR	n 387 % 2.39	84 3.27	34 2.98	1 0.46	4 7.84	3 11.54	1 3.33			514 2.48
	SW	n 963 % 5.96	111 4.33	429 37.63	31 14.42	2 3.92	1 3.85	8 26.67			1545 7.46
	W/-	n 137 % 0.85							334 100.00	196 100.00	471/196 2.27/0.25
	TOT.	n 16165 % 100.00	2566 100.00	1140 100.00	215 100.00	51 100.00	26 100.00	30 100.00	334 100.00	196 100.00	20723 100.00

Birds in swamp were observed infrequently throughout the year, but more often during summer and autumn, than winter or spring. Comparatively few birds were observed in water, for which the seasons of maximum use were spring and summer, and for each season remaining time was spent flying.

Considering each activity separately, most birds fed in dryland, with proportionally fewest feeding there in spring, but more through summer and autumn, to a maximum in winter. In rush margins pukeko fed most in summer and least in winter. In spring, proportionally more birds fed in mud than in other seasons. Birds in swamp fed at consistently low levels throughout the year, while during spring and summer they fed infrequently in water.

For all seasons most birds in attentive/alarm activities were in dryland, the proportion of which increased progressively from spring to maxima in autumn and winter, while the proportion of birds observed in rush margins remained approximately constant over the year. Swamp was also used fairly constantly over the year, whereas mud was used most in spring and least in autumn.

Birds engaged in bodily maintenance were observed mostly in rush margins, especially during winter, and progressively less often in spring, summer and autumn, while dryland, the next most frequently employed habitat, was used mainly in winter, and least often in summer. In swamp, comfort movements contributed most during summer and autumn, and least during spring and winter, whereas in mud proportionally most birds preened etc. here in spring.

Most agonistic/appeasement encounters were recorded in dryland, with fewest birds seen fighting etc. here in summer, and most in spring, which was a reciprocal pattern to that noted for birds in swamp. Encounters in rush margins were recorded at a similar level during summer, autumn and winter, but less frequently in spring, while in mud, they fought etc. infrequently.

Throughout the year pukeko courted more in pasture than in any other habitat, and most often in autumn. For rush margins the peak was in winter, while for mud and swampy

areas it was in spring and summer.

Drinking mostly occurred in rush margins, decreasing from an autumn maximum to a summer minimum. In mud most drinking occurred in summer, while in swamp it continued infrequently over the year, and in dryland only during winter.

Pukeko called mostly from pasture during spring, summer and winter, and from rush margins in autumn. The hypothesis of equal habitat useage over the year was tested for each activity. In all cases seasonal differences in use of habitats were highly significant ( $p < 0.001$ ).

## 5.8 Feeding

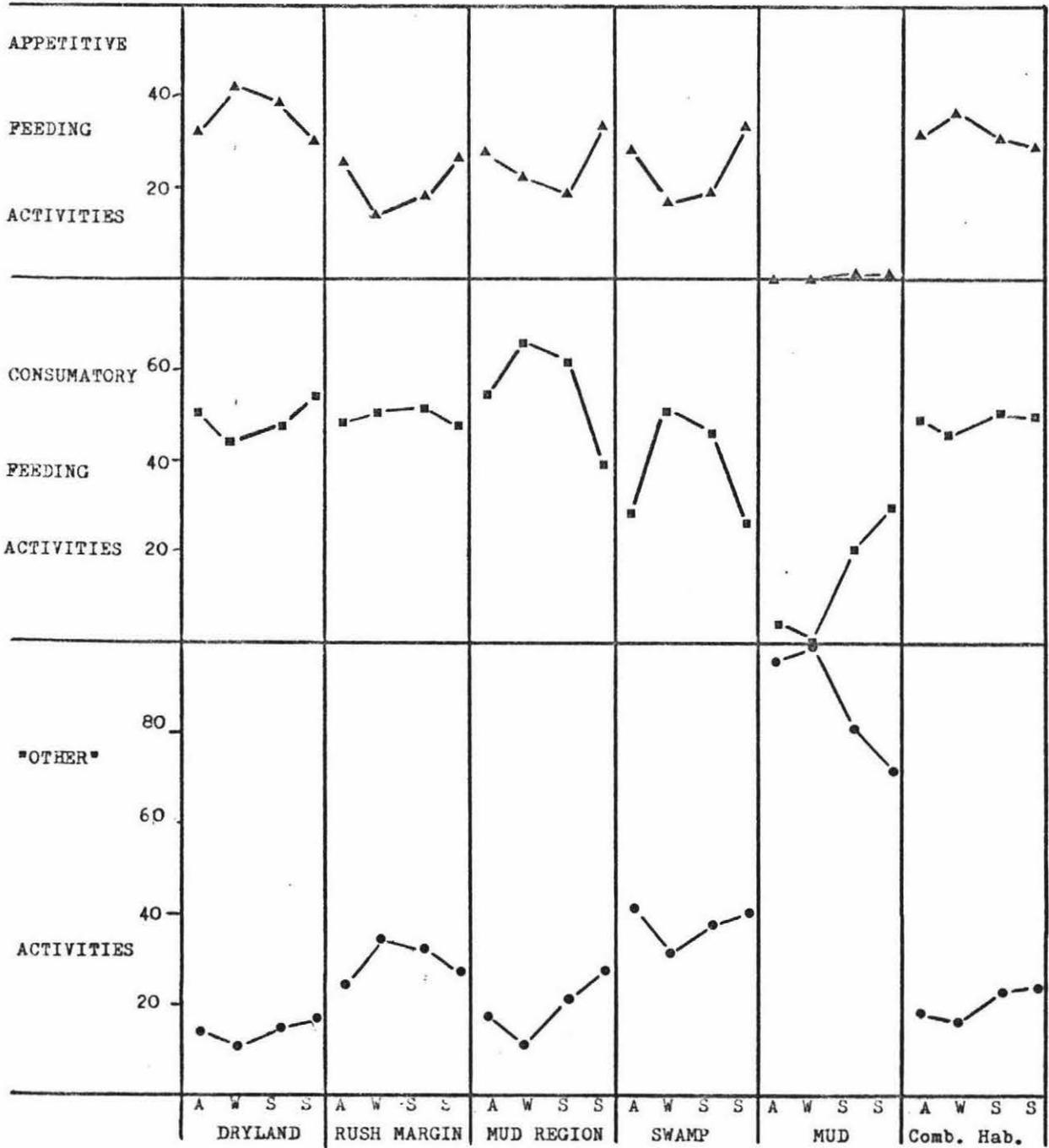
### 5.8.1 Appetitive and Consumatory Feeding, and "Other" Activities

Throughout the year pukeko spent most time eating, particularly during spring, summer, and autumn, and comparatively less time within each season looking for food, with most time being given to this latter activity during winter (Fig. 8; Tab. 8). "Other" activities comprised the balance for each season, occupying more time during spring and summer, than during autumn and winter.

Similar time was assigned to locating food in dryland as that calculated from combined data, namely a winter maximum and a summer minimum. Proportionally more time was spent eating in summer and autumn than in spring and winter. Remaining time was spent in "other" activities and showed little variation throughout the year.

From summer to spring birds in rush areas spent progressively more time eating and gradually less time searching for food, while time allocated to "other" activities progressively decreased from a maximum in winter to a minimum in autumn.

Throughout the year, birds in mud were most often observed eating, especially in winter, spring, and autumn. Looking for food occupied proportionally most time in summer, and least in spring, while "other" activities were



TAB. 8 SEASONAL TIME ALLOCATION TO APPETITIVE AND CONSUMATORY FEEDING, AND "OTHER" ACTIVITIES (COMPOSITE DAY)

SEASON	ACT.		APPET.	CONS.	"OTHER"	TOTAL
	HAB.					
AUTUMN	DL	n	4491	6817	1980	13288
		%	33.8	51.3	14.9	100.0
	RM	n	925	1714	865	3504
		%	26.4	48.9	24.7	100.0
	MR	n	105	208	67	380
		%	27.7	54.7	17.6	100.0
	SW	n	325	331	469	1125
		%	28.9	29.4	41.7	100.0
	W	n		3	80	83
		%		3.6	96.4	100.0
FLY	n			103	103	
	%			100.0	100.0	
CH.	n	5846	9073	3564	18483	
	%	31.6	49.1	19.3	100.0	
WINTER	DL	n	14770	15249	4249	34268
		%	43.1	44.5	12.4	100.0
	RM	n	1142	3096	2671	7719
		%	14.8	50.6	34.6	100.0
	MR	n	365	1054	188	1607
		%	22.7	65.6	11.7	100.0
	SW	n	179	529	326	1034
		%	17.3	51.2	31.5	100.0
	W	n			165	165
		%			100.0	100.0
FLY	n			182	182	
	%			100.0	100.0	
CH.	n	16456	20738	7781	44975	
	%	36.6	46.1	17.3	100.0	
SPRING	DL	n	5979	7331	2423	15733
		%	38.0	46.6	15.4	100.0
	RM	n	973	2878	1789	5660
		%	17.2	51.2	31.6	100.0
	MR	n	562	1953	677	3192
		%	17.6	61.2	21.2	100.0
	SW	n	188	471	386	1045
		%	18.0	45.1	36.9	100.0
	W	n		65	281	346
		%		18.8	81.2	100.0
FLY	n			106	106	
	%			100.0	100.0	
CH.	n	7702	12718	5662	26082	
	%	29.5	48.8	21.7	100.0	
SUMMER	DL	n	3866	7077	2163	13106
		%	29.5	54.0	16.5	100.0
	RM	n	1262	2294	1335	4891
		%	25.8	46.9	27.3	100.0
	MR	n	172	202	140	514
		%	33.4	39.3	27.3	100.0
	SW	n	510	414	621	1545
		%	33.0	26.8	40.2	100.0
	W	n		137	334	471
		%		29.1	70.9	100.0
FLY	n			196	196	
	%			100.0	100.0	
CH.	n	5810	10124	4769	20723	
	%	28.0	48.9	23.1	100.0	

most common in summer, and least frequent in winter.

In swamp proportionally more time was spent looking for food in summer and autumn, than in spring and winter, whereas food consumption showed the reciprocal pattern. "Other" activities were most common in autumn, and least frequent in winter.

In water no food searching behaviour was recorded in any season. The number of birds observed eating increased from spring to peak in summer, but decreased in autumn and were absent in winter. Birds swimming accounted for most observations in all seasons, especially winter. In each habitat pukeko devoted unequal time to locating and consuming food, and following "other" activities within each season ( $p < 0.001$ ) and over the year ( $p < 0.001$ ).

#### 5.8.2 Pecking Rate - Feeding Intensity

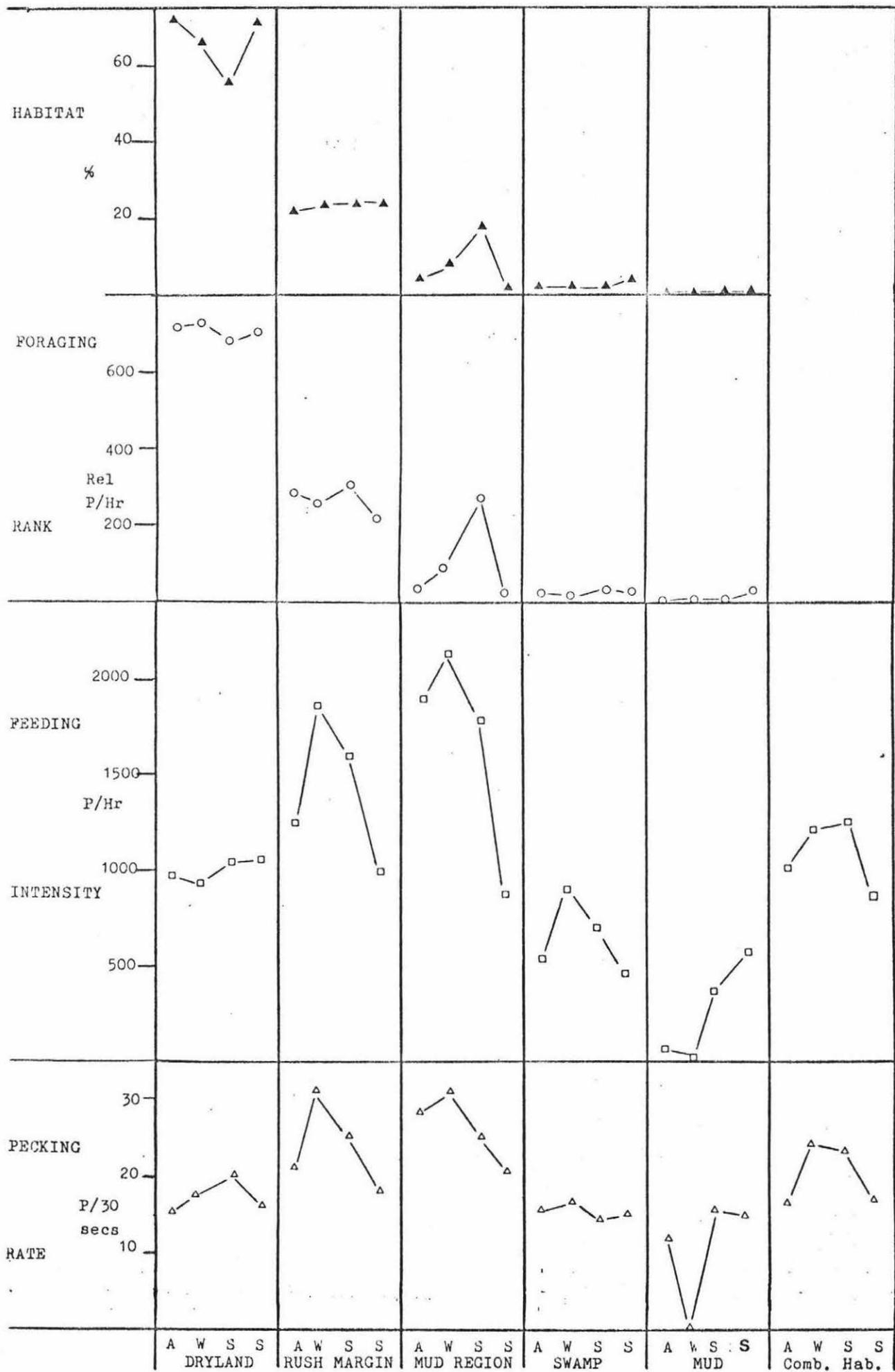
From pooled habitat data, pukeko pecked slower in summer and autumn, than in spring and winter, while in pasture they pecked fastest in spring and slowest in autumn (Fig. 9; Tab. 9). In rush margins pecking rates were highest in winter and lowest in summer, while in mud the birds pecked faster in autumn and winter, than in summer. In swamp pukeko pecked at about the same rate all year whereas pecking rates in water decreased progressively from spring to winter. Pukeko pecked unequally in each habitat within each season ( $p < 0.001$ ) and over the year ( $p < 0.001$ ).

From combined habitat data feeding intensities for an "average" bird, increased progressively from summer through to spring. In pasture it varied little all year, while in rush margin, mud, and swamp areas, it was highest during winter and lowest in summer. Feeding in water peaked in summer. The hypothesis of equal feeding in each habitat throughout the year was tested and accepted for pasture, rush margins, swamp and water ( $p > 0.05$ ) but rejected for mud and combined habitat data ( $p < 0.01$ ).

FIGURE 9

SEASONAL PECKING RATE, FEEDING INTENSITY,  
AND HABITAT FORAGING RANK FOR PUKEKO - COMPOSITE DAY  
(PER CENT)

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TAB. 9 SEASONAL PECK RATES, FEEDING INTENSITIES,  
AND HABITAT FORAGING RANKS (COMPOSITE DAY)

SEASON	HABITAT	PECK RATE P./30 sec	FEED. INT. P./hr	HAB. FOR. RANK	
				Rel. no. P./hr	Percent
AUTUMN	DL	15.85	976	739.5	72.43
	RM	21.00	1233	281.4	21.40
	MR	28.77	1889	39.5	3.87
	SW	15.15	535	23.5	2.30
	W	12.00	52	0.01	0.00
	CH.	17.00	1002	1083.9	100.00
WINTER	DL	17.52	935	754.4	66.99
	RM	31.61	1920	261.1	23.18
	MR	30.48	2399	91.9	8.16
	SW	16.09	988	18.8	1.67
	W				
	CH.	21.84	1208	1126.2	100.00
SPRING	DL	19.68	1042	676.0	55.28
	RM	24.56	1508	290.3	23.74
	MR	25.35	1861	230.1	18.81
	SW	14.35	776	25.4	2.08
	W	16.28	361	1.2	0.09
	CH.	21.25	1244	1223.0	100.00
SUMMER	DL	16.29	1052	719.2	71.76
	RM	18.18	1024	229.4	22.89
	MR	18.36	866	20.7	2.07
	SW	14.60	470	28.0	2.79
	W	15.57	581	4.9	0.49
	CH.	16.75	985	1002.2	100.00

### 5.8.3 Habitat Foraging Rank

Throughout the year, dryland was used for feeding far more often than any other habitat, contributing comparatively fewer pecks to the total calculated per hour during spring and summer than during autumn and winter (Fig. 9; Tab. 9). Rush margins and mud were used least for feeding during summer but became increasingly more important feeding areas in other seasons. Throughout the year swamp and water were infrequently fed upon.

The seasonal contribution of each habitat to the total feeding effort of an "average" bird in the Hamilton's Lagoon flock varied, with birds feeding in pasture more than in any other habitat, especially in summer and autumn. Proportional use of rush margins for feeding varied little all year, while in mud feeding increased progressively from summer through to spring. Feeding in swamp peaked in summer, while the birds fed only rarely in water. The hypothesis that pukeko ate equally on all habitats over the year was tested and rejected ( $p < 0.001$ ).

### 5.8.4 Daily Feeding Effort of an "Average" Bird

#### 5.8.4.1 Summed Feeding Intensities

Addition of feeding intensities for every hour of the day allows expression of the total number of pecks delivered each day by an "average" bird in the flock at Hamilton's Lagoon, feeding exclusively in a particular habitat.

#### Annually

For an average day over the year, combined habitat data indicated pukeko delivered over 11,600 pecks at the average rate of 929/hour (average day length = 12.54 hours) (Tab. 10). Analysis of each habitat separately showed most pecks were delivered in mud, succeeded by the rush margin, dryland, swamp and water areas.

#### Seasonally

For all habitats combined, the number of pecks delivered per day was greatest in spring and least in autumn, while the hourly rate of pecking was also greatest during spring and

TABLE 10  
DAILY FEEDING EFFORT OF AN "AVERAGE" PUKEKO - ANNUAL  
 Photoperiod = 12.54 hours

HABITAT	DRYLAND	RUSH MARGIN	MUD REGION	SWAMP	WATER	COMBINED HABITATS	
SUMMED FEEDING INTENSITIES	P/day	10,461	14,621	18,802	7,100	1,955	11,649
	Av. P/hr	834.2	1165.9	1499.4	566.2	155.9	928.9
SUMMED HABITAT FORAGING RANKS	P/day	7,735	2,515	987	239	5	11,481
	Av. P/hr	616.8	200.5	78.7	19.1	0.4	915.5
	%	67.38	21.90	8.60	2.08	0.04	TOTAL 100.00

lower in other seasons (Tab. 11). In dryland birds delivered most pecks in summer and least in winter, whereas the average feeding intensity decreased progressively from spring to winter. In rush margins birds fed most intensely during winter and least during autumn, while the average pecking rate was highest in winter and spring, and lowest in summer. Mud was exploited for food mostly during spring and winter, with highest pecking rate then. Pukeko fed fastest and longest in swamp during winter and spring whereas they fed in water most intensely during summer.

#### 5.8.4.2 Summed Habitat Foraging Ranks

As pukeko moved between habitats while feeding the relative importance of each habitat as a feeding station was calculated seasonally, by summing daily habitat foraging ranks.

##### Annually

For a typical day of the year, pukeko spent by far the greatest proportion of their feeding time in pasture, followed in turn by rush margins, mud, swamp and water (Tab. 10).

##### Seasonally

Most pecks per day were delivered in summer, followed closely by spring (Tab. 11). Fewest were delivered in winter, with only about 1000 or so more being delivered in autumn. On an "average" day in pasture, birds delivered most pecks in summer and least in winter, whereas the pecking rate was slowest in spring, and fastest in winter. However considering the proportional contribution of each habitat to the overall feeding strategy of an "average" bird (per cent of total pecks delivered), dryland was more important as a feeding station in summer and autumn, than during winter and spring.

In rush margins (the second most important feeding site), birds delivered more pecks per day in spring and summer, than in autumn and winter, but pecked fastest in spring and winter. Proportional use of this habitat was greatest in spring and least in autumn. In mud, the birds fed fastest

TABLE 11a  
 DAILY FEEDING EFFORT OF AN "AVERAGE" PUKEKO - AUTUMN  
 Photoperiod = 12.43

HABITAT		DRYLAND	RUSH MARGIN	MUD REGION	SWAMP	WATER	COMBINED HABITATS
SUMMED FEEDING INTENSITIES	P/ day	1,237	14,130	12,892	6,822	1,459	12,137
	Av. P/ hr	995.4	1136.7	1037.1	548.9	117.3	976.4
SUMMED HABITAT FORAGING RANKS	P/ day	10,302	3,092	557	346	2	14,301
	Av. P/ hr	828.8	248.8	44.8	27.9	0.2	1,150.5
	%	72.04	21.63	3.90	2.42	0.01	TOTAL 100.00

TABLE 11b  
 DAILY FEEDING EFFORT OF AN "AVERAGE" PUKEKO - WINTER  
 Photoperiod = 10.39

HABITAT		DRYLAND	RUSH MARGIN	MUD REGION	SWAMP	WATER	COMBINED HABITATS
SUMMED FEEDING INTENSITIES	P/ day	10,077	19,098	18,656	9,494		12,558
	Av. P/ hr	969.8	1,838.1	1,795.6	913.7		1,010.3
SUMMED HABITAT FORAGING RANKS	P/ day	9,042	3,041	1,072	222		13,377
	Av. P/ hr	870.3	292.7	103.2	21.3		1,287.5
	%	67.60	22.74	8.00	1.66		TOTAL 100.00

TABLE 11c  
 DAILY FEEDING EFFORT OF AN "AVERAGE" PUKEKO - SPRING  
 Photoperiod = 12.52

HABITAT		DRYLAND	RUSH MARGIN	MUD REGION	SWAMP	WATER	COMBINED HABITATS
SUMMED FEEDING	P/ day	1,440	18,834	22,360	9,063	3,686	15,632
INTENSITIES	Av. P/ hr	1,153.3	1,504.3	1,785.9	723.9	294.4	1,248.6
SUMMED HABITAT FORAGING	P/ day	9,410	3,940	3,117	346	20	16,835
	Av. P/ hr	751.6	314.7	249.0	27.7	1.6	1,344.6
RANKS	%	55.90	23.40	18.52	2.06	0.12	TOTAL 100.00

TABLE 11d  
 DAILY FEEDING EFFORT OF AN "AVERAGE" PUKEKO - SUMMER  
 Photoperiod = 14.85

HABITAT		DRYLAND	RUSH MARGIN	MUD REGION	SWAMP	WATER	COMBINED HABITATS
SUMMED FEEDING	P/ day	16,379	15,119	1,156	6,466	5,988	14,864
INTENSITIES	Av. P/ hr	1,103.0	1,018.1	778.8	435.5	403.2	1,001.0
SUMMED HABITAT FORAGING	P/ day	12,298	3,991	338	578	148	17,353
	Av. P/ hr	828.1	268.8	22.8	38.9	9.9	1,168.5
RANKS	%	70.87	23.00	1.95	3.33	0.85	TOTAL 100.00

and longest in spring, but slowest and most briefly in summer, whereas in swamp they fed most in summer and least in winter. The proportional use of swamp as a feeding habitat was similar throughout the year, contributing most to the feeding effort of pukeko in summer, and least in winter. In water pukeko fed fastest and most intensely in summer and least during autumn (winter unrecorded). As a foraging habitat water contributed most in summer.

#### 5.8.5 Seasonal Foraging Impact of the Flock at Hamilton's Lagoon

From the number of pecks delivered per day by an "average" bird in each habitat, and the mean number of birds in the flock for each season, the seasonal foraging impact of this flock in each habitat at Hamilton's Lagoon can be calculated (Tab. 12). The average number of pukeko in the Hamilton's Lagoon flock, (seen during each five minute observational sweep of the lagoon) peaked in winter at c. 30 birds. In spring an intermediate number were seen (c. 15 birds per sweep), while in summer and autumn the flock was smallest (c. 8 and 9 birds per sweep respectively).

For all seasons, dryland was the habitat in which the flock fed most extensively, succeeded by rush margins, mud, swamp and water. Considering combined habitat data pukeko, as a flock, fed most extensively in winter, and progressively less intensely from spring to autumn. Feeding in pasture, rush margins and swamp also followed this seasonal pattern, while the birds fed in mud more extensively during spring and winter, than during summer and autumn. Summer was the only season during which pukeko fed extensively in water.

As the duration of an average day for each season was known, the flock's feeding rate was readily calculated (Tab. 12). Again birds fed most eagerly, for all habitats combined, over the winter months, and progressively less intensely from spring through to autumn. Seasonally, feeding effort in swamp and rush margins closely followed this pattern, while for pasture pecking was most intense in winter, and least in summer and autumn. From summer to spring the total pecks delivered per hour by flock birds in mud progress-

TABLE 12  
SEASONAL FORAGING IMPACT OF A PUKEKO FLOCK AT HAMILTON'S LAGOON

Season Flock Size	Autumn 8.85		Winter 30.06		Spring 14.47		Summer 8.31	
	Impact Tot. p/day	Rate p/hour						
Dryland	91,176	7,335	271,799	26,160	136,168	10,876	102,195	6,882
Rush Margin	27,367	2,202	91,421	8,799	57,016	4,554	33,165	2,233
Mud Region	4,933	397	32,218	3,101	45,110	3,603	2,811	189
Swamp	3,066	247	6,660	641	5,011	400	4,802	323
Water	19	2			291	23	1,227	83
TOTAL	126,561	10,183	402,098	38,701	243,596	19,456	144,200	9,710

ively increased, whereas water was used most for feeding in spring and less thereafter.

## 5.9 Discussion

### Feeding Activities

Seasonal changes in time allocated to various activities and in useage of each of the available areas, are perhaps best explained in terms of food availability, the broad seasonal changes in vegetation, and the times spent feeding in each habitat, particularly as so much of the bird's time (c. 75%) was associated with food location and consumption.

In general dryland was used increasingly as a feeding station from spring to winter whereas rush margins, swamp and water were most used in summer, and mud was fed upon most in spring. Throughout the year pukeko spent most time feeding, but least in summer. As this was the season of maximum photoperiod, time available for food collection was also maximal, and the birds delivered in total more pecks. Further, as nights were shortest then, birds were without food for the least time in the year. They delivered fewer pecks over the day in winter than in summer, even though proportionally more time was spent feeding in winter, when fewest hours of light were available for foraging. All this probably influenced foraging in pasture in that season.

Plant food in some habitats was apparently least available to pukeko in winter, i.e. in the swamp raupo was dead; rush margins were heavily grazed by sheep and cattle; and in mud and water there was little vegetation. However, animal food (e.g. carrion and earthworms on dryland) was periodically available in winter. Surface activity of earthworms is related to air temperature and recent rainfall, (Boyd, 1957), and the presence of stock which pugged the soil. An edited extract from my field notes from 2 September, 1977 at 13.03 hours states:

..."pukeko have flown to the western bank of the lagoon (where the sheep have pugged the soil), and are eating earthworms at a rate of c. 10 worms per 30 seconds..."

Bengtson (1976) found goldern plovers Pluvialis apricaria fed most intensely and successfully on earthworms at midday and in the early afternoon. Pukeko were frequently observed eating earthworms in winter when they exhibited midday and early afternoon feeding intensity peaks, however it is unknown if the birds fed on the worms more at this time than in the early morning and late afternoon.

Pukeko were active at night, e.g. flying and calling, and the possibility of night feeding throughout the year could not be discounted. Thus they may have fed into the long winter night, or even before sunrise, although no birds were observed in pasture until first light in winter (45 minutes before sunrise). At dusk, all birds that were in rush margins or pasture made their way to raupo clumps in swamp, and few birds remained in either dryland or the lagoon's margins after night fall.

With increasing temperature and photoperiod in spring, changes occurred within the habitats. In swamp, fresh young raupo shoots developed which pukeko eagerly tugged from the water, while quantities of forage in rush margins and pasture increased. This also meant the birds did not have to venture so far out onto pasture and away from cover, to feed. Furthermore nest-building and some territorial behaviour associated with the establishment of spring breeding territories, was concentrated in swamp and rush margins and hence fewer birds were seen in pasture.

For rush margins in summer and autumn most time was spent feeding. This corresponded with the drying out of pasture and mud areas in summer (1978 drought), and with an overall reduction in water levels which also affected the swamp and water habitats. In summer, although the pasture was short, it was more heavily grazed by stock, than in spring. This reduction in forage availability in pasture resulted in the birds using rush margins and swamp more frequently for feeding. Further, as autumn rains were delayed drying out of the pasture and lagoon margins continued. In water there was a series of algal blooms in summer, including floating and aerial-leaved aquatic plants (e.g. Lemna spp., Myriophyllum spp.) upon which pukeko fed.

The mud regions (areas of flooded pasture) were used by pukeko mostly for feeding in spring when, following winter rain, increasing temperature and photoperiod initiated the profuse growth of floating sweet grass, watercress, and water buttercup, upon which the birds fed avidly, pulling out the entire plant. This habitat was transitory, disappearing in summer and reappearing in winter.

Swamp, while affording protection to loafing birds, was less frequently used for feeding than dryland, rush margins, or mud. In late winter and spring when fresh young raupo shoots were developing, pukeko in this habitat spent most time feeding. Once raupo stalks were too large to remove (i.e. late spring and summer), or were dead (i.e. autumn and winter), pukeko did not eat them. Thus lack of forage in dryland in spring and summer was apparently counter-balanced by the seasonal availability of food in other habitats.

#### Non-feeding Activities

Seasonal changes in time spent feeding are more easily explained than are subtle seasonal changes in attentive/ alarm, comfort movement and agonistic/appeasement activities.

Birds observed in all habitats except swamp were most attentive in summer, due possibly to a lack of protective over-head cover at this time, especially in dryland. Thistles that had grown here during spring had died and disintegrated by autumn, and other vegetation e.g. grass seed-heads, was cropped short. Plant food was probably harder to find and thus pukeko had to move further out into the paddocks and away from the comparatively safe swamp and rush margins, and hence were correspondingly more attentive. Although they mostly fed independently of adults, pukeko chicks were totally dependent on them for protection from predators, which may have made adults more attentive at this time. Throughout the remaining seasons, i.e. autumn and winter, essentially similar time was spent in attentive postures.

Over the year, the number of birds feeding in pasture and mud appeared directly related ( $r=0.912$ ;  $r=0.937$ ;  $0.10 > p < 0.05$ )

to those recorded in attentive alarm activities. For rush margins and swamp, a weaker correlation coefficient ( $r=0.803$ ;  $r=0.025$ ;  $p>0.10$ ) was determined, suggesting that these habitats afforded more protection to feeding birds which were therefore not as attentive as they were in dryland and mud. In summary, the yearly trend for birds seen in attentive/alarm postures in open habitats closely followed that for birds feeding, while in habitats with taller vegetation the relationship was less distinct.

Few birds loafed or preened in open dryland and mud areas, except during spring, which coincided with increasing amounts of food available in these habitats. Daylight hours were longer in spring than in winter, and hence the birds collected more and/or better quality food over the day. Thus as maintenance requirements were apparently easily satisfied in spring, the amount of time the birds could loaf in these habitats increased over that recorded in winter.

Bodily care in rush margins occupied least time in summer and autumn, corresponding with an increase in time spent feeding, and lowest food availability (see above). Also the presence of nidifugous chicks, or predators (more time spent looking round etc.), may partially explain why comfort movements were least seen in summer and autumn. Most time was spent in these activities in winter. As rush margins were closer than swamp to pasture, it was perhaps more energetically efficient for the birds to stop and preen etc. in the former areas than to fly or swim to the more distant swamp.

On swamp however, gradually more time was devoted to bodily maintenance from winter through to autumn. Pukeko engaged in comfort movements require overhead cover for immediate protection from aerial predators, and presumably they will pursue these activities only after more important activities, such as feeding, have largely been completed. In winter forage was scarce in all habitats, and the birds had to search more extensively for food. Hence little time was spent loafing, preening etc. However, in summer and autumn, when drought conditions prevailed, overhead cover was restricted mainly to swamp, as the seed-heads and rank grass stems of pasture and marginal vegetation had been eaten by cattle. Thus the only comparatively safe area in which the

birds could loaf etc. in summer and autumn, was swamp.

I have suggested above that pukeko, while feeding in open pasture and mud, are more attentive than in the more protected swamp and rush margins. Anderson (1965) recognised the importance of cover for loafing areas and especially nest sites for moorhen, and Schranck (1972) found that predation of water-fowl nests by mammals was inversely related to cover. It is likely that pukeko resting in thick cover are less frequently preyed upon than those resting in lighter cover, but this suggestion requires further work.

Most agonistic/appeasement encounters occurred in dryland throughout the year, with progressively more seen there from summer to spring. More skirmishes were recorded in other habitats in late winter, when breeding territories were established and preliminary nest-building activities commenced. Concurrent with fewer birds present in dryland in summer, there was an increase in aggressive encounters in swamp, which may have been due to nest relief, the presence of chicks, or the increasing number of individuals within the territory.

From combined habitat data, the number of encounters rose in autumn and winter, and was probably associated with the breakdown of spring and summer breeding territories, and the build-up of autumn and winter flocks. However the formation of autumn and winter flocks depended on the habitat territorial birds occupied. Brown (1964, 1969) contended that some resources are distributed in time and space in such a way that they are economically defensible, while others are not. Furthermore Brown and Orians (1970) postulated that resources (e.g. food, water, cover, nest site, mates, etc.) will be defended where they are economically defensible (in terms of individual survival and reproductive output). Craig (1974) discussed the application of these ideas to the year-round social organisation of pukeko - a theme that is now developed further.

Pukeko inhabit highly productive (Odum, 1971) swampy or wet-land areas in which food is seasonally available in

large quantities within a generally small area. Raupo and Carex clumps were available throughout the year for nesting and bordered pasture and marginal habitats. Thus food and nesting materials were available all year round. Territories that include an area of protective and seasonally highly productive swamp and an area of pasture (year-round food), would be expected to persist for longer into, and be less likely to break down during autumn and winter. Those territories (e.g. embracing mud and water habitats) that include seasonally abundant foods would be less permanent, breaking down in the non-breeding season. Other factors which might influence the stability of territories include the amount of protective cover from aerial predators and the isolation of nest and vulnerable young from ground predators. Also territories which include areas providing super-abundant winter food may be unstable, as their defence against large numbers of non-territorial birds would be energetically uneconomic. Maintaining a priority of use over this area through dominance, would be energetically less costly, although partial breakdown of the territory would occur.

At Hamilton's Lagoon both types of winter territories existed. The only "breeding" territory which persisted all year included a large area of pasture, a small central area of swamp, and marginal areas of the lagoon (the rush margin and mud areas). This territory bordered on one side only with a flock of non-territorial birds. In the breeding season three distinct territories (c. four birds per territory) were observed in the area occupied in autumn and winter by a flock of c. 30 birds. Area-dependent hierarchies are thought to have existed here in the non-breeding season, perhaps as the area contained a super-abundant winter food supply, the exclusive defence of which would have been uneconomic. Visually few vegetational differences existed between the two wintering areas, and it is suggested the "con-specific contact" on territory borders (contact on three of four sides) contributed most to the breakdown of the three previously distinct breeding territories. The fourth territory, with only one border in common with non-territorial birds, was more easily defended and withstood encroachment by the flock.

As anticipated courtship, seen mostly in dryland, was most common in spring, corresponding with the greatest seasonal abundance of foods in the rush margins, mud, swamp and dryland areas. Most birds drank on the lagoon margins, however in winter, they also drank on dryland. In spring, summer and winter, most birds called on dryland, whereas in autumn, they called mostly from rush margins. Proportionally more birds called from swamp in summer and autumn, but the cause of this remains unclear.

### Foraging

Time spent locating and eating food, and in "other" activities reflects apparent food availability and pukeko selectivity within each habitat and season. If preferred plant species vary seasonally in abundance the birds, in order to obtain the same quantity of food over the year, would have to vary search time and selectivity.

Remarkably, combined habitat data showed that rather similar time in all seasons was spent eating, but slightly less in winter when more time was spent looking for food, and little time spent on "other" activities. In spring and summer, least time was spent locating food and most time went on "other" activities. Hence in autumn, and especially winter, preferred forage was less frequently encountered as the birds wandered, because proportionally more time was spent locating it, and less time was spent eating, and pursuing "other" activities.

In pasture least time was spent looking for food, and most time spent eating and pursuing "other" activities in summer. If pukeko fed with similar selectivity in summer and spring, time spent looking for food would be higher in summer, as food was less available then. However the reverse occurred (i.e. less time was spent looking for food). Therefore pukeko fed less selectively and ate more frequently in pasture in summer than in spring, indicating that they were more intent on eating, than on selecting what food to eat. Least time was spent eating and following "other" activities, and most time spent looking for food in winter, indicating the birds fed most selectively at that time.

Pukeko pecked slower and fed less intensely in summer and autumn, than in winter and spring. Thus in pasture

they fed more selectively and intensely, and at the fastest rate during that season (spring) in which food was most readily available and, when forage was least available (i.e. summer and autumn) they fed less intensively and less selectively. Although pukeko collected food at a lower rate and less selectively, over the long summer day, they delivered in total more pecks than during winter. That is in winter, due possibly to the restriction of the time available for feeding and low ambient temperature, pukeko had to select the highest quality forage available.

Due to the drought and intensive grazing by stock, rush margin forage was apparently least available in summer and autumn (see section 5.8.1). Time allocated to the three activity categories indicated the same, i.e. compared to spring, in winter most time was spent looking for food, least time eating and less time pursuing "other" activities. Growth of pasture grasses and some aquatic plants in winter and spring increased the food available here - the birds spending most time consuming food and following "other" activities, and least time looking for food. However, pukeko fed most intensely in spring which coincided with increased food availability and increased biological demands, e.g. territory establishment and defence, courtship, nest building, incubation, and chick rearing. Also any loss of body condition over the winter months may have been replaced in spring when food supply improved. Pukeko fed at medial intensity in autumn, when their energetic requirement was less than in spring or winter, with moult being the most energetically demanding process at that time (App. 3).

On mud areas time spent locating and eating food, and in "other" activities indicated least food was available to pukeko during summer and autumn, when this area dried up and only plants such as Azolla and Lemna were found. Most forage was available when winter and spring rains flooded these areas, and water buttercup and fresh young pasture grass shoots predominated, resulting in the birds feeding extensively.

In swamp food was most available in winter and spring (young raupo shoots), when most time was spent eating. Least food was available in summer and autumn (dead mature raupo) and most time was spent locating food. Pukeko spent similar time in "other" activities during spring, summer and autumn, and slightly less in winter.

Use of water peaked in summer, concurrent with the seasonal proliferation and availability of aquatic plants. During this season, pukeko ate more frequently and swam less, than in other seasons.

On pasture pukeko fed at similar intensities all year - most in summer and least in winter - although food was apparently more readily available in winter than in summer. In rush margins and mud, lower food availability in summer and autumn corresponded with lowest pecking rates and feeding intensities, whereas in winter and spring, when food was more readily available, pecking rate and feeding intensity increased - a contradictory pattern to that shown for pasture. Birds feeding in swamp pecked at similar rates throughout the year, apparently independent of forage availability, except in late winter when the readily available forage (developing raupo shoots) was fed upon most keenly. In water they pecked fastest and most intensely in spring and summer, when food availability was greatest.

#### Use of foraging areas

Habitat foraging ranks support further the hypothesis that pukeko fed most in those areas where availability and/or quality of forage was greatest. Throughout the year, dryland was by far the most important feeding site, especially in winter, although variation between seasons was slight. In winter birds in dryland were most selective, perhaps selecting the highest quality forage in the time available. Feeding in rush margins and mud was least in summer and most in spring - corresponding respectively to the seasons of minimal and maximal food availability. Over the year, little effort was devoted to feeding in swamp or water, except during spring and summer in the former, and summer in the

latter, again coinciding with the greatest seasonal availability of food in these habitats.

Interestingly, the relative contribution (per cent pecks) of birds feeding in pasture, to the total number of pecks recorded in all habitats per hour, was greatest in summer and least in spring. For mud, the contribution was least in summer and greatest in spring. Thus, when an alternative feeding station became available (and desirable) in spring, e.g. mud, some birds fed here in preference to feeding in pasture. In summer, when the mud dried out, they switched from feeding here, to feeding again in pasture. As late autumn and winter rain brought fresh new plant growth in the mud, the birds returned to feed here.

Pukeko fed steadily in the rush margin, swamp and water areas throughout the year, with feeding in swamp and water apparently unimportant. The lack of difference in seasonal use of rush margins was perhaps superficial as although the birds fed more extensively on this habitat in spring than summer, a similar proportion of total pecks was delivered by an "average" bird here in both seasons.

Besides broad seasonal changes in the quality of the flora on the various areas, other factors such as the extent of overhead protective cover, or social organisational events (e.g. the presence of territorial birds and the defence of breeding territories) or predator activity, as well as seasonal changes in the bird's biology (e.g. moult, breeding etc.) all have to be remembered when considering the seasonal useage of habitats. However, as the birds spent so much time feeding (70-90%), it seems reasonable to interpret the seasonal use of habitats with respect to the availability (absolute or relative) and/or quality of forage in these areas.

In summary, evidence suggests pukeko seasonally gauged food availability and/or quality in each habitat, feeding most in rush margin, mud, swamp and water areas and at the highest rate and intensity, when food availability and/or quality was either maximal or optimal. Conversely, dryland did not follow this pattern. Data on time spent locating

and eating food, the rate and intensity of feeding, and habitat use indicates pasture was used consistently and extensively as a feeding site throughout the year, although the seasonal availability and/or quality of food varied considerably. It is suggested this habitat formed the "feeding backbone" for pukeko throughout the year, and being opportunistic feeders, they were able to switch their feeding activities from this to any of the remaining areas that showed an appropriate reward for the energetic cost of feeding there.

## 6. TIME BUDGET AND FEEDING ECOLOGY - DIURNAL

### 6.1 Introduction

With annual composite day analyses, all hourly data from all seasons were pooled. As seasons were of varying day lengths, only those hourly periods that were common to all four seasons were combined for the annual diurnal expressions. In total 10,931 observations from a total of 110,263 observations (9.9%) were omitted. For spring 3,376 midday (3.1% of the total) observations were not considered, while for summer and autumn, 5,460 (4.9%) and 2,096 (1.9%) observations respectively, were not used. In winter all observations were considered.

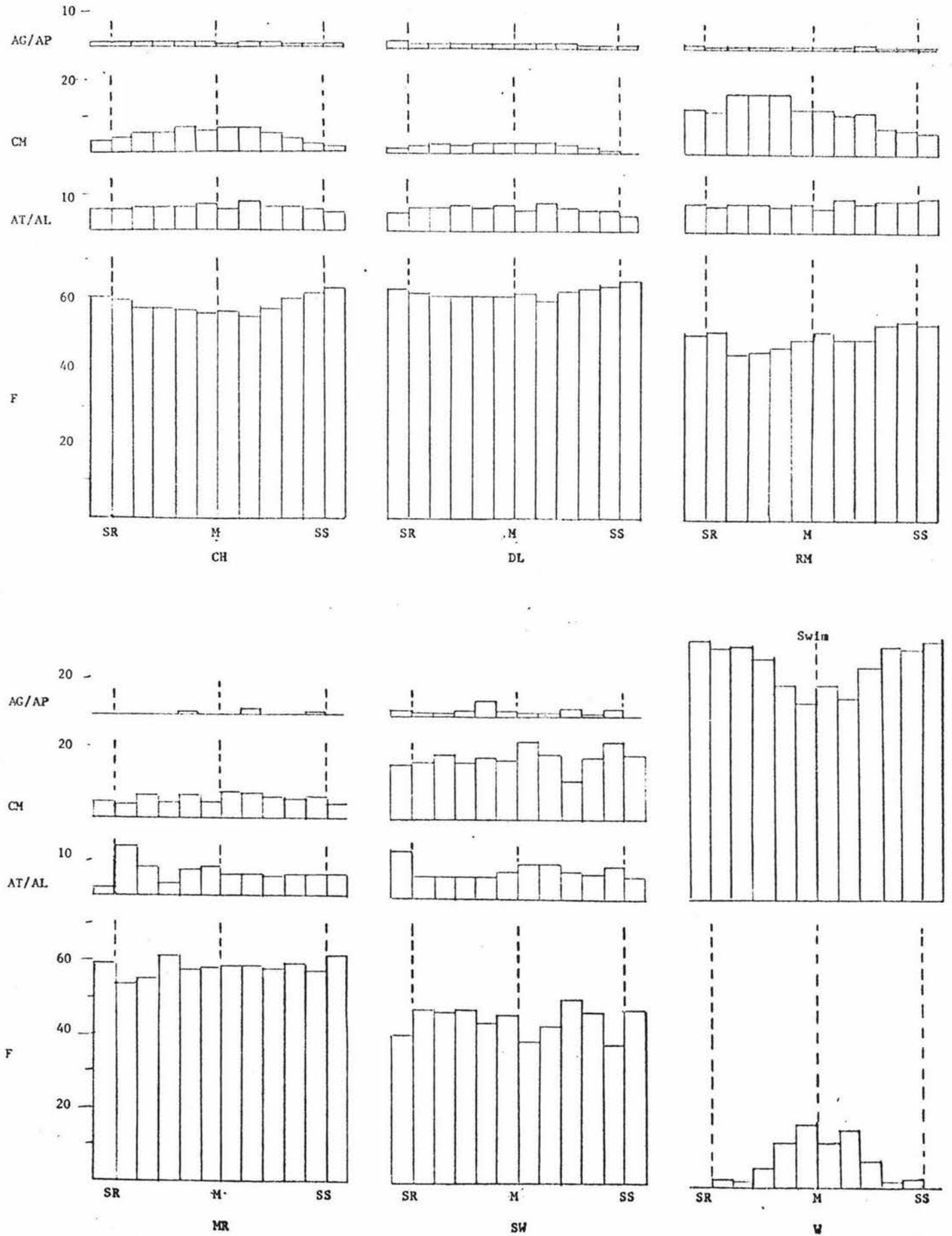
### 6.2 Annual Time Allocation

From pooled habitat data, pukeko spent most time feeding at dawn and dusk, and least at midday, while attentive/alarm postures were seen at a similar level throughout the day, being slightly higher in the morning than in the afternoon. (App. 4 ; Fig.10). Most time was devoted to comfort movements around midday, and agonistic/appeasement encounters were seen more commonly at dawn than later, while pukeko drank and courted most often in the mid and late afternoon. They swam most at midday, and flew and called most at dawn.

In dryland, feeding occupied most of the pukeko's time, but less at midday than at dawn and dusk. The birds were most attentive and spent most time in bodily maintenance at midday. Conflict between individuals decreased gradually from dawn to dusk, while courtship was observed infrequently all day. Drinking or calling birds comprised remaining observations.

More birds fed in rush margins in the afternoon than in the morning, accounting for most observations, while wary birds were seen consistently in the morning and early afternoon, and most at dusk. Time allocated to comfort movements was greater in the morning than in the afternoon, whereas time spent in agonistic/appeasement encounters was similar over the day. More birds were observed drinking and courting

FIG. 10. ANNUAL DIURNAL TIME ALLOCATION OF PUKEKO  
(PER CENT)



at dusk than earlier, whereas most called at dawn.

Pukeko fed in mud more in the afternoon and late morning than earlier. They were most attentive in the early morning, and preened etc. consistently throughout the day. Infrequent observations of birds in conflict, courting or calling comprised remaining observations.

Feeding again accounted for most time in swamp, occupying more time in the morning than in the afternoon. Accounting for most of the remaining observations, bodily maintenance increased gradually over the day. Attentive birds were consistently recorded throughout the day, while encounters were seen mostly in the late morning. The birds called most at dawn and dusk, whereas drinking and courting were infrequently observed.

Pukeko fed in water mostly at midday, while swimming showed a reciprocal diurnal pattern.

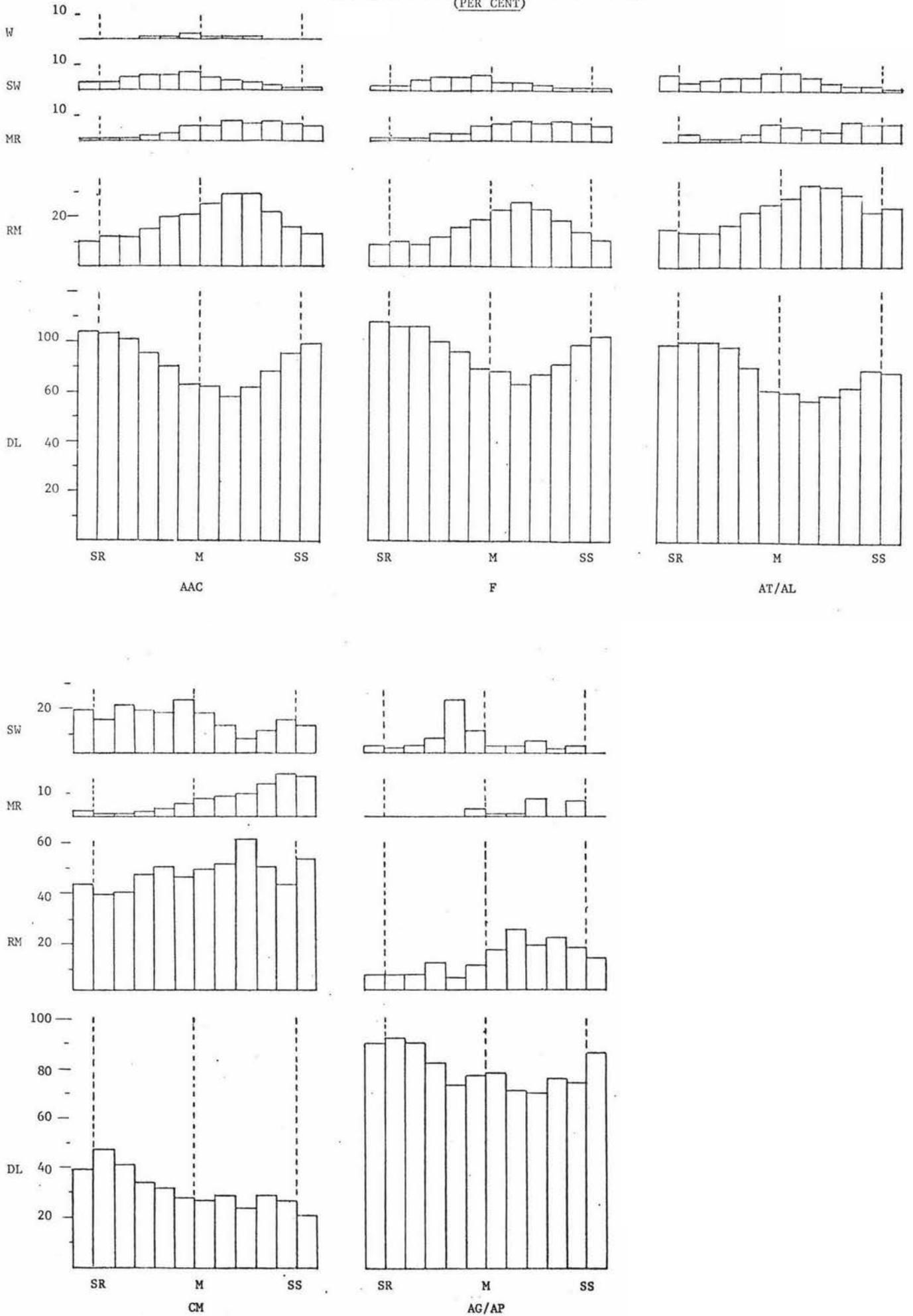
The hypothesis that pukeko spent equal time feeding, in bodily maintenance, courting, drinking, or calling, or were equally attentive or agonistic in all habitats over the day, was tested for each activity and rejected ( $p < 0.001$ ).

### 6.3 Annual Habitat Utilisation

Combined activity data showed dryland was the most frequently used habitat all day, being used more in the early morning and late afternoon than at midday (App. 5; Fig. II). Time spent in rush margins was least in the morning, peaking in the early afternoon decreasing thereafter, while mud was used more extensively towards dusk. Pukeko used swamp and water most in the late morning and at midday respectively. Remaining observations comprised birds in flight, which were seen most in the early morning.

Feeding pukeko mostly used pasture and less frequently rush margins, mud, swamp and water. In dryland, least time was spent feeding during the early afternoon, while rush margins were used most in the early afternoon and least in the early morning. Pukeko fed in mud progressively more frequently over the day, while use of swamp showed a reciprocal pattern. They fed most in water at midday.

FIG. 11 ANNUAL DIURNAL HABITAT UTILISATION  
(PER CENT)



Most attentive/alarm postures were recorded in dryland, especially in the early and late morning, while in rush margins, progressively more were recorded in the morning and early afternoon, and fewer at dusk. Birds in swamp were most vigilant at midday, whereas in mud, attentiveness increased progressively over the day.

Generally birds engaged in bodily maintenance were mostly observed in rush margins, least frequently in mud, with dryland and swamp intermediate. In rush margins comfort movements were seen least in the early morning, increasing to peak in the early afternoon, while in dryland they were seen chiefly in the early morning, and progressively less frequently thereafter. In swamp, bodily care peaked in the late morning, whereas in mud fewest were seen at dawn and most at dusk.

Over the day most agonistic/appeasement encounters were seen in dryland, especially at dawn and dusk. In rush margins fewer birds were engaged in these activities in the morning than in the afternoon, whereas in swamp most were recorded in the late morning. Encounters in mud were recorded most often in the early afternoon.

Pukeko courted more often in dryland, especially in the late morning and late afternoon, than in rush margins, swamp or mud.

Most birds drank in rush margins, particularly towards day's end, with infrequent observations of birds drinking in remaining areas comprising the balance.

More birds called in dryland, especially in the late morning and late afternoon, than in either rush margins or swamp where they were most vocal in the early afternoon and early morning respectively. Pukeko called infrequently in mud.

#### 6.4 Feeding

##### 6.4.1 Appetitive and Consumatory Feeding, and "Other" Activities

From pooled habitat data more time was spent eating than looking for food all day, with the birds eating mostly

at midday, and looking for food mostly at dawn and dusk (App.6; Fig.12). Time allocated to "other" activities made up the balance of time, peaking around midday.

In pasture pukeko spent less time searching for food, than eating. They spent gradually more time eating, and less time looking for food, until mid afternoon. "Other" activities occupied equal time in the morning and early afternoon, but slightly less in the late afternoon.

In rush margins, most time was spent eating food, least was spent searching for food, and "other" activities occupied intermediate time over the day. More birds looked for food in the early morning than throughout the remainder of the day, while more birds were seen eating towards dusk. Most time was allocated to "other" activities in the late morning, and least in the afternoon.

In mud, pukeko spent more time eating than either locating food or in "other" activities. They ate less frequently in the early morning than later, while time spent looking for food showed a reciprocal pattern. Time engaged in "other" activities, decreased progressively from dawn to dusk.

In swamp over the day, similar time was spent eating and following "other" activities, while less time was spent looking for food. Time spent eating peaked in the late morning, decreasing thereafter, while that assigned to "other" activities was consistent over the day. Most time was spent looking for food at dusk.

In water birds mostly swam, especially at dawn and dusk, whereas time spent eating peaked at midday. No appetitive feeding behaviour was recorded here. An hypothesis that pukeko used all habitats equally for all activities over the day, was tested and rejected ( $p < 0.001$ ).

#### 6.4.2 Pecking rate - Feeding intensity

From pooled habitat and dryland data, pukeko pecked progressively faster over the morning to peak at early afternoon, and slower towards dusk (App. 6; Fig.13).

FIG. 12 ANNUAL DIURNAL TIME ALLOCATION TO APPETITIVE  
AND CONSUMATORY FEEDING AND "OTHER" ACTIVITIES  
(PER CENT)

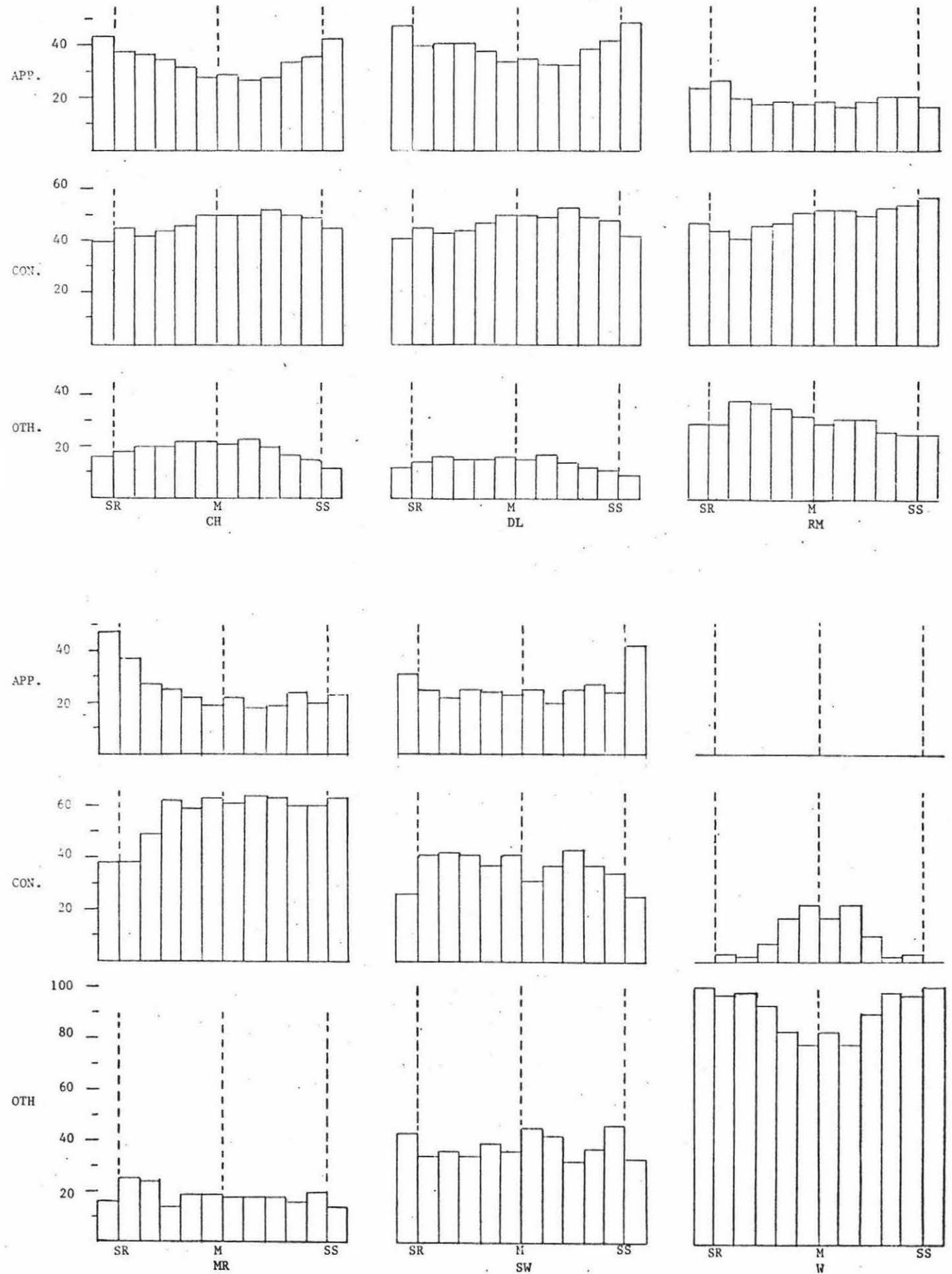
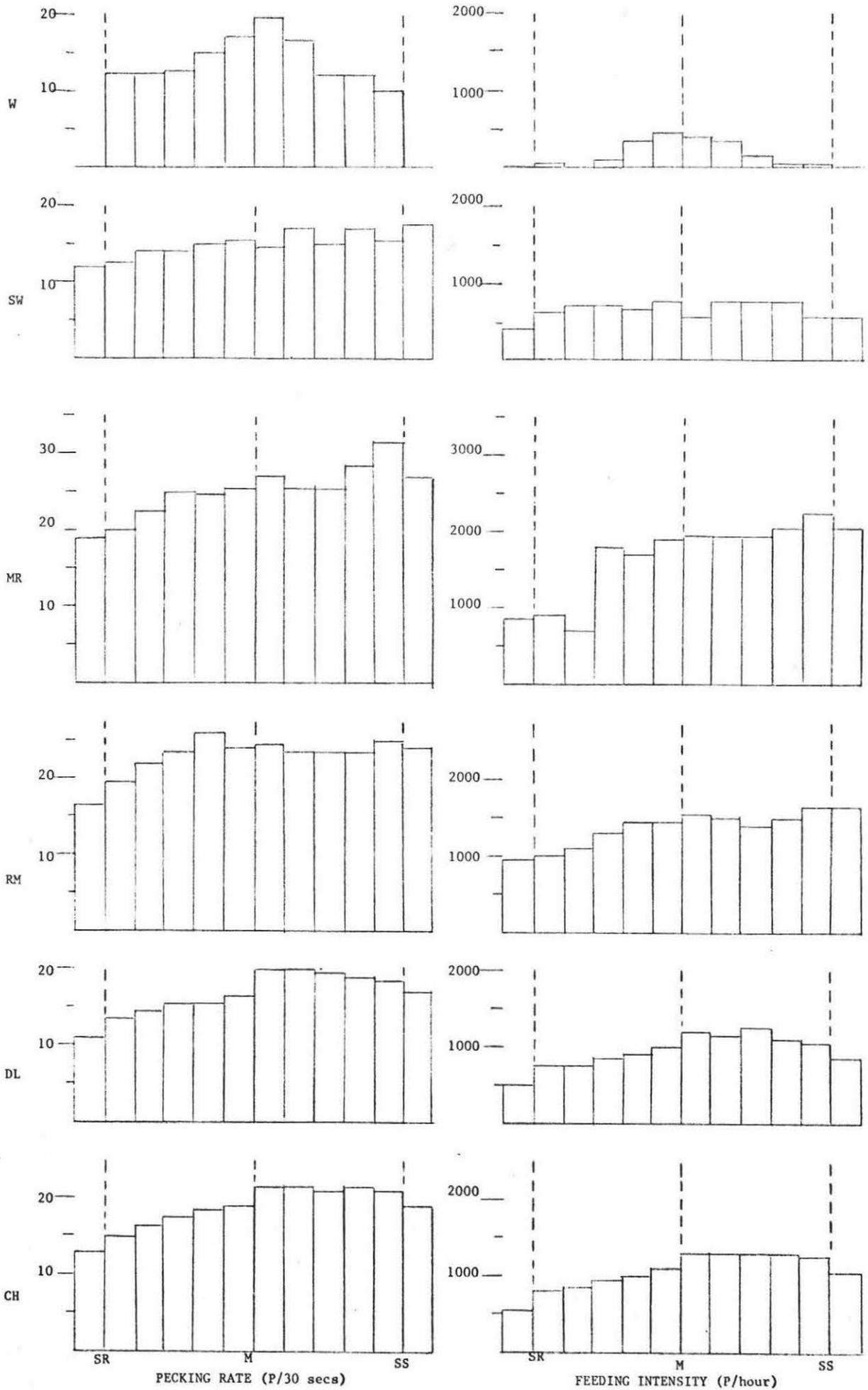


FIG. 13 ANNUAL DIURNAL PECKING RATE, AND FEEDING INTENSITY OF PUKEKO



Birds feeding in rush margins pecked slowest in the early morning, and at a similar rate thereafter, whereas in mud and swamp, pecking rates increased progressively throughout the day. In water they pecked fastest at midday.

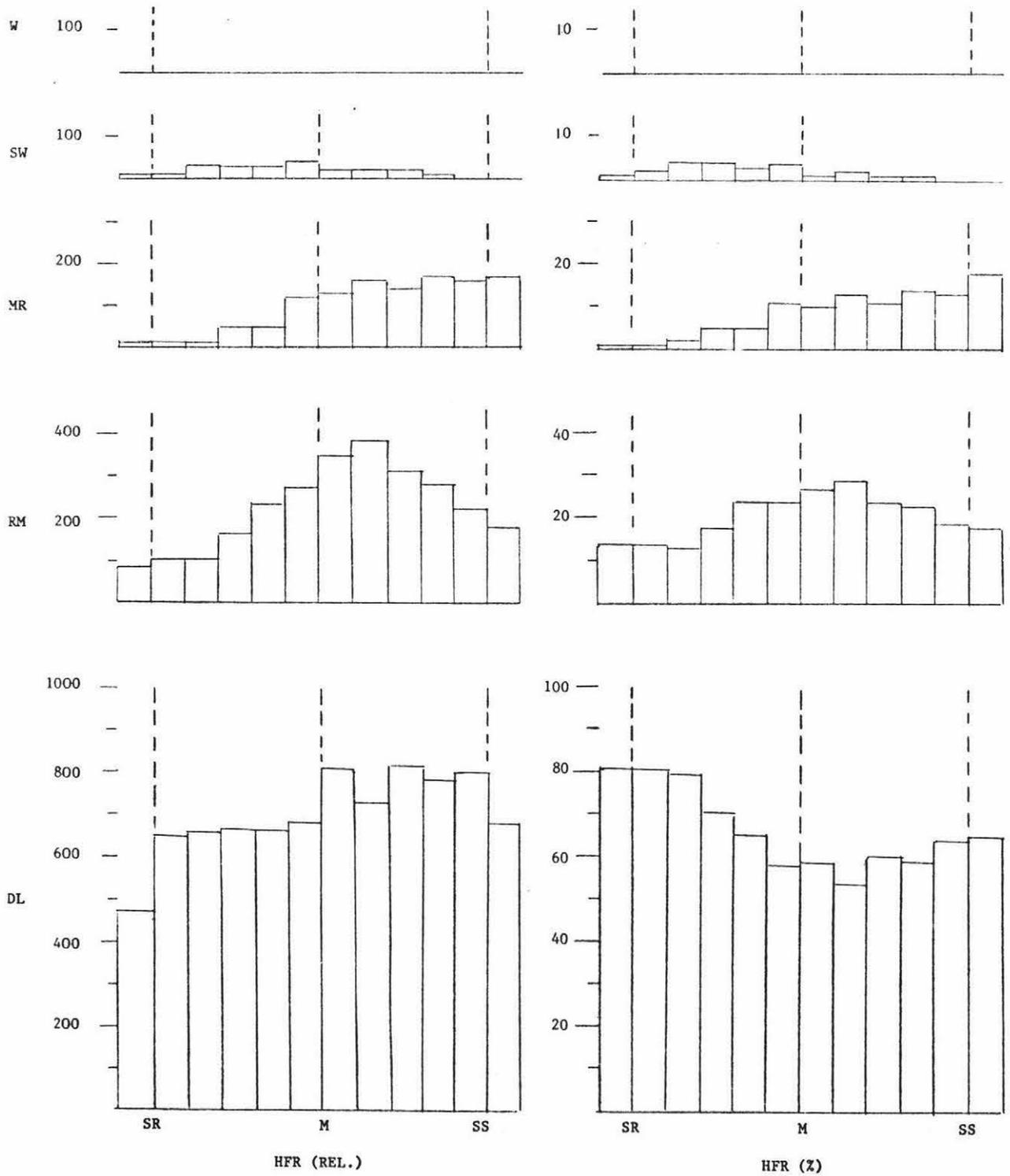
From pooled habitat and dryland data, pukeko fed gradually more intensely in the morning, most in the early afternoon, and at an intermediate intensity in the late afternoon (App. 6; Fig.13). In rush margins and mud, pukeko fed least at dawn and most at dusk, whereas they pecked fastest in swamp and water at midday. Highest feeding intensities were recorded in rush margins and mud. In each habitat pukeko did not feed at the same rate or intensity over the day (for every test  $p < 0.001$ ).

#### 6.4.3 Habitat Foraging Rank

Dryland was the most important feeding site, being used more in the afternoon than in morning (App. 6; Fig.14). Pukeko fed in rush margins most in the early afternoon and least in the early morning, whereas they fed in mud progressively more over the day. Swamp was used infrequently for feeding, being used most in the late morning and least during the late afternoon, while water contributed little, being used most at midday.

The relative contribution (per cent pecks) of each habitat to the total number of pecks delivered per hour showed pasture contributed more than any other habitat, especially in the early morning (App.6; Fig.14). Rush margins, the next major feeding site, contributed proportionally least at dawn and dusk, and most at midday, whereas mud was used progressively more over the day. Swamp was used infrequently for feeding, contributing most in the late morning and least in the late afternoon. Comparatively, water contributed little to the overall feeding strategy.

FIGURE 14  
ANNUAL DIURNAL HABITAT FORAGING RANK OF PUKEKO



## 6.5 Discussion

Diurnal changes in use of available habitats are perhaps best explained through changes in feeding times and rates, and in the quest for protected resting or loafing areas.

Over the day feeding occupied more time at the expense of bodily maintenance, whereas time spent in attentive postures or in maintaining intra- and inter-territorial hierarchies, varied little. Increased foraging time at dusk may reflect "stocking-up" of food reserves for the coming night. If night feeding does not occur, the early morning peak may represent the birds eagerly eating food as their stomachs would have been empty following the night's fast.

### Plant quality

Within a season, plant material was probably equally available throughout the day to feeding pukeko, although forage quality may have varied. Any diurnal differences in feeding times or rates reflected pukeko selectivity of available forage. Time spent looking for food was greatest at dawn and dusk - the birds being perhaps more selective in choosing food items at these times. Possibly they selected higher quality food, so that in the morning, following the night's fast, depleted energy reserves could have been replaced quickly, whereas at dusk higher quality food ingested would have provided more energy for longer into the night. Conversely they fed less selectively but ate more often at midday.

Pukeko pecked fastest and most intensely in the early and mid afternoon in pasture. This, in view of time spent looking for and eating food, suggests pukeko may have fed most at that time of day during which the quality of food available was optimal (or maximal), i.e. early and mid afternoon. Birds in rush margins and mud fed most in the mid and late afternoon, while in swamp they fed mainly in the mid and late morning, again perhaps when food quality was high.

Over the day pukeko mostly used pasture, but especially in the afternoon, whereas they used rush margins mainly in the early afternoon, and mud progressively more over the day. Swamp and water were used infrequently for feeding, but mainly at mid morning in the former, and mostly at midday in the latter. Although maximal feeding intensities were recorded in dryland in the early afternoon, it is difficult to explain why feeding birds left this habitat (although a majority stayed) and switched to rush margins, especially if an optimal food source existed in pasture at this time.

One possibility is that a "super-optimal" food supply existed in rush margins at this time. In early afternoon maximal use was made of this habitat for feeding. Perhaps rush margin plants manufactured some compound(s) which in the early afternoon was found in higher concentrations in these plants than in pasture plants. However, as the day progressed either more was made by pasture and also mud plants, or less was made by rush margin plants, so the birds turned their attention from feeding in the rush margins to feeding in dryland and mud areas. Or perhaps aerial predators or the farmer and his dogs, may have simply disturbed pukeko feeding in pasture around midday, resulting in an increase in the use of other areas.

#### Protected Loafing area

Similarly, a "super-optimal" food supply may have been present in swamp in the mid and late morning, resulting in maximal use of this area then. However, another factor to consider was an increase in bodily maintenance at this time, especially in swamp and rush margins. Diurnal changes in time spent in attentive/alarm in all habitats followed those of feeding activities, and birds loafing etc. within the comparative safety of rush margins and swamp were relatively less attentive than those that fed and rested in open dryland and mud areas. That is birds may have returned to the safety of swamp and marginal areas to rest and preen etc., hence feeding infrequently at this time.

#### Activity cycle

The diurnal activity cycle described above, may have been related to the pukeko's increased demand for energy towards

day's end. When resting, the basal metabolic rate of medium sized birds, such as pukeko, is considered minimal (King and Farner, 1961). However, as the birds are apparently more active towards day's end, the energetic cost to them of becoming so will be expected to rise as they pursue energetically more expensive activities. Energy intake therefore must gradually increase, either through the ingestion of a greater quantity of food (increased pecking rates) or a higher quality of food, to replace the energy that has been used. Research into the energetic cost of various activities especially feeding, but also fighting, courting, bodily maintenance etc., and the diurnal quality of forage could throw some light on this topic. Thus as the day progresses and more energy-demanding biological processes are pursued, the birds mostly followed a feeding pattern which allowed them to at least compensate for this increased energy useage. At the day's end "stocking-up" of food reserves is likely to occur, to supply the bird with an increased store of food after dusk.

## 6.6. Seasonal Time Allocation

### 6.6.1 Autumn

In autumn pukeko fed progressively less frequently over the day, from a maximum in the early morning, to a minimum during early and mid afternoon, increasing again in the late afternoon (App. 7; Fig. 15). Attentive/alarm behaviour accounted for similar time over the day, while that allocated to bodily maintenance increased during the early morning, to a level which was maintained throughout most of the day, before decreasing at dusk. Encounters occupied similar time throughout the day, while pukeko swam mostly at midday, and flew mainly in early morning and late afternoon. Remaining time was spent either courting, drinking, or calling.

### Dryland

Pukeko spent similar time feeding throughout the day accounting for most observations, while attentive birds were also seen consistently throughout the day. Bodily maintenance was seen progressively more frequently from morning through to mid afternoon, and less commonly thereafter, whereas birds

in conflict were observed irregularly.

### Rush Margins

Feeding birds accounted for the bulk of observations throughout the day, being observed most frequently at dawn, least during the mid morning, and progressively more to a second peak at dusk. They were most wary in the mid morning, whereas time allocated to comfort movements peaked at mid morning and mid afternoon. Encounters were irregular in the morning, but more common in the afternoon, while birds drank and called infrequently all day.

### Mud

Pukeko were recorded here exclusively in the afternoon and were mostly feeding, especially in the early and late afternoon, while time spent in attentive/alarm activities was similar throughout the afternoon. Comfort movement and agonistic/appeasement activities were seen infrequently.

### Swamp

Here, time was mostly spent feeding, especially at dawn and dusk, while attentive/alarm activities showed a reciprocal pattern. Time devoted to bodily maintenance peaked in the mid morning and early afternoon, and encounters and calling were infrequently observed.

### Water

Throughout the day only one bird (n=81 bird-observations) fed in water, with others swimming.

## 6.6.2 Winter

### Combined Habitat Data

Proportionally more birds were seen feeding at dawn and dusk than during midday in winter, accounting for most observations, while they were almost consistently attentive over the day (App. 8 ; Fig. 16). Time spent in bodily maintenance and in encounters increased progressively from early and mid morning to midday decreasing thereafter. Pukeko courted and drank progressively more over the day, peaking at dusk and early afternoon respectively, while they flew

FIG. 15 SEASONAL DIURNAL TIME ALLOCATION - AUTUMN  
(PER CENT)

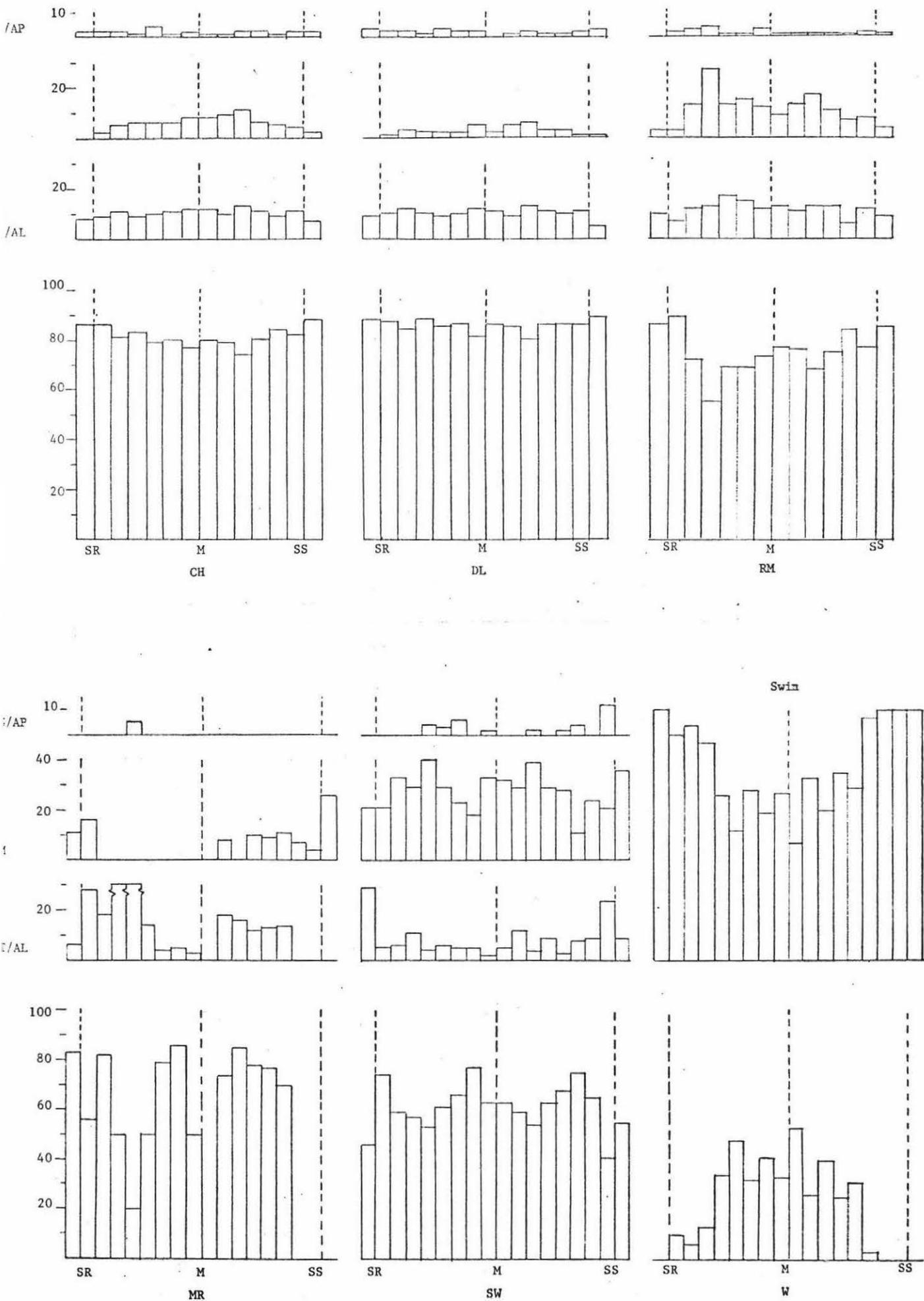
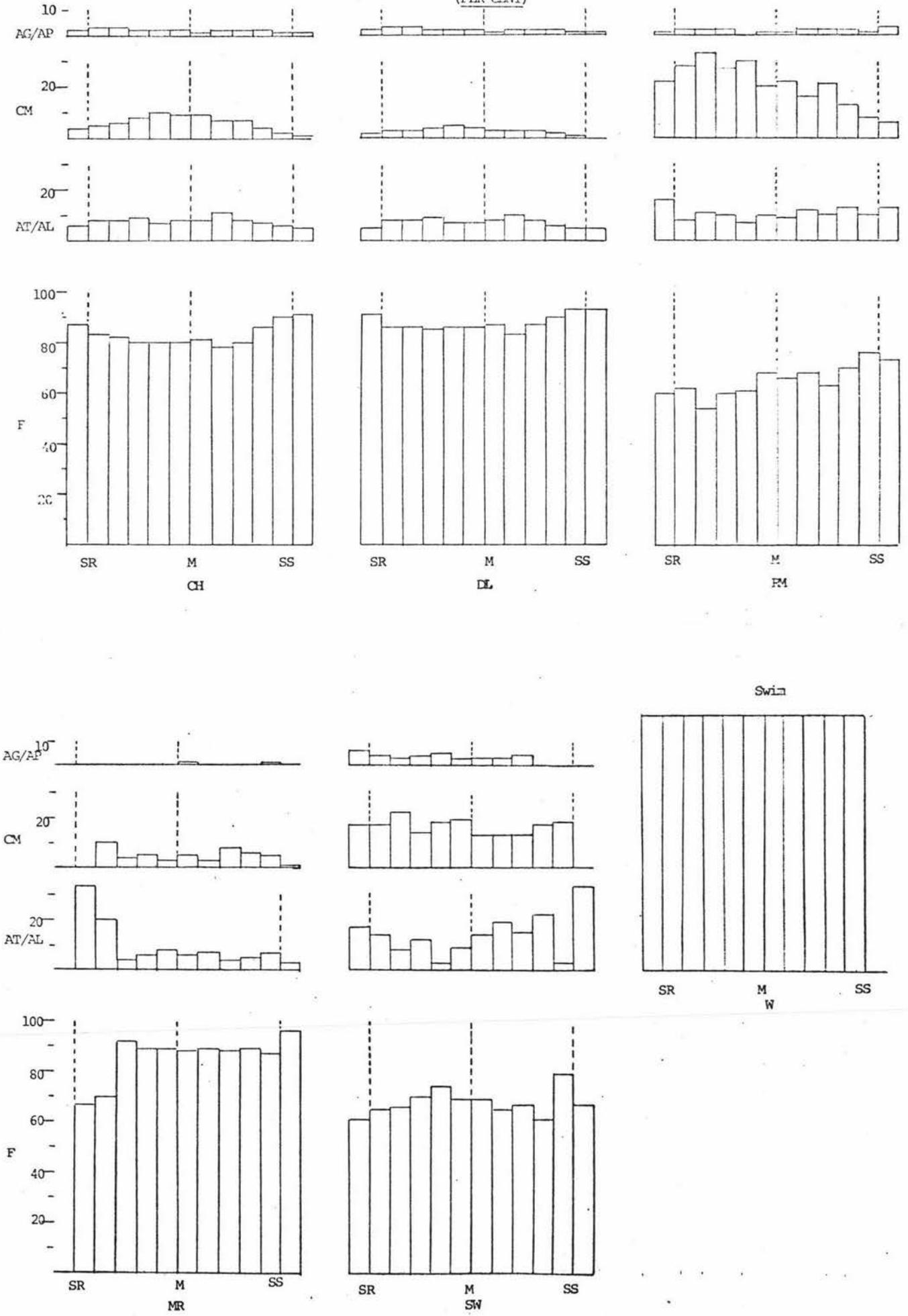


FIG. 16 SEASONAL DIURNAL TIME ALLOCATION - WINTER

(PER CENT)



and called consistently throughout the day. Birds swam mainly at midday.

### Dryland

More time was spent feeding than following any other activity, showing a similar diurnal pattern to that described from combined habitat data. Attentive/alarm activities increased progressively through the morning, peaking in the early afternoon, while bodily maintenance increased steadily during early and mid morning, peaking in the late morning, and decreased gradually in the afternoon. Progressively fewer birds were observed in encounters over the day, while they courted, drank and called infrequently.

### Rush Margins

Pukeko mainly fed here, particularly at dawn and dusk. Attentive birds were seen consistently throughout the day - a little more commonly at dawn and dusk than at midday. Time spent in comfort movements peaked in mid morning, decreasing steadily thereafter. They drank and fought etc. more frequently towards dusk, but courted infrequently.

### Mud

Pukeko spent similar time feeding throughout the day, except during the early and mid morning. Apart from a dawn peak, attentive/alarm activities occupied similar time over the day, while that assigned to comfort movement, agonistic/appeasement, and drinking activities was irregular.

### Swamp

Pukeko mostly fed here, particularly at dawn and dusk. Gradually less time was spent in attentive/alarm postures in the morning, increasing again in the afternoon. Bodily maintenance was more frequently observed in the morning than in the afternoon, while encounters were seen consistently throughout, except in the late afternoon when no birds were seen fighting, etc. Residual time was spent calling or drinking.

### Water

Feeding birds were not recorded in water during winter, consequently all observations were of birds swimming.

### 6.6.3 Spring

#### Combined Habitat Data

Pukeko spent most time by far feeding, particularly at dusk, while over the day attentive/alarm postures occupied similar time (App. 9; Fig.17). Least time was devoted to comfort movements at dawn and dusk, and the birds were observed in conflict most at dawn. They courted and called mainly at dawn and dusk, drank irregularly over the day, swam mostly at midday, and flew mainly at dawn.

#### Dryland

Pukeko followed similar diurnal patterns to those described above, except they courted here mostly at dusk. Also proportionally more time was spent feeding here than recorded above.

#### Rush Margins

Again, pukeko spent most time feeding here, being observed most commonly at dawn and least frequently at dusk. They preened most at midday and were equally attentive all day. Agonistic/appeasement encounters were recorded mostly in the early morning. They courted and drank more in the afternoon than during the morning, and called mainly in the morning.

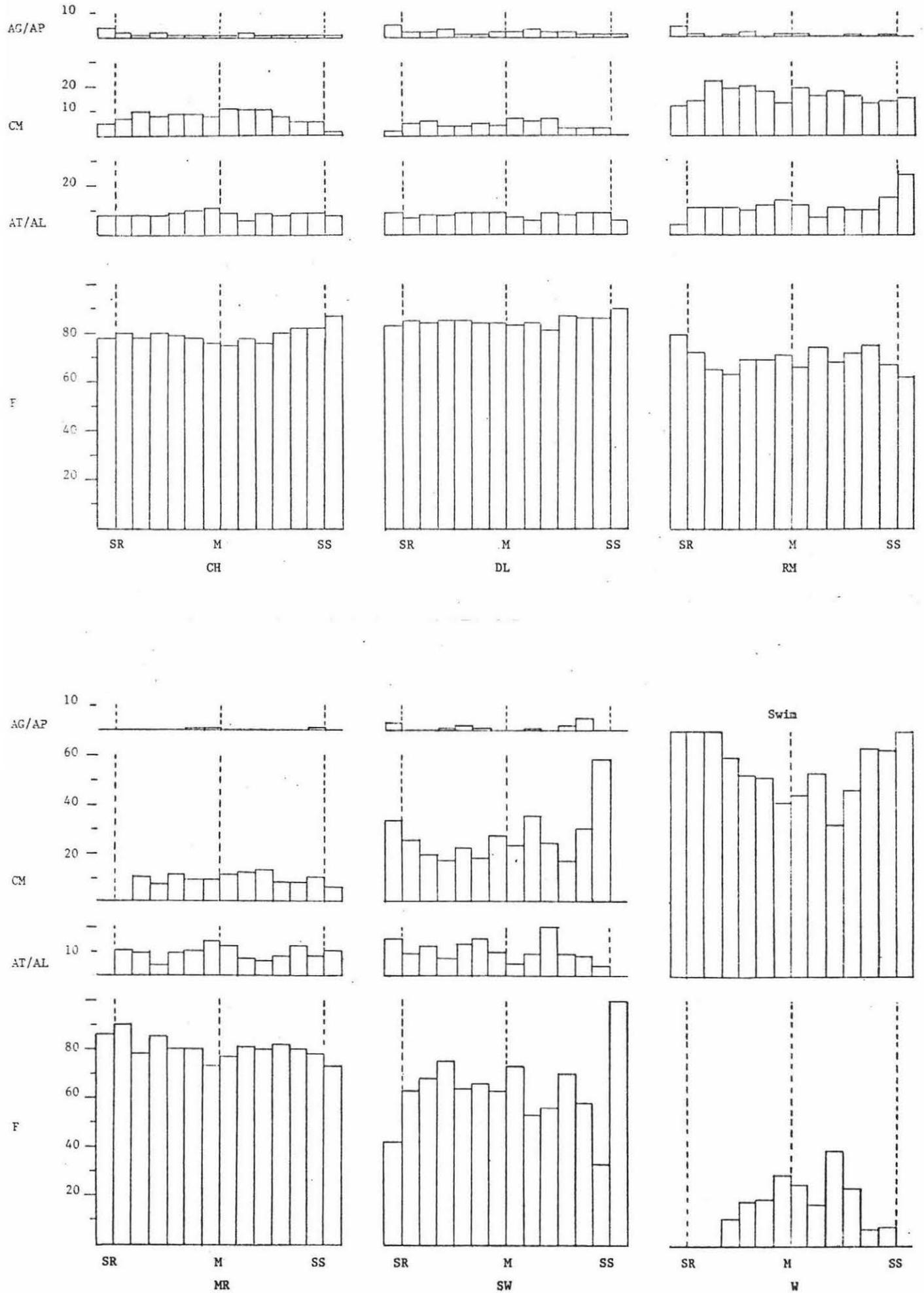
#### Mud

Here birds spent most time feeding, especially in the early morning. Attentive/alarm activities occupied most time at midday, while birds interacted, drank, and called infrequently. Although rarely observed at dawn and dusk, bodily maintenance was seen mostly at midday.

#### Swamp

Although they fed most in the mid morning and mid afternoon, proportionally fewer birds were recorded feeding here than in pasture, rush margins or mud. Pukeko were more vigilant in the morning than in the afternoon, with a peak occurring in the mid afternoon. Bodily maintenance followed a reciprocal pattern to that described for feeding activities, in that three activity peaks were recorded - in the early

FIG. 17 SEASONAL DIURNAL TIME ALLOCATION - SPRING  
(PER CENT)



morning, early and late afternoon. Agonistic/appeasement activities, drinking and calling were seen infrequently over the day.

#### Water

Few pukeko fed in water except at midday, while they swam mostly at dawn and dusk.

#### 6.6.4 Summer

##### Combined Habitat Data

Time spent feeding by pukeko varied little throughout the day, and accounted for most observations, particularly in the early morning and late afternoon, whereas time assigned to attentive activities was similar throughout the day, peaking in the mid morning, early and late afternoon (App. 10; Fig. 18). Time devoted to bodily maintenance increased gradually throughout the morning to peak around midday, steadily decreasing thereafter, while that spent in encounters was similar over the day. Courting birds were observed irregularly, but seemingly most often at dusk. Pukeko drank and called infrequently over the day, and flew most at dawn and dusk.

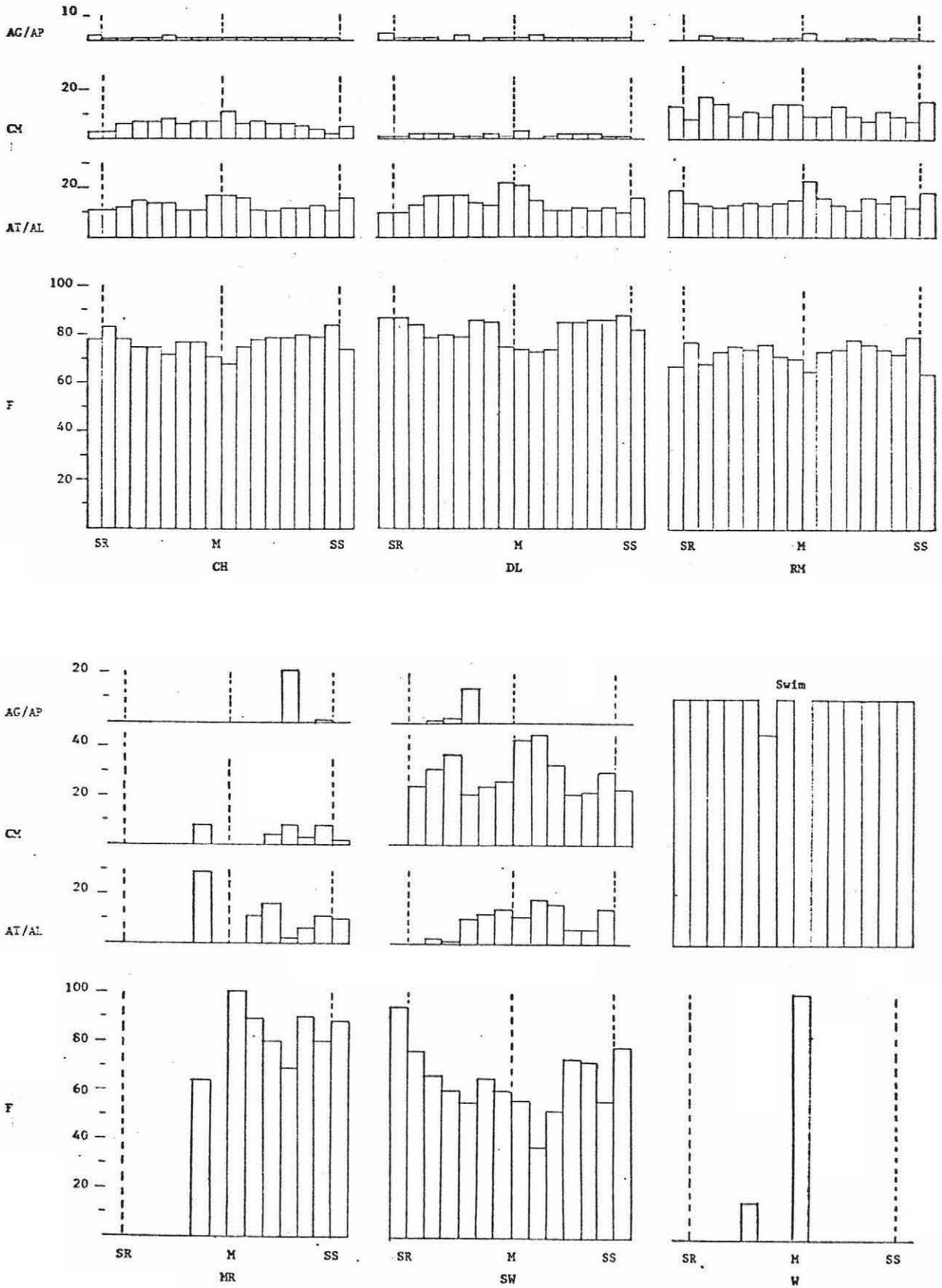
##### Dryland

Feeding, attentive/alarm, agonistic/appeasement and courtship activities in pasture showed similar diurnal changes as those described from data pooled by habitat. Bodily maintenance accounted for a similar proportion of time throughout the day, occupying least time at dawn and dusk, whereas calling was irregularly recorded.

##### Rush Margins

Feeding activities once again accounted for the bulk of observations, occupying most time in the early and mid morning and mid afternoon. The birds were most vigilant in the early morning and early afternoon, whereas bodily maintenance occupied similar time over the day. Except for birds observed drinking, which were recorded most frequently

FIG.18 SEASONAL DIURNAL TIME ALLOCATION - SUMMER  
(PER CENT)



in the late afternoon, remaining activities, i.e. agonistic/appeasement, courtship and calling, were observed infrequently.

#### Mud

Few birds were seen here in summer. In the mid and late afternoon more birds were observed here, apparently spending more time feeding, than in bodily maintenance or attentive/alarm activities. Other activities were irregularly observed.

#### Swamp

Feeding birds again accounted for the bulk of observations here, especially in the early and late morning, and mid afternoon, whereas time allocated to comfort movements was greatest in the mid morning, early and late afternoon. The birds were most attentive, and called more frequently at dawn and dusk. Residual time was spent in encounters, courting and drinking, none of which were observed regularly.

#### Water

Feeding in water peaked at midday, being least frequently observed at dawn and dusk, while time allocated to swimming showed a reciprocal pattern.

### 6.6.5 Statistics

For each season, and for all habitats the hypothesis of equal time allocation to all activities over the day was tested and rejected. Significance at the  $p < 0.001$  level was obtained for 159 tests, the remaining 9 tests being significant at the  $p < 0.01$  level.

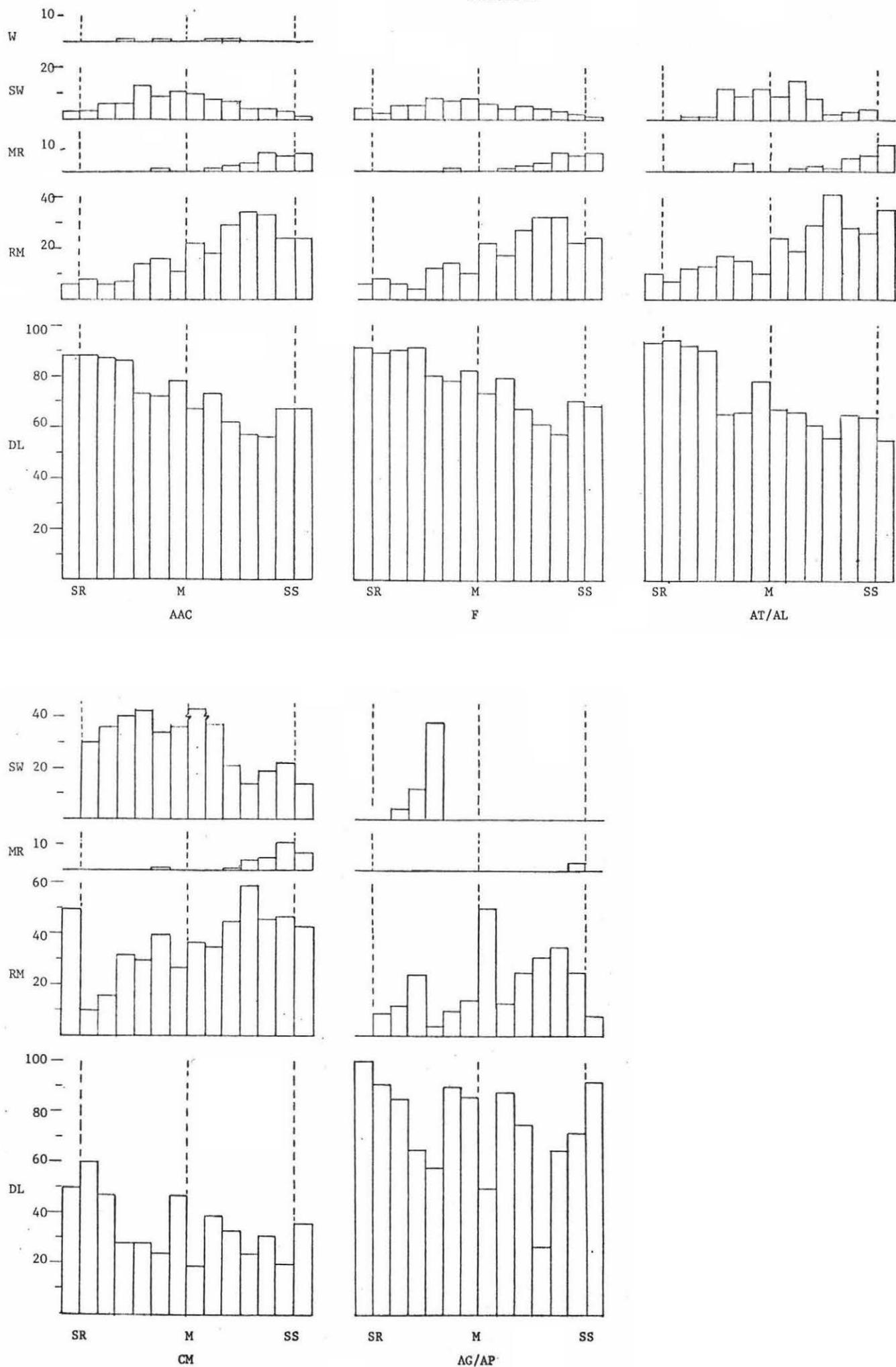
## 6.7 Habitat Utilisation

### 6.7.1 Autumn

#### Combined Activity Data

Dryland was the habitat most frequently used over the day, being used more in the early morning and late afternoon than at midday, whereas use of rush margins showed a reciprocal diurnal pattern (App. II; Fig. 19). Swamp was used least often at dusk, while mud was used mostly in the mid and late afternoon

FIG. 19 SEASONAL DIURNAL HABITAT UTILISATION - AUTUMN  
(PER CENT)



Pukeko swam throughout the day, and flew mostly at dawn.

### Feeding

When considering feeding activities separately, similar diurnal patterns to those described from combined activity data were followed for all the habitats except water. In autumn only three pukeko were observed feeding in water, being observed only at midday.

### Attentive/alarm

Most birds observed in attentive/alarm postures were seen in dryland although fewer were seen towards dusk, while gradually more were seen in rush margins and mud from dawn through to dusk. Swamp was used mostly at midday.

### Comfort Movements

In autumn, birds engaged in bodily maintenance were seen mostly in rush and swamp areas, especially at mid morning and mid afternoon. Swamp was used progressively more often in the early and mid morning, to a slightly lesser extent at midday, and least frequently during the mid and late afternoon. Dawn and dusk were the periods during which dryland was most frequently used for comfort movements, whereas mud was used mostly in the mid and late afternoon.

### Agonistic/appeasement

Agonistic/appeasement bouts were mostly recorded in dryland over the day, and, in swamp, were seen only during the mid morning. Encounters were recorded in rush margins throughout the day, with apparently more there in the afternoon than the morning, and were noted erratically in mud.

### Courtship; Drinking; Calling

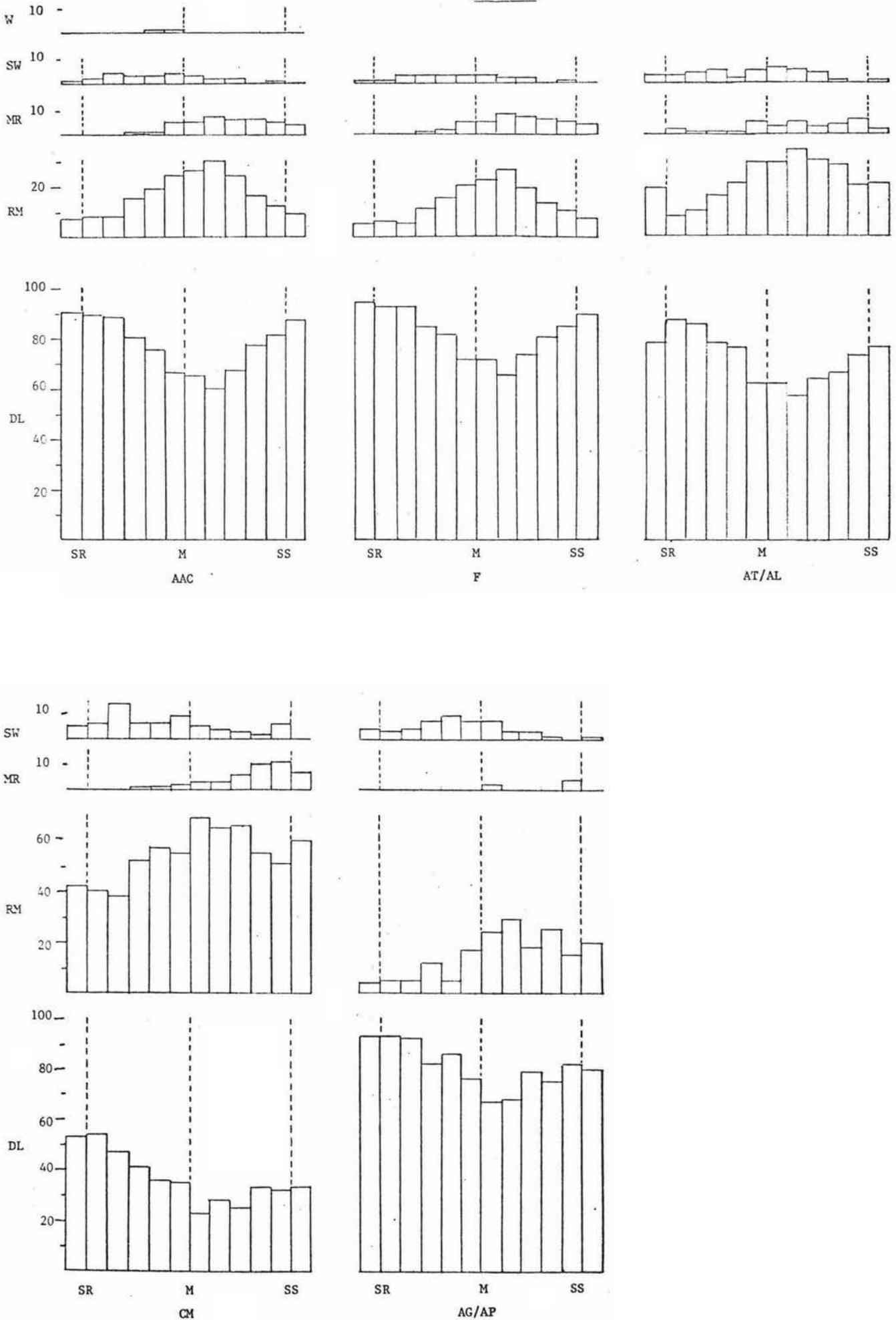
Few pukeko courted, drank and called in autumn.

## 6.7.2 Winter

### Combined Activity Data

Dryland was used most frequently, followed by rush margins, mud, and swamp (App. 12; Fig. 20). Diurnally most time was spent in dryland at dawn, progressively less until

FIG. 20 SEASONAL DIURNAL HABITAT UTILISATION - WINTER  
(PER CENT)



the early afternoon, with gradually more time being spent there during the mid and late afternoon. Use of rush margins followed a reciprocal diurnal pattern. Mud was used irregularly in the morning, and at an essentially constant rate in the afternoon, whereas swamp was used more in the morning than in the afternoon. Pukeko swam most at midday, and flew mostly in the early morning, occupying similar time thereafter.

#### Feeding; Attentive/alarm

The diurnal patterns described above for each habitat, were the same when feeding and attentive/alarm activities were considered separately, with dryland being used far more frequently than either rush margins, swamp, or mud, although the relative proportions of time allocated to each in all habitats was different.

#### Comfort Movements

Birds engaged in bodily maintenance were observed mostly in rush margins and dryland in winter. Progressively more birds loafed in rush margins in the morning and early afternoon, and fewer thereafter, while in pasture a reciprocal pattern of useage was followed. A similar proportion of birds were recorded in swamp during the morning, with comparatively fewer seen there during the afternoon, whereas mud was used progressively more frequently over the day.

#### Agonistic/appeasement

Birds in encounters in dryland accounted for the bulk of observations by far. Gradually more birds were seen fighting etc. in rush margins from dawn through to early afternoon, with fewer birds observed thereafter. Use of swamp increased steadily in the morning to peak during the late morning, but decreased thereafter. Only three birds in agonistic/appeasement activities were recorded in mud during winter, and all were observed in the afternoon.

#### Courtship; Drinking; Calling

Birds courted, drank and called infrequently and erratically in winter, however proportionally more were seen

courting in pasture than in rush margins, while none were recorded in swamp or mud. They drank primarily in rush margins, but were also seen drinking in dryland, swamp and mud, whereas they called more from dryland than from rush margins or swamp.

### 6.7.3 Spring

#### Combined Activity Data

Dryland, the most frequently exploited area, was used progressively less often over the morning, least at midday, and progressively more throughout the afternoon, especially in late afternoon (App. 13; Fig. 21). Rush margins were used consistently during the early and mid morning, to a greater extent at midday, and gradually less frequently thereafter. Progressively more birds were seen in mud throughout the morning, but consistent numbers were seen following midday, whereas birds in swamp were observed progressively less frequently over the day. Pukeko were seen in water mainly at midday, and birds in flight comprised the remaining observations, with more flying at dawn than later.

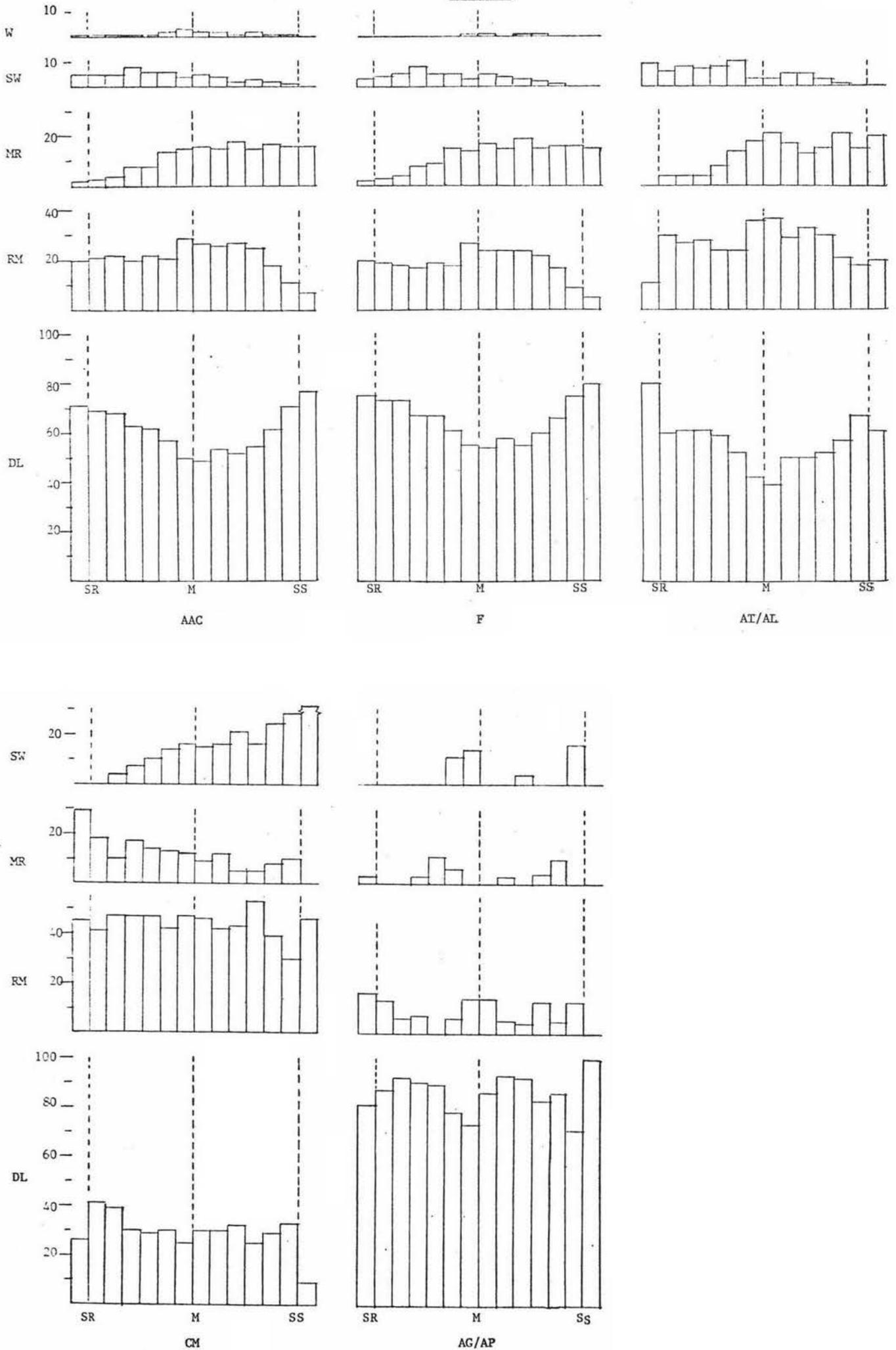
#### Feeding

Pukeko fed in pasture more frequently than in any other habitat, and the diurnal patterns for all habitats except swamp closely followed those described above. In swamp gradually more birds were seen feeding here over the morning (peak at mid morning) and gradually less thereafter.

#### Attentive/alarm

Attentive birds were mostly seen in pasture with least seen here at midday, and most at dawn and dusk. In rush margins birds were most wary at dawn and in the mid afternoon. In mud progressively more attentive birds were seen in the morning to peak in the early afternoon, fewer in the mid afternoon and more again at dusk. In swamp pukeko were less attentive in the afternoon than in the morning, and were unrecorded in water.

FIG. 21 SEASONAL DIURNAL HABITAT UTILISATION - SPRING  
(PER CENT)



### Comfort Movements

The lagoon's rush margins were the areas most frequently used by pukeko for bodily maintenance. Diurnally they used this habitat consistently throughout the morning, but to a gradually lesser extent in the afternoon. Dryland was the next most frequently employed area for loafing in winter, being used most often at dawn and least frequently at dusk. The birds preened etc. in mud progressively more often, and in swamp gradually less often over the day.

### Agonistic/appeasement

By far, birds were mostly involved in conflict encounters in dryland, the relative proportion of which peaked at mid morning and was least at midday. Pukeko also fought etc. in rush margins particularly at dawn and midday, whereas they fought infrequently in mud and swamp.

### Courtship; Drinking; Calling

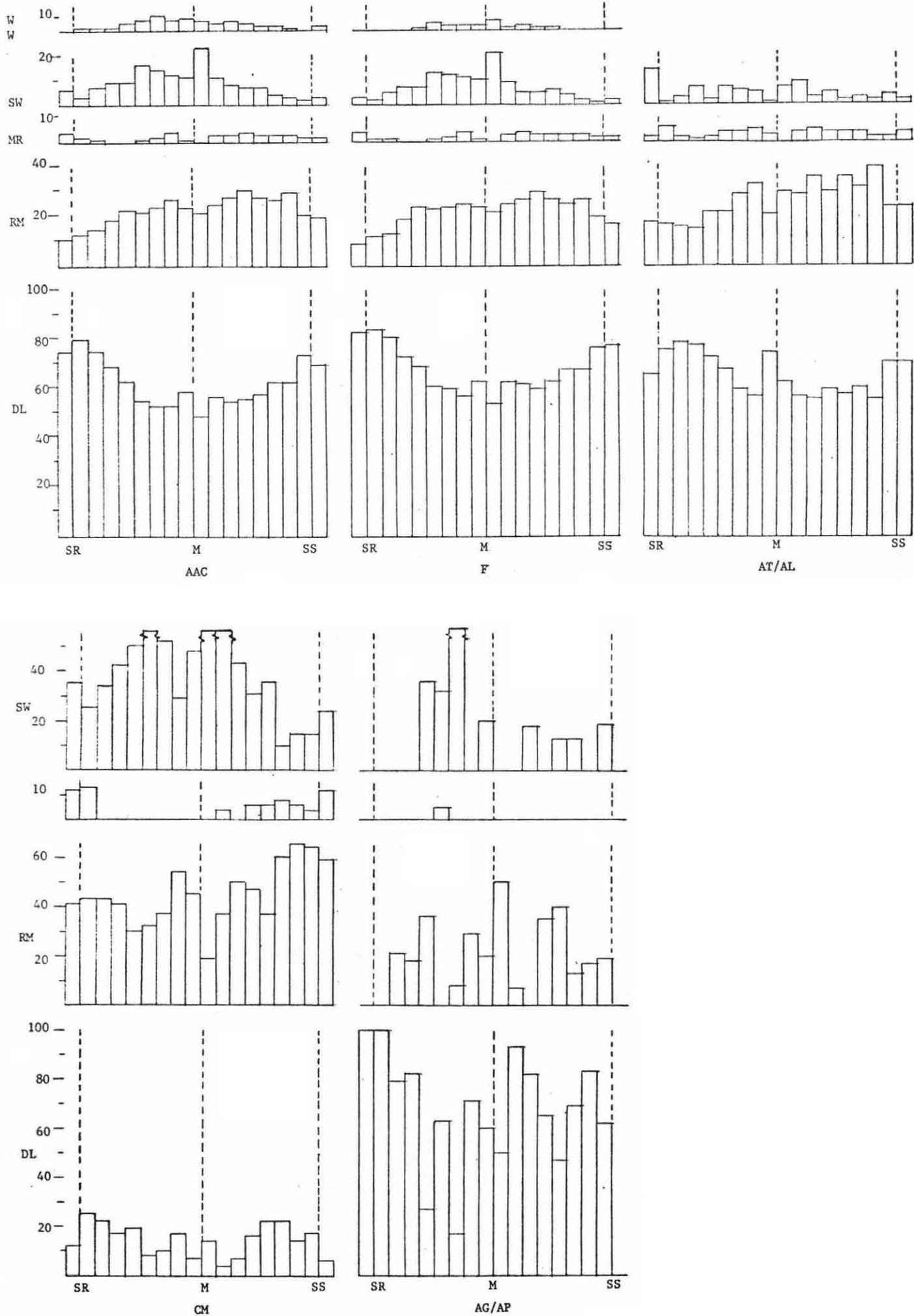
Although few birds were observed courting at any one time, most were seen in dryland, especially in the morning, whereas rush margins were used more in the afternoon than in the morning. No diurnal pattern was discernable for mud or swamp. Clearly most birds drank in rush margins, with others observed drinking in swamp and mud. Although observed irregularly throughout the day, pukeko called more from pasture and rush margins, than from swamp or mud.

#### 6.7.4 Summer

### Combined Activity Data

Dryland was the most frequently used habitat throughout the day during summer, with progressively fewer birds seen there during the morning, least at midday, and gradually more during the afternoon (App. 14; Fig. 22). Use of rush margins rose gradually over the day, to peak in the mid afternoon, while proportionally more were seen in swamp at midday than at either dawn or dusk. Pukeko used mud infrequently over the day, apparently more in the afternoon than in the morning, while they were observed most frequently in water in the late morning. They flew mainly at dawn and dusk.

FIG. 22 SEASONAL, DIURNAL HABITAT UTILISATION - SUMMER  
(PER CENT)



### Feeding

Generally use of each habitat for feeding, closely followed the diurnal patterns described from combined activity data, with dryland and rush margins being the most frequently utilised habitats, followed by swamp, mud and water.

### Attentive/alarm

Attentive birds were mostly seen in dryland, being observed more often at dawn, less during mid morning and dusk, and least frequently in the late morning, and early and mid afternoon. Rush margins were used gradually more extensively over the day, until mid afternoon, while birds were consistently attentive throughout the day in mud. Swamp was used erratically over the day, apparently more in the morning than in the afternoon.

### Comfort Movements

Birds recorded in comfort movements in swamp and rush margins accounted for most observations with similar numbers seen in rush margins from dawn until early afternoon, and more thereafter. Peak use of swamp occurred in the mid morning and early afternoon, whereas use of dryland, the next most frequently used habitat, peaked twice - in the early morning and mid afternoon. Birds in mud preened etc. only at dawn and in the afternoon.

### Agonistic/appeasement; Courtship; Drinking; Calling

Throughout the day few birds were seen fighting etc. or courting, however, most birds by far were recorded in dryland, followed by rush margins, while swamp and mud were infrequently used. Drinking and calling birds were also infrequently and irregularly recorded.

#### 6.7.5 Statistics

For each season and all activities, except swimming and flying the hypothesis of equal use of all habitats over the day was tested and rejected ( $p < 0.001$  in every case).

## 6.8 Feeding

### 6.8.1 Appetitive and Consumatory Feeding, and "Other" Activities

#### 6.8.1.1 Autumn

##### Combined Habitat Data

Pukeko spent by far most time eating, especially towards dusk, while they allocated gradually less time throughout the morning and early afternoon to locating food (App. 15; Fig.23). The balance of time was assigned to "other" activities, which occupied gradually more time over the morning and progressively less time during the afternoon.

##### Dryland

Considering dryland data, similar diurnal time allocation patterns to those described above were followed.

##### Rush Margins

Birds in rush margins spent most time eating, with progressively more doing so from dawn through to dusk. At dawn and in the mid afternoon, pukeko spent a considerable proportion of their time looking for food, with less time allocated to these activities during the mid and late morning, and early and late afternoon. Birds followed "other" activities mostly in the mid morning, devoting gradually less time thereafter.

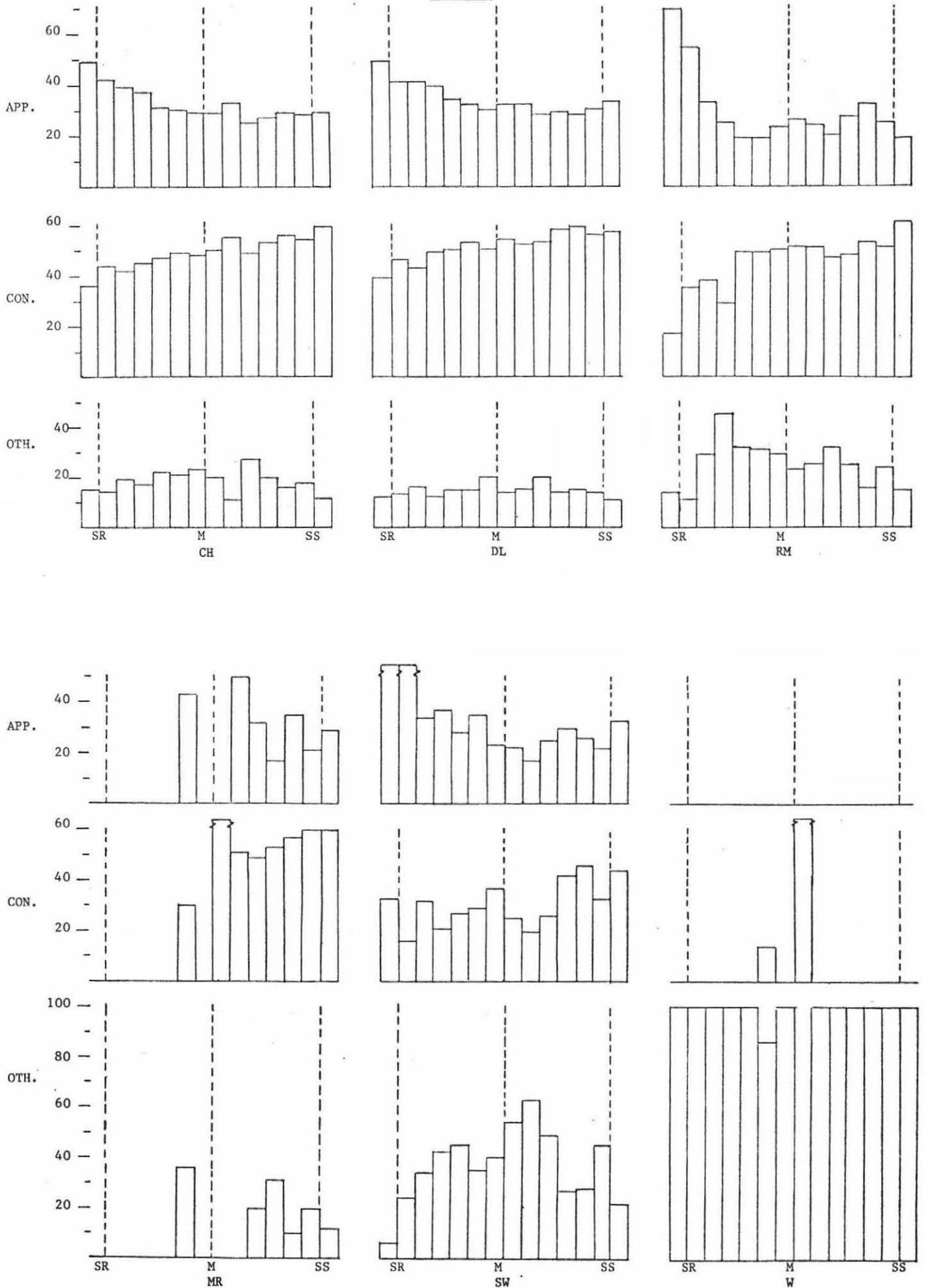
##### Mud

Few birds were seen in mud in the morning, and of those seen in the afternoon, most were recorded eating, with proportionally more doing so towards the day's end. Looking for food and "other" activities were seen irregularly.

##### Swamp

Here least time was spent looking for food around midday. From dawn until the early afternoon pukeko were seen gradually more frequently in "other" activities, while they ate mostly in the mid and late afternoon, and least at midday.

FIG. 23 SEASONAL DIURNAL TIME ALLOCATION TO APPETITIVE AND CONSUMATORY FEEDING AND "OTHER" ACTIVITIES - AUTUMN (PER CENT)



## Water

Few birds fed in water in autumn, and most were observed simply swimming.

### 6.8.1.2 Winter

#### Combined Habitat Data

In winter pukeko spent most time eating, especially at dawn and at midday, while that spent looking for food showed a reciprocal pattern (App. 16; Fig. 24). Most time was spent in "other" activities in the early afternoon, and least at dawn and dusk.

#### Dryland

Diurnally, similar time was spent in all three activities for dryland birds, to that described from combined habitat data.

#### Rush Margins

Over the day gradually more time was spent eating, accounting for most of the bird's time, while that spent locating food increased during the mid morning and occupied constant time over the remainder of the day. Time allocated to "other" activities occupied most time at mid morning and gradually less of the bird's time later.

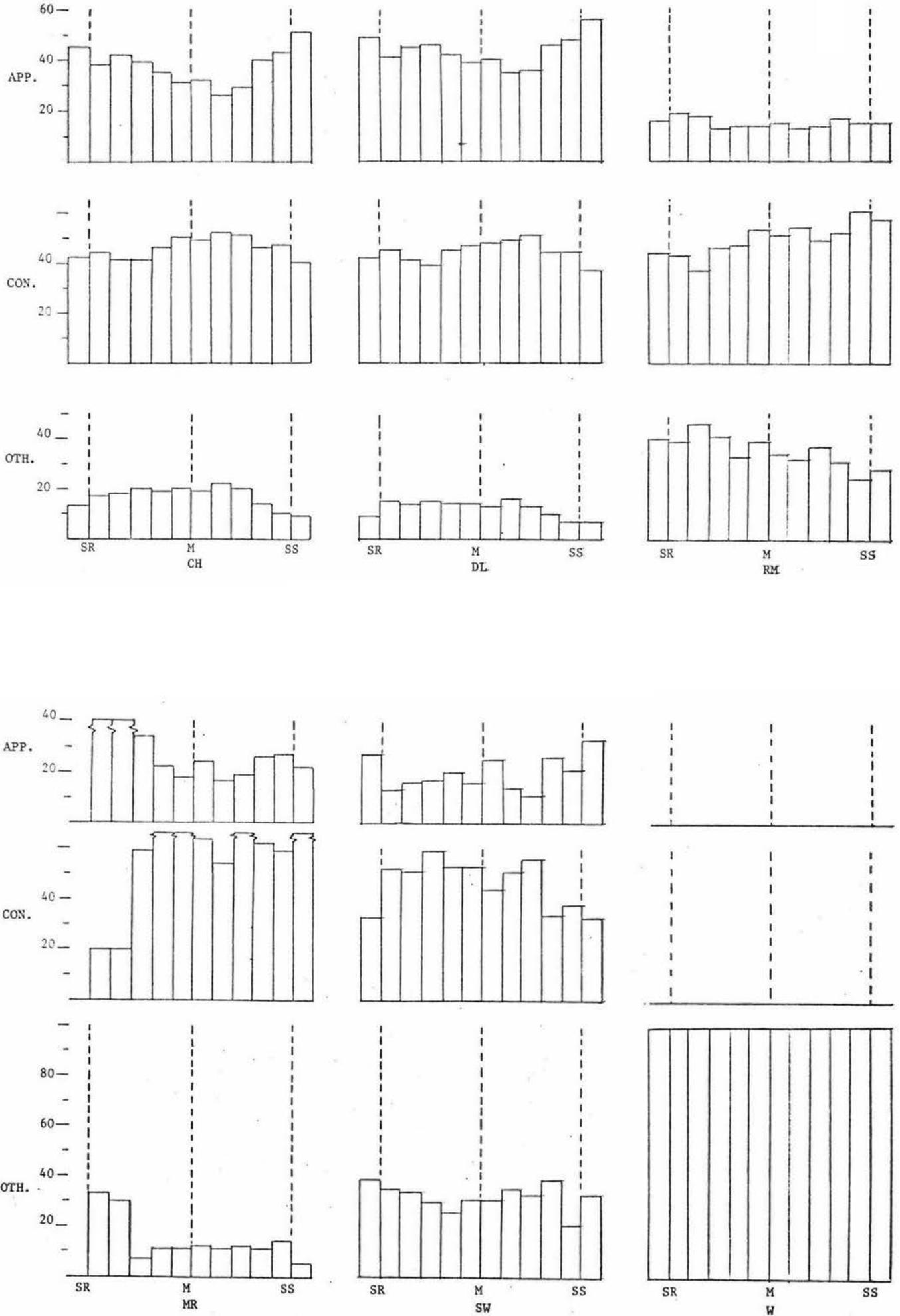
#### Mud

Pukeko consuming food were infrequently seen in the early and mid morning, while later they spent a similar proportion of their time eating. They searched for food more in the early morning and late afternoon, than around midday, whereas "other" activities were seen most in the early and mid morning.

#### Swamp

In winter, throughout the day, pukeko spent by far, most time eating, spending similar time feeding in the morning and less time during the afternoon. Next to consumatory feeding, "other" activities occupied most time, especially in the early morning and mid afternoon, and the birds searched for food mainly at midday.

FIG. 24 SEASONAL DIURNAL TIME ALLOCATION TO APPETITIVE AND CONSUMATORY FEEDING AND "OTHER" ACTIVITIES - WINTER (PER CENT)



## Water

Pukeko spent all their time swimming, i.e. in "other" activities.

### 6.8.1.3 Spring

#### Combined Habitat Data

Pukeko spent the bulk of their time eating, especially in the late morning and afternoon, while looking for food occupied most time in the early morning, and least time at midday (App. 17; Fig.25). Most time was allocated to "other" activities during the late morning and early afternoon, and least at dusk.

#### Dryland

Time allocated to the three activity categories in dryland broadly followed the diurnal patterns described above.

#### Rush Margins

Here, more time was spent eating than in appetitive feeding or "other" activities, particularly at dawn and in the mid afternoon. Most time was spent looking for food during the early morning, while "other" activities occupied gradually more time over the day.

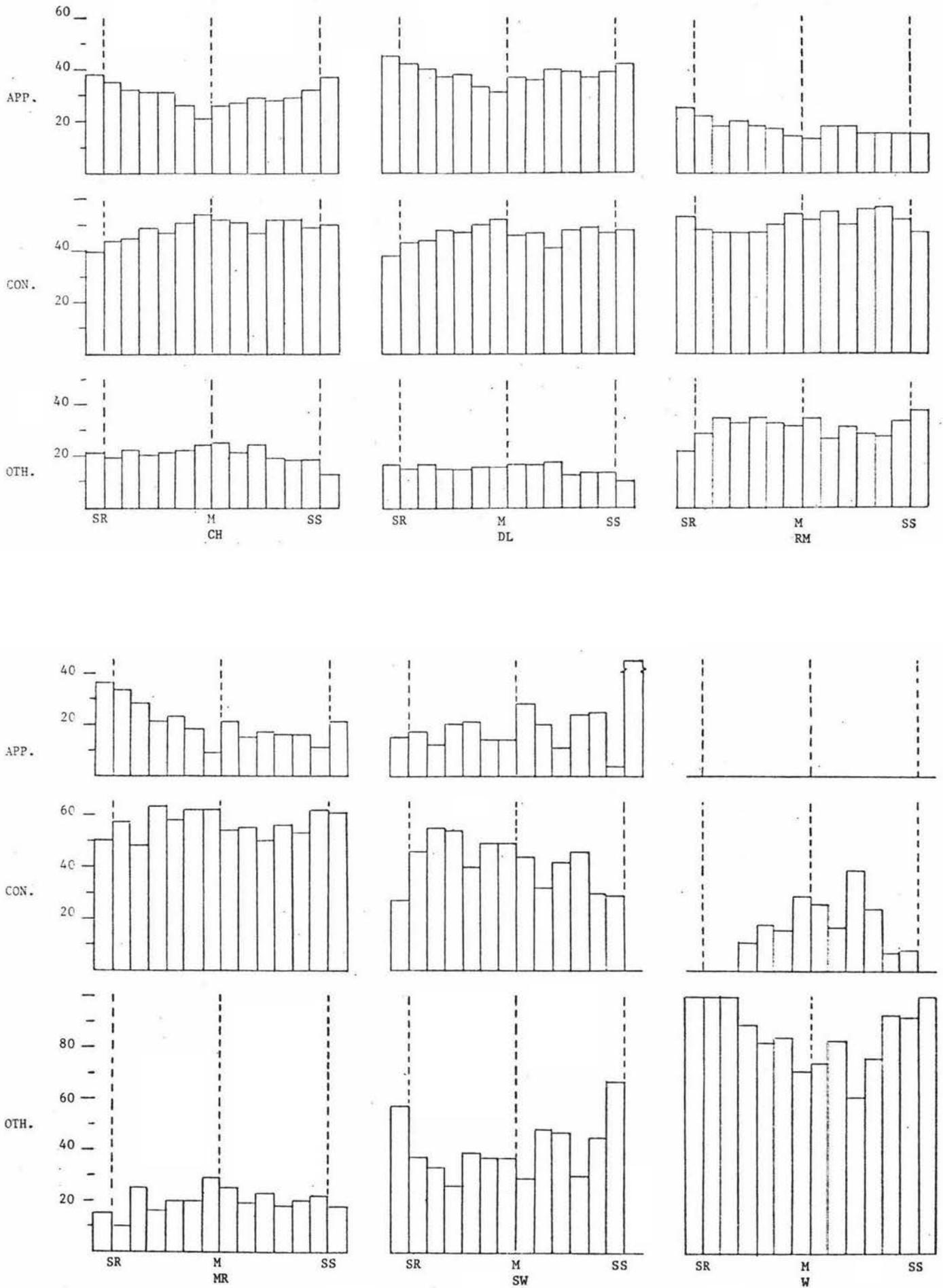
#### Mud

Pukeko ate more often than they looked for food, or followed "other" activities. Similar time was spent eating over the day, except in the early morning, while that spent looking for food showed a reciprocal pattern. Least time was spent in "other" activities at dawn and dusk, and most around midday.

#### Swamp

Time spent eating accounted for most observations over the day, particularly in the morning. Time devoted to "other" activities fluctuated widely over the day, being least in the early morning, while they spent a similar proportion of their time looking for food in the morning (afternoon pattern irregular).

FIG. 25 SEASONAL DIURNAL TIME ALLOCATION TO APPETITIVE  
AND CONSUMATORY FEEDING AND "OTHER" ACTIVITIES - SPRING  
(PER CENT)



## Water

Time spent eating peaked in the mid afternoon and was least at dawn and dusk, whereas time spent swimming showed the reverse pattern.

### 6.8.1.4 Summer

#### Combined Habitat Data

Pukeko spent more time eating food than either looking for it, or engaged in "other" activities (App. 18; Fig.26). Until the mid afternoon, gradually more birds were seen eating. Comparatively more time was spent in locating food at dawn and dusk, than during midday, while that allocated to "other" activities peaked in the mid morning.

#### Dryland

Birds spent most time eating and in "other" activities at midday, although the latter were also commonly seen in the mid morning and mid afternoon. Time spent looking for food peaked at dawn and dusk, and was least at midday.

#### Rush Margins

Here pukeko mostly ate, with gradually more doing so towards dusk, while progressively fewer birds were seen looking for food over the day. "Other" activities occupied similar time from dawn until early afternoon, and less time thereafter.

#### Mud

More birds consumed food in the afternoon than in the morning, while they looked for food and pursued "other" activities more frequently in the morning than in the afternoon.

#### Swamp

Time allocated to "other" activities accounted for the bulk of observations over most of the day, particularly at dawn and dusk. The birds looked for food more in the early morning, midday and mid afternoon than at other times, while they spent most time eating at midday and least at dawn and dusk.



## Water

Pukeko swam mostly in the early morning and late afternoon, and least frequently at midday, while time spent eating showed a reciprocal pattern.

### 6.8.1.5 Statistics

In each season and in all habitats (except water) pukeko spent unequal time in appetitive and consumatory feeding, and "other" activities over the day ( $p < 0.01$  and frequently  $p < 0.001$ ). In water during winter pukeko spent all their time swimming.

## 6.8.2 Pecking Rates

### 6.8.2.1 Autumn

From both combined habitat and dryland data, pukeko gradually increased their pecking rates over the day (App. 15; Fig. 27). Rush margin birds steadily increased their rates of pecking until late morning, pecking at a similar rate in the early and mid afternoon and fastest at dusk. Pukeko fed in mud mainly in the late morning and afternoon, pecking at a similar rate throughout, except in the late afternoon, when the pecking rate increased markedly. In swamp, they pecked increasingly faster until early afternoon, and less rapidly thereafter. Pukeko were infrequently observed feeding in water in autumn.

### 6.8.2.2 Winter

From combined habitat and dryland data, pukeko pecked fastest during midday and the early afternoon, and slowest at dawn and dusk (App. 16; Fig. 28). For rush margins, pecking rates also increased gradually during the early and mid morning, while the birds pecked at an essentially similar rate during the rest of the day. Those feeding in mud progressively increased their rates of pecking from dawn to dusk, whereas in swamp highest pecking rates were recorded during the late morning. In winter feeding birds were not observed in water.

FIG. 27 SEASONAL DIURNAL PECKING RATE AND FEEDING INTENSITY OF PUKEKO - AUTUMN

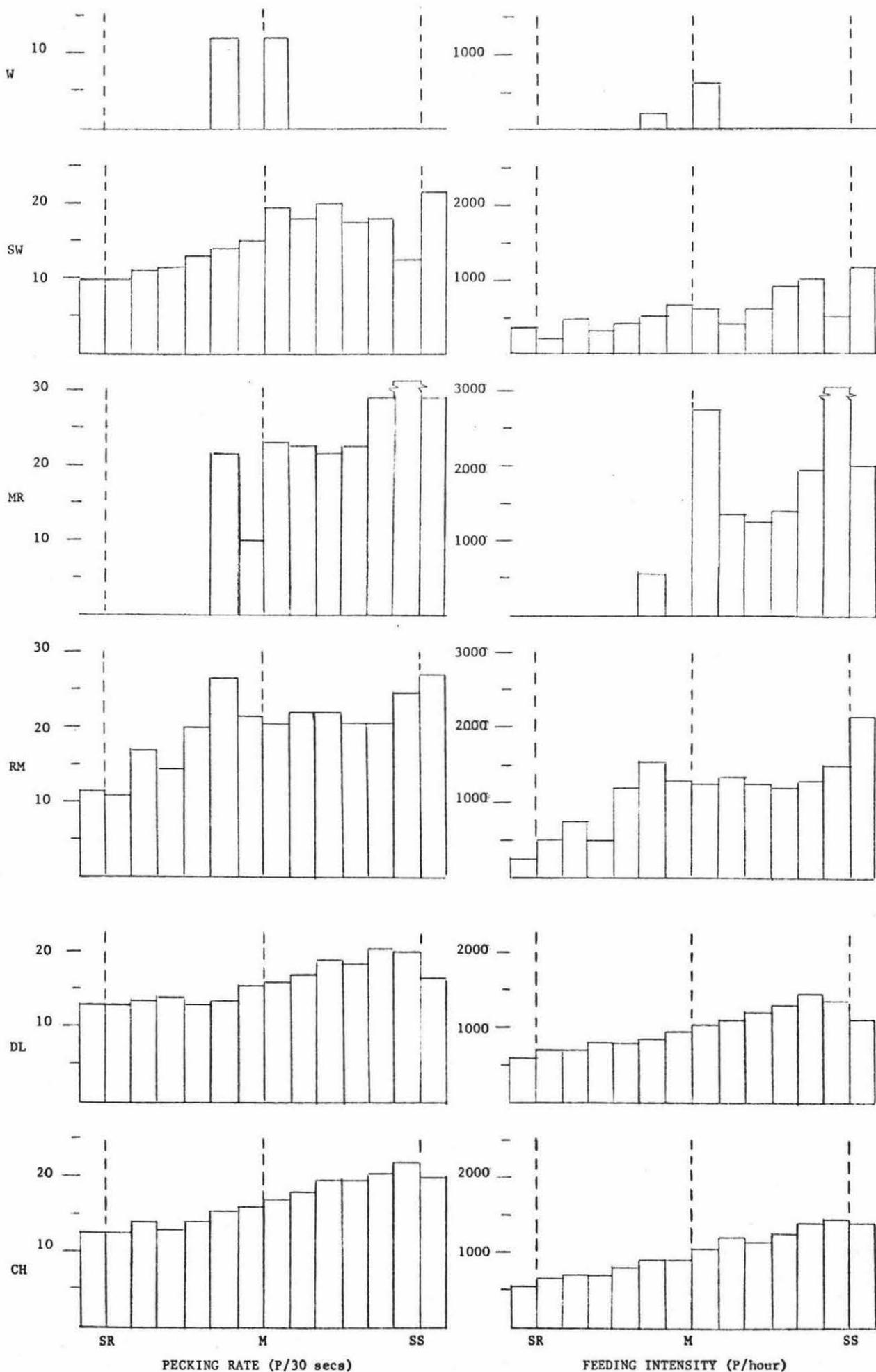
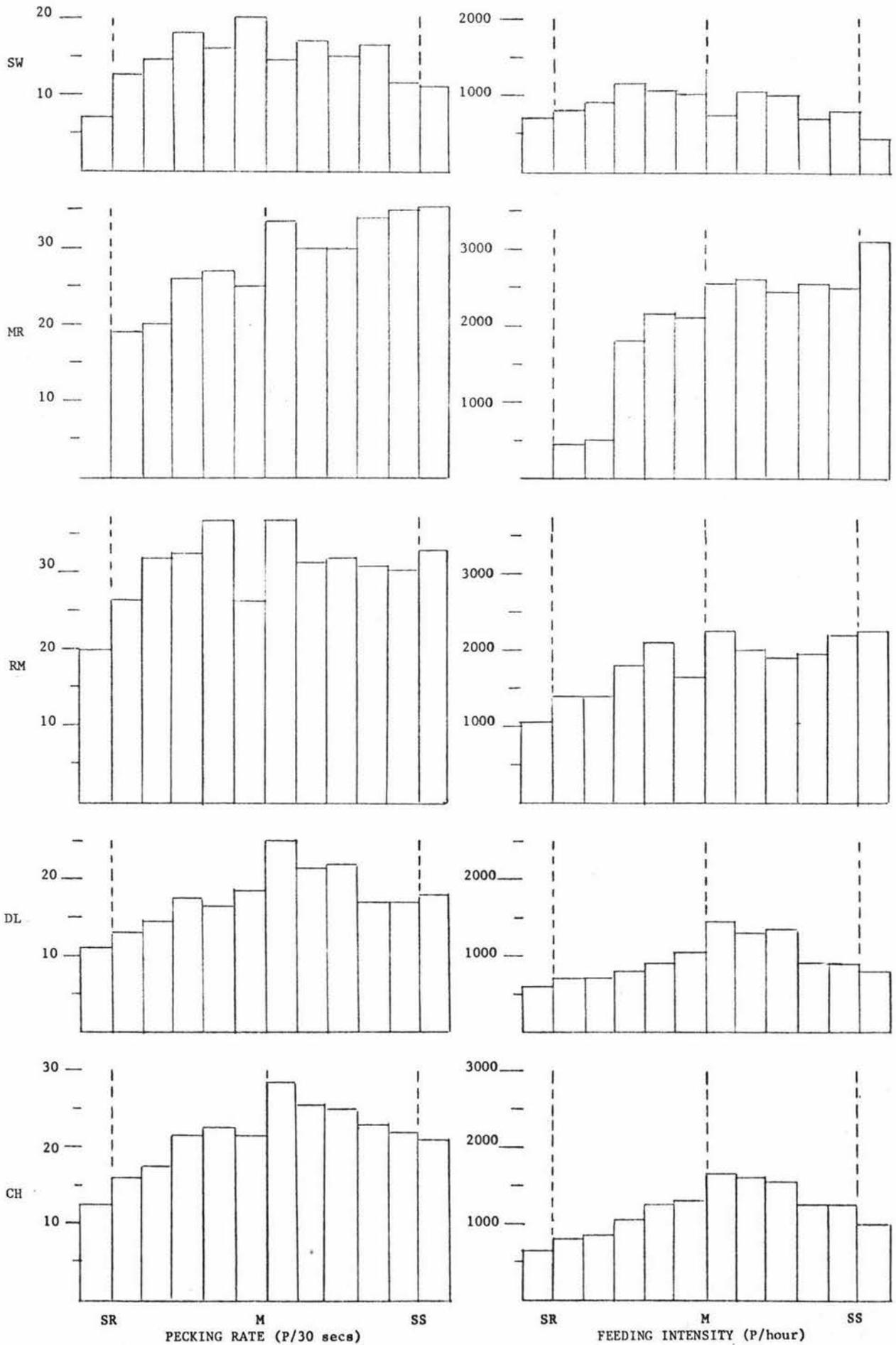


FIG. 28 SEASONAL DIURNAL PECKING RATE AND FEEDING INTENSITY OF PUKEKO - WINTER



### 6.8.2.3 Spring

From combined habitat data, pukeko gradually increased their pecking rates over the day (App. 17; Fig.29). In dryland pukeko also increased their pecking rates until the early afternoon, pecking slower thereafter, while in rush margins they pecked at a constant rate around midday, slowest at dawn, and fastest at dusk. In mud, the morning pecking rate varied little, however in the mid and late afternoon the birds pecked at an increasing rate, decreasing again at dusk. Birds in swamp pecked fastest in the mid morning, and the mid and late afternoon, whereas in water they pecked consistently until the early afternoon, and slower during the mid and late afternoon.

### 6.8.2.4 Summer

From combined habitat and dryland data, pukeko steadily increased their pecking rate throughout the day, peaking in the mid afternoon (App. 18; Fig.30). Rush margin birds pecked slowest in the early and mid morning, and the late afternoon. In summer, pukeko fed infrequently in mud, apparently pecking faster towards dusk. In swamp and water, pecking rates increased steadily, peaking at midday, and decreased thereafter.

### 6.8.2.5. Statistics

In all seasons and for all habitats pukeko diurnal pecking rates varied significantly ( $p < 0.01$ ;  $n=23$  tests) from that expected if they pecked at the mean rate for that habitat all day. Also the hypothesis of equal pecking rate between habitats for the same diurnal period was tested and rejected ( $p < 0.001$ ).

## 6.8.3 Feeding Intensity

### 6.8.3.1 Autumn

The diurnal feeding intensity patterns for birds feeding in dryland and rush margins, and for combined habitat data, closely followed those described from pecking rate data (App. 15; Fig.27). Pukeko did not feed extensively in mud

FIG. 29 SEASONAL DIURNAL PECKING RATE AND FEEDING INTENSITY OF PUKEKO - SPRING

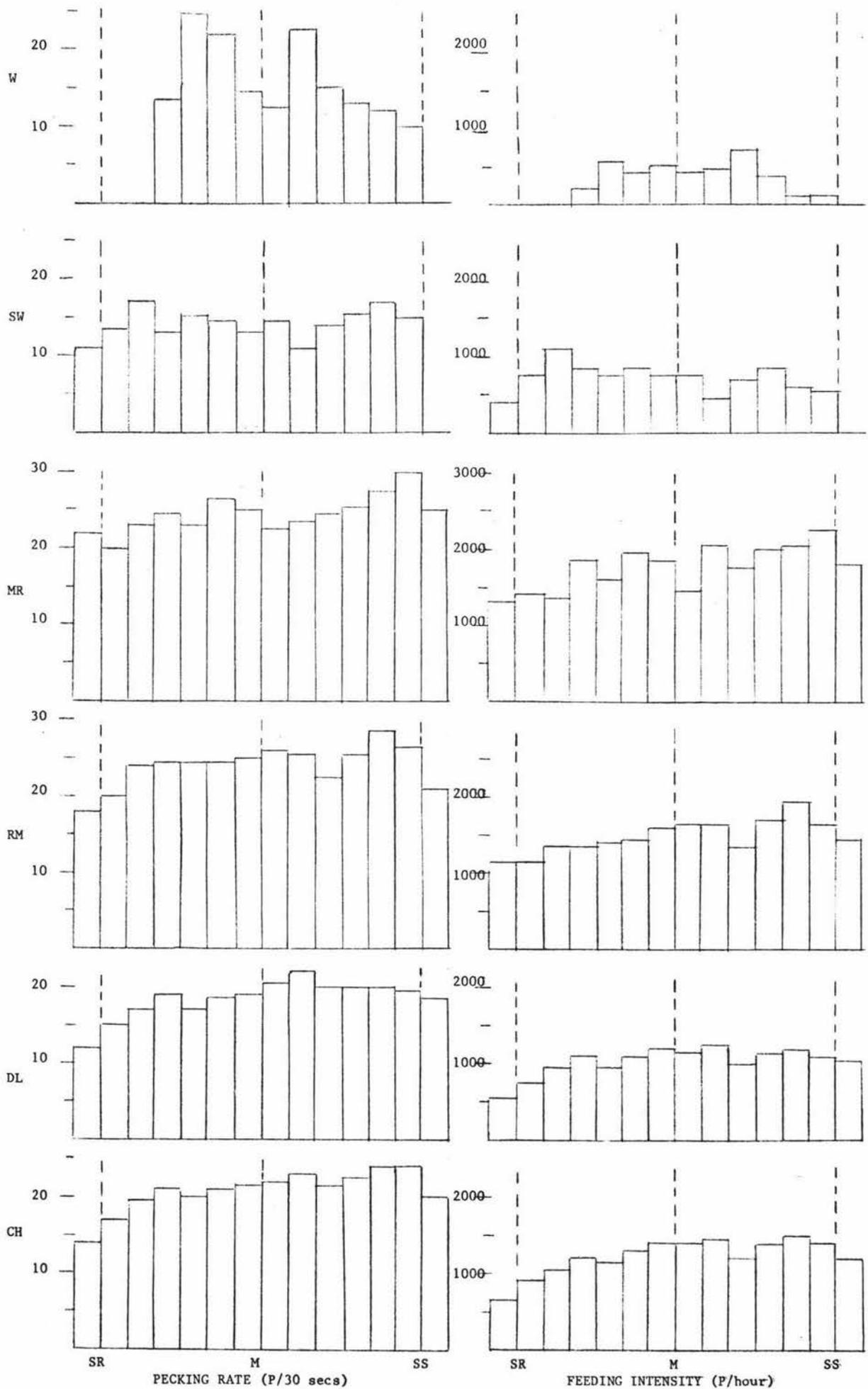
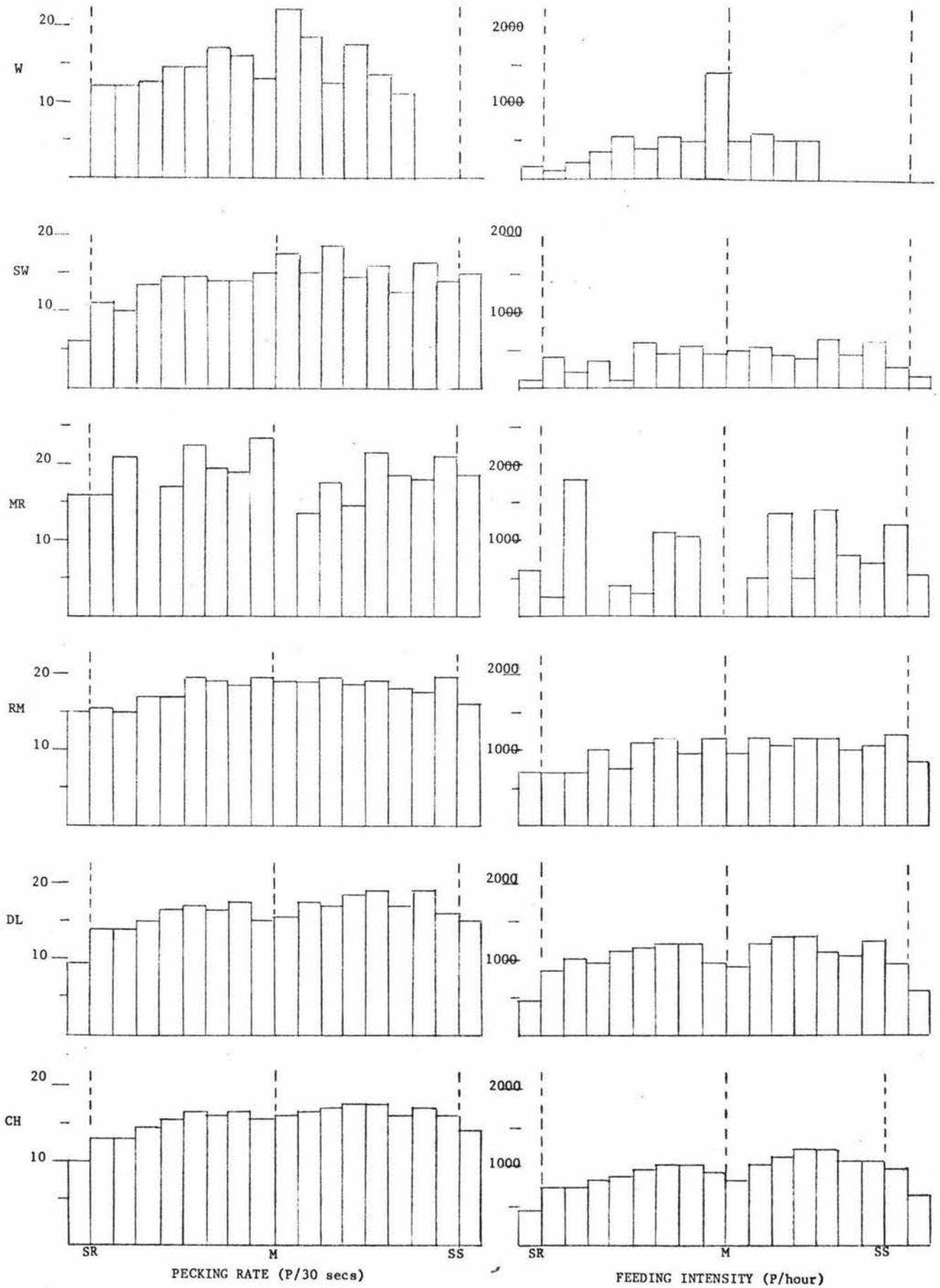


FIG. 30 SEASONAL DIURNAL PECKING RATE AND FEEDING INTENSITY OF PUKEKO - SUMMER



before midday, feeding mostly during the early and late afternoon, whereas in swamp they gradually increased their feeding intensities throughout the day, peaking in the mid and late afternoon. Birds fed infrequently in water.

#### 6.8.3.2 Winter

From combined habitat and dryland data, pukeko fed most intensely during the early afternoon, while in rush margins they fed gradually more towards dusk (App. 16; Fig. 28). Those recorded in mud fed less keenly in the morning than later, whereas for swamp the maximum feeding intensity was recorded during the mid and late morning. In winter, no birds fed in water.

#### 6.8.3.3 Spring

From combined habitat data, the birds delivered gradually more pecks per hour throughout the day, whereas in pasture they steadily increased their feeding intensity during the morning, maintaining throughout the afternoon, the intensity recorded in the late morning (App. 17; Fig. 29). In rush margins and mud, pukeko progressively increased their feeding intensities from dawn to peak in the mid afternoon, and in swamp they fed most extensively in the mid morning. Meanwhile, in water pukeko fed most at midday.

#### 6.8.3.4 Summer

Combined habitat and dryland data indicated pukeko fed gradually more keenly over the day, until the mid afternoon, whereas in rush margins they fed gradually more intensely in the early and mid morning, and at a virtually similar rate thereafter (App. 18; Fig. 30). They fed inconsistently in mud and most intensely in swamp around midday, while in water they fed most keenly during the mid and late morning.

#### 6.8.3.5 Statistics

In each season pukeko fed at unequal intensities in all habitats, and at all times of the day ( $p < 0.001$  in all (23) cases).

#### 6.8.4 Habitat Foraging Rank

##### 6.8.4.1 Autumn

In pasture, rush margins, and mud an "average" bird of the flock pecked in each habitat at an increasing rate throughout the day, feeding more intensely in pasture than in any other area (App. 15; Fig. 31). In swamp, virtually the same feeding rate was recorded throughout the day, being slightly less at dawn and dusk, while birds feeding in water contributed little to the overall foraging effort.

Throughout the day, an "average" bird derived a progressively smaller proportion of their food (per cent pecks) from pasture, with a reciprocal foraging pattern being recorded for rush margins and mud. Swamp was used consistently over the day, while the water habitat was unimportant.

##### 6.8.4.2 Winter

By far most pecks were delivered by birds feeding in pasture, with progressively more recorded here until the early afternoon (App. 16; Fig. 32). Feeding in rush margins also followed this pattern, whereas mud was fed upon more in the afternoon, than in the morning. Conversely, swamp was used for feeding mainly in the morning and water, not at all.

Proportionally dryland was the most important feeding habitat in winter, contributing comparatively more to the pukeko's overall feeding strategy in the early morning, progressively less until the early afternoon, and more towards dusk. The relative importance of rush margin and swamp habitats followed the diurnal pattern described from original data (above), while towards dusk, an increasing proportion of pecks were delivered in mud. In winter water was not used as a feeding area.

##### 6.8.4.3 Spring

Dryland was the most extensively fed upon habitat all day, especially in the mid morning and late afternoon (App. 17; Fig. 33). Pukeko used the rush margins for feeding mostly during the early afternoon, whereas in mud they fed progressively more from dawn to dusk. Swamp was used most in the mid morning and gradually less extensively thereafter, and

FIG. 31 SEASONAL DIURNAL HABITAT FORAGING RANK OF PUKEKO - AUTUMN

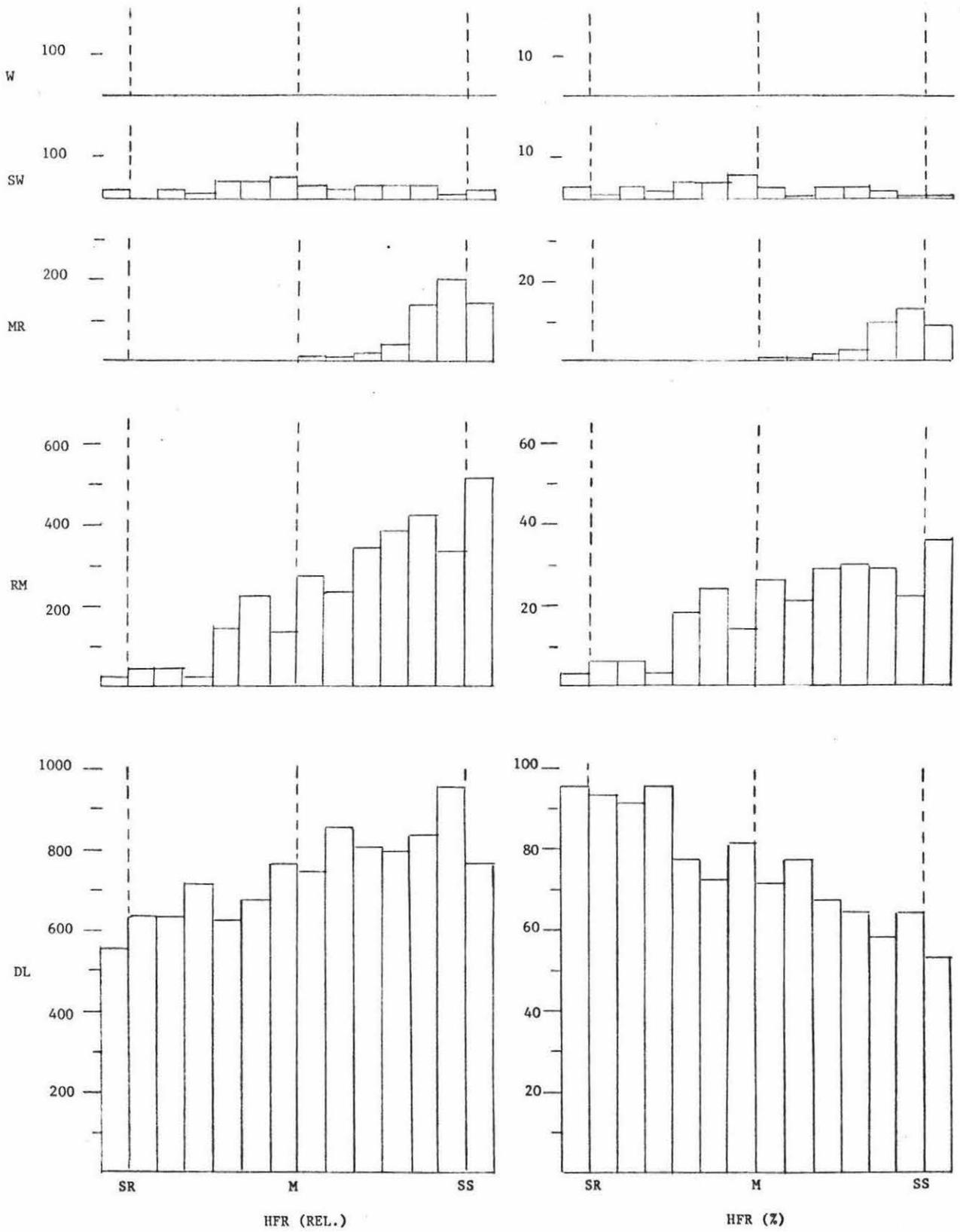


FIG. 32 SEASONAL DIURNAL HABITAT FORAGING RANK OF PUKEKO - WINTER

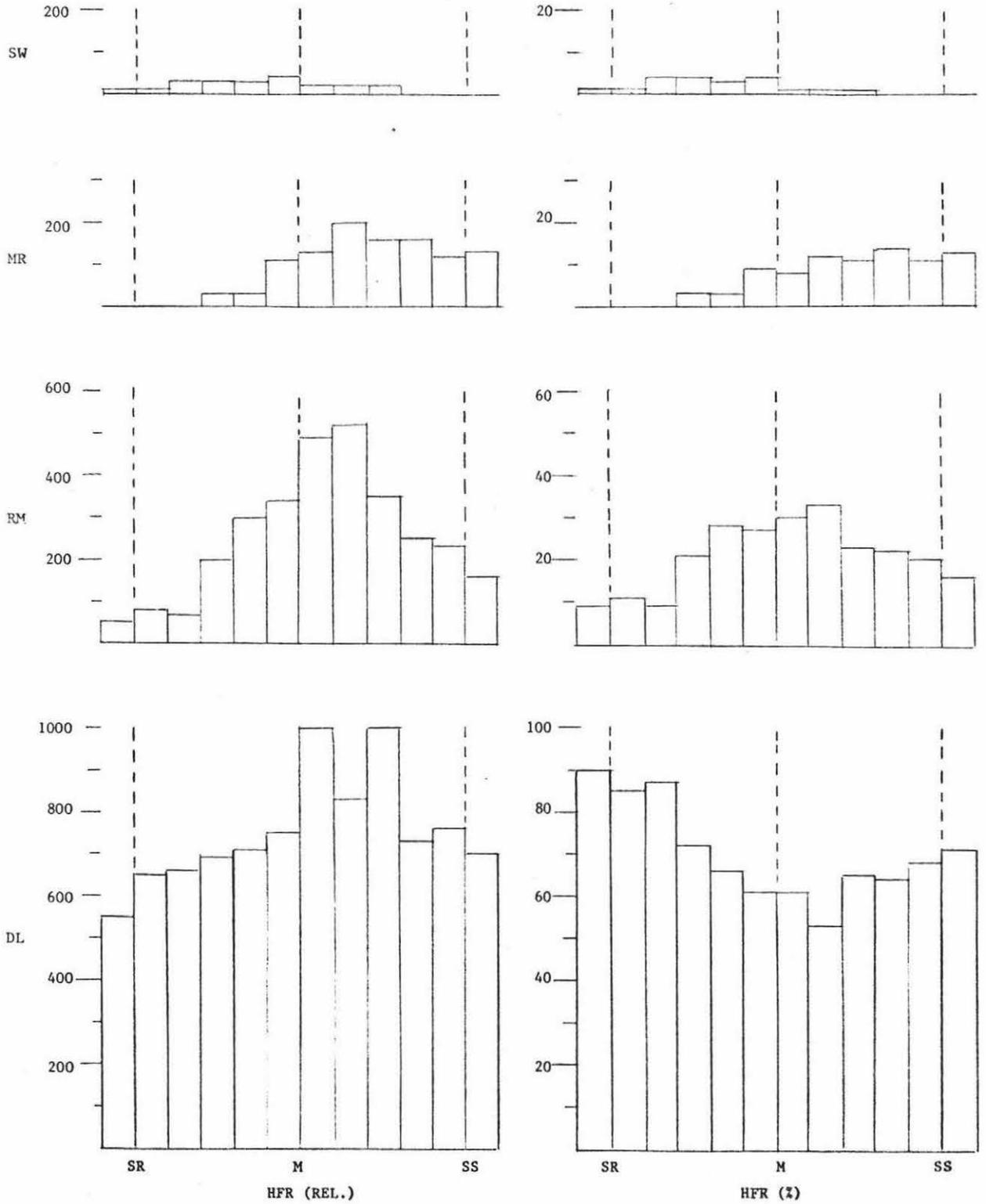
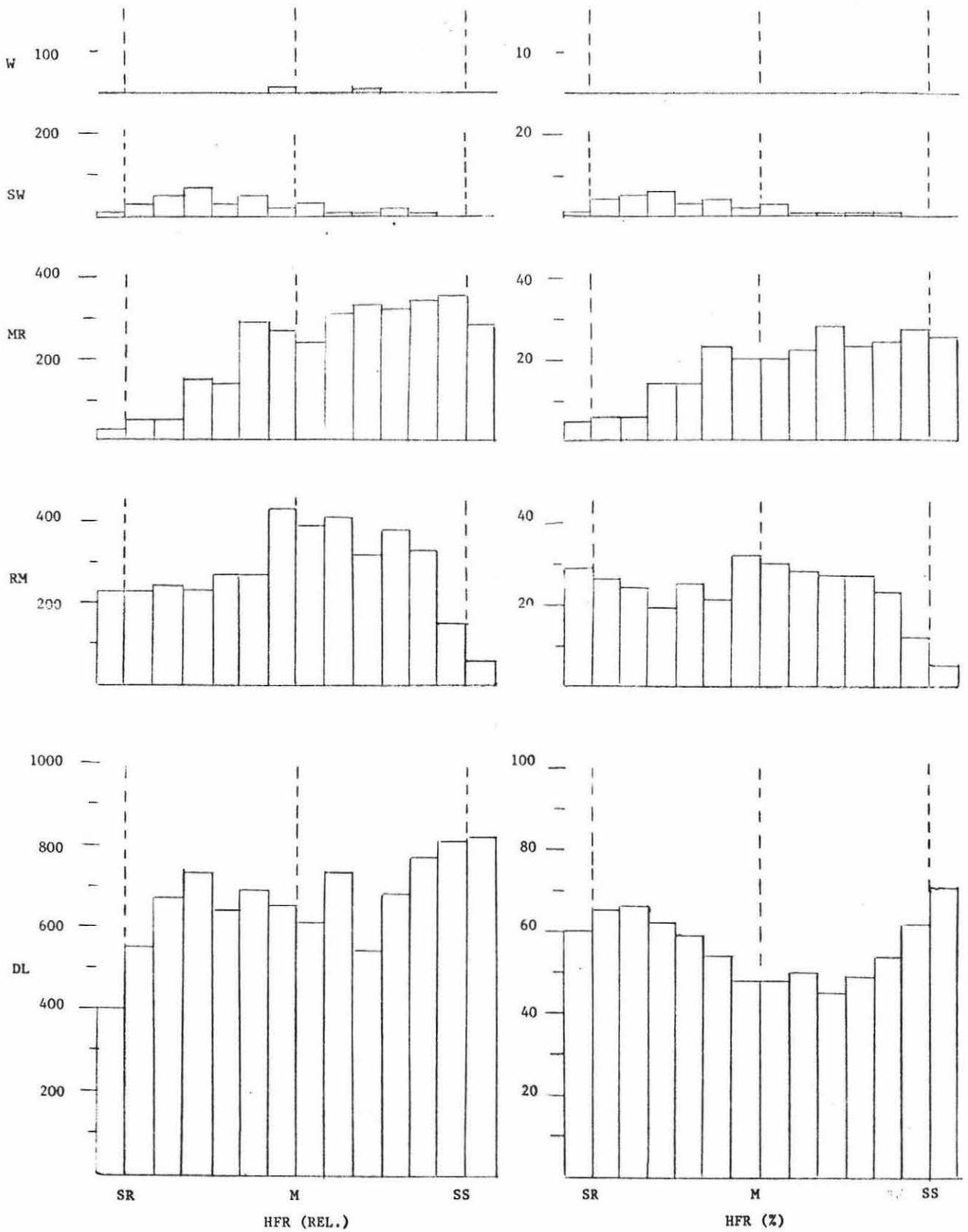


FIG. 33 SEASONAL DIURNAL HABITAT FORAGING RANK OF PUKEKO - SPRING



birds fed most keenly in water around midday, but contributed little.

The relative contribution of each habitat showed pasture contributed more than any other habitat to the bird's overall feeding effort, particularly during the early and mid morning and late afternoon. Pukeko fed proportionally most extensively in rush margins at dawn and in the early afternoon, whereas the diurnal changes in relative contributions of bird's feeding in mud, swamp and water habitats closely followed those described from original habitat foraging rank data (above).

#### 6.8.4.4. Summer

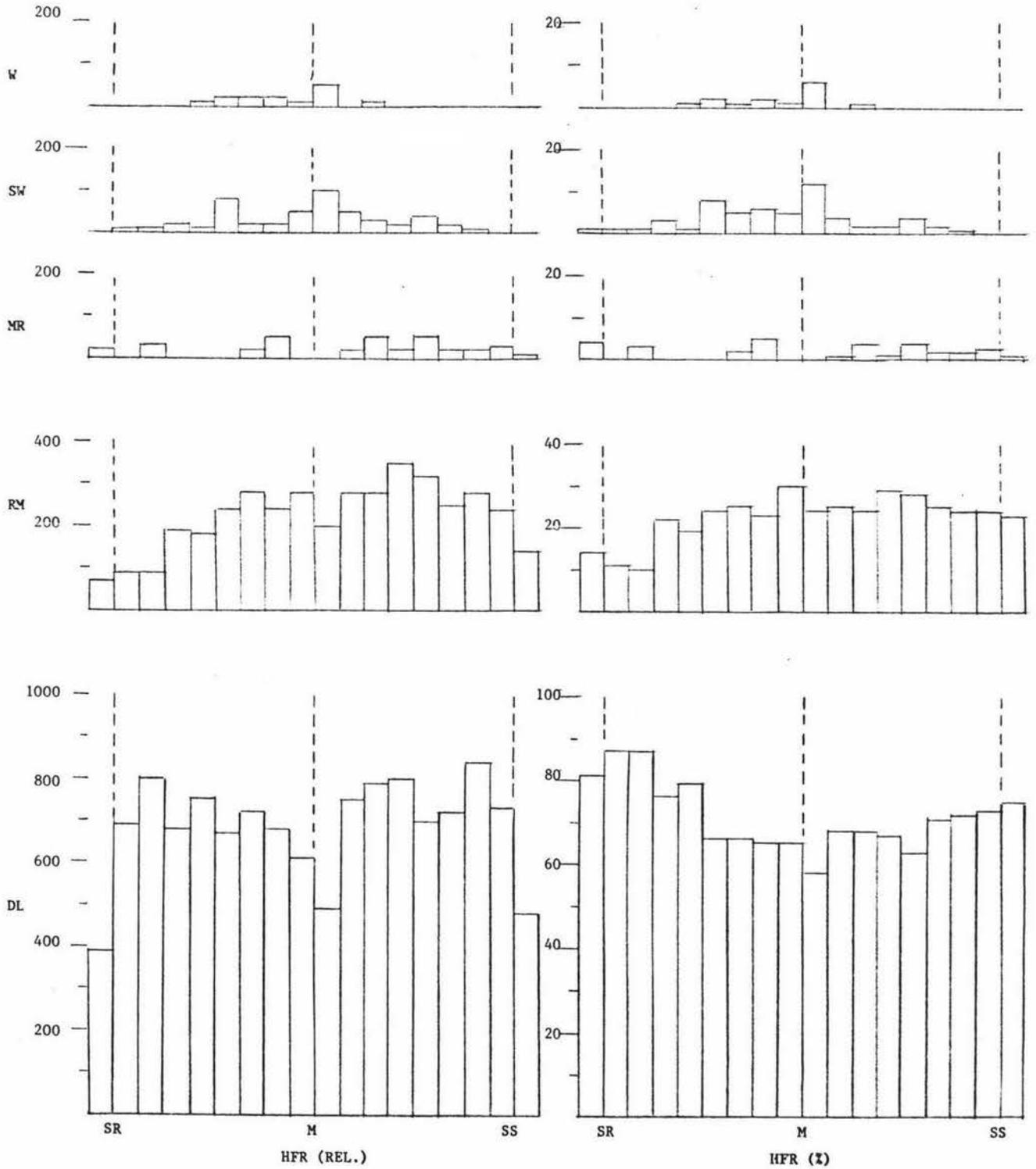
Throughout the day pukeko fed mostly in pasture in summer, feeding more here in the afternoon than in the morning (App. 18; Fig. 34). In rush margins progressively more pecks were delivered per hour until the mid afternoon, while in mud birds fed infrequently, apparently more in the afternoon than in the morning. They fed in swamp mostly during the mid morning, and progressively less keenly thereafter whereas they fed in water mainly around midday.

Considering the relative contribution of each habitat to an "average" bird's overall feeding strategy, dryland was still the most frequently fed upon habitat, accounting for proportionally more of the total pecks delivered per hour at dawn and dusk, than at midday. The daily pattern of relative importance of remaining habitats follows those described from original habitat foraging rank data (above).

#### 6.8.4.5 Statistics

Diurnal habitat foraging rank data for each season and habitat were tested against the null hypothesis of equal distribution on all habitats over the day, of total pecks per hour, and rejected (in three tests  $p < 0.01$  and in 17 tests  $p < 0.001$ ).

FIG. 34 SEASONAL, DIURNAL HABITAT FORAGING RANK OF PUKEKO - SUMMER



## 6.9 Discussion

### 6.9.1 Autumn

#### Time allocation

In autumn most time by far, was spent feeding and diurnal variation was slight with only small increases in activity at dawn and dusk. The birds were equally attentive and aggressive all day while time spent in comfort movements rose at midday above those levels recorded in the early morning and late afternoon.

#### Habitat use

In autumn, dryland was by far the most frequently used of all the available habitats, particularly in the early and mid morning, followed in turn by rush margins, swamp, mud and water. Birds were seen mostly in rush margins and mud in the mid and late afternoon, while they occupied swamp more around midday than during the early morning or late afternoon.

#### Feeding

Time spent in appetitive and consumatory feeding, and "other" activities showed pukeko spent more time locating food at dawn than later suggesting, if the food was consistently available to them all day, that they were most selective in their choice of food items at this time. Time spent eating food rose steadily throughout the day, while more time was spent in "other" activities at midday than at dawn and dusk. Both pecking rate and feeding intensity data showed the birds fed faster and more intensely over the day - culminating in the maximum rate recorded at dusk. Thus not only did the birds spend more time eating towards day's end, but they also consumed more.

It is thought this autumn diurnal activity pattern estimated for an "average" bird of the flock, represented as closely as possible of the four seasons, the "basal" pattern, as the only auxiliary biological process the birds were known to be following at this time was moult (App. 3). Moreover, this was the season in which fewest pecks were delivered by

an "average" feeding bird over an entire day, suggesting that the demand for food (energy) at this time was least.

#### Foraging effort

Over the day gradually more pecks were delivered in dryland, rush margins, and mud, however by far most were delivered in dryland at any one time. The proportional contribution of dryland habitat to the total allocation of feeding effort, decreased gradually over the day, suggesting the birds shifted their feeding effort from this area to alternative ones, although for the time they were in pasture, they delivered an increasing number of pecks.

Feeding in rush and mud areas peaked at dusk, which was also the time of the day that these two habitats contributed most to the overall feeding effort of the birds. Swamp was used mostly around midday, although it was used for feeding much less than either dryland or rush margins. Few birds fed in water in autumn.

Differential use of habitats may reflect pukeko capitalising on available plant quality, their quest for overhead protective cover, their "activity cycle" and consequent energy demand, or may simply be due to their disturbance by predators, the farmer or his dogs (see p.73).

### 6.9.2 Winter

#### Time allocation

In winter, as in autumn, similar time was spent feeding over the day, showing a slight dawn, and a more prominent dusk peak. The birds appeared equally attentive all day, and were more aggressive in the afternoon than in the morning. Time spent in bodily maintenance rose markedly at midday from that recorded at dawn and dusk - a pattern which was notably different from that recorded in autumn, when the rise was not as pronounced. Courtship, an activity which was absent in autumn, was seen occasionally in winter.

#### Habitat use

As in autumn, most birds were recorded in pasture all day with more observed there at dawn and, particularly in winter, at dusk. Coincidental with fewer birds seen in pasture

in the early afternoon, was the period of maximum use of rush margins. Mud was used most after midday, whereas swamp was used consistently over the day, but less in winter than in autumn.

### Feeding

Pukeko spent most time looking for food at dawn and dusk, and most time eating food around midday and in the mid afternoon. Perhaps they were most selective in their choice of forage at both dawn and dusk, replenishing an "energy-debt" from the previous night at dawn and possibly "stocking up" in the late afternoon for the coming night.

In winter photoperiods were shortest and nights were longest. Thus without feeding at night, pukeko had to ensure that they accumulated sufficient reserves during the previous daylight period to last them through the forthcoming night. Hence at dusk they would have been expected to search for the highest quality forage available, which was reflected in time spent locating food. Least time was allocated to "other" activities at dawn and dusk suggesting the bird's time was devoted to more important activities, e.g. locating food. Towards midday the birds fed less selectively which suggested they ate only sufficient food to replace the energy expended in its collection and in the pursuit of other activities. Similar time was spent eating and in "other" activities as in autumn, however the major difference between the two seasons was the amount of time allocated at day's end to locating food.

In winter pukeko pecked faster throughout the entire day, than in autumn, and also the diurnal patterns were different. Maximum pecking rates were recorded at midday in winter, and not at dusk as in autumn. Generally pecking rates recorded in winter increased gradually from a minimum at dawn, to peak at midday, decreasing to an intermediate level at dusk. Greater feeding intensities were calculated for the birds in winter than in autumn, and diurnally followed the pattern described for pecking rate data. In summary the birds fed faster and more intensely, but less selectively at midday, than at dawn and dusk.

### Foraging effort

In winter pasture was the major foraging site, followed by rush margins, mud and swamp. In all habitats pukeko fed least in the early morning, and most at midday, except in mud, when they fed here most at dusk. The major difference between this and the autumn pattern is that pasture was used more extensively in winter in the late afternoon, thereby replacing the rush margins which had been used more extensively in autumn. Mud was more important as a feeding site in winter than in autumn, which may also account for proportionally fewer pecks delivered to the rush margins. In winter, when mature raupo was dead, swamp was used less extensively than in autumn. Increased use of mud in winter coincided with the most rapid seasonal rise in lagoon water levels and the growth of aquatic and emergent-rooted plants.

Considering the total number of pecks delivered over a day by an "average" feeding bird, pukeko fed most at midday, least at dawn and to an intermediate degree in the late afternoon, whereas in autumn the birds fed progressively more eagerly over the day.

#### 6.9.3 Spring

##### Time allocation

In spring time spent foraging at dawn and dusk increased slightly over that recorded in winter, although in general similar time was spent feeding all day. Similar time to that spent in winter, was also allocated to attentive/alarm activities and flying throughout the day whereas comfort movements were most frequent in the morning, attaining a greater midday peak in spring than in winter. Courting birds were seen mostly at dawn and dusk, and far more often in spring than in winter. Pukeko were more aggressive in winter than in spring, being more so at midday during the former than in the latter, and drank more frequently in winter than in spring.

##### Habitat use

In spring pasture was again the most frequently used area, especially at dawn and dusk, and least at midday. Decreased usage in the late morning coincided primarily with

increased usage of rush margins but also with more time spent in swamp. Use of rush margins decreased gradually in the afternoon (especially around dusk), which was concurrent with more time spent in pasture again. Birds infrequently used mud in the early and mid morning, but later many more birds were found here. They fed infrequently in water, except at midday.

### Feeding

In spring, pukeko spent more time eating food in the late morning and afternoon than earlier, and least time searching for food at midday. This indicated they were gradually less selective in their choice of forage at midday. Compared to winter they spent less time locating food over the day, similar time eating food, and more time in "other" activities. Pukeko should perhaps spend time in non-feeding "other" activities only when body demands were fulfilled, i.e. one would expect them to firstly fill their stomachs, and then to preen etc. Thus the food available to pukeko appears greater in spring than in winter, allowing the birds to search less selectively for preferred food items.

In spring the rate and intensity of feeding gradually increased towards day's end - an opposite pattern to that described for the selectivity of pukeko over the day. Although pecking rates and feeding intensities were similar between the two seasons, their diurnal patterns were different. In winter there was a single midday peak, whereas in spring pecking rates and feeding intensities gradually increased over the day. Therefore in spring the birds ate progressively faster and less selectively over the day, whereas in winter, they ate fastest and most selectively around midday.

### Foraging effort

Thus although pecking rates and feeding intensities of birds in all habitats increased steadily over the day, pukeko again appeared to modify their allocation of feeding effort from pasture in the mid morning (although a majority stayed here) to feed in swamp and rush margins. Around midday fewer birds fed in swamp and pasture, with an increase in feeding effort in rush margins and mud. Throughout the afternoon mud

was used to a similar degree, however rush margins were used less extensively, resulting in an increase in the proportion of pecks being delivered in dryland. Thus over a spring day, pukeko differentially allocated their feeding effort between habitats, perhaps in response to the quality of available forage.

Comparison of habitat use between winter and spring, showed pukeko used dryland less extensively in spring than in winter, although similar diurnal usage patterns were noted. Use of remaining habitats was considerably greater in spring than in winter, particularly water and mud, and less so of rush margins and swamp.

Habitat foraging ranks for both seasons showed for the whole day, pukeko pecked more in dryland during winter than during spring. Rush margins appeared more important as a foraging habitat in the early morning in spring, than in winter, however over the rest of the day, similar effort was spent feeding here in both seasons. Feeding in mud was much more extensive in spring than in winter, whereas swamp and water habitats remained relatively unimportant.

#### 6.9.4 Summer

##### Time allocation

Pukeko allocated more time to feeding activities over the day, than to any other activity, occupying less time in summer than in spring. Throughout the day similar time was spent feeding although the birds fed more often at dawn and dusk than at midday. The birds were more wary in summer than in spring, particularly around midday. As expected courtship activities accounted for less time in summer than in spring, and birds that did court did so mostly around dawn and dusk. In summer bodily maintenance occupied less time throughout the day than in spring, with most birds preening etc. around midday. For both seasons, similar time was allocated to agonistic/appeasment, drinking, calling, swimming and flying.

### Habitat use

In summer most birds were seen in pasture throughout the day, especially around dawn and dusk, and a similar proportion was seen here as in spring. However in rush margins in summer, gradually more birds used this area over the day, peaking in the mid afternoon, at a higher proportion of birds compared to spring. In summer comparatively more birds were seen in swamp over the day, than in spring, especially during the mid and late morning, whereas mud was used very infrequently in summer.

### Feeding

Pukeko spent similar time eating all day, except at dawn and dusk, when fewer were observed. Conversely time spent locating food was greatest at dawn and dusk, indicating they searched more selectively for preferred food items then, than at other times. Time allocated to "other" activities accounted for more of the bird's time in the mid morning and midday than during the remaining periods, which corresponded to an increase in the time spent in the more protected swamp and rush margins.

Although a similar diurnal pattern in pecking rates and feeding intensities was seen in summer compared to spring, pukeko pecked slower and less intensely in summer than in spring. They delivered fewer pecks over the "typical" summer day, compared to a spring day, even though they had more daylight hours in which to feed. In spring when the birds had to replace lost winter condition, defend newly established territories, build nests, incubate eggs and rear chicks etc. biological demands on pukeko were presumably greater than in summer. The absence or quiescence of most of these activities in summer may have allowed the birds to feed less intensively.

### Foraging effort

In all habitats the birds fed far less intensely in summer than in spring. Pasture was still the most important foraging site by far, particularly in the early morning, and

was more important in summer than in spring. Rush margins were used least at dawn and to a similar extent thereafter, contributing proportionally the same to the overall feeding strategy of an "average" bird in summer as in spring. Conversely mud, in which approximately 20% of the feeding effort was centred in spring, contributed less than 5% to the overall feeding effort in summer, whereas swamp and water were used more in summer than in spring, especially around midday.

Thus the daily wandering of an "average" bird on a "typical" day in summer, took the bird first in the early morning to pasture where it fed for over 85% of the time, feeding in rush margins for the bulk of the remaining time. Towards mid morning the bird changed from feeding almost exclusively in pasture, to feeding more frequently in rush margins, and to a minor extent, in swamp, although the bulk of food was still obtained in dryland. At midday least time was spent feeding in dryland compared to the whole day, with rush margins and swamp areas accounting for the major portion of the remaining feeding effort. Also at this time the bird occasionally swam out to feed in water. Towards dusk less time was spent feeding in water and swamp areas, and similar time to that recorded earlier was spent feeding in the marginal vegetation, while feeding in pasture gradually increased, peaking at dusk. Assuming that food was equally available to the pukeko over the day in all habitats, then it may have been the relative quality of forage, or some other factor(s), which determined where and to what extent pukeko fed.

## 7. SAMPLED POPULATION

### 7.1 Standard observations

#### 7.1.1. Introduction

In mid autumn and early spring standard observations for two weeks of birds in pasture only were performed at Fell's Lagoon enabling comparison of time allocated to various activities, pecking rates and feeding intensities by this flock, with those recorded for the Hamilton's Lagoon flock.

As visibility of pukeko in marginal areas of Fell's Lagoon was severely restricted, data on use of other habitats were not collected.

#### 7.1.2. Composite Day

##### 7.1.2.1 Autumn

###### 7.1.2.1.1 Time Allocation

In mid autumn the birds again spent most time feeding, and in turn less time in attentive postures, encounters and bodily maintenance, with the balance of time spent flying (Tab. 13).

###### 7.1.2.1.2 Foraging

Eating again accounted for most observations over the day, followed in turn, by appetitive feeding and "other" activities (Tab. 14). They pecked at an average rate of 17.7 pecks/30 secs., and at an average feeding intensity of 1003 pecks/hr (Tab. 14).

##### 7.1.2.2 Spring

###### 7.1.2.2.1 Time Allocation

Summed hourly data for the two-week period in early spring indicated pukeko spent most time feeding, and less time in attentive/alarm activities, bodily care, and agonistic/appeasement encounters, with remaining time spent courting, calling or flying (Tab. 13).

TABLE 13

TIME ALLOCATION OF PUKEKO AT FELL'S LAGOON (COMPOSITE DAY)

Season	Act. Hab.		F	AT/AL	CM	AG/AP	CO	D	CA	S	FLY	TOTAL
Autumn	DL	n	2715	336	46	81					7	3185
		%	85.24	10.55	1.44	3.44					0.23	100.00
Spring	DL	n	5664	765	239	208	40		19		3	6938
		%	81.64	11.03	2.54	3.00	0.58		0.27		0.04	100.00

TABLE 14

TIME ALLOCATION TO APPETITIVE AND CONSUMATORY FEEDING AND  
"OTHER" ACTIVITIES, PECKING RATE, AND FEEDING INTENSITY

Season	Act. Hab.		APP.	CON.	OTH.	TOT.		PECKING RATE	FEEDING INTEN- SITY
Autumn	DL	n	1200	1505	473	3178			
		%	37.77	47.35	14.88	100.00		17.65	1003
Spring	DL	n	2466	3190	1279	6935			
		%	35.56	46.00	18.44	100.00		16.10	889

#### 7.1.2.2.2 Foraging

Pukeko spent most time eating and in "other" activities, while food location occupied less time (Tab. 14). They pecked at an average rate of 16.1 pecks/30 secs., and at an average feeding intensity of 889 pecks/hr throughout the day (Tab. 14).

#### 7.1.3 Diurnal

##### 7.1.3.1 Autumn

###### 7.1.3.1.1 Time Allocation

Again data showed pukeko spent most time feeding while in pasture, particularly at dawn and dusk, while they were more wary in the mid morning and mid afternoon, than during the remaining periods (App. 19; Fig.35a). Comfort movements were seen mainly in the mid and late afternoon, whereas encounters were commonest in the mid morning and mid afternoon. Residual time was spent flying.

###### 7.1.3.1.2 Foraging

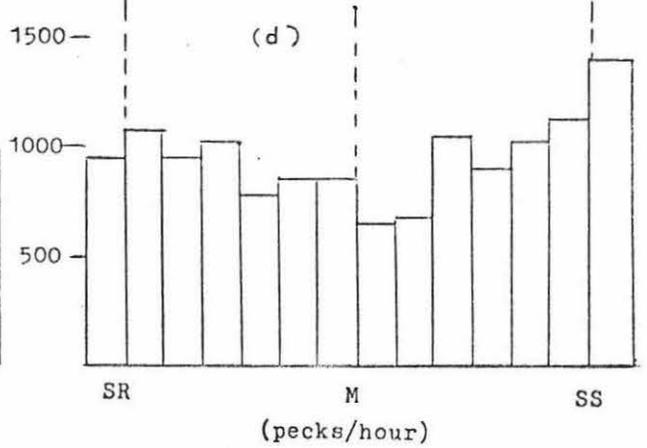
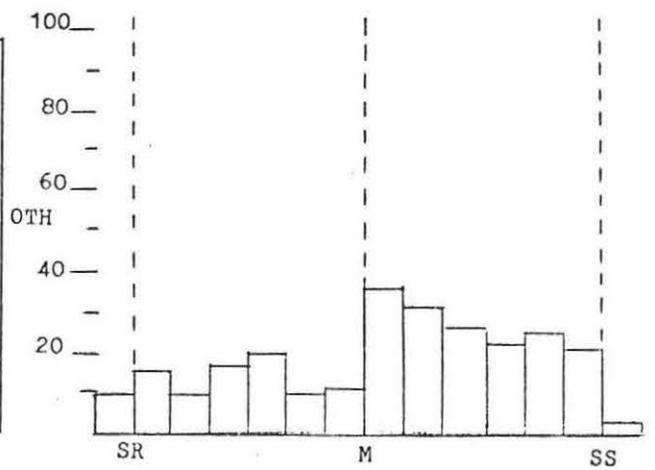
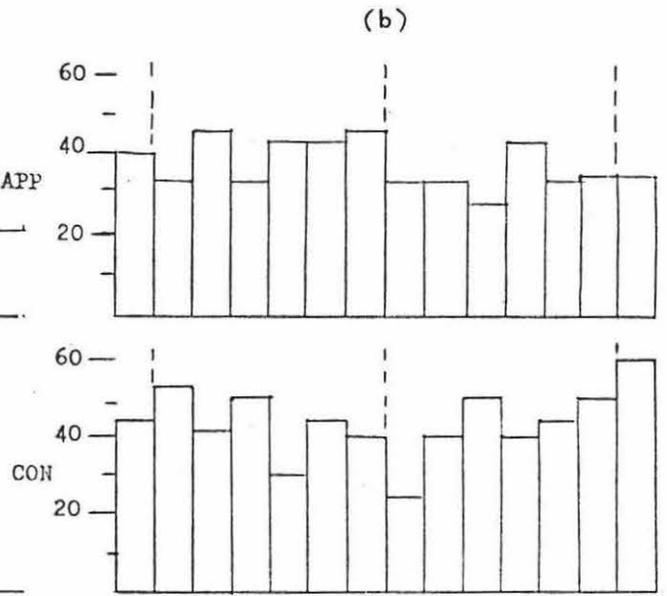
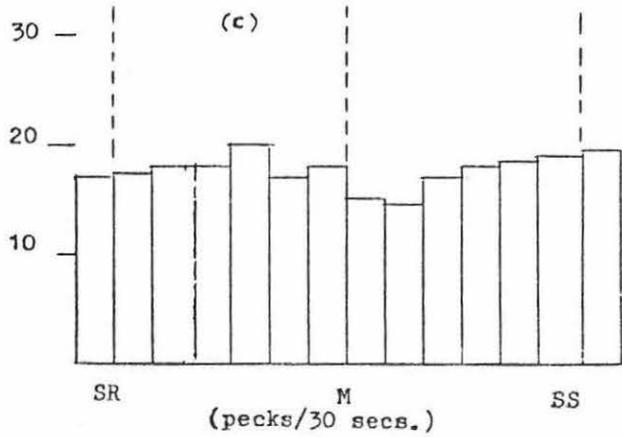
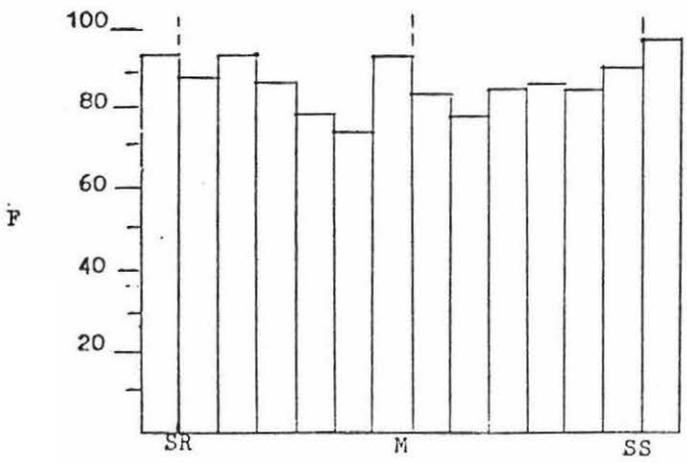
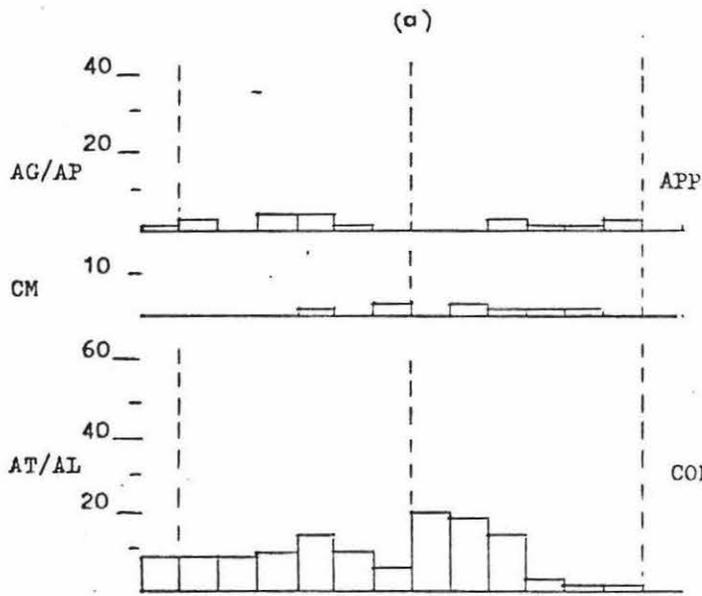
In mid autumn most time was spent locating and consuming food. Over the morning gradually less time was spent eating, occupying least time at midday, increasing again during the afternoon (App. 20; Fig.35b). Time spent looking for food increased steadily in the morning, but was less in the afternoon, whereas that assigned to "other" activities peaked in the early afternoon, and occupied gradually less time thereafter.

Birds pecked at a steady rate all morning, slowest in the early afternoon, and gradually faster thereafter (App. 20; Fig.35c). Feeding intensities decreased gradually throughout the morning to be least at midday, increasing in the afternoon, to peak at the maximum rate at dusk (App. 20; Fig.35d).

##### 7.1.3.2 Spring

###### 7.1.3.2.1 Time Allocation

Observations indicated pukeko spent more time feeding while in the pasture, than following any other activities, occupying similar time in the morning and early and mid



afternoon, but even more during the late afternoon (App. 21; Fig.36a). Attentive/alarm activities accounted for the bulk of the remaining observations, especially in the early and late morning. Pukeko allocated most time to bodily maintenance in the mid morning and mid afternoon while they were more aggressive etc. at dawn than later. Courting and calling birds were seen infrequently, apparently more at dawn and dusk than at other times, while they flew irregularly.

#### 7.1.3.2.2 Foraging

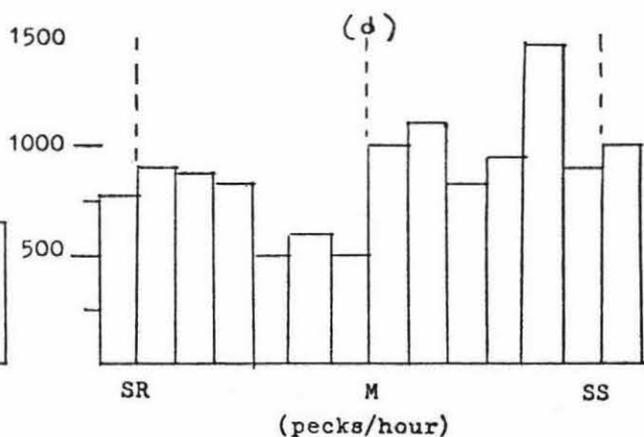
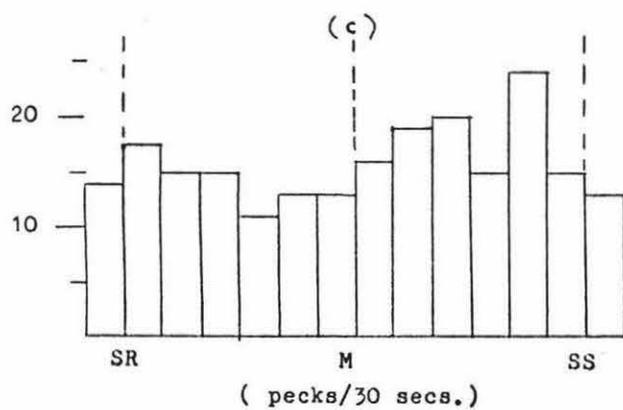
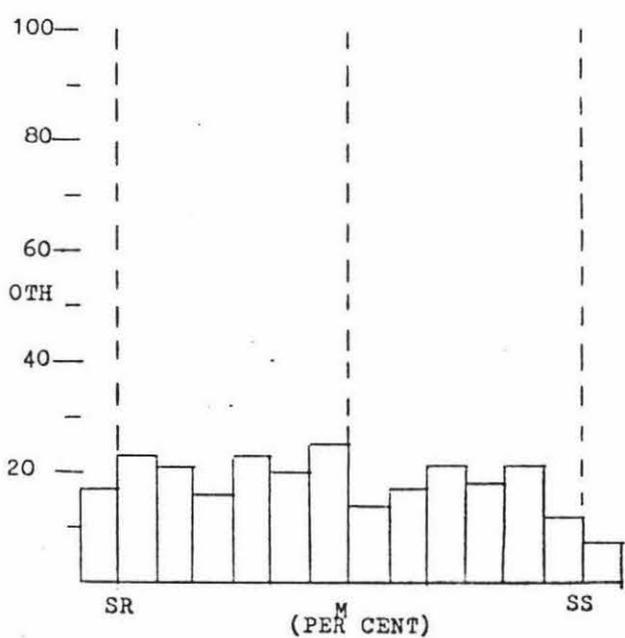
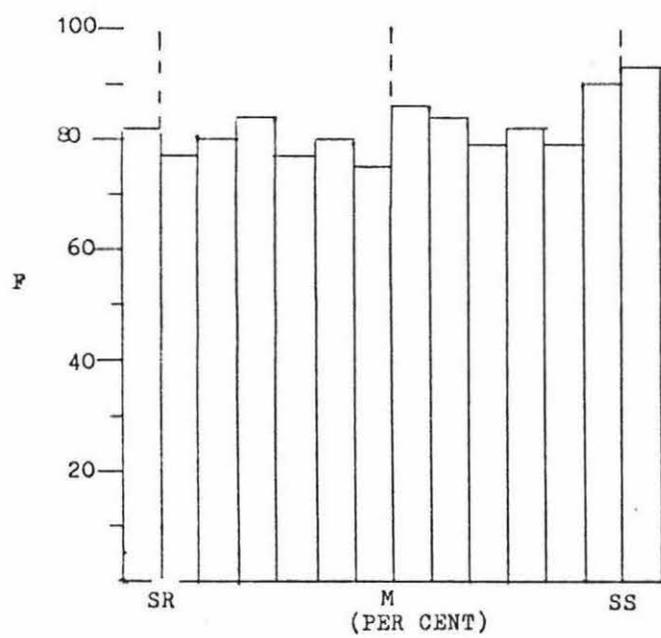
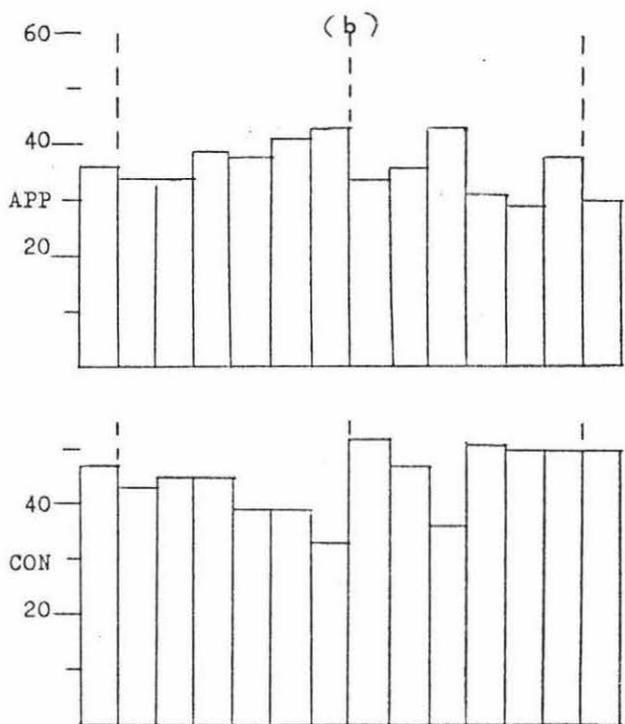
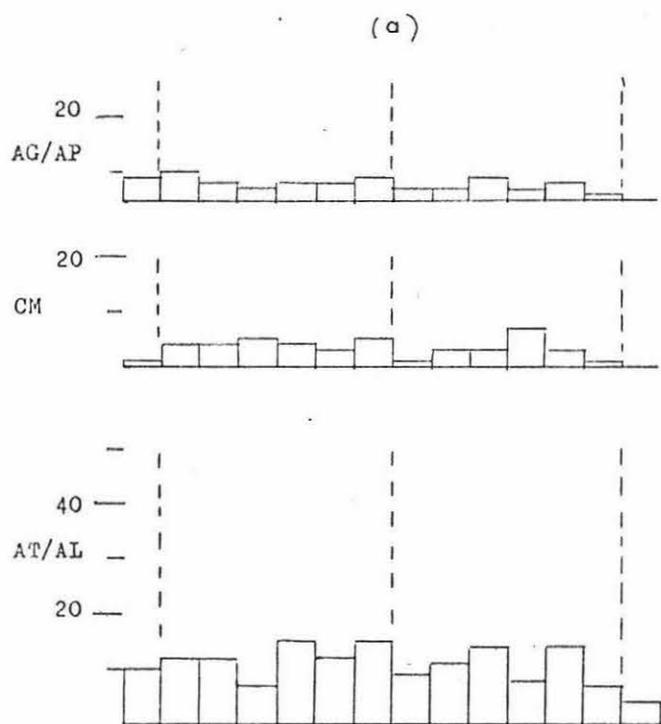
Throughout the day pukeko mostly ate, particularly at dawn and dusk (App. 22; Fig.36b). By far the bulk of the remaining observations were of birds looking for food, with more doing so during the morning, and progressively less thereafter. Most time was spent in "other" activities at midday.

Pukeko in dryland pecked faster and more intensely at dawn, less avidly in the mid morning, and progressively more rapidly throughout the midday and mid afternoon periods, decreasing again at dusk (App.22; Fig.36c & d).

#### 7.1.4 Discussion

##### Autumn

Time spent feeding by birds over the day at Fell's Lagoon was similar to that for birds at Hamilton's Lagoon. Diurnal patterns for other activities were different from those recorded at Hamilton's Lagoon. Proportionally more birds were seen in attentive/alarm activities at Fell's, compared to Hamilton's Lagoon, particularly in the mid and late afternoon, whereas time spent in comfort movements, and in encounters was irregular in the former area. Most birds flew at dawn and dusk at Fell's Lagoon, while courting, calling or drinking birds were not seen. As at Hamilton's, birds at Fell's Lagoon spent more time looking for food in the morning, than in the afternoon, while eating occupied most time at dawn and dusk. Thus the birds foraged more selectively in the morning than in the afternoon, spending most time in "other" activities then.



Diurnally, patterns for pecking rate and feeding intensity disagreed with those recorded at Hamilton's Lagoon, although the birds pecked at similar rates and intensities in the afternoon. In the morning, the birds pecked faster and fed more intensely at Fell's than at Hamilton's Lagoon, the reason for which remains unclear.

### Spring

Comparison of data collected during standard observations at Fell's Lagoon, with those collected at Hamilton's Lagoon, in the same season agreed well, i.e. in spring by far most birds at Fell's were observed feeding, with proportionally more doing so at dusk. Attentive/alarm, agonistic/appeasement and comfort movement activities were recorded at essentially the same rate all day, while courting, calling and birds in flight were infrequent.

Time allocated to appetitive and consumatory feeding and "other" activities broadly agreed with the data obtained from the Hamilton's Lagoon flock, although in spring pukeko at Fell's appeared to be more selective in their choice of forage, and hence spent less time eating. Similar time was allocated to "other" activities over the day, although there was a decrease at day's end with more time spent looking for food. This indicated the birds fed more selectively towards dusk, perhaps choosing higher quality food which would have provided them with more energy for longer into the night.

Diurnally pecking rates for both populations agreed well, with birds at Fell's Lagoon gradually increasing their pecking rates over the day. However the dawn peak was less than that recorded at Hamilton's Lagoon. Rates of pecking at Hamilton's were consistently higher than those recorded at Fell's Lagoon - an observation possibly related to the length of grass tiller available in the sward. At Fell's Lagoon in spring pasture, which was grazed mainly by horses, appeared longer (not measured) than that found in the sheep-grazed paddocks at Hamilton's Lagoon. Thus if the length of tiller taken by the birds at Fell's was greater than at Hamilton's Lagoon, the birds may not have needed to

peck as rapidly to ingest the same quantity of forage. Direct sampling of pukeko at Hamilton's Lagoon will elucidate this point.

The diurnal variation in feeding intensities calculated for the Fell's Lagoon flock was not the same as that described for the Hamilton's Lagoon flock. Again differences in sward length may be important to pukeko feeding intensity.

In summary, data from standard observations at Fell's Lagoon in spring agreed broadly with those collected concurrently at Hamilton's Lagoon. Data from only two weeks observations were used, which, when compared to the twelve weeks data collected at Hamilton's Lagoon, may explain a few of the irregularities. Moreover populations of pukeko inhabiting superficially similar areas will be expected to exploit the available habitats differently. As dense cover surrounding Fell's Lagoon precluded observations of some birds, the importance of marginal areas as feeding sites remains unclear.

## 7.2 Gut Analysis

### 7.2.1 Introduction

As the frequency of occurrence of the various size classes were known an "average" composite length of the food items (Siegfried, 1972) contained in the gizzards of shot pukeko, for each of the bi-hourly periods of spring and autumn and for the day as a whole, was calculated.

$$\text{Average Composite Peck Length (mm)} = \frac{\begin{array}{l} \text{(mean number of food items} \\ \text{in a particular size class x} \\ \text{the mean length value} \\ \text{for that class)} \end{array}}{\text{total number of food items}}$$

### 7.2.2 Frequency of Occurrence of Peck Lengths

#### 7.2.2.1 Composite Day

In autumn and spring the most frequently measured size class for food items in pukeko gizzards, was between 2.5 and 7.5 mm (Tab. 15). Plant material outside this range were progressively less frequently encountered.

TABLE 15. FREQUENCY OF OCCURRENCE OF PECK LENGTHS - COMPOSITE DAY

Length \ Season		0.0	2.6	5.1	7.6	10.1	12.6	15.1	17.6	20.1	22.6	25.1	27.6	30.1	32.6	35.1	TOTAL
		2.5	5.0	7.5	10.0	12.5	15.0	17.5	20.0	22.5	25.0	27.5	30.0	32.5	35.0	37.5	
AUTUMN	n	10	90	102	47	27	15	4	3	1	1	0	0	2	0	0	302
	% freq. of occ.	3.31	29.80	33.77	15.56	8.94	4.97	1.32	0.99	0.34	0.34	0	0	0.66	0	0	100.00
SPRING	n	37	236	227	114	54	41	14	9	8	4	3	2	1	2	1	753
	% freq. of occ.	4.91	31.34	30.15	15.14	7.17	5.44	1.86	1.20	1.06	0.53	0.40	0.27	0.13	0.27	0.13	100.00

#### 7.2.2.2 Diurnal

##### 7.2.2.2.1 Autumn

Average composite peck lengths for those periods in which sufficient birds were shot were similar over the day (c. 8.2 mm). However for midday and mid afternoon, data from only one bird for each period was available (Tab.16). Other birds shot in these periods had oat-filled gizzards, and were therefore not considered. Over the day the average composite peck length was 8.31 mm.

##### 7.2.2.2.2 Spring

The average composite peck length increased steadily over the day, from an average length in the early morning of 6.69 to 10.21 mm in the late afternoon (Tab. 17). Data from only one bird collected during the mid morning was used, the other birds at this time having oat-filled gizzards. For the whole day the average composite peck length was 8.47 mm.

#### 7.2.3 Diurnal Changes in Food Intake

##### 7.2.3.1 Ingesta in each Gut Segment (per gram body weight)

Shot birds whose gizzards contained only oats were not considered. All weights referred to below are "dry weights".

##### 7.2.3.1.1 Autumn

Gizzard and intestinal fractions accounted for most food found in the digestive tract, with most being found in the gizzard at midday, and least at dawn and dusk, while in the intestine most was found at dawn, midday and dusk (Tab. 18; ). Little food was found in the oesophagus, but a similar amount of food was found throughout the day in the stomach. When ingesta weights from all gut segments were combined, most food per gram body weight, was found in those birds shot around midday.

##### 7.3.2.1.2 Spring

Throughout the day most ingesta by far was found in the intestinal segment, with least there in the early morning and most in the late afternoon (Tab.19). Food in the oesophagus in any period was negligible, while

TABLE 16. DIURNAL FREQUENCY OF OCCURRENCE OF PECK LENGTHS - AUTUMN

Length Period	0.0 2.5	2.6 5.0	5.1 7.5	7.6 10.0	10.1 12.5	12.6 15.0	15.1 17.5	17.6 20.0	20.1 22.5	22.6 25.0	25.1 27.5	27.6 30.0	30.1 32.5	32.6 35.0	35.1 37.5	37.6 40.0	TOTAL
SR - +2	n 3	23	25	11	2		1	2									67
	% 4.48	34.33	37.31	16.42	2.99		1.49	2.98									100.00
+2 - +4	n 4	26	22	14	7	3							2				78
	% 5.13	33.33	28.21	17.95	8.97	3.85							2.56				100.00
+4 - M - -4	n 2	8	3														13
	% 15.38	61.54	23.08														100.00
-4 - -2	n 1	10	8	8	7	3	1	1	1	1							41
	% 2.44	24.39	19.51	19.51	17.07	7.32	2.44	2.44	2.44	2.44							100.00
-2 - SS	n 2	29	39	11	11	8	2										102
	% 1.96	28.43	38.24	10.79	10.78	7.84	1.96										100.00

TABLE 17. DIURNAL FREQUENCY OF OCCURRENCE OF PECK LENGTHS - SPRING

Length Period	0.0	2.6	5.1	7.6	10.1	12.6	15.1	17.6	20.1	22.6	25.1	27.6	30.1	32.6	35.1	37.6	TOTAL
	- 2.5	- 5.0	- 7.5	- 10.0	- 12.5	- 15.0	- 17.5	- 20.0	- 22.5	- 25.0	- 27.5	- 30.0	- 32.5	- 35.0	- 37.5	- 40.0	
SR - +2	n %	19 7.57	116 46.22	73 29.08	28 11.15	7 2.79	6 2.39	1 0.40				1 0.40					251 100.00
+2 - +4	n %	2 2.99	6 8.95	20 29.85	11 16.42	6 8.95	8 11.94	4 5.97	2 2.99	2 2.99	1 1.49	1 1.49	1 1.49	2 2.99	1 1.49		67 100.00
+4 - M - -4	n %	11 5.67	62 31.96	63 32.47	33 17.01	11 5.67	5 2.58	3 1.55	3 1.55	1 0.51	2 1.03						194 100.00
-4 - -2	n %	1 0.80	34 27.20	41 32.80	18 14.40	10 8.00	9 7.20	3 2.40	3 2.40	3 2.40	1 0.80	2 1.60					125 100.00
-2 - SS	n %	4 3.42	18 15.38	30 25.64	24 20.51	20 17.09	13 11.11	3 2.56	1 0.86	2 1.71		1 0.86				1 0.86	117 100.00

TABLE 18  
DIURNAL CHANGES IN FOOD INTAKE - AUTUMN

Seg. Period	OESOPHAGUS		GIZZARD		STOMACH		INTESTINE		TOTAL
	$\times 10^{-4}/g$ BW	% tot. cont.							
SR - +2			4.33	20.16	2.15	10.01	15.00	69.83	21.48 100.00
+2 - +4			5.92	39.57	0.66	4.41	8.38	56.02	14.96 100.00
+4 - M - -4			17.97	49.55	1.10	3.03	17.20	47.42	36.27 100.00
-4 - -2	0.15	0.83	9.47	52.41	1.82	10.07	6.63	36.69	18.07 100.00
-2 - SS			1.99	12.33	0.93	5.77	13.21	81.90	16.13 100.00

TABLE 19  
DIURNAL CHANGES IN FOOD INTAKE - SPRING

Seg. Period	OESOPHAGUS		GIZZARD		STOMACH		INTESTINE		TOTAL
	$\times 10^{-4}/g$ BW	% tot. cont.							
SR - +2	0.07	0.78	3.23	35.81	0.96	10.64	4.76	52.77	9.02 100.00
+2 - +4	0.14	1.17	2.44	20.47	1.00	8.39	8.34	69.97	11.92 100.00
+4 - M - -4			2.02	21.38	0.27	2.86	7.16	75.76	9.45 100.00
-4 - -2			3.30	30.67	1.17	10.87	6.29	58.46	10.76 100.00
-2 - SS	0.03	0.14	5.50	25.97	1.27	6.00	14.38	67.89	21.18 100.00

that in the stomach was essentially constant all day. More food was found in the gizzard in the mid afternoon, at dusk and at dawn, than at other times, although over the day, the total weight of ingesta found in the entire gut per gram body weight, gradually increased.

#### 7.2.3.2 Per cent weight in each segment of total weight of ingesta (per gram body weight)

##### 7.2.3.2.1 Autumn

Throughout the day intestinal and gizzard segments held most food (Tab.18). Except for a decrease at midday, gradually more food was located in the intestine towards dusk. Similar quantities of food were found in the stomach over the day, but that in the gizzard was variable. The oesophageal fraction was comparatively unimportant.

##### 7.2.3.2.2 Spring

Throughout the day food was mostly found in the intestine, with less in turn being recorded in the gizzard, stomach and oesophagus (Tab.19). During mid morning and midday comparatively most ingesta was located in the intestine, and least found in the gizzard. Generally less food was contained in the stomach over the day, whereas that found in the oesophagus was negligible.

#### 7.2.4 Discussion

In both autumn and spring, pukeko took at each peck essentially the same length of tiller throughout the day, although it increased by 3.52 mm and 0.78 mm from dawn to dusk in spring and autumn respectively. The importance of this remains unclear but may possibly be related to lower quality forage available towards day's end, to increasing energy and nutrient demands by active pukeko towards dusk, or to the birds accumulating food reserves for the forthcoming night's fast.

Recalling that in spring birds at Fell's Lagoon fed less selectively, spent more time eating, and pecked faster and more intensely at dusk than earlier, it is not surprising to find total food in the pukeko's gut increased gradually

towards day's end. Moreover in autumn, but particularly in spring, birds steadily increased the tiller length taken towards dusk. Thus when forage quality was low, besides spending more time eating, pecking faster, feeding more intensely and less selectively, pukeko may have obtained the same quantity of nutrients and energy per unit time, by increasing the length of tiller taken, although they would have had to ingest a greater quantity of food.

Pukeko may have increased their pecking rate and length towards day's end so their digestive tract was full at nightfall. Thus while resting and sleeping they were effectively taking in nutrient and energy. Moreover as pukeko lack a storage crop - the oesophagus ending directly at the proventriculus - continual feeding until nightfall must occur to ensure retirement with a full tract. Maximum quantities of food were found in the gut of shot birds at this time, which further supports the hypothesis of "stocking-up" of food reserves at dusk. Although in the early morning birds were shot one and a half to two hours after sunrise, the weight of food in the whole gut and especially the intestine, was less than that recorded for the last period of the day. The gizzard contained proportionally more food in the early morning than later. Presumably digestion continued at night, and as less food was found in the gut in the morning than at dusk, it is thought extensive night feeding did not occur in either autumn or spring at Fell's Lagoon.

In autumn the length of tillers taken over the day varied little (0.78 mm) however sample size was small (301 measurements from 12 birds). Possibly food quality was similar throughout the day, so birds did not need to increase their peck length to ingest the same quantity of nutrients and energy, notwithstanding that they may have increased eating times, feeding rates and intensities and/or decreased their selectivity in response to lower forage quality.

In summary shot samples of pukeko indicated:

1. The length of tiller taken at each peck (average composite peck length), was essentially constant

over the autumn day, but increased towards dusk in spring.

2. Little food was found in the oesophageal or gastric portions of the tract, with more in the gizzard but most in the intestine.
3. More food was found in the entire gut towards dusk.
4. Food found in the oesophagus and stomach was essentially constant throughout the day, while that found in the gizzard and intestine increased gradually over the day in spring, but was irregular in autumn.
5. Proportionally more food was found in the intestine at dusk than at dawn.
6. Pecking rates and feeding intensities increased gradually over the day indicating support for the use of time spent feeding and pecking rates as indices of pukeko feeding effort.
7. Pukeko may respond to changes in food quantity and/or quality by varying searching and eating time, pecking rate and feeding intensities, as well as peck lengths.

## 8. GENERAL DISCUSSION

### Optimal Foraging Theories

The way in which a predator behaves is likely to be a compromise of conflicting selection pressures and environmental conditions (Krebs, 1973). Natural selection will favour those individuals in a population which contribute most to subsequent generations, hence natural selection will result in a change with time, of the average foraging behaviour (optimal time spent feeding for energy obtained) in a population, towards that which gives maximum fitness (Rosen, 1967; Pyke *et al*, 1977). Thus the average foraging behaviour observed for a population should be very close to the behaviour which results in maximum fitness, subject to whatever constraints are operating. A foraging strategy that optimises the amount of energy obtained per unit collection time in the long term (e.g. a week, month, or year) may be different from that which optimises the amount obtained in the short term (e.g. an hour or day). Since biological fitness may be measured over the entire life history of an individual, it is this length of time that is relevant (Schoener, 1971).

Elmen (1966, 1968), MacArthur and Pianka (1966), Schoener (1971), and Charnov (1976a, b) have proposed models to describe the optimal choice of food items. In general, these models measure the profitability of a particular prey type purely in terms of energy gained per unit searching effort, and do not take into account such factors as palatability, searching image formation, and avoidance of novel prey.

### Optimal patch use

Optimal foraging theory predicts animals allocate the greatest amount of time to the area of highest food abundance (and/or quality) and progressively less time to progressively worse areas. This behaviour may be an adaptation to a fluctuating environment, and represents a long-term adaptation via phenotypic plasticity, rather than a short term

one (Schoener, 1971). Pukeko showed "phenotypic plasticity", adapting to a seasonally fluctuating food supply by feeding most intensely in pasture, where food abundance and/or quality was highest, and less intensely in rush margin, mud, swamp and water areas where food availability and/or quality varied seasonally.

#### Optimal diet

The amount of food that an animal must procure per unit of body weight and time, to maintain the minimal physiological and behavioural outputs consistent with self maintenance and reproduction depends on an intricate interplay of many abiotic (e.g. micrometeorological) and biotic (e.g. body size, food availability and quality, morphological events, social hierarchy, competition and predation, etc.) factors (King, 1974). Whether or not a food type should be eaten is independent of the abundance of that food type and depends only on the absolute abundances of the food types of higher rank (Schoener, 1971). As the abundance of a preferred food type included in the diet rises, the number of less preferred food types in the diet falls i.e. increased food abundance should lead to greater food specialisation.

Diurnal and seasonal food preferences of pukeko are unknown, but from gut analysis (Carroll, 1966; this study) it appears pukeko forage broadly - their dietary composition undoubtedly reflecting seasonal (e.g. pasture grass seed-heads, clover stolons) and diurnal availability and nutrient composition (e.g. insect abundance and leaf or stem concentration of photosynthetic products) of local food types.

#### Optimal feeding period

No general theory exists on optimal placement of feeding periods over the activity cycle, but basic components are the metabolic costs of activity under different climatic conditions, the time distribution of these factors, and food and predator abundance. For animals like pukeko, which require food at frequent intervals, time from prior feeding periods may be important. When food is scarce or energetic

requirements are relatively greater, animals should expand their feeding periods towards less profitable times (Schoener, 1971).

The importance of climatic factors on duration and placement of the feeding period is well documented (see p.130). The ideal placement of the foraging period(s) for pukeko at Hamilton's Lagoon over the day and for each season is unknown, but, as the optimal foraging theory predicts, it will be close to the "average" foraging behaviour observed for this population. Its placement over the day will likely depend on such factors as diurnal quality of plant food (assuming plant availability is essentially constant over the day), and perhaps animal food availability (e.g. crepuscular invertebrates) and quality. The relative importance of each food type will determine when and where pukeko forage most actively, but factors such as climate, predator activity, and ecologically similar species may modify these feeding patterns. An "average" pukeko fed more keenly all day in winter, when overall food availability was least, than in autumn, summer, but especially spring, when apparently most food was available. Although spending most time feeding at dawn and dusk in all seasons, an "average" bird fed most intensely at dusk in spring, summer and autumn, and at midday in winter, suggesting pukeko did indeed, expand their feeding periods towards less profitable times when food availability (and/or quality) was least.

#### Specific searching image

Gibb (1962), discussing L. Tinbergen's (1960) hypothesis on the role of the specific searching image in great tits Parus major, suggested predators hunted by expectation, rejecting low and high density prey as uneconomic for the effort involved in pursuing prey. Murton (1971) rejected the presence of a specific searching image in gregariously feeding woodpigeons (Columbus palambus). Although woodpigeon mimic each other's pecking movements, feeding rate becomes adjusted to the overall food density. Such imitative feeding behaviour was considered advantageous in a coarse-grained habitat, and disadvantageous in a fine-grained

environment. Feare et al (1974) showed rooks (Corvus frugilegus) in flocks fed at a higher rate than solitary birds, due possibly to social facilitation and/or decreased predation pressure, and Smith (1974 a,b) found European song thrushes (Turdus philomelus) fed according to the specific searching image hypothesis. However Smith (1977) found pecking rates of great-tailed grackles were independent of flock density.

Pukeko generally formed loose feeding flocks, however time of day and presence of chicks influenced (but not significantly) the distance between birds and their rate of feeding. They were seldom seen feeding far from the main flock, and may have fed together primarily to avoid predation. Pukeko are discriminant feeders, spending a major portion (30-40%, with diurnal and seasonal differences) of their time looking for food. Hence it is possible pukeko developed a "searching image" for a preferred food item, which at intermediate densities was taken in a direct proportion relative to its density. Ryegrass and clover are primary sward constituents (60-75% and 17-27% cover respectively) at Hamilton's Lagoon and featured predominantly (especially clover stolons) in gizzards of birds shot at Fell's Lagoon. Unless pukeko searched for a specific portion of ryegrass (unknown) or clover (underground stolons) it is unclear why they should have developed a specific searching image for components that featured so predominantly in the habitat. Obviously this question requires further study.

#### Time Budget and Feeding Ecology

Selection will favour individuals that diurnally optimise energetic efficiency and time allocation in all seasons, in response to local environmental conditions (Verner, 1965; Wolf and Hainsworth, 1971; Verbeek, 1972). The amount of time birds devote to a particular activity depends, among other things, on the life style (Pearson, 1954; Orians, 1961), body size (Gibb, 1954), food availability (Gibb, 1956), and temperature (Verbeek, 1964). Reproduction requires

extra time, above that needed for self-maintenance but an organism can accommodate the increased seasonal demands of reproduction and territory by increasing its total energy requirement, or by changing the allocation of time and energy to different activities, while maintaining total energy expenditure relatively constant (Stiles, 1971).

In homeotherms, a long term balance exists between heat generated through the metabolism of food, and heat loss to the environment (Collins and Clow, 1978). However in the short term energy flux between the two are influenced by the degree of feather insulation, latitude, environmental variables (e.g. temperature, humidity, cloud cover, etc.), lunar periodicity, population dynamics and body cycles. However because of its close relationship to bioenergetics, feeding (and hence forage availability and quality) is probably one of the most important aspects of any time budget.

### Feeding

Pukeko spent the bulk of their time (c. 75% feeding, with most of the remaining time being allocated to attentive/alarm, comfort movement, and agonistic/appeasement encounters. Residual time was assigned to less important or less time-consuming activities, such as drinking or courting. Dryland was the habitat most frequently used (especially as a feeding station), followed in turn by rush margins, mud, swamp and water. From considerations of time devoted differentially to appetitive and consumatory feeding, and "other" activities, the seasonal availability (quality) of forage, and selectivity of pukeko, which varied for each habitat, both seasonally and diurnally, was inferred. Pecking rate, feeding intensity and habitat foraging rank data provided an insight into the seasonal allocation of feeding effort by an "average" bird of the Hamilton's Lagoon flock. It appears pukeko are able to differentially allocate their feeding effort between various habitats, in relation to food availability and quality, and the biological demands on the birds at that time.

Pukeko "have presumably evolved some mechanism enabling them to relate searching effort to the amount of food found, . . . , recognising a situation where no food exists and responding by searching elsewhere" (Murton and Isaacson, 1962). However as food selection is a time consuming process it must be balanced against the ability of the birds to ingest sufficient food in the time available, i.e. it is inefficient to select a diet of 10% better quality if total food intake is thereby reduced by more than 10% (Owen, 1972).

Diurnally for all seasons, pukeko exhibited a bimodal distribution of activity, peaking at dawn and dusk, whereas feeding effort was unimodal. They fed more intensely in winter (peaking just after midday), spring (peaking in the late afternoon), and autumn (peaking at dusk), than in summer when the birds fed much less intensely (peaking in the mid afternoon). Towards dusk increases in peck length especially in spring were found.

Information on time allocated to feeding activities in rails is scarce. Recapping briefly, Carroll (1966) determined from gut analysis that the volume of food contained in pukeko gizzards during any one of three daily periods over the day decreased towards dusk, suggesting pukeko forage more in the morning than in the afternoon. However, as indicated in my study, wholesale combination of pukeko samples collected from a wide range of areas, in which the relative importance of the available habitats will determine where and the extent to which pukeko have fed most recently, is undesirable. Her data were probably affected by unequal samples of birds from each season for each period of the day. Craig (1974) found the birds to be more active (in particular spending more time feeding) at dawn and dusk than during the central daily periods. Fordham (unpub. data) found that pukeko fed 65-85% of the time while on pasture, and 45-64% while on swamp (seasonal variations), which compares favourably with the values recorded at Hamilton's Lagoon.

Mills (1973) found the flightless takahe can spend up to 90% (c. 21 hours) of the day feeding, eating at a fairly constant rate throughout. However as yet, no detailed diurnal activity patterns have been determined for this bird.

Ridpath (1972a) noted that the Tasmanian native hen fed steadily all day but least during the hottest time. Bent (1926) found the king rail (Rallus elegans) to be most active "just after sunset and just before sunrise, and when not molested (the birds) were seen in daylight."

Fordham (1978) found moorhen fed more intensively prior to sunset than immediately following sunrise, pecking fastest on the grass/herb sward, slowest on water, with mud intermediate. He suggested high pecking rates and feeding intensities may have represented the "stocking-up" of food reserves for the forth-coming night. To start the day with the smallest energy debt the birds may reduce their energy expenditure at night, so that the need to feed was less than that prior to dusk. However few birds fed in the early morning perhaps as other activities (particularly social, e.g. territorial re-establishment and defence, may have been more important, and moreover the diurnal changes in food quality or quantity.

Recently grouse and ptarmigan have received particular attention, and considerable information on their diurnal feeding habits is now available. Peters (1958) noted that Newfoundland willow ptarmigan (Lagopus lagopus) started feeding as soon as it was light, and food intake in the morning was apparently little more than what could be digested. Around noon feeding decreased but resumed in the early afternoon, and intensified during the late afternoon. Red grouse (Lagopus l. scoticus), according to Hartley (1948), Fowle (1960), and Savory et al (1978), feed throughout the day, ingesting the largest volume of food towards dusk - a similar sequence to that noted for pukeko. Irving et al (1967) found the weight of food in Alaskan willow ptarmigan (Lagopus lagopus) crops in autumn, spring, and winter increased over the day, however in summer feeding occurred at a steady rate throughout the day. They also noted a concentration of feeding in relation to the shortening of the day length. Pendergast and Boag (1970) could not determine any diurnal foraging pattern in any season for spruce grouse (Canachites canadensis), but noted they ate more by volume and weight, in winter than in any other season, and that shot samples contained lowest

diversity of food items at this time. In summer the birds ate least food but took the widest variety of items (autumn and spring were intermediate). Savory (1975) found the daily food intake of red grouse was positively related to body weight and to day length, and negatively related to air temperature, the birds eating more in summer than in spring, autumn or winter.

Murton and Isaacson (1962) found woodpigeon fed for c. 70% of the time in mid winter while in pasture, resting for only 5% of the day. Pecking rates in pigeons are higher than those recorded for pukeko (e.g. 81 versus 50-70 peck/min. respectively). Woodpigeon pecking rates rose gradually over the day from c. 70 to c. 100 pecks/min. in the late afternoon, being dependent to some extent on the social position the bird occupied in the flock, with those birds in the middle to front fan, feeding at a higher rate than those at the rear. The rates at which redshank (Tringa totanus), pied stilts and wild domestic fowl feed have also been found to be dependent on the number of birds in the feeding flocks (Goss-Custard, 1970c ; McConkey, 1972; Savory et al, 1978). However this idea was not tested in pukeko flocks.

During late summer the amount of effort spent searching for food by cattle egrets (Ardeola ibis) indicated by the number of paces taken, was about twice that recorded in early summer (Siegfried, 1971). As the length of pace remained relatively constant, it was assumed that each egret searched in late summer, twice the area searched in early summer, for half the return in food capture. The number of, and length between paces for pukeko were not measured during this study, as the birds commonly paused to eat food held "parrot-like" in the foot. Time spent searching for food was measured only in proportional time spent looking for food, showing that pukeko searched for food most extensively in winter, and least in summer when food availability was least.

Recently Kenward and Sibly (1977) hypothesised that feeding preference of woodpigeon feeding on Brassica and

clover sites, could be explained by a "digestive bottleneck" in the digestion of Brassica. It is possible that pukeko eating some plant species (e.g. water buttercup) could be limited like woodpigeons, by a digestive bottleneck. As pukeko lack a crop, ingestion could be limited by the quantity of food the oesophagus and proventriculus could hold. Furthermore if some plants take longer to digest than others, it is possible food intake could be restricted, preventing pukeko from eating more.

Using a similar method to that developed for this study, Savory et al (1978) calculated the time spent feeding, pecking rates and feeding intensities for wild domestic fowl. They commented that on wet days the birds fed in short frequent bouts whereas on fine days they spent less time feeding and pecked at a slower rate and intensity in the morning than in the afternoon, reaching a maximum feeding effort in the early evening. Pecking rate was inversely related to walking rate throughout the day. Daily overall means for time spent pecking (48%), pecking rate (50 pecks/min.), and feeding intensity (1,450 pecks/hour) were comparable with the overall annual means for pukeko (48%; 38 pecks/min.; 1085 pecks/hour respectively). The authors also calculated the number of pecks each bird would deliver during a ten hour day, as 14,000-15,000 pecks, compared to 13,380 pecks for pukeko feeding during a similar photoperiod (winter). Furthermore differences in pecking rates, and feeding intensities between two habitats indicated domestic fowl responded to variations in food density by altering their feeding effort allocation (time spent feeding, and pecking rate) between the habitats.

#### Forage availability and quality

Foraging efficiency, according to Wolf et al (1975), is an increasing function of the quality of food, being dependent on other factors such as body size, daylength, temperature, and time devoted to non-feeding activities (see later).

Large differences between individual plants and parts of plants (e.g. Chionochoa - Connor et al, 1970) may be

important to grazers (e.g. takahe - Williams et al, 1976b) that can distinguish between high and low quality food portions. Plant palatability is related to grazing intensity (Cook et al, 1953; Mills and Mark, 1977) and nutrient availability at a particular site (Williams et al, 1976a; Mills and Mark, 1977). Preference rating of a plant species is increased with higher carbohydrate, protein, and phosphorus levels (Thomas et al, 1964), and may possibly be linked with selection for factors such as Vitamin A (Nesler, 1946; Nesler et al, 1949; Hungerford, 1964).

Little detailed work is available on changes in the seasonal and diurnal composition of pasture plants. Huxley (1976) suggested photoperiod may affect the quantity and quality of moorhen forage. For clover and ryegrass, the mineral composition of forage is essentially constant throughout the year, with higher nitrogen and phosphorus levels in winter and spring, than in summer and autumn (Melville and Sears, 1953). The absolute level of any nutrient is dependent on the state of maturity, besides many other physical and biological factors (Evans et al, 1964). Smith (1973) states that the amount of total sugar and soluble sugar carbohydrates in temperate grassland herbage (e.g. ryegrass and legumes) increases during the morning hours until sometime in the afternoon, decreasing from that time until daylight the following day. However with ryegrass, large differences were reported according to the portion (and hence the state of maturity) of the plant analysed.

In soybean (Glycine soja) plants highest photosynthetic rates occurred at dawn (least concentration of photosynthetic products), whereas respiration rates increased gradually over the light period. Leaf weights increased during the second half of the photoperiod (especially from accumulated starch), and declined during the dark period (Warrington et al, 1977). In Paspalum dilatatum, the amount of starch present in the leaves increased gradually towards dusk, the photosynthetic rate remaining approximately constant all day (Forde et al, 1975). The nitrogen content of a wide variety of grasses from tropical or temperate origin, varied little throughout the day (Forde

et al, 1976).

Little more is known on the diurnal or seasonal composition of temperate pasture plants, so considering all the above, it is possible pukeko fed most at that time of day when the quality of forage, (i.e. the concentration of a specific compound(s), e.g. starch) was greatest. Exactly what this product(s) is, remains unclear but research into the diurnal concentration of photosynthetic products for pasture plants may provide some insight into what factor(s) induces pukeko to feed more selectively at one time of day than another.

#### Feeding effort

Moss (1972), Moss et al (1972), and Savory (1978), working with red grouse found food digestibility was inversely related to its intake rate. In the same way, wild domestic fowl became less selective and ate fewer higher quality food items as feeding activity increased in the afternoon and evening, than earlier (Savory et al, 1978). Thus when feeding sporadically fowl appeared to be searching for choice food items, so food type and quality eaten then, may well have differed from that eaten during intensive feeding. Savory (1978) also demonstrated that red grouse actively selected between foraging site for heather of specific age classes. A similar hypothesis, that over the day feeding effort is differentially allocated between available habitats according to availability and/or quality of forage, is suggested for pukeko.

Takahe have been shown recently to consume food according to the relative amount of many nutrients and sugars the plants contain, and moreover selection occurred between plants of the same species for the highest levels of phosphorus in spring, early summer, and autumn (Mills and Mark, 1977).

Red grouse apparently selected for higher nitrogen and phosphorus levels from winter to spring (Miller, 1968; Moss and Parkinson, 1972), while selection for calcium, soluble carbohydrates, and crude fat did not change over the year (see also Pulliainen, 1970). Pulliainen and Salo (1973) noted willow grouse actively select certain food

items, while at the onset of territory establishment and consequent breeding, blue grouse (Dendragapus obscurus fuliginosus) selected for high energy food (King, 1973).

Alternatively Marriott (1969), and Newton and Campbell (1973) found Cape Barren geese (Cereopsis novaehollandiae) fed non-selectively - the species composition of the pasture being very similar to that determined from the crops of shot samples. Perhaps it was inefficient for the birds to feed selectively on one particular plant species, if that resulted in decreased food intake (Owen, 1972), or increased energetic cost of locomotion (Krebs, 1973; Norberg, 1977). However artificially fertilised pasture plots were fed upon more than control plots (Owen, 1975), indicating geese were capable of selecting between differing forage quality, but plainly most rejected concentration of feeding effort on a particular plant food species in ordinary pasture as being uneconomic.

Recently Collins and Clow (1978) noted selectivity of foraging habitats by the western spinebill (Acanthorhynchus superciliosus) was determined by food quantity and quality available in each, for the cost of obtaining it. Differences in foraging rates between two habitats have also been noted for redshank (Goss-Custard, 1970b), grey-crowned babbler (Ptomatostomus temporalis) (Councilman, 1974), starlings (Brownsmith, 1977) and oystercatchers (Haematopus ostralegus occidentalis) (Heppleston, 1971).

#### Feather insulation

Kendeigh (1970) found that the relatively higher rates of metabolism and the greater sensitivity to cold experienced by small species, was related to their less effective feather insulation, as well as to their surface area to volume ratio. Bligh (1976) commented that small organisms with a large surface area relative to mass will warm up and cool down much more rapidly, and become active earlier but retire earlier, than will larger organisms with a smaller surface area to mass ratio (see also Gibb, 1954). Fredrickson (1969) examined carcasses of coots

that had died following a severe spring, during which cold weather refroze the lake shallows and grass. Most birds had died of starvation and cold as, in the latter case anyway, plumage was inadequate for temperatures experienced.

Hamilton and Harper (1967) hypothesised that "black homeotherm colouration functioned primarily to maximise the absorption of radiation of solar energy". Since homeotherms maintain a nearly constant body temperature, there might seem to be little advantage in absorbing additional heat from the environment. Under certain conditions however, it is possible that the "cost" of energy to maintain body temperature might be reduced by obtaining environmental heat from sunlight. Radiant energy, reported by Morton (1967a), was used as a supplementary energy source by white crowned sparrows (Zonotrichia leucophrys gambelii), only when they were expending extra energy to maintain body temperature. In pre-European times pukeko presumably inhabited dense swamps and areas which permitted sunbathing probably would have been few. In this case black pigmentation of swamp-dwelling birds would have reduced the metabolic costs of staying warm. However to be of adaptive value this saving must be expressed ultimately as a decrease in food intake. Indeed pukeko at Hamilton's Lagoon took less food and were least active at noon, than at other times.

### Lattitude

Variations in the times of daily onset and end of activity are most pronounced at high lattitudes with animals being active for longer in spring than in autumn, at equal photoperiods (Enright, 1966; Daan and Aschoff, 1975). At higher lattitudes, the birds start earlier and go to rest later in relation to sunrise, the shorter, colder, and windier the days are (Palmgren, 1949; Hart, 1964; Calder, 1975; Daan, 1976). Pukeko were active for longer after sunset (+30 minutes), and earlier before sunrise (-30 minutes) in winter, than in summer, when they

were active for only 10 minutes after sunset, and 10 minutes prior to sunrise. Similar "anticipation" of dawn and cessation of activity before dark, was also noted for willow ptarmigan (West, 1968).

Daan (1976) has explained similar responses to changes in light intensity in finches (Fringillidae) by the presence of morning and evening oscillators, the frequency of oscillation of which are dependent on light intensity. Hence if a "morning oscillator" responsible for the onset and morning peak of activity is accelerated by light, and an "evening oscillator" to which the afternoon peak and cessation of activity are coupled, slowed by light, his theory predicts pukeko will become active later in the morning and retire earlier at dusk as photoperiod increases, i.e. the start of activity shifts forward in time and the end of activity shifts backward, but not as much as sunrise shifts forward, and sunset shifts backward.

#### Environmental variables

Environmental variables such as temperature, cloud cover, humidity etc., affect the time allocated to and the intensity of feeding. For example Austin (1978) found the time verdin (Auriparus flaviceps) spent foraging remained constant until temperatures exceeded 30-35°C., in which case time was mostly spent sitting. This suppression of activity when environmental heat gain is greatest, has definite energetic and thermoregulatory implications (see "feather insulation"). Verdin actually did most of their feeding in the cool early morning and evening, and less at midday when the temperature increased above 30°C. Observations on a flock of wintering Brewer blackbirds (Euphagus cyanocephalus) showed a clear inverse relationship between environmental temperature, and feeding time (Verbeek, 1964). As feeding time increased, time spent on other activities decreased at low air temperatures. Calder (1968) found desert-dwelling road runners (Geococcyx californianus) were most active in the mid morning and mid afternoon, and least active at noon when temperatures were greatest. However prey avoidance of midday heat may also have influenced the bird's activity patterns.

On the other extreme Beer (1961) found wintering house sparrows fed most intensely in the early morning and late afternoon, but when ambient temperatures decreased to  $-20^{\circ}\text{C}.$ , feeding occurred well before sunrise. Rain and stronger winds caused a further decrease in the feeding activity. Some other bird species in which an inverse relationship has been determined between temperature and feeding activity include white-crowned sparrows (Morton, 1967); redshank (Goss-Custard, 1969, 1970a); yellow-billed magpie (Pica nutalli) (Verbeek, 1972); Downy woodpecker (Picoides pubescens), Carolina chickadee (Parus carolinensis), tufted titmouse (P. bicolor), white-breasted nuthatch (Sitta carolinensis) (Grubb, 1975); black-capped chickadee (Parus atricapillus) (Grubb, 1977); American avocet (Recurvirostra americana) (Gibson, 1978). Hence it is likely that pukeko exhibited changes in feeding intensity associated with environmental temperature.

Work on the effects of other environmental variables on feeding time is scarce. Grubb (1977) working with the forest-dwelling species mentioned above, found higher wind velocities, lower humidity and solar radiation (and hence ambient temperature), resulted in decreased foraging activity, and affected the bird's choice of foraging habitat - the birds positioning themselves in more sheltered areas when conditions were adverse. However, Schnell (1967) found rough-legged hawks (Butea lagopus) flew more often in stronger winds and higher temperatures.

Increased cloud cover prolongs awakening and lengthens sleeping time (Palmgren, 1949), and delays onset of feeding activities (Schnell, 1967; Raveling et al, 1972; Maxon, 1977).

#### Lunar periodicity

The daily timing and duration of feeding activities may also be dependent on lunar periodicity. For example McIntyre (1978) found feeding activity of common loons (Gavia immer) showed a tidal relationship, peaking when the rate of tidal rise began to slow. Inactivity (i.e. maintenance etc.) was greatest at high tide when the birds did not feed. However like other feeding activity cycles, with

increasing daylength, the birds stopped feeding earlier. Work by Ranwell and Downing (1959) on Brent goose (Branta bernicla) provides another example in which the bird's feeding cycle was related to the lunar (tidal) cycle and climatic conditions.

### Population dynamics

Besides being dependent on a variety of external environmental factors, feeding rate and intensity, and habitat usage have also been noted to differ between sexes (Jackson, 1970 - downy woodpeckers; Heppleston, 1971 - oystercatchers; Siegfried, 1974 - lesser scaups (Aythya affinis); Smith, 1977 - great-tailed grackles (Cassidix mexicanus); Gibson, 1978 - American avocets; Seymour and Titman, 1978 - black ducks (Anus rubripes)). Savory et al (1978) found that incubating wild domestic hens pecked at twice the rate of non-breeding adults. It is unknown if differences in feeding ecology existed between the sexes in pukeko, but it is reasonable to expect that with the onset of egg-laying the female's foraging habit may change markedly. However large differences between the sexes is thought unlikely, as both sexes participated in territory establishment and defence, incubation and chick rearing, and presumably when outside the breeding season biological demands on each will be expected to be similar.

The quantity and quality of food available to herbivores can also determine the breeding density of adults and chick rearing success (e.g. Kean, 1956; Williams, 1960; Kahi, 1964; Miller et al, 1970; Craig, 1974; Sinclair, 1974; Mills, 1975, 1977; Miller and Watson, 1978). Unlike pukeko, which feed quite broadly (Carroll, 1966), woodpigeon rely heavily on one food type, with population levels determined by the availability of this late autumn and winter food supply (Murton et al, 1964a,b, 1966).

### Body Cycles

Several authors, e.g. Baldwin and Kendeigh (1938), Fisher and Bartlett (1957), Collins and Clow (1978), have found diurnal variations in the body weights of various bird species - all of which indicated the birds were

significantly lighter (7-10% at dawn than at dusk, and that weight changes were inversely related to the prevailing air temperatures (e.g. O'Connor, 1970). Also prevailing wind, humidity, food availability etc. affect diurnal variation in body weights.

Heat production is associated with the daily activity cycle, with highest temperatures occurring during the active part of the day, and the lowest during the inactive part. In addition its magnitude is functionally related to the environmental temperatures. Oxygen consumption also varies diurnally, peaking around mid morning to midday (Aschoff and Pohl, 1970).

#### Diurnal Activity Patterns of Other Animals

Bimodal diurnal activity patterns have been found for a wide variety of animal taxa, including molluscs, insects, arthropods, reptiles, (e.g. Cnemidophorus sexlineatus, Barden, 1942 and the Anolis lizard, Andrews, 1971), mammals (e.g. N.Z. fur seals Arctocephalus forsteri, Crawley et al, 1977), and birds. The details of the diurnal activity patterns are different for different species, but all are ultimately related to the time phasing of environmental conditions (Palmgren, 1949; Aschoff, 1966; Verner, 1965). Authors who have noted bimodal dawn and dusk activity (or feeding) peaks in birds include Lees (1948) for robins, blackbirds, and blue tits; Cullen (1954) for many arctic bird species; Gibb (1956) for rock pipits (Anthus spinoetta); Schmidt (1965) for mourning doves (Zenaidur macroura marginella); Verner (1965) for male long-billed marsh wren (Telmatodytes palustris); Aschoff and Wever (1966), and Daan (1976) for finches; Morton (1967) for white-crowned sparrows; West (1968) for willow ptarmigan; Hintz and Dyer (1970) for red-winged blackbirds (Agelaius phoeniceus); Siegfried (1972) for cattle egrets; Utter (1973) for purple martins (Progne subis); McConkey (1973) for pied stilts; Ballard and Biellier (1975) for both pinealectomised and control domestic hens; Maxson (1977) for female ruffled grouse; Gibson (1978) for American avocets; Gass (1978) for rufous hummingbirds (Selasphorus rufins); and Collins and Clow (1978) for Western spinebills. But some birds,

e.g. rough-legged hawks (Schnell, 1967), may be equally active all day. Shimek and Monk (1977) noted bimodal peaks of activity in sea otters.

However seasonal differences in diurnal activity patterns occur and may resemble that pattern described by Campbell (1976) for Kea (Nestor notabilis) and Thompson (1977) for grey squirrel (Sciurus carolinensis) in winter, or that described by Schartz and Zimmerman (1971) for male dickcissels (Spiza americana), and Yeates (1971) and Spurr (1978) for Adelie penguins (Pygoscelis adeliae).

Seasonal differences in the overall time (composite day) spent foraging are also noted, with generally more time being spent eating in winter and spring, than in summer and autumn (e.g. Great, blue, coal and long-tailed tits - Gibb, 1954; rock pipits - Gibb, 1956; female ruffed grouse - Maxon, 1977), while the reverse was recorded for rooks (Feare et al, 1974) and Maccoa duck (Oxyura maccoa) (Siegfried, et al, 1976).

As with pukeko, the proportion of time South Island robins (Petroica a. australis) males, females immatures, but not bachelors, spent feeding in winter was greater than in autumn and summer (R. Powlesland, pers. comm.). Consequently in winter less time<sup>was</sup> devoted to bodily maintenance for both species, and resting and singing for the latter. Like pukeko, robins fed least when environmental factors were most unfavourable and food availability was lowest, but unlike pukeko they spent proportionally more time in the early morning in territorial defence and singing. For both species, most time was spent feeding at dusk, perhaps "stocking-up" for the coming night and morning - a similar pattern to that noted by Verner (1965) and Schartz and Zimmerman (1971) with male long-billed marsh wrens and male dickcissels. When time budgets of robin populations inhabiting different areas were compared, differences in time allocated to feeding and non-feeding activities were found. Birds inhabiting areas in which food was less readily available, spent more time feeding, (especially in the early morning), and defending feeding sites and food caches, and less time in activities not associated with individual maintenance.

In conclusion, field evidence suggests pukeko at Hamilton's Lagoon were able to gauge seasonally and diurnally, the availability of food present in each habitat, feeding most in rush margins, mud, swamp and water, and at the highest rate and intensity when the availability (and/or quality) of food was either maximal or optimal for the energy expended in its collection. Conversely, however, pasture was used extensively and consistently as a foraging habitat all year, although availability and presumably quality of food varied considerably. Hence it is thought pasture formed the flock's "feeding backbone" and when food became available on other areas they switched to those habitats that showed an appropriate reward for the energetic cost of feeding there. Pukeko appear able to differentially allocate their feeding effort between various habitats, in relation to food availability and quality, prevailing meteorological conditions and the biological demands on the birds at that time.

SUMMARY

1. The year-round time budget, habitat utilisation, and feeding ecology of pukeko (Porphyrio porphyrio melanotus), for both a composite day and diurnally, were investigated from March, 1977, to March, 1978 at Hamilton's Lagoon, Tiakitahuna, Palmerston North. Shot samples from an adjacent population provided direct information on diurnal foraging patterns in autumn and spring.

Composite day

2. In all seasons, and in all habitats (except water) most time by far was spent feeding (c. 75%), followed in turn by attentive/alarm, comfort movement, and agonistic/appeasement activities, with other activities (i.e. courtship, drinking, calling, swimming and flying) comprising remaining time. In water pukeko mainly swam, with little time spent feeding.
3. In all seasons and for all activities except comfort movements, drinking, and swimming, dryland was by far the most frequently used habitat, followed in turn by rush margins, mud, swamp, and water, although between seasons extent of utilisation of habitats varied considerably. For remaining activities large seasonal differences in habitat use occurred, but for bodily maintenance and drinking rush margins were used far more frequently than any other habitat.
4. By classifying all activities according to appetitive, and consumatory feeding, and "other" categories, time spent locating and eating food, and in "other" activities allowed insight into forage availability and pukeko selectivity in each habitat over the year. Generally pukeko fed most selectively in winter when time for food consumption and forage availability was least and the necessity for highest quality forage was greatest. They fed least selectively in summer, when food availability was low, but time available for collection was greatest.

5. Pecking rates and feeding intensities were scored for birds feeding exclusively within each habitat. Pukeko pecked faster and most intensely in rush margins and mud areas, and least in swamp and water, with dryland intermediate. Birds in dryland fed fastest in spring and slowest in winter, whereas in rush margin, mud, and swamp they fed fastest in winter and slowest in summer. Conversely in water, they fed fastest in summer and slowest (unrecorded) in winter.
6. As feeding pukeko wandered from foraging habitat to foraging habitat over an hour, a rank of importance of each habitat to the overall feeding strategy of an "average" bird was derived. Dryland was by far the most importantly fed upon area, followed in turn by rush margins, mud, swamp and water. Seasonal changes in extent of use of each habitat were compared with broad vegetational and social-organisational events.

#### Diurnal

7. Analysis was also performed for each hourly period of the day during all seasons. Throughout the day and for all seasons and habitats (except water) feeding activities accounted for the bulk of observations followed by attentive/alarm, comfort movement and agonistic/appeasement activities. In all seasons pukeko exhibited a bimodal activity pattern with periods of greatest activity occurring at dawn and dusk, and they were least active around midday and in the early afternoon. Birds in water spent most time swimming, but fed more at midday than at other times.
8. In all seasons and for most activities, dryland was the most frequently used habitat all day, particularly at dawn and dusk. Around midday fewer birds were seen here, and correspondingly more were seen in mud, but particularly in rush margin and swamp areas. Generally water was used most around midday. Over the day birds engaged in bodily maintenance were seen mainly in rush margins and swamp, and less often in pasture and mud. Drinking birds were usually seen in marginal and

- swamp habitats, but in winter they were also seen drinking from grass tips in pasture.
9. Over the day in all seasons and in all habitats unequal time was spent in appetitive and consumatory feeding, and "other" activities. Pukeko searched for food mostly at dawn and dusk in winter, spring, and summer, but more at dawn than later in autumn. Time spent eating peaked around midday in winter, was greater in the morning than in the afternoon in spring, was essentially constant all day in summer, but increased gradually over the day in autumn. From all this, pukeko selectivity over the day was inferred, with birds feeding most selectively at dawn and dusk in winter and summer, and eating gradually less selectively towards dusk in autumn and spring.
  10. Pukeko in all seasons exhibited unimodal pecking rate and feeding intensity patterns, increasing gradually over the day to peak at dusk in spring, summer, and autumn, but peaking at midday to early afternoon in winter. As with composite day analysis, over the day pukeko fed most intensely in rush margin and mud areas, least intensely in swamp and water, with dryland intermediate, although the pattern altered diurnally.
  11. In all seasons and over each day, an "average" pukeko spent most time by far feeding in pasture than elsewhere, particularly at dawn and dusk. Approaching mid morning and midday less effort was devoted to feeding here, the bird switching to feed mainly in rush margin and swamp habitats. However towards dusk the birds fed infrequently in swamp, foraging more in rush margin and mud areas, but especially more frequently in pasture. The main difference between the seasons in use of habitats for foraging was tentatively related to the availability of preferred plant items within each habitat.

Gut Analysis

12. In mid-autumn and spring, standard observations were performed at Fell's Lagoon, Tiakitahuna, so that behavioural comparisons between this and the Hamilton's Lagoon population could be made prior to direct sampling of the former population.
13. In both seasons diurnal activity and foraging patterns were similar in both populations, however due to restricted vision into marginal habitats no indication of differential use of foraging habitats was possible.
14. Shot samples in mid-autumn indicated pukeko took essentially the same length of tiller over the day, whereas in spring the length of tiller taken increased gradually toward dusk. The digestive tract contained more food at dusk (dry weight of ingesta per gram body weight) than at dawn, particularly in the gizzard. At dawn the intestine contained proportionally less food than at dusk indicating the birds did not feed extensively at night in either season. Gut analysis data support the use of "time spent feeding" and "pecking rate" as indices of pukeko foraging effort.
15. Assuming plant availability was essentially constant over the day it is unclear why pukeko in one season foraged more extensively at one time of the day than at another, and moreover, why at a certain time they switched from feeding in one habitat to feed more extensively in another. Perhaps pukeko were able to gauge the seasonal availability (and/or quality) of food present in each habitat, thereby feeding most in rush margins, mud, swamp, and water and at the highest rate and intensity, when the availability (and/or quality) of food was either maximal or optimal for the effort involved in its collection. However, as a foraging habitat pasture was used consistently and the most extensively of all habitats throughout the year, although seasonal availability, and presumably quality, of food varied considerably. Hence it is thought pasture formed the flock's "feeding backbone" and when food became avail-

able on other areas, they switched to feed there. That is, pukeko are able to differentially allocate their feeding effort between various habitats, in relation to food availability and quality, meteorological events, and the biological demands on the birds at that time.

Appendix IMETEOROLOGICAL DATASeasonally

Meteorological data collected at Hamilton's Lagoon and Grassland's Division, D.S.I.R., Palmerston North, are generally comparable but differences in the rainfall in winter, spring, and summer at Hamilton's Lagoon were noted (Tab. 1). These may have been due to wind-accelerated evaporation of rain-gauge water at the lagoon, as the gauge was checked only four days a week. Often greater extremes in air temperature (maximum and minimum) were recorded at Hamilton's Lagoon compared to D.S.I.R. records. Presence/absence of dew varied between sites. It was frequently less humid at Hamilton's Lagoon, than at D.S.I.R., and windier in winter and summer, but calmer in spring and autumn, at Hamilton's Lagoon. Prevailing wind direction was different, being predominantly 250-290° at Hamilton's Lagoon, but varying between 210-360° at D.S.I.R.

Diurnally

Meteorological results were also collected diurnally (Tab. 2). Temperatures were noted at both the onset and end of the observation periods. Differences between these two temperatures were greatest at dawn and dusk watches, and least at noon. Humidity in summer and autumn showed a midday low, while in winter and spring it was higher in the early morning than later. Cloud cover in autumn and winter was maximal in the early morning and early afternoon, while in spring and summer it was maximal in the mid morning and early afternoon. Wind volume for all seasons gradually increased from dawn until the early afternoon, decreasing thereafter.

TABLE 1

## METEOROLOGICAL OBSERVATIONS - SEASONAL

Season	Station	Cloud Cover @ 09.00 (%)	Rain-fall (mm)	Air Max/Min (°C)	Frost (% days present)	Grass Min (°C)	Dew (% days present)	Rel. Hum. @ 09.00	SS (hrs)	Wind Vol. (M/sec)	WIND DIRECTION								
											Calm	34/02	03/06	07/11	12/15	16/20	21/24	25/29	30/33
AUTUMN	DSIR	65	104.8	20.8 11.5	1	9.2	22.3	75	6.1	3.06	8	15	4	18	14	11	13	18	19
	HAM. LAG.	61	111.7	21.9 8.8	2	n/a	42.0	67	n/a	3.00	3	3	4	15	3	2	4	16	7
WINTER	DSIR	67	301.4	12.5 5.1	24	2.8	43.0	87	3.1	2.63	16	14	5	10	7	11	14	8	7
	HAM. LAG.	72	196.5	13.7 2.9	25	n/a	23.0	73	n/a	3.30	0	1	3	15	1	5	6	14	4
SPRING	DSIR	72	207.4	13.8 6.4	13	4.3	23.9	78	4.1	3.41	4	14	3	10	6	13	12	18	12
	HAM. LAG.	68	128.9	15.4 4.5	8	n/a	54.0	73	n/a	3.30	2	2	3	10	0	1	6	31	2
SUMMER	DSIR	63	178.6	20.1 11.1	1	9.4	18.5	74	7.0	3.67	5	12	5	5	3	12	12	24	14
	HAM. LAG.	63	113.8	22.3 9.3	2	n/a	48.0	62	n/a	3.90	5	1	2	6	0	1	6	20	6

TABLE 2

## DIURNAL METEOROLOGICAL OBSERVATIONS

Season	AUTUMN				WINTER				SPRING				SUMMER			
Time	EM	LM	EA	LA	EM	LM	EA	LA	EM	LM	EA	LA	EM	LM	EA	LA
Start	n 7	10	11	10	12	5	5	7	10	10	11	8	14	15	12	14
Temperature °C	t 14.36	17.25	19.55	18.40	5.29	8.70	12.00	11.32	6.35	11.90	13.27	13.94	11.75	17.73	19.25	18.54
End	n 13	12	14	11	13	12	12	9	11	11	10	12	17	15	13	14
	t 16.35	19.58	18.86	14.09	9.31	11.04	11.33	8.83	10.86	12.82	13.35	10.08	16.17	18.67	18.58	15.07
Humidity	n 9	12	14	5	12	13	11	3	9	10	9	6	12	15	13	12
(%)	% 67.11	47.00	52.71	67.40	73.00	70.46	60.73	63.33	73.22	67.00	55.56	58.67	61.67	48.27	49.85	67.67
Cloud	n 14	14	15	14	10	12	12	10	11	12	11	12	14	15	13	14
Cover	% 61.43	51.07	57.67	40.21	71.50	51.50	75.42	66.00	68.18	88.75	62.27	69.58	62.50	69.47	71.08	63.57
Wind	n 26	28	30	24	26	28	22	20	18	22	20	24	24	30	26	28
Volume (m/secs)	v 180.0	207.4	176.8	145.6	180.9	167.9	193.7	139.3	198.6	219.6	181.7	189.5	231.5	233.1	265.9	123.3

EM = Early Morning; LM = Late Morning; EA = Early Afternoon; LA = Late Afternoon

APPENDIX 2 PUKEKO BODY MEASUREMENTS

Body Measurements	IMMATURES				ADULT MALE				ADULT FEMALE			
	$\bar{X}$	R	SD	n	$\bar{X}$	R	SD	n	$\bar{X}$	R	SD	n
C + S (mm)	60.41	64.45 57.00	2.81	6	73.59	78.70 64.65	4.26	14	67.54	78.15 55.50	5.32	20
W (mm)	19.24	22.54 16.45	2.46	6	25.66	29.15 24.15	2.19	14	23.84	28.00 17.61	2.74	21
D (mm)	20.06	22.96 18.10	1.78	6	22.47	30.21 19.35	2.90	14	20.40	28.00 18.55	2.10	18
N-T (mm)	28.97	38.70 26.00	4.95	6	32.17	37.75 28.35	2.32	14	29.39	38.90 20.56	3.37	18
Wgt (gm)	756.0	954.0 660.0	106.0	6	1047.0	1268.0 915.0	104.5	14	909.7	1133.0 749.0	92.1	21

Appendix 3PUKEKO MOULT CYCLEIntroduction

Thirty-three pukeko skins held at the National Museum, Wellington, were examined to establish the moult season. Following Tunncliffe (1965) the skins were classified, according to the condition of the primary feathers, into five categories:

- (i) Black primaries, partly enclosed in sheaths;
  - (ii) Black primaries, with relic sheaths;
  - (iii) New black primaries, with no sheaths and no signs of wear;
  - (iv) Black primaries, with brown tips and signs of wear;
  - (v) Old brown primaries, with notched vanes and tips;
- Tunncliffe noted that "birds with primaries in this condition often had peeling frontal shields and leg scutes."

Results and Discussion

Data from moulting classes i and ii, and iv and v, were combined (i.e. i+ii; iv+v) in the percentage frequency of occurrence of the classes during each season (Tab. 1).

Both the National Museum's skins and Tunncliffe's (1965) observations indicated that in the bulk of birds, moulting occurred in autumn, i.e. classes i and ii were most frequent then. In winter, the primaries of most birds showed little fading and no signs of wear, whereas in spring most showed signs of wear and were discoloured. In summer, the primaries were worn, old and discoloured.

The major difference between Tunncliffe's data and mine was that classes iv and v were prominent in Tunncliffe's summer sample, but absent in the Museum's summer skins.

TABLE 1

PUKEKO MOULT CYCLE

SEASON	MOULT CYCLE	NATIONAL MUSEUM		TUNNI-CLIFFE'S (1965)		COMBINED DATA	
		n	%	n	%	n	%
SPRING	I						
	II						
	III	2	100.0	16	40.0	18	42.9
	IV			20	60.0	20	57.1
	V			4		4	
	TOTAL	2	100.0	40	100.0	42	100.0
SUMMER	I		28.6				6.5
	II	2				2	
	III	5	71.4			5	16.1
	IV			4		4	
	V			20	100.0	20	77.4
	TOTAL	7	100.0	24	100.0	31	100.0
AUTUMN	I		40.0	6	63.6	6	56.5
	II	6		15		21	
	III	8	53.3	6	18.2	14	29.2
	IV		6.7	5	18.2	5	14.6
	V	1		1		2	
	TOTAL	15	100.0	33	100.0	48	100.0
WINTER	I						
	II						
	III	8	88.9	11	61.1	19	70.4
	IV	1	11.1	7	38.9	8	29.6
	V						
	TOTAL	9	100.0	18	100.0	27	100.0



APP. 4 cont.

-3 - -2							-2 - -1					-1 - SS					SS - +1								
Hab. Act.	DL	RM	KR	SW	W/-	TOT.	DL	RM	KR	SW	W/-	TOT.	DL	RM	KR	SW	W/-	TOT.	DL	RM	KR	SW	W/-	TOT.	
n	5373	1007	560	197	10	7967	6291	1690	725	116	1	8823	7564	1331	662	83	1	9661	2248	296	170	16		2730	
%	86.72	69.42	82.15	71.12	10.42	80.19	88.00	74.65	34.21	65.54	2.38	83.81	89.46	75.50	81.23	53.89	3.03	85.62	91.16	74.94	86.74	66.67		87.89	
n	540	295	46	28		909	584	276	72	16		948	655	205	69	19		948	151	53	16	2		222	
%	8.72	11.33	6.52	10.11		9.15	8.17	12.19	8.36	9.04		9.00	7.72	11.63	8.46	12.34		8.40	6.12	13.42	8.16	8.33		7.15	
n	164	414	58	42		678	135	235	59	42		471	101	159	62	46		368	12	30	9	6		57	
%	2.65	15.90	8.22	15.16		6.83	1.89	10.38	6.85	23.73		4.47	1.19	9.02	7.61	29.87		3.28	0.49	7.59	4.59	25.00		1.84	
n	108	29	11	7		155	103	30		2		135	106	25	8	4		143	31	5				36	
%	1.74	1.11	1.56	2.53		1.56	1.44	1.32		1.13		1.28	1.25	1.42	0.98	2.60		1.27	1.26	1.27				1.16	
n	7	15	8			30	28	13	2			43	28	6	14	1		49	23	7				30	
%	0.11	0.56	1.13			0.30	0.39	0.57	0.23			0.41	0.33	0.34	1.72	0.65		0.43	0.93	1.77				0.96	
n		39	2	1		42	1	18	3			22		36				36		4				4	
%		1.50	0.28	0.36		0.42	0.01	0.60	0.35			0.21		2.04				0.32		1.01				0.13	
n	4	4	1	2		11	7	2		1		10	4	1		1		6	1		1			2	
%	0.66	0.16	0.14	0.72		0.11	0.10	0.09		0.56		0.09	0.05	0.05		0.65		0.05	0.04		0.51			0.06	
n					86	86					41	41					32	32						7	7
%					87.58	0.87					97.67	0.39					96.97	0.28						100.00	0.23
n					57	57					36	36					40	40						18	18
%					100.00	0.57					100.00	0.34					100.00	0.35						100.00	0.56
n	6196	2603	706	277	96/57	9935	7149	2264	861	177	42/36	10529	8478	1763	815	154	33/40	11283	2466	395	196	24	7/18	3106	
%	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	

APPENDIX 5 ANNUAL DIURNAL HABITAT UTILISATION BY PUKEKO

-1 - SR							SR - +1					+1 - +2					+2 - +3								
Hab. Act.	DL	RM	KR	SW	W/-	TOT.	DL	RM	KR	SW	W/-	TOT.	DL	RM	KR	SW	W/-	TOT.	DL	RM	KR	SW	W/-	TOT.	
n	2505	246	27	55		2833	6255	752	00	168	1	7256	6159	664	81	287	1	7192	5750	887	192	346	5	7100	
%	85.42	8.68	0.96	1.94		100.00	86.20	10.36	1.10	2.33	0.01	100.00	85.64	9.23	1.13	3.99	0.01	100.00	80.08	12.36	2.67	4.82	0.07	100.00	
n	201	38	1	16		256	619	109	20	21		769	665	118	12	34		829	650	147	10	42		849	
%	78.52	14.04	0.39	6.25		100.00	80.49	14.10	2.60	2.73		100.00	80.22	14.23	1.45	4.10		100.00	76.56	17.31	1.18	4.95		100.00	
n	47	52	2	20		121	202	165	5	55		427	256	245	9	110		620	223	312	13	114		662	
%	38.84	42.98	1.65	16.53		100.00	47.31	38.64	1.17	12.88		100.00	41.29	39.52	1.45	17.74		100.00	33.69	47.13	1.96	17.22		100.00	
n	73	6		2		81	168	12		3		183	159	13		5		177	125	19		9		153	
%	90.12	7.41		2.47		100.00	91.60	6.56		1.64		100.00	89.83	7.34		2.83		100.00	81.70	12.42		5.88		100.00	
n	3		2			5	18	6				24	19	2	2			23	10	6	5	4		25	
%	60.00		40.00			100.00	75.00	25.00				100.00	82.61	8.70	8.69			100.00	40.00	24.00	20.00	16.00		100.00	
n		3				3	3	4				7	3					3	4	11				15	
%		100.00				100.00	42.86	57.14				100.00		100.00				100.00	26.67	73.33				100.00	
n	4	2	4			10	9	2		3		14	4	7		2		13	10	2				13	
%	40.00	20.00	40.00			100.00	64.29	14.28		21.43		100.00	30.77	53.85		15.38		100.00	76.92	15.39		7.69		100.00	
n					16	16					33	33					59	59						63	63
%					100.00	100.00					100.00	100.00					100.00	100.00						100.00	100.00
n					59	59					64	64					40	40						38	38
%					100.00	100.00					100.00	100.00					100.00	100.00						100.00	100.00
n	2833	347	32	97	16/59	3384	7274	1050	105	250	34/64	8777	7262	1052	104	438	60/40	8956	6772	1384	220	516	68/38	8998	
%	83.72	10.25	0.95	2.87	0.40/1.74	100.00	82.88	11.96	1.20	2.85	0.39/0.73	100.00	81.09	11.75	1.16	4.88	0.67/0.45	100.00	75.26	15.38	2.44	5.73	0.76/0.43	100.00	

APP. 5 cont.

		+3 - +4						+4 - +5						-5 - -4						-4 - -3					
Hab.	Act.	DL	RM	MR	SW	W/-	TOT.	DL	RM	MR	SW	W/-	TOT.	DL	RM	MR	SW	W/-	TOT.	DL	RM	MR	SW	W/-	TOT.
F	n	5334	1150	195	321	15	7015	4107	1124	379	354	29	5993	4349	1502	430	216	16	6513	4651	1902	623	227	21	7424
	%	76.04	16.39	2.78	4.58	0.21	100.00	68.53	18.76	6.32	5.91	0.48	100.00	66.77	23.06	6.60	3.32	0.25	100.00	62.65	25.62	8.39	3.06	0.28	100.00
AT/AL	n	540	170	23	39		772	462	186	51	54		753	415	107	39	50		691	694	347	57	49		1047
	%	99.95	22.02	2.90	5.05		100.00	61.36	24.70	6.77	7.17		100.00	60.06	27.06	5.64	7.24		100.00	56.73	33.15	5.44	4.68		100.00
CR	n	256	392	22	126		796	173	282	29	125		609	199	359	50	119		727	241	421	66	91		819
	%	32.16	49.85	2.76	15.03		100.00	21.41	46.31	4.76	20.52		100.00	27.37	49.30	6.88	16.37		100.00	29.43	51.50	8.06	11.11		100.00
AC/AP	n	117	10		33		160	89	13	3	11		116	91	20	1	4		116	112	40	1	5		158
	%	73.13	6.25		20.62		100.00	76.72	11.21	2.59	9.48		100.00	78.45	17.24	0.86	3.45		100.00	70.89	25.32	0.63	3.16		100.00
CO	n	5					5	12	5				17	20	2		2		24	15	11				26
	%	100.00					100.00	70.59	29.41				100.00	83.34	8.33		8.33		100.00	57.69	42.31				100.00
D	n		14				14		15	1	1		17		12		1		13		28	1			29
	%		100.00				100.00		88.24	5.88	5.88		100.00		92.31		7.69		100.00		96.55	3.45			100.00
CA	n	2	2				4	5	2		2		9	4	4				8	5	3				8
	%	80.00	50.00				100.00	55.56	22.72		22.22		100.00	50.00	50.00				100.00	62.50	37.50				100.00
S	n					72	72					92	92					70	70					73	73
	%					100.00	100.00					100.00	100.00					100.00	100.00					100.00	100.00
FLY	n				43	43						41	41					30	38					38	38
	%				100.00	100.00						100.00	100.00					100.00	100.00					100.00	100.00
TOT.	n	6254	1736	240	519	87/43	8881	4848	1627	463	547	121/41	7647	5078	2086	520	392	94/38	8208	5618	2752	748	372	94/44	9628
	%	70.42	19.57	2.70	5.84	0.99/0.48	100.00	63.41	21.27	6.05	7.15	1.56/0.54	100.00	61.87	25.40	6.34	4.78	1.15/0.46	100.00	58.35	28.58	7.77	3.86	0.98/0.46	100.00

APP. 5 cont.

		-3 - -2						-2 - -1						-1 - SS						SS - +1					
Hab.	Act.	DL	RM	MR	SW	W/-	TOT.	DL	RM	MR	SW	W/-	TOT.	DL	RM	MR	SW	W/-	TOT.	DL	RM	MR	SW	W/-	TOT.
F	n	5373	1807	580	197	10	7967	6291	1690	725	116	1	8823	7584	1331	662	83	1	9661	2248	296	170	16		2730
	%	67.44	22.68	7.28	2.47	0.13	100.00	71.30	19.16	8.22	1.31	0.01	100.00	78.50	13.78	6.85	0.86	0.01	100.00	82.34	10.84	6.23	0.59		100.00
AT/AL	n	540	295	46	28		909	584	276	72	16		948	655	205	69	19		948	151	53	16	2		222
	%	59.41	32.45	5.06	3.08		100.00	61.64	29.10	7.58	1.68		100.00	69.09	21.62	7.28	2.01		100.00	68.02	23.87	7.21	0.90		100.00
CR	n	164	414	58	42		678	135	235	59	42		471	101	159	62	46		368	12	30	9	6		57
	%	24.19	61.06	8.56	6.19		100.00	28.66	49.89	12.53	8.92		100.00	27.45	43.20	16.85	12.50		100.00	21.05	52.63	15.79	10.53		100.00
AC/AP	n	108	29	11	7		155	103	30		2		135	106	25	8	4		143	31	5				36
	%	69.68	18.71	7.10	4.51		100.00	76.30	22.22		1.48		100.00	74.13	17.48	5.59	2.80		100.00	56.11	13.89				100.00
CO	n	7	15	8			30	28	13	2			43	28	6	14	1		49	23	7				30
	%	23.33	50.00	26.67			100.00	65.12	30.23	4.65			100.00	57.14	12.25	28.57	2.04		100.00	76.67	23.33				100.00
D	n		39	2	1		42	1	18	3			22		36				36		4				4
	%		92.86	4.76	2.38		100.00	4.54	81.82	13.64			100.00		100.00				100.00		100.00				100.00
CA	n	4	4	1	2		11	7	2		1		10	4	1		1		6	1		1			2
	%	36.37	36.36	9.09	18.18		100.00	70.00	20.00		10.00		100.00	66.67	16.67		16.66		100.00	50.00		50.00			100.00
S	n					86	86					41	41					32	32					7	7
	%					100.00	100.00					100.00	100.00					100.00	100.00					100.00	100.00
FLY	n					57	57					36	36					40	40					18	18
	%					100.00	100.00					100.00	100.00					100.00	100.00					100.00	100.00
TOT.	n	6196	2603	706	277	96/57	9935	7149	2264	861	177	42/36	10529	8478	1763	815	154	33/40	11283	2466	395	196	24	7/18	3106
	%	62.37	26.20	7.10	2.79	0.97/0.57	100.00	67.90	21.50	8.18	1.68	0.40/0.34	100.00	75.14	15.63	7.22	1.36	0.29/0.36	100.00	79.39	12.72	6.31	0.77	0.23/0.58	100.00

APPENDIX 6 ANNUAL DIURNAL TIME ALLOCATION TO APPETITIVE AND CONSUMATORY FEEDING AND "OTHER" ACTIVITIES, PECKING RATE, FEEDING INTENSITY, AND HABITAT FORAGING RANK

-1 - SR							SR - +1					+1 - +2					+2 - +3							
Hab. act.	DL	RM	MR	SW	W	TOT.	DL	RM	MR	SW	W	TOT.	DL	RM	MR	SW	W	TOT.	DL	RM	MR	SW	W	TOT.
n	1357	82	15	30		1484	2931	285	39	63		3318	3007	215	28	98		3348	2760	244	54	129		3167
Ap.	47.90	23.96	46.88	30.92		44.63	40.30	27.14	37.14	25.19		38.08	41.39	20.44	26.93	22.33		37.55	40.75	17.63	24.55	25.00		35.57
n	1148	163	12	25		1346	3305	458	40	102	1	3906	3129	435	57	183	1	3799	2981	632	135	214	5	3967
Con.	40.52	47.01	57.50	55.76		40.54	45.45	45.63	53.10	40.80	2.91	44.83	43.09	41.26	49.04	41.78	1.07	42.61	44.00	46.06	61.26	41.40	7.25	44.27
n	325	102	5	42	16	493	1038	307	26	85	33	1489	1127	401	25	157	59	1769	1031	506	31	173	63	1366
Oth.	11.55	29.43	15.62	43.30	100.00	14.03	14.27	29.23	34.76	34.01	97.05	17.09	15.52	38.20	24.03	35.84	93.33	19.24	15.23	36.71	14.09	32.53	32.65	20.16
n	2833	347	32	57	16	3325	7274	1050	105	250	34	8713	7262	1052	104	438	60	8916	6772	1334	220	516	68	8960
Tot.	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00
FR i/30 secs.	10.83	16.41	19.00	12.23		13.02	13.61	19.27	19.75	12.41	12.00	14.77	14.67	21.80	22.35	14.19	12.00	16.26	15.72	23.39	24.76	14.06	12.60	17.67
FI i/hr	526	926	855	378		633	742	1009	903	608	42	795	759	1082	1316	711	24	831	830	1282	1823	700	111	939
HFR Rel. i/hr	463.7	80.0	8.1	7.3		559.1	636.6	104.0	9.9	14.0	0.4	764.9	647.1	99.4	14.7	28.3	0.0	789.5	661.4	157.5	48.5	33.5	0.1	901.0
HFR	82.93	14.31	1.45	1.31		100.00	83.23	13.59	1.30	1.83	0.05	100.00	81.96	12.59	1.87	3.58	0.00	100.00	73.41	17.48	5.38	3.72	0.01	100.00

APP. 6 cont.

+3 - +4							+4 - +5					-5 - -4					-4 - -3							
Hab. act.	DL	RM	MR	SW	W	TOT.	DL	RM	MR	SW	W	TOT.	DL	RM	MR	SW	W	TOT.	DL	RM	MR	SW	W	TOT.
n	2371	325	53	125		2874	1663	286	87	127		2163	1787	399	112	97		2395	1871	474	134	76		2555
Ap.	37.91	18.70	22.03	24.08		32.52	34.29	17.59	18.79	33.22		28.44	35.19	19.13	21.53	24.75		29.31	33.31	17.22	17.92	20.39		26.65
n	2950	797	142	190	15	4094	2431	828	290	223	29	3801	2554	1091	315	118	16	4094	2769	1420	479	139	21	4328
Con.	47.17	45.86	57.17	26.61	17.24	46.32	50.15	50.91	62.64	40.77	22.32	49.97	50.29	52.29	60.58	30.10	17.02	50.11	49.20	51.60	64.03	37.33	22.34	40.38
n	933	616	45	204	72	1870	754	513	86	197	92	1642	737	596	93	177	78	1681	978	855	135	157	73	2201
Oth.	14.92	35.44	18.75	9.31	82.76	21.16	15.56	31.50	18.57	36.01	77.63	21.59	14.52	23.58	17.89	45.15	32.98	20.58	17.40	31.18	18.05	42.23	77.66	22.97
n	6254	1738	240	519	87	8838	4848	1627	463	547	121	7606	5078	2086	520	392	94	8170	5618	2752	746	372	94	9564
Tot.	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00
FR i/30 secs.	15.50	25.92	33.89	15.04	16.14	18.40	16.60	23.91	25.33	15.45	17.00	18.80	20.05	24.40	27.10	14.66	19.40	21.55	19.76	23.70	25.37	16.85	13.86	21.25
FI i/hr	877	1426	1696	661	334	1023	999	1461	1904	756	455	1082	1210	1531	1970	547	396	1296	1169	1468	1949	755	372	1285
HFR Rel. i/hr	663.6	232.8	47.0	30.1	0.7	974.4	681.7	272.7	120.0	44.5	2.2	1121.1	807.0	352.6	130.0	18.1	1.0	1308.7	730.3	375.0	163.1	23.0	1.0	1292.4
HFR	68.12	23.89	4.82	3.09	0.08	100.00	60.81	24.32	10.70	3.97	0.20	100.00	61.66	26.95	9.93	1.38	0.08	100.00	56.51	29.01	12.62	1.78	0.08	100.00

APP. 6 cont.

-3 - -2							-2 - -1						-1 - SS						SS - +1					
lab. act.	DL	RH	HR	SW	W	TOT.	DL	RH	HR	SW	W	TOT.	DL	RH	HR	SW	W	TOT.	DL	RH	HR	SW	W	TOT.
n	2073	503	132	70		2778	2783	479	204	47		3513	3519	364	166	30		4079	1216	69	45	10		1340
Ap. %	33.46	19.33	16.70	25.27		28.12	38.93	21.16	23.69	26.56		33.48	41.51	20.64	20.38	19.48		36.26	49.22	17.47	22.96	41.67		43.40
n	3285	1295	448	119	10	5157	3494	1194	516	65	1	5270	4042	959	488	53	1	5543	1030	226	124	6		1386
Con. %	53.02	49.75	63.45	42.96	10.42	52.21	48.88	52.73	59.93	26.72	2.30	50.22	47.65	54.41	59.87	34.41	3.03	49.30	41.76	57.22	63.27	35.00		44.38
n	838	805	126	88	86	1943	872	591	141	65	41	1710	917	440	161	71	32	1621	220	100	27	8	7	362
Uth. %	13.52	30.92	17.85	31.77	89.58	19.67	12.19	26.11	16.38	26.72	97.62	16.30	10.82	24.95	19.75	46.11	96.97	14.42	8.92	25.31	13.77	33.33	100.00	11.72
n	6196	2603	706	277	96	9878	7149	2264	861	177	42	10493	8478	1763	815	154	33	11243	2466	395	196	24	7	3038
Tot. %	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00
FR P/30 secs.	19.41	23.28	25.49	15.00	12.00	21.03	18.96	23.42	28.68	17.13	12.00	21.51	18.46	24.88	31.70	12.77	10.00	21.22	16.89	24.07	27.16	17.25		19.23
FI P/hr	1235	1390	1941	773	150	1318	1112	1482	2062	755	34	1296	1033	1625	2278	527	36	1255	846	1653	2062	518		1036
HFR rel. i/hr	331.5	314.7	141.1	19.1	0.2	1306.6	792.7	283.8	169.5	9.9	0.0	1255.9	810.2	223.5	156.0	4.5	0.00	1194.2	694.4	178.5	128.0	3.0		1003.0
HFR %	63.64	24.05	10.80	1.46	0.01	100.00	63.11	22.60	13.50	0.79	0.00	100.00	67.84	18.72	13.06	0.28	0.00	100.00	69.17	17.78	12.75	0.30		100.00







APP. 8 cont.

		-3 - -2						-2 - -1						-1 - SS						SS - +1																			
Sub-Act.	n	DL	RI	NR	SI	W/-	TOT.	DL	RI	NR	SI	W/-	TOT.	DL	RI	NR	SI	W/-	TOT.	DL	RI	NR	SI	W/-	TOT.														
F	2648	67.16	63.41	67.78	66.67		3617	3276	533	259	14		4062	3614	447	214	26		4301	1351	106	64	2		1523														
%							100.00	89.90	69.50	60.70	60.67		86.16	92.62	76.02	67.34	78.79		89.74	93.49	72.60	95.52	66.67		91.25														
AC/AL	23	7.66	10.23	3.70	15.48		364	235	100	15	5		355	212	50	18	1		289	68	19	2	1		90														
%							8.09	6.45	13.05	5.14	21.71		7.49	5.43	9.87	7.35	3.03		6.03	4.70	13.01	2.99	33.33		5.39														
JK	82	2.70	20.64	7.78	13.09		334	58	96	18	4		176	31	49	11	6		97	5	9	1			15														
%							7.42	1.59	12.53	6.16	17.39		3.71	0.80	8.33	4.49	18.18		2.02	0.35	6.16	1.49			0.40														
AG/AP	71	2.34	1.50		3.57		90	57	19				76	45	8	2			55	16	4				20														
%							2.00	1.57	2.49				1.60	1.19	1.36	0.82			1.15	1.11	2.74				1.20														
CO	4	0.13	0.75				12	10	2				12		1				1	5	7				12														
%							0.27	0.27	0.26				0.25		0.17				0.02	0.35	4.80				0.72														
D			34	2			36	1	14				15		25				25		1				1														
%			3.19	0.74			0.80	0.03	1.83				0.32		4.25				0.52		0.69				0.06														
CA	1	0.03	0.28		0.19		5	4	2				6																										
%							0.11	0.11	0.26				0.13																										
S						21	21					6	6						7	7																			
%						100.00	0.46					100.00	0.13						100.00	0.15																			
FLY						22	22					10	10						18	18				8	8														
%						100.00	0.47					100.00	0.21						100.00	0.37				100.00	0.11														
TOT.	3036	100.00	1066	100.00	270	100.00	84	21/22	4501	100.00	3641	100.00	766	100.00	292	100.00	23	6/10	4738	100.00	3902	100.00	50	100.00	245	33	7/10	4793	100.00	1445	100.00	146	100.00	67	100.00	3	-/8	1669	100.00











APPENDIX 11 SEASONAL DIURNAL HABITAT UTILISATION BY PUKEKO - AUTUMN

		-1 - SR						SR - +1						+1 - +2						+2 - +3					
Hab. Act.	n	DL	RI	NR	SW	W/-	TOT.	DL	RI	NR	SW	W/-	TOT.	DL	RI	NR	SW	W/-	TOT.	DL	RI	NR	SW	W/-	TOT.
F	n	406	25		17		448	1125	107		29		1261	1107	69		58		1234	1041	52		53		1146
%		90.63	5.56		3.79		100.00	89.21	8.49		2.30		100.00	89.71	5.56		4.70		100.00	90.04	4.54		4.62		100.00
AT/AL	n	41	3				44	129	8				137	156	4		2		169	113	12		1		126
%		93.10	6.02				100.00	94.16	5.94				100.00	92.31	6.51		1.16		100.00	89.68	9.57		0.79		100.00
CI	n	1	1				2	18	3		9		30	35	12		27		74	23	26		33		82
%		50.00	50.00				100.00	60.00	10.00		30.00		100.00	47.30	16.21		36.49		100.00	28.05	31.71		40.24		100.00
AS/AP	n	13					13	21	2				23	22	3		1		26	11	4		2		17
%		100.00					100.00	91.30	8.70				100.00	84.61	11.54		3.85		100.00	64.71	23.53		11.76		100.00
CO	n																								
D	n																				1				1
%																					100.00				100.00
CA	n				1		1								1					1					
%					100.00		100.00								100.00					100.00					
S	n				2		2					4	4					6	6					7	7
%					100.00		100.00					100.00	100.00					100.00	100.00					100.00	100.00
FLY	n				13		13					13	13					7	7					6	6
%					100.00		100.00					100.00	100.00					100.00	100.00					100.00	100.00
TOT.	n	461	29		18	2/13	523	1293	120		38	4/13	1468	1320	96		88	6/7	1517	1108	95		89	7/6	1389
%		68.15	5.54		3.44	0.30/ 2.49	100.00	88.08	8.17		2.59	0.22/ 0.89	100.00	87.01	6.33		5.80	0.40/ 0.46	100.00	85.78	6.86		6.43	0.51/ 0.43	100.00

APP. 11 cont.

		+3 - +4						+4 - +5						+5 - +6						-6 - -5					
Hab. Act.	n	DL	RI	NR	SW	W/-	TOT.	DL	RI	NR	SW	W/-	TOT.	DL	RI	NR	SW	W/-	TOT.	DL	RI	NR	SW	W/-	TOT.
F	n	748	113		78		939	849	153	9	77	2	1090	647	79		65		791	617	184	2	47	1	851
%		79.56	12.03		8.31		100.00	77.89	14.04	0.83	7.06	0.18	100.00	80.47	9.98		8.22		100.00	72.50	21.62	0.24	5.52	0.12	100.00
AT/AL	n	81	28		15		124	102	34	4	14		154	100	13		15		128	82	30		11		123
%		65.32	22.58		12.10		100.00	66.23	22.08	2.60	9.09		100.00	78.12	10.16		11.72		100.00	66.67	24.39		8.94		100.00
CI	n	20	21		30		71	20	33	1	28		82	37	13		28		78	15	22		44		81
%		28.17	29.58		42.25		100.00	24.39	40.24	1.22	34.15		100.00	47.43	16.67		35.90		100.00	18.52	27.16		54.32		100.00
AS/AP	n	30	2		20		52	18	2				20	19	3				22	3	3				6
%		57.69	3.85		38.46		100.00	90.00	10.00				100.00	86.36	13.64				100.00	50.00	50.00				100.00
CO	n																								
D	n		1				1		1				1												
%			100.00				100.00		100.00				100.00												
CA	n													1						1					
%														100.00						100.00					
S	n				5		5					12	12					5	5						
%					100.00		100.00					100.00	100.00					100.00	100.00						
FLY	n				4		4					8	8					4	4					5	5
%					100.00		100.00					100.00	100.00					100.00	100.00					100.00	100.00
TOT.	n	879	165		143	5/4	1196	999	223	14	119	14/8	1367	804	108		108	5/4	1029	717	239	2	102	1/5	1066
%		73.49	13.79		11.96	0.42/ 0.33	100.00	72.35	16.31	1.02	8.71	1.02/ 0.59	100.00	78.06	10.40		10.48	0.49/ 0.39	100.00	67.26	22.42	0.19	9.57	0.09/ 0.47	100.00



APPENDIX 12 SEASONAL DIURNAL HABITAT UTILISATION BY PUKEKO - WINTER

		-1 - SR						SR - +1						+1 - +2						+2 - +3					
Hab. Act.	DL	RI	NR	SW	W/-	TOT.	DL	RI	NR	SW	W/-	TOT.	DL	RI	NR	SW	W/-	TOT.	DL	RI	NR	SW	W/-	TOT.	
F	n 1364 94.20	73 5.04		11 0.76		1448 100.00	2958 92.24	193 6.02	10 0.31	46 1.43		3207 100.00	3059 91.64	167 5.00	7 0.21	105 3.15		3338 100.00	2945 84.43	367 11.10	52 1.49	104 2.98		3468 100.00	
AD/AL	n 79 78.22	19 18.81		3 2.97		101 100.00	276 86.79	27 8.49	5 1.57	10 3.15		318 100.00	200 65.11	34 10.33	2 0.61	13 3.95		329 100.00	299 78.27	63 16.49	2 0.53	18 4.71		382 100.00	
CR	n 34 53.12	27 42.19		3 4.69		64 100.00	114 54.03	85 40.28		12 5.69		211 100.00	122 47.29	100 38.76	1 0.39	35 13.56		258 100.00	138 40.83	177 52.37	2 0.59	21 6.21		338 100.00	
AG/AP	n 25 92.59	1 3.70		1 3.71		27 100.00	103 92.79	5 4.51		3 2.70		111 100.00	101 91.82	5 4.54		4 3.64		110 100.00	69 81.18	10 11.76		6 7.06		85 100.00	
CO	n							1 100.00				1 100.00							2 33.33	4 66.67				6 100.00	
D	n	2 100.00				2 100.00	3 60.00	2 40.00				5 100.00		1 100.00					1 100.00	4 30.78	9 69.23				13 100.00
CA	n					5 100.00						5 100.00	2 50.00	1 25.00		1 25.00		4 100.00	5 100.00						5 100.00
S	n				5 100.00	5 100.00					4 100.00	4 100.00					15 100.00	15 100.00						19 100.00	
FLY	n				14 100.00	14 100.00					15 100.00	15 100.00					6 100.00	6 100.00						18 100.00	
TOT.	n 1502 90.43	122 7.35		18 1.08	5/14 0.30/ 0.84	1661 100.00	3459 89.22	313 8.07	15 0.39	71 1.83	4/15 0.10/ 0.39	3877 100.00	3564 87.76	300 7.58	10 0.25	158 3.89	15/6 0.37/ 0.15	4061 100.00	3462 79.51	650 14.93	56 1.29	149 3.42	19/18 0.44/ 0.41	4354 100.00	

APP. 12 cont.

		+3 - +4						+4 - +5						-5 - -4						-4 - -3					
Hab. Act.	DL	RI	NR	SW	W/-	TOT.	DL	RI	NR	SW	W/-	TOT.	DL	RI	NR	SW	W/-	TOT.	DL	RI	NR	SW	W/-	TOT.	
F	n 2920 80.89	522 14.46	56 1.55	112 3.10		3610 100.00	1834 71.31	512 19.91	138 5.36	88 3.42		2572 100.00	1757 70.52	550 21.71	124 4.89	73 2.88		2534 100.00	2265 64.85	895 25.62	262 7.50	71 2.03		3493 100.00	
AD/AL	n 227 76.43	61 20.54	4 1.35	5 1.63		297 100.00	152 61.60	72 28.80	13 5.20	11 4.40		250 100.00	165 62.26	76 28.68	9 3.40	15 5.66		265 100.00	270 57.32	159 33.76	21 4.46	21 4.46		471 100.00	
CR	n 154 36.44	255 56.67	3 0.67	28 6.22		450 100.00	94 34.56	150 55.15	4 1.47	24 8.82		272 100.00	61 22.76	186 69.40	7 2.61	14 5.23		268 100.00	94 28.23	215 64.57	10 3.00	14 4.20		333 100.00	
AG/AP	n 68 86.02	4 5.06		7 8.66		79 100.00	45 76.27	10 16.95		4 6.78		59 100.00	29 67.44	10 23.25	1 2.33	3 6.93		43 100.00	63 67.74	27 29.03		3 3.23		93 100.00	
CO	n 1 100.00					1 100.00							2 100.00						2 75.00	6 25.00				8 100.00	
D	n	11 100.00				11 100.00		10 90.91		1 9.09		11 100.00		7 87.50		1 12.50			8 100.00		22 100.00				22 100.00
CA	n 1 100.00					1 100.00	1 50.00	1 50.00				2 100.00	2 50.00	2 50.00					4 100.00	2 66.67	1 33.33				3 100.00
S	n				28 100.00	28 100.00					31 100.00	31 100.00					7 100.00	7 100.00						22 100.00	
FLY	n				19 100.00	19 100.00					14 100.00	14 100.00					15 100.00	15 100.00						23 100.00	
TOT.	n 3381 75.26	853 18.97	63 1.40	152 3.38	28/19 0.62/ 0.43	4496 100.00	2128 66.27	755 23.51	155 4.93	128 3.99	31/14 0.96/ 0.44	3211 100.00	2046 65.03	831 26.42	141 4.48	106 3.37	7/15 0.22/ 0.48	3146 100.00	2700 60.43	1321 29.57	293 6.56	109 2.44	22/23 0.49/ 0.51	4468 100.00	

APP. 12 cont.

		-3 - -2						-2 - -1						-1 - SS						SS - +1					
Hab.	act.	DL	RM	MR	SW	W/-	TOT.	DL	RM	MR	SW	W/-	TOT.	DL	RM	MR	SW	W/-	TOT.	DL	RM	MR	SW	W/-	TOT.
F	n	2640	676	237	56		3617	3276	533	259	14		4082	3614	447	214	26		4301	1351	106	64	2		1523
	λ	73.21	18.69	6.55	1.55		100.00	80.25	13.06	6.35	0.34		100.00	84.03	10.35	4.98	0.60		100.00	88.71	6.96	4.20	0.13		100.00
RT/AL	n	232	109	10	13		364	235	100	15	5		355	212	58	18	1		289	68	19	2	1		90
	λ	63.71	29.54	2.75	3.57		100.00	66.20	28.17	4.22	1.41		100.00	73.36	20.07	6.23	0.34		100.00	75.56	21.11	2.22	1.11		100.00
UN	n	82	220	21	11		334	58	96	18	4		176	31	49	11	6		97	5	9	1			15
	λ	24.55	65.87	6.29	3.29		100.00	32.95	54.55	10.23	2.27		100.00	31.96	50.51	11.34	6.19		100.00	33.33	60.00	6.67			100.00
3/AF	n	71	16		3		90	57	19				76	45	8	2			55	16	4				20
	λ	78.89	17.78		33.33		100.00	75.00	25.00				100.00	81.82	14.54	3.64			100.00	80.00	20.00				100.00
33	n	4	8				12	10	2				12		1				1	5	7				12
	λ	33.33	68.67				100.00	33.33	16.67				100.00		100.00				100.00	41.67	58.33				100.00
D	n		34	2			36	1	14				15		25				25		1				1
	λ		94.44	5.56			100.00	6.67	93.33				100.00		100.00				100.00		100.00				100.00
CA	n	1	3		1		5	4	2				6												
	λ	20.00	60.00		20.00		100.00	66.67	33.33				100.00												
S	n					21	21					6	6					7	7						
	λ					100.00	100.00					100.00	100.00					100.00	100.00						
FLY	n					22	22					10	10					18	18						8
	λ					100.00	100.00					100.00	100.00					100.00	100.00					100.00	100.00
TOT.	n	3038	1066	270	84	21/22	4501	3641	766	292	23	6 / 10	4738	3902	588	245	33	7 / 18	4793	1445	146	67	3	- / 8	1669
	λ	67.50	23.68	6.00	1.87	0.46/ 0.49	100.00	76.85	16.17	6.16	0.40	0.13/ 0.21	100.00	81.41	12.27	5.11	0.60	0.15/ 0.37	100.00	86.58	8.75	4.01	0.18	- / 0.48	100.00

APPENDIX 13 SEASONAL DIURNAL HABITAT UTILISATION BY PUKEKO - SPRING

-1 - SR							SR - +1							+1 - +2							+2 - +3						
Hab. Act.	DL	RR	NR	SW	W/-	TOT.	DL	RR	NR	SW	W/-	TOT.	DL	RR	NR	SW	W/-	TOT.	DL	RR	NR	SW	W/-	TOT.			
n	416	112	12	14		554	1133	208	52	64		1547	1192	297	60	77		1626	1134	205	139	127	3	1608			
%	75.09	20.22	2.16	2.53		100.00	75.24	19.26	3.36	4.14		100.00	73.31	18.26	3.69	4.74		100.00	67.10	16.88	6.23	7.52	0.19	100.00			
n	44	6		5		55	91	46	6	9		152	102	48	7	14		176	100	46	7	11		164			
%	80.00	10.91		9.09		100.00	59.87	30.27	3.95	5.92		100.00	60.00	27.27	3.98	7.95		100.00	60.97	38.05	4.27	6.71		100.00			
n	10	17		11		38	60	60		26		146	82	100	8	22		212	49	70	11	28		166			
%	26.31	44.74		28.05		100.00	41.10	41.09		17.81		100.00	30.68	47.17	3.77	10.38		100.00	29.52	46.69	6.62	16.87		100.00			
n	26	5		1		32	33	5				38	25	2				27	36	3		1		40			
%	81.25	15.62		3.13		100.00	36.04	13.16				100.00	92.59	7.41				100.00	90.00	7.50		2.50		100.00			
n	3		2			5	13	5				18	15	2	2			19	6	2	5	2		15			
%	60.00		40.00			100.00	72.22	27.78				100.00	78.95	10.53	0.52			100.00	40.00	13.33	33.33	13.34		100.00			
n		1				1								2				2		1				1			
%		100.00				100.00								100.00				100.00		100.00				100.00			
n	3	1		2		6	4	2		3		9	2	3				5	3	2				5			
%	50.00	16.67		33.33		100.00	44.45	22.22		33.33		100.00	40.00	60.00				100.00	60.00	40.00				100.00			
n					7	7					16	16						23	23				24	24			
%					100.00	100.00					100.00	100.00						100.00	100.00				100.00	100.00			
n					12	12					16	16						7	7				5	5			
%					100.00	100.00					100.00	100.00						100.00	100.00				100.00	100.00			
n	502	142	14	33	7/12	710	1334	416	58	102	16/16	1942	1423	454	77	113	23/7	2097	1320	417	162	169	27/5	2108			
%	70.70	20.00	1.97	4.65	0.97/1.69	100.00	68.69	21.42	2.99	5.25	0.92/0.83	100.00	67.06	21.65	3.67	5.39	1.10/0.33	100.00	63.00	19.78	7.69	8.01	1.20/0.24	100.00			

APP. 13 cont.

+3 - +4							+4 - +5							+5 - +6							-6 - -5						
Hab. Act.	DL	RR	NR	SW	W/-	TOT.	DL	RR	NR	SW	W/-	TOT.	DL	RR	NR	SW	W/-	TOT.	DL	RR	NR	SW	W/-	TOT.			
n	1076	312	138	75	4	1605	945	280	225	63	6	1539	696	314	113	37	13	1273	698	307	212	58	9	1204			
%	67.04	19.44	8.60	4.67	0.25	100.00	61.41	18.19	14.62	5.39	0.39	100.00	54.67	27.02	14.38	2.91	1.02	100.00	54.86	23.91	16.51	4.52	0.70	100.00			
n	110	45	15	15		165	103	47	20	19		197	78	66	34	6		184	60	56	32	4		152			
%	59.86	24.32	8.11	8.11		100.00	52.28	23.06	14.22	9.64		100.00	42.39	35.87	18.46	3.26		100.00	39.47	36.04	21.05	2.64		100.00			
n	5	91	19	26		192	52	72	24	23		171	34	64	22	16		136	60	90	29	18		197			
%	29.17	47.40	9.89	13.54		100.00	30.41	42.11	14.03	13.45		100.00	25.00	47.06	16.18	11.76		100.00	39.46	45.60	14.72	9.14		100.00			
n	16			2		18	14	1	2	1		18	16	3	2			22	8	3				21			
%	78.09			11.11		100.00	77.78	5.55	11.11	5.56		100.00	72.73	13.63	13.64			100.00	85.71	14.29				100.00			
n	2					2	8	2	1			11		5	7			12	4	3	2			9			
%	100.00					100.00	72.73	18.18	9.09			100.00		41.67	58.33			100.00	44.45	33.33	22.22			100.00			
n								4	1			5		2				2		2				2			
%								80.00	20.00			100.00		100.00				100.00		100.00				100.00			
n	1	2				3	3					3	3	1				4		3				3			
%	33.33	66.67				100.00	100.00					100.00	75.00	25.00				100.00		100.00				100.00			
n					18	18					26	26						32	32				26	26			
%					100.00	100.00					100.00	100.00						100.00	100.00				100.00	100.00			
n					8	8					6	6						5	5				12	12			
%					100.00	100.00					100.00	100.00						100.00	100.00				100.00	100.00			
n	1261	450	172	118	22/8	2031	1125	406	281	126	32/6	1976	827	485	249	59	45/5	1670	840	464	275	80	35/12	1706			
%	62.09	22.16	8.47	5.81	1.00/0.39	100.00	56.43	20.55	14.22	6.38	1.62/0.30	100.00	49.53	29.04	14.91	3.53	2.69/0.30	100.00	49.24	27.20	16.12	4.69	2.05/0.70	100.00			



APPENDIX 14 SEASONAL DIURNAL HABITAT UTILISATION BY PUKEKO - SUMMER

-1 - SR							SR - +1					+1 - +2					+2 - +3							
Habitat	DL	RH	MR	SW	W/-	TOT.	DL	RH	MR	SW	W/-	TOT.	DL	RH	MR	SW	W/-	TOT.	DL	RH	MR	SW	W/-	TOT.
n	319	36	15	13		383	1039	154	18	29	1	1241	801	131	14	47	1	994	630	163	1	62	2	658
%	93.29	9.40	3.92	3.39		100.00	83.72	12.41	1.45	2.34	0.08	100.00	60.58	13.18	1.41	4.73	0.10	100.00	73.43	19.00	0.12	7.23	0.22	100.00
n	37	10	1	8		56	123	28	9	2		162	122	25	3	5		155	138	26	1	12		177
%	66.07	17.06	1.70	14.29		100.00	75.93	17.28	5.56	1.23		100.00	78.70	16.13	1.94	3.23		100.00	77.97	14.69	0.56	6.78		100.00
n	2	7	2	6		17	10	17	5	8		40	17	33		26		76	13	31		32		76
%	11.76	41.18	11.77	35.29		100.00	25.00	42.50	12.50	20.00		100.00	22.37	43.42		34.21		100.00	17.10	40.79		42.11		100.00
n	9					9	11					11	11	3				14	9	2				11
%	100.00					100.00	100.00					100.00	78.57	21.43				100.00	81.82	18.18				100.00
n						5						5	4					4	2			2		4
%						100.00						100.00	100.00					100.00	50.00			50.00		100.00
n								2				2												
%								100.00				100.00												
n	1	1		1		3							2		1			3	2			1		3
%	33.33	33.33		33.33		100.00							66.67		33.33			100.00	66.67			33.33		100.00
n					2	2					9	9					15	15					13	13
%					100.00	100.00					100.00	100.00					100.00	100.00					100.00	100.00
n					20	20					20	20					20	20					9	9
%					100.00	100.00					100.00	100.00					100.00	100.00					100.00	100.00
n	368	54	18	28	2/20	490	1188	201	32	39	10/20	1490	955	194	17	79	16/20	1281	794	222	2	109	15/9	1151
%	75.10	11.02	3.67	5.71	0.41/4.06	100.00	79.73	13.49	2.15	2.62	0.67/1.34	100.00	74.54	15.14	1.32	6.79	1.25/1.56	100.00	68.98	19.29	0.17	9.48	1.30/0.78	100.00

APP. 14 cont.

+3 - +4							+4 - +5					+5 - +6					+6 - +7							
Habitat	DL	RH	MR	SW	W/-	TOT.	DL	RH	MR	SW	W/-	TOT.	DL	RH	MR	SW	W/-	TOT.	DL	RH	MR	SW	W/-	TOT.
n	590	203	1	56	11	861	479	179	7	106	21	792	516	207	19	101	21	864	485	211	38	96	10	818
%	68.52	23.58	0.12	6.50	1.28	100.00	60.48	22.60	0.89	13.38	2.65	100.00	59.72	23.96	2.20	11.69	2.43	100.00	57.19	24.88	4.48	11.32	2.13	100.00
n	122	36	4	4		166	103	33	6	10		152	75	36	5	0		124	71	41		6	6	124
%	73.49	21.69	2.41	2.41		100.00	67.76	21.71	3.95	6.58		100.00	60.48	29.03	4.03	6.45		100.00	57.26	33.06		4.84	4.84	100.00
n	16	25		42		83	7	27		50		84	7	25		35		67	13	42		23		78
%	19.28	30.12		50.60		100.00	8.34	32.14		50.52		100.00	10.45	37.31		52.24		100.00	16.66	53.85		29.49		100.00
n	3	4		4		11	12		1	6		19	2	1		9		12	5	2				7
%	27.27	36.37		36.36		100.00	63.16		5.26	31.58		100.00	16.67	8.33		75.00		100.00	71.43	28.57				100.00
n	2					2	4	2				6												
%	100.00					100.00	66.67	33.33				100.00												
n		2				2							1					1		3				3
%		100.00				100.00							100.00					100.00		100.00				100.00
n							1	1		2		4		1				1						
%							25.00	25.00		50.00		100.00		100.00				100.00						
n					21	21						23	23					44	44					26
%					100.00	100.00						100.00	100.00					100.00	100.00					100.00
n					12	12						13	13					10	10					4
%					100.00	100.00						100.00	100.00					100.00	100.00					100.00
n	733	270	5	106	32/12	1158	606	242	14	174	44/13	1093	600	271	24	153	65/10	1123	574	299	44	125	44/4	1090
%	63.20	23.32	0.43	9.15	2.76/1.04	100.00	55.44	22.14	1.28	15.92	4.03/1.19	100.00	53.43	24.13	2.14	13.62	5.79/0.89	100.00	52.66	27.44	4.04	11.47	4.04/0.37	100.00

APP. 14 cont.

+7 - +8							-8 - -7					-7 - -6					-6 - -5							
Hab. Act.	DL	RM	NR	SW	W/-	TOT.	DL	RM	NR	SW	W/-	TOT.	DL	RM	NR	SW	W/-	TOT.	DL	RM	NR	SW	W/-	TOT.
n P	172	65	2	27	6	272	122	49		48	8	227	501	229	29	81	9	929	617	271	38	55	20	1001
%	63.24	23.90	0.74	9.92	2.20	100.00	53.74	21.59		21.15	3.52	100.00	62.54	24.65	3.12	8.70	0.97	74.64	61.64	27.07	3.90	5.49	2.00	100.00
n AT/AL	51	14	2	1		68	38	17		4		56	104	52	7	17		180	76	48	7	4		135
%	15.00	20.39	2.94	1.47		100.00	62.50	30.36		7.14		100.00	57.74	20.09	3.09	9.44		100.00	50.30	35.56	5.18	2.96		100.00
n CI	2	13		14		29	5	7		24		36	3	30	3	40		74	7	47		40		94
%	6.90	14.82		48.28		100.00	13.09	19.44		66.67		100.00	4.05	37.04	4.06	54.05		100.00	7.45	50.00		42.55		100.00
n AG/AP	3	1		1		5	2	2				4	13	1				14	9			2		11
%	60.00	20.00		20.00		100.00	50.00	50.00				100.00	92.86	7.14				100.00	81.82			18.18		100.00
n CO													2					2						
%													100.00					100.00						
n D														2				2				1		1
%														100.00				100.00				100.00		100.00
n CA							1					1		1				1		1				1
%							100.00					100.00		100.00				100.00		100.00				100.00
n S					12	12					7	7					26	26					30	30
%					100.00	100.00					100.00	100.00					100.00	100.00					100.00	100.00
n FLY					2	2					4	4					14	14					9	9
%					100.00	100.00					100.00	100.00					100.00	100.00					100.00	100.00
n TOT.	228	93	4	43	18/2	388	165	75		76	15/4	335	703	313	39	138	35/14	1242	709	367	45	102	50/9	1282
%	58.76	23.97	1.03	11.08	4.64/ 0.52	100.00	49.25	22.39		22.69	4.40/ 1.19	100.00	56.60	25.20	3.14	11.11	2.60/ 1.13	100.00	54.75	28.34	3.48	7.88	0.69	100.00

APP. 14 cont.

-5 - -4							-4 - -3					-3 - -2					-2 - -1							
Hab. Act.	DL	RM	NR	SW	W/-	TOT.	DL	RM	NR	SW	W/-	TOT.	DL	RM	NR	SW	W/-	TOT.	DL	RM	NR	SW	W/-	TOT.
n P	665	332	30	59	9	1103	760	327	41	78	9	1215	803	326	39	55	1	1304	928	369	46	30		1373
%	60.29	30.10	3.45	5.25	0.81	100.00	62.55	26.91	3.37	6.42	0.74	100.00	67.71	25.00	2.99	4.22	0.08	100.00	67.59	26.80	3.35	2.18		100.00
n AT/AL	90	45	6	8		149	108	67	7	3		105	118	62	8	6		194	125	88	5	4		222
%	60.40	30.20	4.03	5.37		100.00	58.33	36.22	3.70	1.62		100.00	60.02	31.96	4.13	3.09		100.00	56.31	39.61	2.25	1.00		100.00
n CI	14	40	5	27		66	19	32	5	32		88	17	47	6	8		78	10	46	4	11		71
%	16.20	40.51	5.01	31.40		100.00	21.59	36.37	5.68	36.36		100.00	21.79	60.26	7.69	10.26		100.00	14.08	64.79	5.64	15.49		100.00
n AG/AP	11	6				17	7	6		2		15	11	2		3		16	15	3				18
%	64.71	35.29				100.00	46.67	40.00		13.33		100.00	68.75	12.50		18.75		100.00	83.33	16.67				100.00
n CO	4					4	3					3			2			2	5	6				11
%	100.00					100.00	100.00					100.00			100.00			100.00	45.45	54.44				100.00
n D		3				3								1				1		2	3			5
%		100.00				100.00								100.00				100.00		40.00	60.00			100.00
n CA		1				1	2					2	1	1	1	1		4	2			1		3
%		100.00				100.00	100.00					100.00	25.00	25.00	25.00	25.00		100.00	66.67			33.33		100.00
n S					27	27					20	20					28	28					19	19
%					100.00	100.00					100.00	100.00					100.00	100.00					100.00	100.00
n FLY					7	7					11	11					12	12					9	9
%					100.00	100.00					100.00	100.00					100.00	100.00					100.00	100.00
n TOT.	784	427	49	94	36/7	1397	899	432	53	115	29/11	1539	1020	439	56	73	56/12	1639	1085	514	58	46	19/9	1731
%	56.12	30.57	3.58	6.73	2.58/ 0.50	100.00	58.42	28.07	3.44	7.48	1.85/ 0.71	100.00	62.84	26.70	3.42	4.45	3.42/ 0.73	100.00	62.68	29.69	3.35	2.66	0.52	100.00



APPENDIX 15 SEASONAL DIURNAL TIME ALLOCATION TO APPETITIVE AND CONSUMATORY FEEDING AND "OTHER" ACTIVITIES, PECKING RATE, FEEDING INTENSITY, AND HABITAT FORAGING RANK - AUTUMN

-1 - SR							SR - +1					+1 - +2					+2 - +3							
Hab. Act.	DL	RM	MR	SW	W	TOT.	DL	RM	MR	SW	W	TOT.	DL	RM	MR	SW	W	TOT.	DL	RM	MR	SW	W	TOT.
n	226	20		11		257	530	65		23		618	537	32		30		599	459	24		33		516
FP	19.02	13.97		61.11		50.39	40.95	54.17		50.53		42.47	40.68	33.23		34.09		39.67	38.64	25.26		37.08		37.42
n	179	5		6		190	595	42		6		643	567	30		28		631	582	28		19		629
Con.	38.83	17.24		33.33		27.25	40.00	35.00		15.79		44.19	42.95	37.51		31.82		41.79	48.99	29.48		21.35		45.61
n	56	4		1	2	63	168	13		9	4	194	216	28		30	6	280	147	43		37	7	234
uth.	12.15	13.79		5.56	100.00	12.36	12.99	10.83		23.68	100.00	13.34	16.37	29.16		34.09	100.00	18.54	12.37	45.26		41.57	100.00	15.97
n	461	29		18	2	510	1293	120		38	4	1455	1320	96		83	6	1510	1165	95		59	7	1379
Tot.	100.00	100.00		100.00	100.00	100.00	100.00	100.00		100.00	100.00	100.00	100.00	100.00		100.00	100.00	100.00	100.00	100.00		100.00	100.00	100.00
FR P/30 secs.	13.03	12.40		10.00		12.67	12.77	12.17		9.75		12.60	13.65	17.15		11.13		13.86	14.31	14.38		11.73		13.18
FI P/Hr	607	269		340		566	705	511		185		668	704	772		425		695	783	513		301		721
HFR Rel. P/Hr	550.2	15.0		15.2		580.4	629.1	43.4		4.3		676.8	631.1	43.2		20.0		694.3	711.0	23.3		13.9		748.2
HFR %	94.80	2.59		2.61		100.00	92.96	6.41		0.63		100.00	90.90	6.22		2.88		100.00	95.03	3.11		1.86		100.00

APP. 15 cont.

+3 - +4							+4 - +5					+5 - +6					-6 - -5							
Hab. Act.	DL	RM	MR	SW	W	TOT.	DL	RM	MR	SW	W	TOT.	DL	RM	MR	SW	W	TOT.	DL	RM	MR	SW	W	TOT.
n	302	32		40		374	318	43	6	42		409	245	25		25		295	230	62		22		314
FP	34.28	19.39		27.82		31.38	32.16	19.28	42.86	35.29		30.10	30.47	23.14		23.15		28.78	32.08	35.94		21.57		29.59
n	443	81		38		562	526	110	3	35	2	676	400	54		40		494	386	121	2	25	1	535
Con.	50.40	49.09		26.72		47.14	53.18	49.33	21.43	29.42	14.29	49.74	49.75	50.01		27.04		48.20	53.83	50.64	100.00	24.51	100.00	50.43
n	134	92		65	5	256	145	70	5	42	12	274	159	29		43	5	236	101	56		55		212
uth.	15.24	31.52		15.46	100.00	21.48	14.66	31.39	35.71	35.39	85.71	20.16	19.78	26.85		39.81	100.00	33.02	14.09	33.42		53.92		13.98
n	879	165		143	5	1192	989	223	14	119	14	1329	804	108		100	5	1025	717	239	2	102	1	1051
Tot.	100.00	100.00		100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00		100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00
FR P/30 secs.	12.86	20.28		13.18		13.93	13.61	26.50	21.00	14.20	12.00	15.40	15.65	21.55	10.00	15.00		16.05	15.87	20.55	23.00	19.58	12.00	17.13
FI P/Hr	778	1195		423		788	869	1569	540	501	206	919	934	1293		667		928	1025	1249	2760	576	1440	1037
HFR Rel. P/Hr	619.5	143.7		35.1		798.3	676.7	220.2	4.2	35.4	0.4	936.9	764.0	129.0		54.8		947.8	743.2	269.9	6.6	31.8	1.7	1053.3
HFR %	77.60	18.00		4.40		100.00	72.23	23.50	0.45	3.78	0.04	100.00	80.60	13.62		5.78		100.00	70.56	25.63	0.63	3.02	0.16	100.00



APPENDIX 16 SEASONAL DIURNAL TIME ALLOCATION TO APPETITIVE AND CONSUMATORY FEEDING AND "OTHER" ACTIVITIES, PECKING RATE, FEEDING INTENSITY, AND HABITAT FORAGING RANK - WINTER

		-1 - SR						SR - +1						+1 - +2						+2 - +3					
Hab. Act.	DL	RM	NR	SW	W	TOT.	DL	RM	NR	SW	W	TOT.	DL	RM	NR	SW	W	TOT.	DL	RM	NR	SW	W	TOT.	
n	731	15		5		755	1406	53	7	9		1460	1605	54	5	25		1689	1533	25	19	25		1717	
AP	48.67	15.52		27.77		45.84	40.65	12.53	46.67	12.0		33.32	45.04	17.53	50.02	15.82		41.65	45.85	13.07	33.93	16.73		39.60	
n	633	54		6		693	1551	134	3	37		1725	1453	113	2	80		1648	1356	301	33	79		1769	
Con.	42.14	44.26		33.34		42.08	44.25	42.61	20.00	52.12		44.67	40.77	36.69	20.00	50.64		40.64	29.17	46.31	58.93	53.02		40.80	
n	138	49		7	5	199	502	121	5	25	4	657	506	141	3	53	15	718	518	264	4	45	19	350	
Oth.	9.19	10.16		38.09	100.00	12.08	14.50	38.66	33.32	35.21	100.00	17.01	14.19	45.78	30.00	33.54	100.00	12.71	14.95	40.62	7.14	30.20	100.00	19.60	
n	1502	12		18	5	1647	3459	313	15	71	4	3062	3564	308	10	158	15	4055	3462	650	56	149	19	4336	
%	100.00	100.00		100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	
FR P/30 secs	11.05	20.20		6.75		12.53	13.19	26.89	19.00	12.43		16.13	14.70	31.95	20.00	14.44		17.48	17.27	32.42	25.75	18.17		21.45	
FI F/Hr	589	1073		720		633	710	1381	456	777		865	719	1407	480	878		852	812	1802	1821	1156		1050	
HFR Rel. F/Hr	554.8	54.1		5.5		614.4	654.7	83.2	1.4	11.1		750.4	659.1	70.5	1.0	27.7		758.1	685.3	200.0	27.1	34.4		946.9	
HFR %	90.31	8.80		0.89		100.00	85.25	11.08	0.19	1.48		100.00	86.94	9.28	0.13	3.65		100.00	72.38	21.12	2.87	3.64		100.00	

APP. 16 cont.

		+3 - +4						+4 - +5						-5 - -4						-4 - -3					
Hab. Act.	DL	RM	NR	SW	W	TOT.	DL	RM	NR	SW	W	TOT.	DL	RM	NR	SW	W	TOT.	DL	RM	NR	SW	W	TOT.	
n	1406	117	14	31		1568	824	108	28	20		980	814	125	34	26		999	939	178	50	15		1122	
P	41.58	13.72	22.22	20.39		35.02	38.72	14.38	19.06	15.63		30.66	39.78	15.04	24.11	24.53		31.90	34.78	13.47	17.00	13.76		26.59	
n	1514	404	42	81		2041	1010	401	110	68		1589	973	425	90	47		1535	1326	715	212	56		2309	
Con.	44.78	47.36	66.67	53.29		45.59	47.46	53.14	70.97	53.12		49.70	47.56	51.15	63.58	44.34		47.03	49.11	54.13	72.36	51.38		51.95	
n	461	332	7	40	28	868	294	246	17	40	31	628	259	281	17	33	7	597	435	420	31	38	22	954	
Oth.	13.64	38.92	11.11	26.32	100.00	19.39	13.82	31.58	10.97	31.25	100.00	19.64	12.66	33.21	12.06	31.13	100.00	19.07	16.11	32.40	10.58	14.86	100.00	21.46	
n	3381	853	63	152	28	4477	2128	755	155	120	31	3197	2046	631	141	106	7	3131	2700	1321	293	109	22	4445	
Tot.	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	
FR P/30 secs	16.35	36.78	26.75	16.29		22.73	18.50	26.42	24.83	20.10		21.71	25.15	36.70	33.69	14.50		28.48	21.63	31.15	29.75	16.88		25.35	
FI F/Hr	879	2090	2140	1041		1244	1054	1685	2115	1281		1295	1435	2257	2571	772		1676	1275	2023	2583	1040		1580	
HFR Rel. F/Hr	710.9	302.2	33.2	32.3		1078.5	751.3	335.4	113.4	43.8		1243.7	1012.2	490.1	125.7	22.2		1650.2	826.7	518.4	193.7	21.1		1550.9	
HFR %	65.91	28.02	3.08	2.99		100.00	60.40	26.97	9.11	3.52		100.00	61.34	9.70	7.62	1.34		100.00	53.00	33.23	12.42	1.35		100.00	

APP. 16 cont.

-3 - -2							-2 - -1						-1 - SS						SS - +1						
Sub. Tot.	DL	RM	MR	SW	#	TOT.	DL	RH	MR	SW	#	TOT.	DL	RI	LR	SW	#	TOT.	DL	RI	LR	SW	#	TOT.	
n	1091	152	51	9		1303	1607	131	77	6		1881	1879	90	65	7		2041	213	22	15	1		251	
f	35.91	14.25	15.85	10.71		29.09	45.79	17.10	26.37	26.09		39.78	48.15	15.31	26.52	21.21		42.74	50.26	15.06	22.39	33.33		51.23	
n	1556	521	186	47		2310	1606	401	182	8		2197	1733	354	145	19		2251	538	83	49	1		671	
f	51.21	46.80	66.80	55.96		51.58	44.11	52.35	62.33	34.78		46.47	44.41	60.20	59.17	57.58		47.14	37.23	56.85	73.13	33.33		40.40	
n	391	393	33	28	21	866	368	234	33	9	6	650	250	144	35	7	7	483	94	41	3	1		139	
f	12.37	36.87	12.22	33.33	100.00	19.33	10.10	30.55	11.0	39.13	100.00	13.75	7.44	24.45	14.31	21.21	100.00	10.12	6.51	28.09	4.48	33.33		8.37	
n	3028	1066	270	84	21	4479	3641	766	292	23	6	4728	3902	538	245	33	7	4775	1445	146	67	3		1661	
f	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00
FR P/30 secs.	22.14	32.08	29.68	15.22		25.09	17.07	30.70	33.96	16.50		22.84	16.91	30.29	34.93	11.33		22.08	17.87	33.00	35.50	11.00		20.77	
FI P/Hr	1361	1882	2454	1022		1553	904	1929	2540	689		1274	901	2188	2480	783		1249	798	2251	3115	440		1007	
HFR Rel. P/Hr	996.3	351.7	160.7	15.8		1524.5	725.1	251.9	161.3	2.3		1140.6	757.3	227.3	123.5	4.7		1112.8	708.2	156.7	130.8	0.6		996.3	
HFR	65.35	23.07	10.54	1.04		100.00	63.57	22.08	14.14	0.21		100.00	68.05	20.43	11.10	0.40		100.00	71.08	15.73	13.13	0.06		100.00	

APPENDIX 17 SEASONAL DIURNAL TIME ALLOCATION TO APPETITIVE AND CONSUMATORY FEEDING AND "OTHER" ACTIVITIES, PECKING RATE, FEEDING INTENSITY, AND HABITAT FORAGING RANK - SPRING

-1 - SR							SR - +1					+1 - +2					+2 - +3							
Hab.	DL	RM	MR	SW	W	TOT.	DL	RM	MR	SW	W	TOT.	DL	RM	MR	SW	W	TOT.	DL	RM	MR	SW	W	TOT.
n	226	36	5	5		272	557	93	19	17		686	556	80	21	14		671	490	84	34	33		641
Ap.	45.02	25.36	35.73	15.15		38.97	41.75	22.35	32.76	16.67		35.52	39.10	17.62	27.27	12.35		32.11	36.88	20.74	20.99	19.52		30.48
n	190	75	7	9		281	573	201	33	47		854	632	213	37	62		944	638	194	102	92	3	1029
Con.	37.85	52.81	49.99	17.28		40.26	42.95	48.33	56.90	46.08		44.34	44.40	46.99	48.05	54.85		45.17	48.05	46.53	62.90	54.44	11.11	45.93
n	86	31	2	19	7	145	204	122	6	38	16	386	235	161	19	37	23	475	200	139	26	44	24	433
Cth.	17.13	21.83	14.25	57.57	100.00	20.77	15.30	29.32	10.34	37.25	100.00	20.04	16.50	35.45	24.68	32.72	100.00	22.72	15.07	33.33	16.05	26.04	88.89	20.59
n	502	142	14	33	7	698	1334	416	58	102	16	1926	1423	454	77	113	23	2090	1328	417	162	169	27	2103
Tot.	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00
FR F/30 secs.	11.95	17.90	22.00	11.80		13.83	14.83	20.18	20.24	13.57		16.90	16.84	23.71	23.00	17.07		19.48	19.12	24.51	24.29	13.00	13.40	20.81
FI F/Hr	543	1134	1320	386		668	764	1171	1382	750		899	930	1335	1326	1124		1056	1102	1368	1848	875	173	1222
HFR Rel. F/Hr	407.9	329.4	28.5	9.3		685.1	559.8	225.5	46.4	31.1		862.8	681.9	243.8	48.9	53.3		1027.9	740.6	231.0	152.2	65.8	0.3	1189.9
HFR %	60.42	23.98	4.22	1.38		100.00	64.89	26.13	5.38	3.60		100.00	66.35	23.72	4.76	5.18		100.00	62.24	19.41	12.79	5.53	0.3	100.00

APP. 17 cont.

+3 - +4							+4 - +5					+5 - +6					-6 - -5							
Hab.	DL	RM	MR	SW	W	TOT.	DL	RM	MR	SW	W	TOT.	DL	RM	MR	SW	W	TOT.	DL	RM	MR	SW	W	TOT.
n	484	83	39	25		631	373	71	50	18		512	260	66	23	8		357	309	61	58	22		450
Ap.	38.33	13.44	22.67	21.19		31.19	33.15	17.49	17.75	14.29		25.99	31.43	13.60	9.24	13.56		21.44	36.79	13.15	21.08	27.50		26.56
n	591	212	95	47	4	953	566	203	174	62	6	1013	434	262	154	29	13	892	387	241	149	35	9	621
Con.	46.27	47.11	57.56	39.83	18.18	47.11	50.49	50.00	61.02	49.20	15.62	51.42	52.48	54.03	51.94	49.15	28.89	53.58	46.08	51.94	54.19	43.75	25.71	45.47
n	186	155	34	46	18	439	184	132	57	46	26	445	133	157	72	22	32	416	144	162	68	23	26	423
Cth.	14.75	34.45	19.77	38.98	81.82	21.70	16.36	32.51	20.29	36.51	84.48	22.59	16.09	32.37	28.92	37.29	71.11	24.98	17.12	34.91	24.73	28.75	74.29	24.97
n	1261	450	172	118		2023	1125	406	281	126	32	1970	627	485	249	59	45	1665	840	464	275	80	35	1694
Tot.	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00
FR F/30 secs.	17.12	24.50	23.27	25.00	15.45	20.08	18.67	24.53	26.32	14.35	22.00	21.17	19.09	24.79	24.88	12.80	14.50	21.63	20.55	26.08	22.64	14.67	12.33	22.21
FI F/Hr	963	1385	1607	739	545	1135	1131	1472	1956	847	412	1306	1202	1608	1847	755	503	1391	1136	1626	1472	770	381	1292
HFR Rel. F/Hr	645.4	272.0	136.6	34.5	1.4	1089.9	694.8	267.7	285.9	45.7	1.6	1295.7	657.6	434.4	265.6	21.9	5.1	1384.6	617.7	388.7	243.0	34.8	2.7	1286.9
HFR %	59.22	24.96	12.54	3.17	0.11	100.00	53.62	20.66	22.07	3.52	0.13	100.00	47.50	31.37	19.18	1.58	0.37	100.00	48.00	30.20	18.89	2.70	0.21	100.00



APPENDIX 18 SEASONAL DIURNAL TIME ALLOCATION TO APPETITIVE AND CONSUMATORY FEEDING AND "OTHER" ACTIVITIES, PECKING RATE, FEEDING INTENSITY, AND HABITAT FORAGING RANK - SUMMER

		-1 - SR						SR - +1						+1 - +2						+2 - +3					
Hab. Act.		DL	RH	HR	SW	W	TOT.	DL	RH	HR	SW	W	TOT.	DL	RH	HR	SW	W	TOT.	DL	RH	HR	SW	W	TOT.
n	173	11	10	3			197	439	70	13	14		536	222	46	2	29		302	222	51	1	38		312
Ap.	%	47.01	20.77	55.55	32.14		43.68	36.95	34.82	40.62	35.90		36.46	23.24	25.26	11.77	36.71		23.95	27.96	22.97	50.00	34.86		27.32
n	146	21	5	1			173	585	76	4	12	1	678	563	73	12	14	1	663	404	105		24	2	539
Con.	%	33.68	36.90	27.77	14.29		38.36	49.25	37.81	12.50	30.77	10.00	46.12	58.96	37.62	70.58	17.72	6.25	52.58	50.09	49.25		22.02	13.33	47.20
n	49	22	3	5	2		81	164	55	15	13	9	256	170	72	3	36	15	296	168	62	1	47	13	291
Uth.	%	13.31	40.33	16.67	53.57	100.00	17.96	13.80	27.37	46.84	33.33	90.00	17.42	17.80	32.12	17.65	45.57	93.75	23.47	21.15	27.73	50.00	43.12	86.67	25.48
n	368	54	10	9	2		451	1188	201	32	39	10	1470	955	194	17	79	16	1261	794	242	2	105	15	1142
Tot.	%	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00
FR	F/20	9.73	14.89	16.00	6.00		10.86	14.03	15.67	16.00	11.00	12.00	14.33	14.05	15.10	21.00	10.00	12.00	14.22	15.15	17.26		13.33	12.33	15.51
FI	F/Hr	463	695	533	103		500	829	711	240	406	144	793	994	682	1779	213	90	897	925	1020		352	197	878
HFR	Rel. i/dr	385.9	65.3	20.9	3.5		475.6	694.4	88.2	3.5	9.5	0.1	795.7	801.0	89.8	25.1	10.1	0.1	926.1	679.2	193.9		25.5	0.4	899.0
HFR	%	81.13	13.74	4.40	0.73		100.00	87.27	11.08	0.44	1.19	0.02	100.00	86.50	9.70	2.70	1.09	0.01	100.00	75.55	21.57		2.83	0.05	100.00

APP. 18 cont.

		+3 - +4						+4 - +5						+5 - +6						+6 - +7					
Hab. Act.		DL	RH	HR	SW	W	TOT.	DL	RH	HR	SW	W	TOT.	DL	RH	HR	SW	W	TOT.	DL	RH	HR	SW	W	TOT.
n	173	93		30			302	147	63	3	47		260	148	68	70	56		342	150	78	17	51		296
Ap.	%	24.42	34.44		25.20		26.35	24.26	26.03	21.43	27.01		24.07	24.67	25.09	33.34	36.60		26.31	26.13	26.08	38.63	40.80		27.26
n	402	100	1	23	11		537	327	112	3	58	21	521	364	127	97	43	21	662	331	129	21	43	18	542
Con.	%	54.34	37.04	20.00	21.70	34.37	46.86	53.95	46.28	21.43	33.34	45.46	48.24	60.66	50.55	45.83	28.11	32.31	50.92	57.66	43.15	47.73	34.40	40.91	49.50
n	152	77	4	53	21		307	132	67	8	69	23	299	88	66	44	54	44	296	93	92	6	31	26	248
Uth.	%	20.74	28.52	50.00	50.00	65.63	26.79	21.79	27.69	57.14	39.65	54.54	27.69	14.67	24.36	20.83	35.29	37.65	22.77	16.21	30.77	13.64	24.80	59.09	22.84
n	733	270	5	106	32		1146	606	242	14	174	44	1080	600	271	211	153	65	1300	574	299	44	125	44	1086
Tot.	%	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00
FR	F/20	16.62	16.94	17.00	14.90	14.67	16.48	17.20	19.40	22.50	14.61	14.50	17.33	16.65	19.15	19.67	13.85	17.13	17.05	17.62	18.45	18.75	13.76	16.17	17.31
FI	F/Hr	1093	753	408	121	605	927	1134	1077	289	585	791	1003	1212	1162	1082	467	664	1042	1219	955	1074	568	794	1037
HFR	Rel. i/Hr	749.3	177.5	0.5	7.9	7.7	942.9	673.4	243.5	2.6	78.2	21.0	1018.7	723.9	278.3	23.8	54.6	16.1	1096.7	679.1	237.7	48.1	64.3	16.9	1046.1
HFR	%	79.46	18.83	0.05	0.84	0.83	100.00	66.11	23.90	0.25	7.68	2.06	100.00	66.00	25.38	2.17	4.98	1.49	100.00	64.91	22.72	4.60	6.15	1.62	100.00

APP. 18 cont.

+7 - +8							-8 - -7					-7 - -6					-6 - -5							
Hab. ct.	DL	RM	MR	SW	W	TOT.	DL	RM	MR	SW	W	TOT.	DL	RM	MR	SW	W	TOT.	DL	RM	MR	SW	W	TOT.
n	48	17	2	16		83	41	18		29		88	178	70	16	38		302	176	105	9	33		323
Ap. %	21.66	18.25	50.00	7.21		21.50	24.85	24.00		38.19		26.59	25.37	2.37	41.58	27.54		24.59	24.83	28.61	21.11	32.35		35.37
n	123	46		11	6	186	81	31		18	8	138	402	155	12	41	9	619	439	161	29	22	20	671
Con. %	53.96	49.46		25.98	33.33	48.19	49.09	41.33		23.67	53.33	41.69	57.19	49.51	39.25	29.71	35.71	50.41	61.91	43.87	63.33	21.57	40.00	32.71
n	57	30	2	16	12	117	43	26		29	7	105	123	88	11	59	26	307	94	101	7	47	30	279
Oth. %	24.98	32.26	50.00	37.21	56.67	30.31	26.06	34.67		38.14	46.67	31.72	17.49	28.12	27.57	42.75	24.29	25.00	13.26	27.52	15.56	46.08	60.00	31.92
n	225	95	4	43	18	386	165	75		76	15	331	703	315	39	136	39	1220	709	307	45	102	50	1273
Tot. %	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00
PR F/30 secs.	14.91	19.69	23.00	14.80	13.00	16.37	15.48	18.89		17.25	22.00	17.09	17.55	19.11	13.17	15.14	16.17	17.47	17.18	19.52	17.71	18.29	12.50	18.01
FI F/Hr	965	1169		454	520	947	912	937		490	1408	855	1205	1135	487	540	499	1057	1276	1028	1346	466	600	1139
HFR Rel. i/Hr	610.5	279.3		45.1	11.4	946.4	490.0	202.3		103.6	49.6	845.5	753.4	279.8	15.2	47.1	4.8	1100.3	786.6	278.2	51.2	25.6	12.0	1153.6
HFR %	64.51	29.51		4.76	1.21	100.00	57.96	23.92		12.26	5.86	100.00	68.47	25.43	1.38	4.28	0.44	100.00	68.19	24.11	4.43	2.22	1.05	100.00

APP. 18 cont.

-5 - -4							-4 - -3					-3 - -2					-2 - -1							
Hab. ct.	DL	RM	MR	SW	W	TOT.	DL	RM	MR	SW	W	TOT.	DL	RM	MR	SW	W	TOT.	DL	RM	MR	SW	W	TOT.
n	207	108	25	36		372	219	105	11	30		365	229	118	19	28		394	310	100	23	13		454
Ap. %	25.97	25.25	51.02	38.30		26.76	24.32	24.30	20.77	26.08		23.89	22.25	26.88	33.93	38.36		24.22	28.57	21.01	39.66	28.26		26.36
n	456	221	13	23	9	722	444	219	29	39	9	740	543	205	20	21	1	790	609	258	19	14		900
Con. %	58.16	51.76	26.53	24.47	25.00	51.94	49.43	50.69	54.70	33.92	31.03	48.43	52.72	46.69	35.71	28.76	3.45	48.96	56.13	50.20	32.76	30.44		52.26
n	125	98	11	35	27	296	236	108	13	46	20	423	258	116	17	24	20	443	166	148	16	19	19	358
Oth. %	15.94	22.95	22.45	37.23	75.00	21.29	26.25	25.01	24.53	40.00	68.97	27.68	25.03	26.43	30.26	32.88	96.55	27.23	15.30	28.79	27.58	41.30	100.00	21.37
n	784	427	49	94	36	1390	899	432	53	115	25	1528	1030	439	56	73	29	1627	1085	514	58	46	19	1722
Tot. %	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00
PR F/30 secs.	18.59	18.58	14.60	14.33	17.33	18.26	18.85	19.11	21.63	16.22	13.40	18.58	16.85	17.90	18.30	12.71	11.00	17.07	18.43	17.41	18.00	16.33		17.94
FI F/Hr	1320	1154	465	421	520	1138	1118	1162	1419	660	499	1080	1066	1003	784	439	46	995	1241	1049	708	597		1125
HFR Rel. i/Hr	795.8	347.3	16.0	22.5	4.2	1185.8	699.3	312.8	48.0	42.4	3.6	1106.1	721.9	250.7	23.5	18.5	0.1	1014.7	839.0	281.9	23.7	13.0		1157.6
HFR %	67.10	29.29	1.35	1.90	0.36	100.00	63.22	28.28	4.34	3.83	0.33	100.00	71.15	24.71	2.31	1.83	0.00	100.00	72.48	24.35	2.05	1.12		100.00



APPENDIX 10 STATISTICAL ANALYSIS OF

WILSON AT FELL'S LAKE - AUTUMN

Period	-1 - SR	SR - +1	+1 - +2	+2 - +3	+3 - +4	+4 - +5	+5 - +6	-5 - -5	-5 - -4	-4 - -3	-3 - -2	-2 - -1	-1 - SS	SS - +1
Hab. Act.	DL													
F. n	96	354	210	133	56	107	144	94	50	245	176	107	63	154
F. %	88.39	86.34	90.94	83.63	77.72	69.17	88.81	72.82	74.36	81.24	83.81	84.34	80.73	87.20
AT./AL. n	8	36	17	17	10	11	10	22	13	33	8	12	10	
AT./AL. %	7.41	8.78	7.36	10.69	13.86	9.44	8.00	19.30	10.21	10.77	3.84	3.99	1.53	
OM n		4	3		1		7	1	3	5	5	7	9	1
OM %		0.98	1.30		1.39		4.19	0.93	4.35	1.80	2.38	1.74	1.15	0.93
AG./AP. n	2	14	1	9	5	2	2		1	13	8	10	12	
AG./AP. %	1.85	3.41	0.43	5.62	3.21	1.67	1.20		1.15	4.83	3.81	3.99	1.53	
CC n														
D n														
CA n														
S n														
FLY n	2	2										1	1	
FLY %	1.35	0.49										0.59	0.43	
TOT n	108	410	231	159	72	120	159	114	69	269	210	102	74	107
TOT %	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00

APPENDIX 20. SEASONAL DIURNAL TIME ALLOCATION BY ACTIVITY IN DOMESTIC FEEDING AND  
 "OTHER" ACTIVITIES: FEEDING RATE: 400 PPM 17 FIVE CITY OF WINDS AT WELLS LAGOON

AUTUMN

Period	-1 - SR	SR - 0+1	+1 - +2	+2 - +3	+3 - +4	+4 - +5	+5 - +6	+6 - +7	+7 - +8	+8 - +9	+9 - +10	+10 - +11	+11 - +12	+12 - +13
Hab. Act.	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL
AP <sub>n</sub>	16	133	100	55	33	81	77	40	25	77	93	139	101	10
AP <sub>%</sub>	12.60	33.66	47.12	31.59	45.84	45.90	18.38	25.00	30.23	20.62	41.79	31.58	37.10	37.35
CON <sub>n</sub>	50	216	101	78	23	53	64	41	27	114	83	188	399	61
CON <sub>%</sub>	46.29	52.68	43.72	49.06	14.24	41.17	40.07	25.94	30.13	50.40	39.52	45.76	49.63	59.81
OTH <sub>n</sub>	12	56	21	20	11	12	19	30	17	51	24	70	101	3
OTH <sub>%</sub>	11.11	13.59	9.09	16.35	27.77	10.75	11.35	20.84	11.01	43.03	18.19	41.15	13.17	1.80
TOT <sub>n</sub>	100	440	31	159	77	100	115	111	69	180	210	402	794	107
TOT <sub>%</sub>	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00
FR /30 secs.	17.00	17.12	18.00	17.77	22.22	11.90	17.39	14.14	14.01	17.00	17.93	18.07	19.11	19.10
FI P/hr	914	1105	914	1053	721	102	208	364	227	1050	750	1021	1110	1052

APPENDIX 24 SEASONAL DIVERSITY ESTIMATION  
ON BEINGS AT BEHNS LAGOON - SPRING

Period	-1 - SR	SR - +1	-1 - +1	+	+ - +1	+1 - +1	+ - +1	-1 - +1	+1 - +1	-1 - +1	-1 - +1	-1 - +1	-1 - SS	SR - +1
Hab. Act.	DL													
F. n %	183 82.25	169 77.14	173 75.52	521 83.92	176 77.17	174 80.03	177 79.14	182 85.34	137 83.56	134 78.79	170 81.99	124 72.37	573 89.95	220 92.83
AT/AL n %	23 10.09	84 12.33	77 12.42	45 7.21	84 15.22	74 12.33	33 14.47	20 9.17	52 11.09	75 13.71	55 7.94	87 13.70	45 7.06	12 4.22
CM n %	2 0.88	25 4.11	25 4.03	45 5.13	20 3.62	16 2.78	11 4.82	3 1.38	14 2.68	17 3.11	42 6.25	21 3.31	4 0.63	
AG/AP n %	8 3.51	32 5.26	19 3.06	15 2.10	17 3.08	23 2.87	9 3.25	5 2.32	13 2.48	24 3.94	16 2.27	20 3.15	11 1.73	
CO n %	5 2.19		5 0.81	6 0.85	3 0.55	5 0.87	2 0.92				3 0.43		3 0.47	6 2.53
D n %														
CA n %	2 0.58	1 0.16	1 0.16	2 0.32	1 0.18	1 0.17	1 0.44		1 0.19	1 0.16	3 0.47	3 0.47	1 0.16	1 0.17
S n %														
FLY n %					1 0.19					2 0.37				
TOT. n %	228 100.00	608 100.00	620 100.00	624 100.00	552 100.00	576 100.00	228 100.00	218 100.00	523 100.00	547 100.00	705 100.00	535 100.00	637 100.00	237 100.00



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