ECOLOGICAL STUDIES ON THE WHITE-FACED HERON

(*Ardea novaehollandiae novaehollandiae* LATHAM 1790)

IN THE MANAWATU

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

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Frontispiece : White-faced Heron on the nest incubating eggs.
Adults have a white face and lanceolate plumes on the back.

ABSTRACT

White-faced Herons were studied near Pukepuke Lagoon, Manawatu, from March 1980 to February 1981, and at Palmerston North between April and June 1980. Usually three days a week were spent in the field to observe herons, sample feeding areas, and to visit roosts and nests.

Diurnal and seasonal time budgets and feeding ecology patterns were compiled for herons feeding in pasture, from 39 581 bird observations and 5004 recordings of feeding rates respectively. The influence of time of day, season, food availability, breeding, and moult, on the time budget and feeding ecology is discussed. Data from Pukepuke and Palmerston North are compared. The location of herons in fields was plotted to determine whether certain areas of pasture were favoured as foraging sites.

Feeding areas at Pukepuke were sampled weekly with a sweep net and a soil quadrat to determine the potential prey for herons foraging in pasture. A comparison was made between the number and dry weight of animals collected at different times of the day, in different seasons, and between feeding and non-feeding areas. The diet was assessed by direct observation of prey, analysis of regurgitated pellets and food, and from the stomach contents of one heron. A total of 30 748 prey animals were recorded, with the great majority of them from pellets. Monthly and seasonal changes in the diet are discussed in relation to changes in the relative availability of prey species.

Some breeding data were obtained, including the measurements of 21 eggs. The biology of herons is summarized and discussed as it relates to White-faced Herons.

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CHAPTER ONE

INTRODUCTION

Herons are a distinctive and easily recognisable family of birds, even to people with only a passing interest in ornithology. They are generally large, conspicuously coloured, and hunt in open areas, making them fairly easy to locate and observe. These graceful and attractive birds have long been favourite subjects of many bird-watchers.

1.1 Herons in New Zealand

The White-faced Heron (*Ardea novaehollandiae*), also called the Blue Heron or Blue Crane, is the most widespread and most populous heron in New Zealand, and is therefore the one usually seen by most people. The species is widely distributed over the south-west Pacific region. Around New Zealand, the species is established on the Chatham Islands (B.D. Bell in Carroll 1970), and has reached the Snares (Horning and Horning 1974), Kermadec, Auckland, Campbell, and Macquarie Islands (Hancock and Elliott 1978). It is found throughout Australia wherever there is suitable habitat, and is established on New Guinea, New Caledonia and many nearby islands (Hancock and Elliott 1978).

Nine other heron species have been recorded in New Zealand, including four vagrants (Falla *et al*. 1979). The others breed here but have small populations (Falla *et al*. 1979), and scattered distributions in this country (Bull *et al*. 1978). The two bitterns (*Botaurus stellaris* and *Ixobrychus novaezelandiae*) are secretive and restricted to swamps and marshes. The White Heron (*Egretta alba*) is our best known heron and apparently only breeds near Okarito in South Westland, but afterwards disperses throughout the country. Reef Herons (*Egretta sacra*) are strictly coastal dwellers, favouring rocky shorelines especially north of the Bay of Plenty. Cattle Egrets (*Bubulcus ibis*) arrived about 20 years ago and as numbers increase their range is expanding.

1.2 History of the White-faced Heron in New Zealand

The White-faced Heron almost certainly colonized this country from Australia in pre-European times. Carroll (1970) has thoroughly documented its subsequent occurrence, establishment, and spread within New Zealand so only a brief account is given here. The first published reference to White-faced Herons was by Buller (1868), who obtained several from the North Island. The species was also known to be in the Nelson district at about that time (Oliver 1955). Early reports indicate that the first points of landfall and settlement were in South Westland and possibly Tasman Bay, Nelson (Carroll 1970). Breeding was not confirmed until 1941 (Ellis 1945), but Falla (1942) after investigations at Okarito wrote, "It seems likely that it has been a common breeding species there during the whole period of European settlement, and before ... ".

Population growth was slow until the 1940's but during the next ten years it accelerated before peaking in the 1960's and subsequently stabilizing (Carroll 1970). It is unclear if the population explosion was augmented by further arrivals of Australian stragglers. Settlement progressed from coastal to inland districts and generally from south to north (Carroll 1970). In 1947 one heron was seen at Palmerston North, and during the next decade solitary birds and small groups appeared along the Manawatu coast and at inland localities. The species now occurs throughout the country and is widespread in both coastal and inland habitats (Carroll 1970, Bull _et al_. 1978).

1.3 Previous research and aims of the study

There are only two published studies of the White-faced Heron, both in New Zealand by Carroll (1967, 1970). The first followed complaints that the population explosion of White-faced Herons had led to a serious depletion of trout stocks in some areas, and so their diet was studied. Carroll's 1970 paper covered the species' history in New Zealand. Spurr (1967) and Louisson (1972) in two unpublished B.Sc.(Honours) theses, studied the behaviour of coastal herons at Kaikoura, Marlborough, and at Akaroa Harbour, Canterbury respectively. References to the species in the Australian literature are usually just records of its presence in regional bird lists.

Many other herons have been extensively studied, but much of the research has concentrated on their feeding ecology and breeding biology (Jenni 1969, Kushlan 1978). There are few time budget studies of herons, and there is a lack of data for herons foraging in a terrestrial habitat. Both aspects can be studied in the White-faced Heron. When feeding and resting they tend to remain in rather small areas for extended periods and they forage primarily in open areas, which facilitates an observational study. White-faced Herons feed extensively on pasture, which is unusual among herons, so I concentrated on this habitat as a comparison with studies of herons in aquatic environments.

The aim of this study is to investigate aspects of the biology of the White-faced Heron. There are five sections:

1. Compilation of a diurnal and seasonal time budget.
2. Description of the diurnal and seasonal feeding ecology of herons foraging in pasture.
3. Determination of the potential prey in pasture.
4. Determination of the diet of herons at Pukepuke.
5. Collection of incidental breeding information.

CHAPTER TWO

STUDY AREAS

2.1 Manawatu-Rangitikei sand country

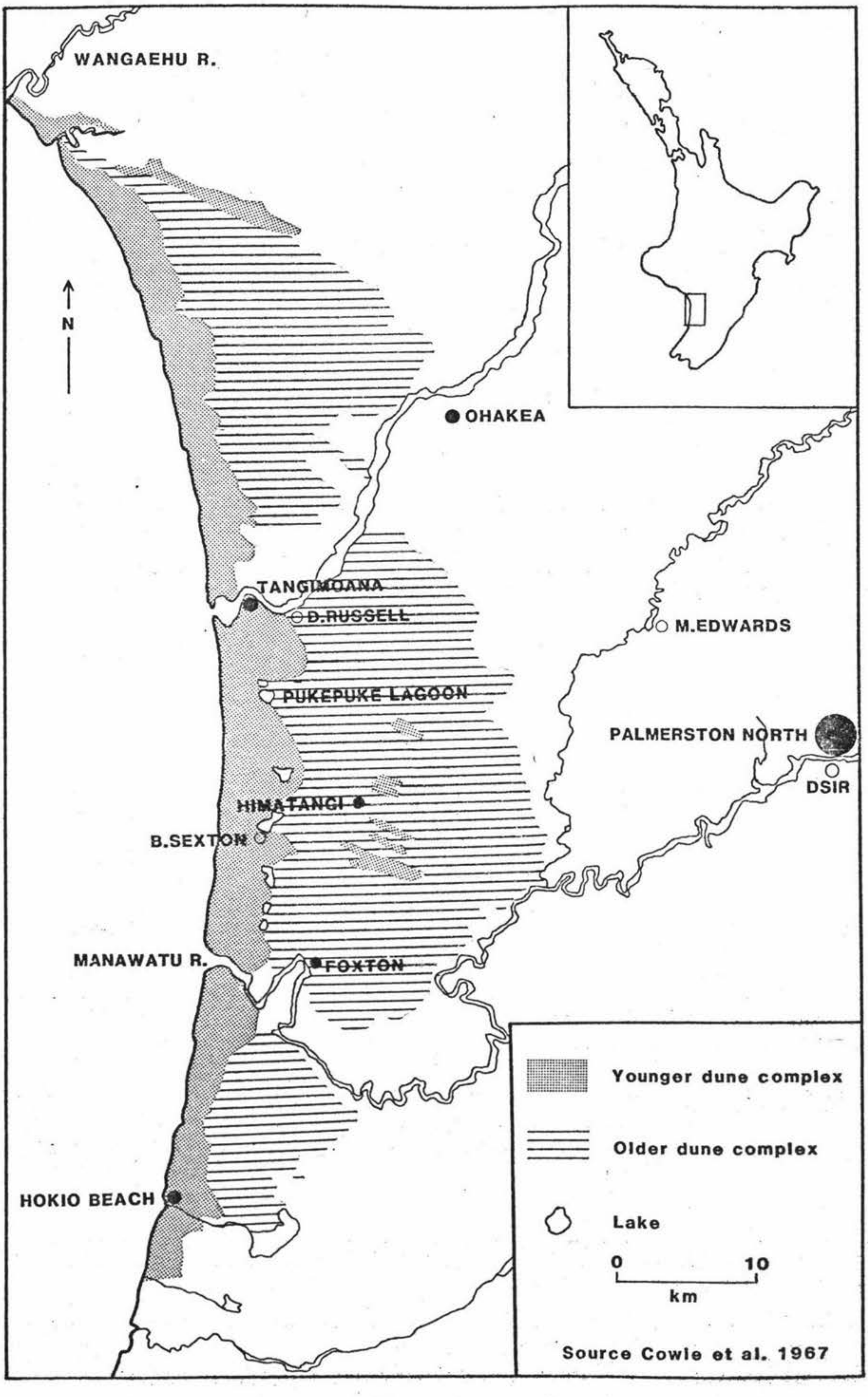
The Manawatu-Rangitikei sand country comprises a complex of dunes, sand plains, peaty swamps, and shallow lakes on the west coast of the southern North Island (Figure 2.1). It covers approximately 420 000 ha from the Wangaehu River to Hokio Beach (Cowie et al. 1967). The intensive study was centred around the Wildlife Service's game management reserve at Pukepuke Lagoon about 30 km west of Palmerston North. The lagoon is one of the larger coastal dune lakes in the sand country and lies on the boundary between two dune complexes (Cowie and Smith 1958). The younger formation extends inland 0.4-6.4 km from the coast, as a complex of recent and unconsolidated dunes and flats which have large areas with insufficient plant cover to prevent wind erosion of the sand. Further inland are the consolidated dunes and flats of an older dune complex which are well vegetated and where there is little serious wind erosion (Cowie et al. 1967).

The principal land use in the region is sheep and cattle farming. Farms sited on younger dunes have developed pastures only on the sand plains, while the dunes themselves have been fenced off and left in scrub or planted with pines.

2.2 Pukepuke

The study area occupied parts of the Department of Lands and Survey Tangimoana Block and P. Barber's farm (Figure 2.2 and Plate 1). Herons were observed at area one on P. Barber's farm from March to May 1980 and during January and February 1981. Area two was used between April and July, then I moved to area three from July to October. Observations were made at area four from September to December, and at area

FIGURE 2.1 THE MANAWATU -RANGITIKEI SAND COUNTRY



Source Cowie et al. 1967

FIGURE 2.2 TANGIMOANA LANDS AND SURVEY BLOCK

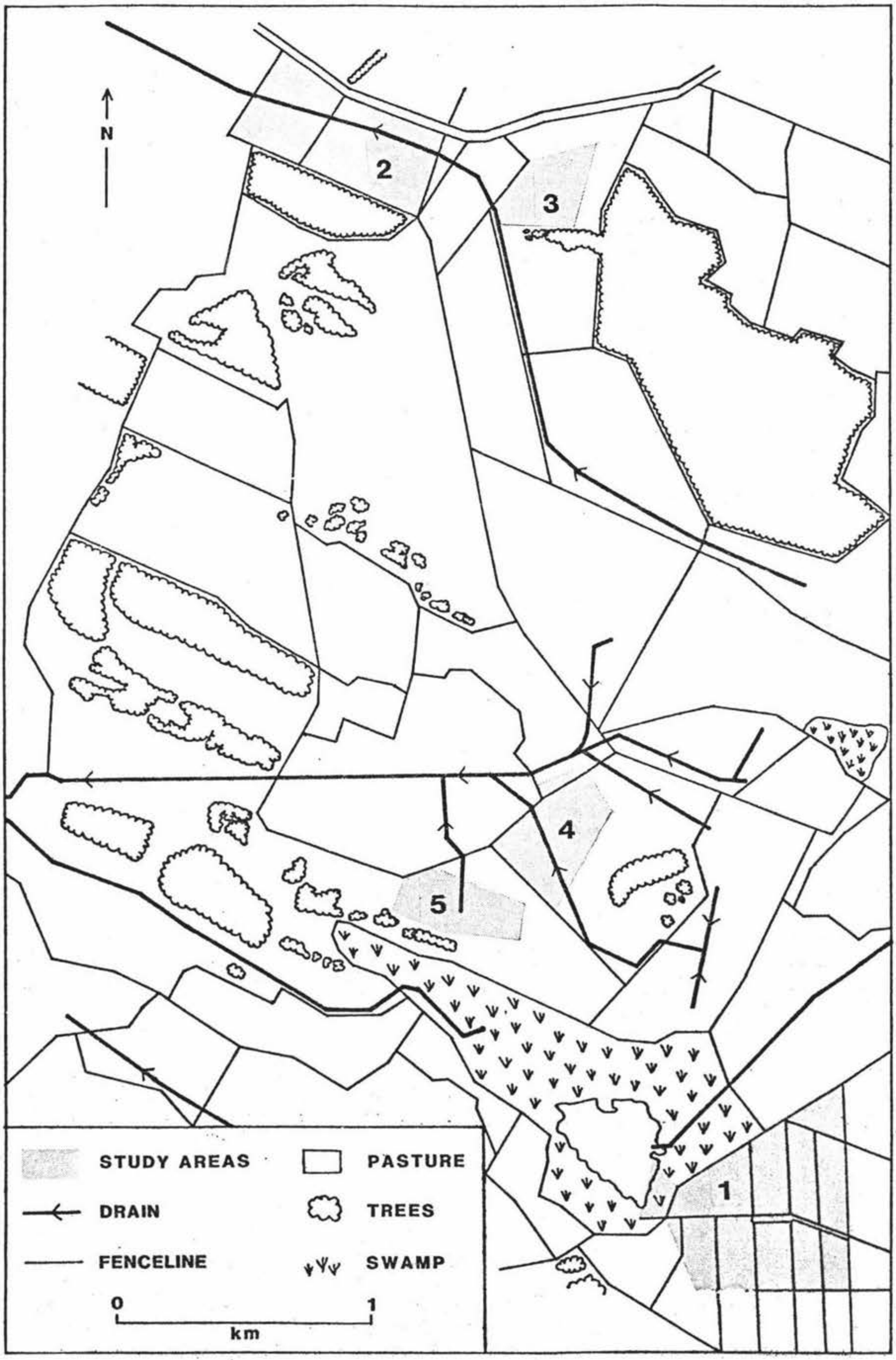


Plate 1 : Group of herons in a typical pastoral situation, with short pasture and areas of surface water.

five between October and December. Each area comprised fields of short grazed pasture with various amounts of surface water.

2.3 Soils

The parent material of most of the soils of the region is wind blown sand derived from greywacke of the central ranges. As a result of sorting during transport down rivers, along beaches, and inland by wind, these sands are of a fairly uniform size grade, with negligible amounts of silt and clay. Quartz and feldspar are the dominant minerals. The soils of the study area are described by Cowie et al. (1967) as being imperfectly drained and low in organic matter.

2.4 Climate

The Manawatu-Rangitikei sand country has a moderate climate, not marked by extremes of weather or by sharp seasonal contrasts (Cowie et al. 1967). Winters are mild and moist with many frosts, especially on the low-lying sand plains. In spring, the winds increase in frequency and strength, and during the warm summer, rainfall is comparatively low and drought conditions can occur on freely drained lands. Autumn is warm, having higher temperatures and humidity than in spring.

Air temperatures peak in February and are lowest in July, and frosts are common between June and August (Cowie et al. 1967). Rainfall usually increases steadily from the driest month, March, to the wettest month, June, followed by a decrease to September, a marked increase during October and then a decrease over the summer months (Cowie et al. 1967). Tangimoana, about 3 km north of the study area, averaged 893 mm of rain and 141 rain days per year (Cowie and Smith 1958). The prevailing winds are from the west-northwest, and commonly reach gale force especially during spring and early summer. These winds decrease in frequency and strength over late summer and autumn, when easterlies are more frequent. From late autumn to early spring, light winds prevail and calm spells are common between winter storms (Cowie et al. 1967). Sunshine on the coast totals over 2 000 hours annually (Tomlinson 1976).

Meteorological data over the study period were obtained from the Ohakea station 16 km northeast of the study area, and from the Wildlife Service's station at Pukepuke Lagoon (Appendix 1). Air temperatures were similar to the pattern described by Cowie et al. (1967), but the rainfall was markedly different. March was exceptionally wet, but the rest of autumn and winter (usually the wettest season) was drier than normal. Spring was considerably wetter than usual and was the wettest season, while summer had much less rain than in recent years and was the driest season. The water table in the study area was high during winter and spring, and many pastures had extensive areas of surface water at this time of year.

2.5 Vegetation

Virtually all of the original pre-European climax vegetation of the Manawatu-Rangitikei sand country has been extensively modified. In European times, many unconsolidated dunes have been planted with marram grass (Ammophila arenaria), tree lupin (Lupinus arboreus), and pines (Pinus radiata), which have successfully stabilized them against wind erosion. The sand plains have been cleared, drained and sown with introduced grasses such as ryegrass (Lolium spp.) and clover (Trifolium spp.), which are the main pasture species in the study area.

The pre-European vegetative succession that existed on the dune complexes, from the pioneering plants on the newly formed and unconsolidated foredunes, to the climax shrubland vegetation on the older dunes and flats was described by Carnahan (1957). Today examples of this flora can be seen only on former wandering dunes that are now stabilized, on formerly grazed land that has reverted to scrub, or in peaty swamps where farming has not been possible.

2.6 Fauna

The Pukepuke Lagoon reserve and surrounding areas of farmland, pine plantations, and scrub, supports a broad diversity of wildlife. Short-finned Eels (*Anguilla australis*) are common and some Long-finned Eels (*A. dieffenbachii*) are present. A few small native fish (*Galaxias*, *Retropinna*, *Neochanna*, and *Gobiomorphus* spp.) inhabit the main dune lakes (Cunningham 1957, McDowell 1978), and carp (*Carassius* spp.) are also present in Pukepuke Lagoon (Baker-Gabb 1978). Golden Bell frogs (*Litoria raniformis*), Whistling frogs (*L. ewingi*), hedgehogs (*Erinaceus europaeus*), rats (*Rattus norvegicus* and *R. rattus*), ferrets (*Mustela putorius*), stoats (*M. erminea*), and weasels (*M. nivalis*) are all present. Other animals found in the area are possums (*Trichosurus vulpecula*), rabbits (*Oryctolagus cuniculus*), hares (*Lepus europaeus*), feral cats (*Felis catus*) (Robertson 1978), and a few Sambar deer (*Cervus unicolor*) (pers. obs.). The lagoon and surrounding swamp support a large population of waterfowl and swamp birds, and Falla (1957) noted that introduced passerines, mainly finches, are numerous in the sand dunes.

Herons in the study area were most likely to be associated with Pukekos (*Porphyrio Porphyrio*) when they were near the lagoon, otherwise with Magpies (*Gymnorhina tibicen*), Starlings (*Sturnus vulgaris*), various finches, Harriers (*Circus approximans*), and Spur-winged Plovers (*Vanellus miles*).

2.7 Supplementary study areas

Additional observations were made on a group of herons near Palmerston North from April to June 1980. These birds frequented an area of experimental plots with heavily grazed to moderately long pasture at the DSIR, 3 km south of the city (Figure 2.1). Regular visits were also made to the farms of : M. Edwards, Oroua Road; D. Russell, Tangimoana Road; and B. Sexton, Wylies Road (Figure 2.1); to visit heron nests and a roost to gather breeding data and regurgitated pellets.

CHAPTER THREE

GENERAL BIOLOGY

3.1 Classification and Evolution

Herons, egrets and bitterns belong in the family Ardeidae, and are related to storks, ibises, and spoonbills as members of the order Ciconiiformes (Hancock and Elliott 1978). The Ardeidae comprises 61-64 species (depending on whose classification is followed), in two subfamilies; the Botuarinae bitterns and Ardeinae typical herons, and the tribe Ardeini (day herons) which includes the White-faced Heron, is the largest group in the family.

Sharpe (1875) assigned the White-faced Heron to the genus Notophoyx based on its absence of nuchal plumes in breeding plumage. Such plumage characters are, however, now considered insufficient to justify recognition at a generic level (Hancock and Elliott 1978), and the species is currently included in the genus Ardea (CSNZ 1980). Curry-Lindahl (1971) who made a comparative study of behaviour and ethology, states that it " ... is the dwarf of the genus but nevertheless a typical Ardea". Payne and Risley (1976) however, place it in the genus Egretta on the basis of skeletal comparisons, so further comparative work is necessary to determine its proper position. The subspecies A. novaehollandiae novaehollandiae found in New Zealand and most of Australia, is distinguished by its lighter plumage from A. n. parryi found in northwest Australia (Hancock and Elliott 1978). The subspecific status of the apparently smaller herons in New Caledonia A. n. nana (Oliver 1955), has yet to be confirmed (Hancock and Elliott 1978).

The heron family is at least 60 million years old, and the genus Ardea is known from the Miocene 20-30 million years ago (Lowe 1954). The Ardeidae apparently originated in tropical parts of the Old World (Curry-Lindahl 1971), and while still found mostly in the tropics and subtropics, have expanded over all regions except the far north and Antarctica.

3.2 Morphology and Plumage

Herons are medium to large birds standing 40-140 cm tall (Hancock and Elliott 1978) and weighing 100-2600 g (Grzimek 1972). Typically the body is slender and held upright, and the neck and legs are long. Part of the tibia is bare and all four toes are long with the middle one flattened and serrated. The head and neck have a number of adaptations for feeding. The eye position permits binocular focus beneath or at the tip of the bill (Kushlan 1978), which except for a few species is long, strong, straight and pointed. Thick heron bills are probably an adaptation for handling large prey, while thin bills are adapted for catching fast-moving prey (Kushlan 1978). The distinctive kink in the neck is due to the sixth cervical vertebra articulating differently from the others, which permits the oesophagus to slide before or behind the vertebrae to facilitate swallowing large prey, and also acts as a fulcrum for rapidly thrusting the head and neck forward (Cameron and Harrison 1978).

The digestive system lacks a crop but the proventriculus (glandular stomach) is well developed while the gizzard (muscular stomach) is relatively undifferentiated. This arrangement only occurs in birds whose food requires little mechanical treatment, such as fish and meat eaters, and the primary requirement is for an expansible organ for holding food while it is digested chemically (McLelland 1979). The gizzard also acts as a barrier to indigestible fragments in the food which are regurgitated as pellets (see Chapter 7).

Herons do not oil their plumage for their preen gland is vestigial, instead they have specialized regions of plumage called powder-down areas (Grzimek 1972). All species have pairs of such areas on the breast and rump, and some species have a third pair in the groin region. Feathers in powder-down areas grow continuously and are composed of fine filaments without lateral offshoots which crumble into a powder when rubbed with the bill. Herons work this powder into their plumage during preening, cleaning it of slime and oil and keeping it water repellent. The powder is combed out with the specialized middle toe.

The plumage colour is some combination of grey, blue, green, purple, rufous, or white (Thomson 1964). The sexes are generally alike and the juvenile plumage rarely differs greatly from that of the adults, although colour phase polymorphism is a characteristic feature of several species. Kushlan (1978) suggests that the primary adaptive pressures associated with plumage colour are conspicuousness to prey and to other birds, while secondary factors include the heat load on birds in highly insolated environments. Kushlan (1978) accurately predicted the dorsal and ventral plumage shading of most species in a representative sample of herons by categorizing their feeding ecology. Gregarious species and those living in the tropics tend to be white to make them conspicuous and to reduce heat loads, while herons that live amongst dense cover tend toward cryptic colouration for concealment to prey. Active diurnal foragers like the White-faced Heron are less conspicuous to prey if they have a light ventral plumage. White-faced Herons are not particularly gregarious so a dark dorsal plumage makes them less obvious from above. Kushlan's predicted pattern for the White-faced Heron is close to what occurs, although the dorsal plumage is only slightly darker than the ventral colour.

The White-faced is a medium sized heron, standing approximately 66 cm high (Falla et al. 1979) and weighing about 625 g (A. Carroll in Spurr 1967b). A band of white extends from the forehead around the eyes and onto the chin and throat (see Frontispiece). The rest of the head, neck, and upper plumage is bluish grey with long pale grey lanceolate plumes on the back, while the undersurface is light grey with chestnut feathers on the breast. Wing quills and tail feathers are a dark slate-grey which can be clearly seen in flight. The bill is black and the legs are greenish-yellow or occasionally reddish. The sexes are indistinguishable, but immature birds have a paler plumage and lack the distinctive white face and long plumes of the adults (Louisson 1972, pers. obs.). Oliver (1955) and Stonehouse (1968) state that juveniles have more white on the head and neck, but Plates 2 and 3 show that this was not true in Pukepuke birds.

3.3 Breeding

Breeding in herons is preceded by pair bond formation at the nest site, with displays involving body postures, nuptial plumes, and vocalizations; while the selection, presentation, and incorporation in the nest of nesting material is also important (Hancock and Elliot 1978). During the sexual display period, the non-feathered parts of the body (e.g. bill, lores, legs, and feet) change colour in many species.

All types of nesting situation from solitary through loose groupings to dense colonies occur, and most herons are colonial. A notable feature is that heron colonies contain all or most of the colonial nesting heron species in the area. The nest which is usually built by both parents, is generally a platform of sticks placed in a tree, although marsh dwelling species construct nests of reeds on the ground.

Clutch size ranges from one to nine and both sexes incubate. Eggs are lost through robbing by avian, mammalian, and reptilian predators; rolling out during high winds which may also blow down nests, or through other herons stealing nest material; while some eggs are infertile (Meanley 1955, Jenni 1969). Incubation starts after the first or second egg is laid so hatching is asynchronous. In tree nesters the downy young remain in the nest for the first few weeks, then they begin to wander around the nest site, returning to the nest for meals (Lowe 1954, Meanley 1955). Both parents attend the chicks

Plate 2 : Fledglings about four to five weeks old. It was unusual for a nest to have more than two chicks of this age.

Plate 3 : Juvenile White-faced Heron. Immature birds can be distinguished from adults by their paler plumage and lack of a white face and plume feathers.

Plate 4 : Nest containing two chicks, with a sack tied about 1.7 m directly below it to catch pellets.

Plate 5 : Eggs and nest which is a flattish platform constructed of sticks.

and feed them regurgitated food. During the first few days after hatching, food is regurgitated directly into the nest, later the chicks stimulate regurgitation by grasping the parent's bill crosswise with their own and are fed directly (Lowe 1954, Meanley 1955, Moon 1967).

White-faced Herons nest singly or in a loose group, but unlike other herons not necessarily near water (Hancock and Elliott 1978, pers. obs.). They choose a variety of trees usually building high in the crown (up to 22 m, Moon 1979) and often away from the trunk (Moon 1967, pers. obs.) (Plate 4). Falla *et al.* (1979) also record a nest in a beached passenger ferry, while in the Chatham Islands, nests have been found on a cliff ledge (Gordon 1979) and among boulders (Wright 1979). Possible reasons suggested for these unusual sites were a lack of suitable trees, high winds, and predation.

Eggs are normally laid from June to December, and the usual clutch is three to five pale blue eggs (Falla *et al.* 1979) (Plate 5). At Pukepuke breeding starts in August and September, and the feeding of young reaches a peak in October. The clutch size was known in only five nests with three, three, four, four, and five eggs, because other nests were either inaccessible or the eggs had hatched before I found the nest. Twenty-one eggs from nine nests averaged 45.5 x 33.4 mm (Appendix 2). These figures are shorter and narrower than those quoted for White-faced Heron eggs in : Western Australia, 48.1 x 34.6 mm (**Serventy** and Whittell 1962); south-eastern Australia, 48-51 x 34.3 - 35.1 mm (Hancock and Elliott 1978); Tasmania, 48.5 x 34, 47 x 33.5 mm (Oliver 1955); and the Chatham Islands, 47.9 x 36.1 mm (Wright 1979). Egg size varies according to Bergmann's rule of increasing size with increasing latitude (Dann 1977), but because the number of eggs on which these figures are based is either not given or less than 20, little significance can be given to the differences.

Devonshire (1976) observed a pair of White-faced Herons which successfully nested twice in the same season, the later clutch being laid in late January and the chicks fledging in April. It is not unusual for a pair which has lost their first clutch to re-nest, but this is the only report of a pair fledging two broods in the same season. Some eggs are blown out of the nest during storms (M. Edwards pers. comm.), and nests are occasionally robbed by Harriers (M. Edwards, B. Sexton pers. comm.) and Magpies (Hudson 1972). But the theft of nest material is probably unimportant as a cause of nest failure since the White-faced Heron is not a colonial nester.

Incubation lasts about 25 days, and the young fledge at about six weeks (Falla _et al._ 1979) (Plate 2). Initially the chicks are fed throughout the day, and are constantly brooded by one parent while the other feeds. As the young develop the interval between meals gradually lengthens and they are not brooded, although one parent stands guard nearby. After three or four weeks the chicks are left unattended, and by their final week in the nest are fed only early in the morning and in the evening (Moon 1967). Once the chicks fledged and began foraging for themselves I never saw them being fed, although what were presumably family groups did feed together.

3.4 Mortality

Adult herons are seldom predated upon (Kushlan 1978), although White-faced Herons occasionally fall prey to Harriers (Redhead 1969), New Zealand Falcons (_Falco novaeseelandiae_) (Fox 1975), and Peregrine Falcons (_Falco peregrinus_) (Pruett-Jones _et al._ 1981). The main cause of mortality in herons is starvation (and attendant diseases) of the young, either in the nest or once they leave it. Nestling mortality is greatest in the first two weeks (Kushlan 1978). At this time, growth is rapid, the relative size difference between siblings is great, and only one parent is foraging, so the smallest chicks often starve. Nests that I observed usually fledged only one or two young compared with the usual clutch of three to five eggs. Chicks at all stages of development were found dead beneath nests, including one nestling with a deformed bill which is described in Appendix 3. Mortality is also high in the first months after independence. First-year birds in six heron populations (composed of four species), had an average mortality rate of 70% compared with 29% in older birds (Kahl 1963, and references cited therein). Presumably this is because juveniles forage less efficiently than adults (see section 5.4.2).

3.5 Migration and Dispersal

About half of world's herons have a regular seasonal migration, and virtually all herons show some dispersal activity after the breeding season (Hancock and Elliott 1978). High latitude nesters must retreat from adverse weather, while the relief of feeding grounds which may have been under intense pressure during breeding could be a factor in the movements of other herons.

White-faced Herons, at least in New Zealand, do not appear to migrate, but there is a regular post-breeding movement to the coast which is reversed in winter as birds move onto wet inland pastures. Between 1976 and 1981, the Manawatu River estuary (Figure 2.1) had an average of 34 and up to 68 White-faced Herons over summer and autumn, compared with only four birds during winter and spring (Dr L. Davies pers. comm.).

3.6 Feeding

The dominating factor behind the evolution of heron feeding methods is the association of feeding areas with water, whether it be a lake, river, stream, swamp or the sea. There are two basic feeding methods used by all herons (Hancock and Elliott 1978, Kushlan 1978). The classic technique is to stand still and patiently wait for prey to approach, the other is to walk slowly through a field or shallow water stalking prey. But herons have a remarkable diversity of additional feeding behaviour. Each species has a repertoire of techniques and a range of food preferences related to its structure, particularly the size and shape of the bill and length of leg and neck.

The more sophisticated techniques are grouped under "disturb and chase" by Meyerriecks (1962), who suggests that they follow an evolutionary sequence. The first stage in the sequence is "wing-flicking", where a heron partially extends and retracts its wings rapidly while walking slowly, presumably to startle prey from cover by suddenly casting a shadow on the water. This extends into "open-wing feeding" where a walking or running bird briefly opens one or both wings completely. In "under-wing feeding" the wings are held open while the heron stabs at prey underneath them. The advantage seems to be that either the shade created improves vision by reducing reflections from the water, or it attracts fish into a false refuge. The final step is "canopy feeding", best seen in the Black Heron (Melanophoyx ardesiaca) which brings its open wings forward so that the fore-edges meet while it tucks its head under the enclosed canopy.

A variety of other techniques from "hawking" for flying insects to associating with large animals such as cattle which act as beaters are also used. Prey are also flushed by disturbing the substrate with the foot, while over deeper water, prey are caught by diving, and hovering above the water (Kushlan 1976). Meyerriecks (1962) and Kushlan (1976) also record many variations in the way these methods are used.

Herons are typically gregarious when feeding, and cooperation with other water birds such as mergansers and cormorants in catching prey has been observed by Christman (1957), Parks and Bressler (1963), and Emlen and Ambrose (1970). Nevertheless, many herons maintain feeding territories (Meyerriecks 1962, Recher and Recher 1972, Cook 1978a, Kushlan 1978), which partitions food resources between conspecifics. Resource partitioning between species in achieved differently. Since herons are basically similar in morphology and use many of the same hunting techniques, species foraging in the same place could potentially have a considerable overlap of prey resources. Overlap of prey is minimized however, because herons whose foraging grounds coincide have distinct feeding ecologies. Studies by Meyerriecks (1962), Jenni (1969), Willard (1977), and Recher and Recher (1980) have shown that herons are separated on the basis of habitat (water depth, open or vegetated, aquatic or terrestrial), body size (leg length, size and shape of the bill), time of feeding (day or night), foraging strategy (methodical searcher or active pursuer), prey selection (species, size, slow or fast moving), and by an interspecific dominance hierarchy based on size.

White-faced Herons are not particularly gregarious, but groups of over 20 birds occasionally fed together. At Pukepuke their standard method of hunting was a steady walk while capturing prey either off vegetation or from the ground. The "stand and wait" method was not used on pasture and nor were any "disturb and chase" techniques. Occasionally they performed what I called "foot-shake" (described in Appendix 4), when feeding in surface water. This behaviour presumably disturbs hidden prey and is equivalent to what Meyerriecks (1959) calls "foot-stirring". Another feeding behaviour observed even more rarely was "neck-swaying". After sighting an animal, the heron would sway its neck sideways a few times before striking. Cattle Egrets perform a similar behaviour but it is developed further and used much more frequently than in White-faced Herons (Blaker 1969). Blaker (1969) suggests that " ... neck-swaying is used chiefly on prey animals which the bird recognises as active and likely to escape". Another adaptation to terrestrial foraging adopted by Cattle Egrets is to follow large animals and catch insects that they disturb. White-faced Herons do not use this technique and were not observed obviously associating with stock. Feeding territories were not observed in this study, but it seems they do occur in White-faced Herons (Spurr 1967b).

When foraging in water, White-faced Herons use more methods than when foraging on pasture, although their principal technique is still a slow walk. Herons feeding at the edge of Pukepuke Lagoon used "walk slowly" or occasionally "stand and wait", but Spurr (1967a) and Louisson (1972) also observed "foot-stirring", "wing-flicking", "open-wing feeding", and "hovering" in the feeding repertoire.

To summarize, the White-faced Heron is a generalist in its habitat and food. It occurs in all aquatic habitats as well as pastures and rough grazing land, hunting in a slow methodical manner for a variety of prey. Recher and Recher (1980) suggest that Australia's highly variable rainfall and the consequent fluctuations in the extent of aquatic habitats from year to year "probably ... explains the ecology of the White-faced Heron as a bird able to exploit a wide range of habitats and foods and not be confined to aquatic environments".

CHAPTER FOUR

DIURNAL TIME BUDGET AND FEEDING ECOLOGY

4.1 Introduction

An important part of the ecology of an animal is the way it divides the time and energy available to it among the various activities associated with self-maintenance and reproduction. Since there is a limited amount of time to perform all these activities, animals should apportion their time in such a way as to optimize their chances of surviving and reproducing. How a species organizes its time can be determined by compiling a time budget, which is a record of the time spent on each activity. Time and energy are interrelated resources, so to fully understand the adaptive significance of a time budget it should be considered together with an energy budget (King 1974). However, energy budgeting was beyond the scope of this study and was not attempted.

The way a species utilizes its food resources is also of interest to ecologists. Feeding methods used by White-faced Herons were discussed in section 3.6, and here I examine how the birds adjust their feeding to time of day and to relative prey availability. Like time budgets there should be an optimum feeding strategy, which takes into account various factors such as daylength, substrate, prey species, and characters of the predator itself.

4.2 Methods

4.2.1 Time budget

The largest group of herons known at Pukepuke was observed from one of the Wildlife Service's permanent hides, my own portable hide (Plate 6), and from a car. Because the herons periodically changed their feeding area, observations were made at the five main areas described in section 2.2. Equipment used during hide watches comprised

Plate 6 : Portable hide from which time budget and feeding ecology data were collected.

a 15-60 x telescope, 8 x 40 binoculars, wristwatch, automatic timer, counter, tape recorder, and a camera.

Time budget data were obtained by taking scan samples (Altmann 1974) at five minute intervals, at which the activities of all herons in view were recorded. An implicit assumption was that the five minute interval did not parallel any behavioural periodicity, and as far as possible each bird was observed for an equally brief period. Since the probability of recording an activity depended on how much time a bird spent on it before switching to another activity (Fordham 1978), the summed frequencies of the different activities, converted to percentages, gave an estimate of the percentage of time spent on each activity (Altmann 1974). By combining the data from a number of herons, taken from many scan samples, a diurnal and seasonal time budget was compiled for the "average" heron. The time budget refers only to time spent at feeding areas and does not include time spent at roosts or nests. The sexes cannot be distinguished in the field, and I did not differentiate between the activities of adults and juveniles.

4.2.2 Behavioural categories

The herons' behaviour was recorded in the 24 activities described in Appendix 4. These activities were grouped into the six categories below for analysis and discussion of the time budget:

Foraging: Comprises activities associated with gathering food; searching for, capture, and swallowing of prey.

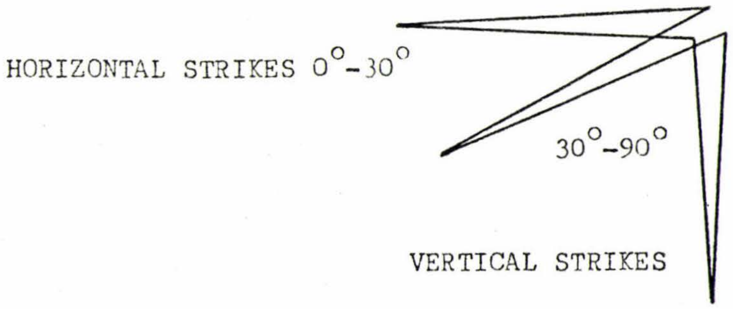
Looking: Includes resting birds and those pausing between some other activity, since on occasions it was difficult to distinguish between them. Resting birds stood still but those pausing to look around were either stationary or moving.

Body care:	Activities concerned with care for the plumage and comfort movements.
Flying:	All flying except aerial chases between herons which were classified as agonistic behaviour.
Agonistic:	Behaviour associated with intraspecific interactions.
Other:	Rarely recorded behaviour including the greeting ceremony between members of a pair and drinking.

4.2.3 Feeding ecology

Feeding rates on pasture were recorded in between the five minute intervals used to gather time budget data. Individual herons were watched continuously for one minute while I counted the number of strikes made at prey and the number of successful strikes. Successful capture of prey was determined by noting if swallowing (described in Appendix 4) occurred immediately after striking. Strikes were scored as "horizontal" or "vertical" (Figure 4.1).

Figure 4.1 : Horizontal and vertical strikes.



A horizontal strike made an angle of 0°-30° with the ground, while vertical strikes were recorded when the bill was directed downwards at between 30°-90° to the ground. The purpose was to relate the direction of strikes to the kind of prey sought, on the assumption that vertical strikes were directed at prey on or in the ground, whereas horizontal strikes were aimed at mobile prey on or above the ground. The number of steps taken during the minute of observation was also recorded as an index of the area searched (Murton et al. 1963), with the assumption that the length of each step was constant.

The one-minute period for observing feeding rates was chosen after initial work showed that feeding generally proceeded continuously, with only brief stops. Observations were taken only from herons which were already foraging. If foraging stopped for more than about five seconds during an observation the data were discarded. The feeding rate of a particular heron (classified as adult or juvenile) was recorded only once in each five minute interval. From the results of a large number of feeding rates the diurnal and seasonal pattern for an "average" heron was determined.

4.2.4 Data analysis

The daylight period for each month was taken as extending from half an hour before the mean sunrise to half an hour after the mean sunset, because the light was generally too poor for accurate observations to be made outside these times. The day was then divided into six equal periods for each month. The mean sunrise and sunset times were calculated from information supplied by the Carter Observatory, Wellington. The data were collated by month and then into seasons: Autumn - March, April, May; Winter - June, July, August; Spring - September, October, November; and Summer - December, January, February.

For statistical purposes I assumed that the periodic activity observations and feeding rate recordings were independent. Unequal amounts of data were collected in each season, so for each diurnal period the overall values for time budget activities and measures of the feeding rate were calculated as the mean of the four seasonal values. Two indices of feeding "intensity" were calculated by combining the activity and feeding rate data:

Hourly strikes : (strikes/hour)	The proportion of time spent foraging in a period or season was converted to minutes of an hour. This was multiplied by the strike rate (mean number of strikes per minute) in that period or season, to give the number of strikes made per hour by an "average" heron.
Hourly catch : (swallows/hour)	This was calculated in the same way as the hourly strike index by substituting the swallow rate (mean number of swallows per minute) for the strike rate.

The overall diurnal and seasonal changes in time budget activities and feeding rate data, including feeding intensity indices, were analysed by an analysis of variance, with tests for linear and quadratic trends to the diurnal data. Chi square with Yates' correction was used to compare time budget data between seasons, while feeding rate data between diurnal periods and seasons were compared with Mann-Whitney U tests. The time budget categories of "flying", "agonistic", and "other" were pooled as "other activities". A Spearman correlation coefficient was calculated between the number of strikes and steps. Significance was set at 0.05 for all tests, and the value of the test statistics are given in Appendices 5 and 6.

4.3 Results

4.3.1 Time budget

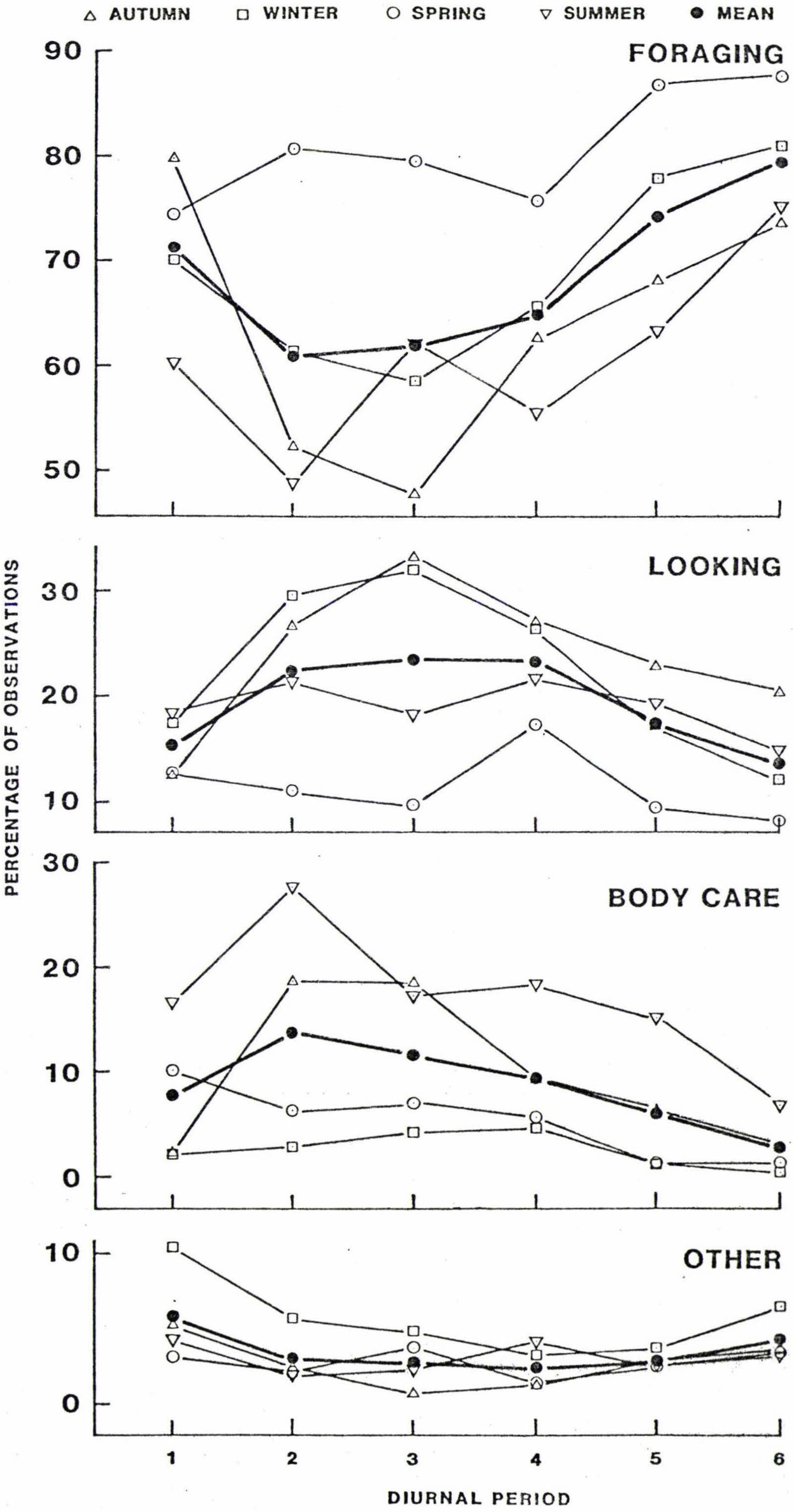
A total of 38 011 bird observations were recorded from predominantly adult birds during 668 hours of observation (Appendix 5). Over the year, herons spent 68.7% of their time foraging, 19.1% looking, 8.7% on body care, and 3.5% on other activities (3.1% flying, 0.3% agonistic, and 0.1% other). Clearly herons did not apportion their time equally among their various activities. The time spent on their four main activities varied over the day, but not in the same way for each activity (Figure 4.2). The variation was significant at the 0.01 level for foraging and body care, and at the 0.05 level for looking and other activities.

Foraging was the most frequently observed activity throughout the day, and overall herons spent more than twice as much time foraging as on all their other activities combined. The overall diurnal pattern was bimodal with an early morning peak and another higher one in the evening. There was a significant linear trend ($P < 0.01$) indicating that an increasing amount of time was spent foraging over the day, and superimposed upon this pattern was a quadratic trend ($P < 0.01$) indicating a significant curve to the data. This overall foraging pattern was followed in each season except spring, when the time spent foraging was comparatively high throughout the day. In all seasons there was a marked increase in foraging from period four onwards.

Looking occupied the second largest proportion of the time budget and peaked between mid-morning and early afternoon. A significant quadratic trend was found ($P < 0.001$) but not a linear one. Diurnal changes were similar in autumn and winter, with large increases in the morning then a more gradual decrease over the afternoon. In spring, looking accounted for a small proportion of time except in the fourth period, and in summer it occupied a similar proportion of time during the first five periods. In each season the time spent on looking decreased progressively over the afternoon.

The pattern for body care activities included a single peak early in the day then a steady decrease over subsequent periods. The pattern was a combination of a decreasing linear, and quadratic trends (both $P < 0.01$). Diurnal patterns were similar in summer and

FIGURE 4.2 DIURNAL TIME BUDGET



and autumn, and in winter and spring. In winter and spring, body care occupied a small proportion of time throughout the day, whereas in summer and autumn there was a large increase from early to mid-morning then a decrease over the rest of the day.

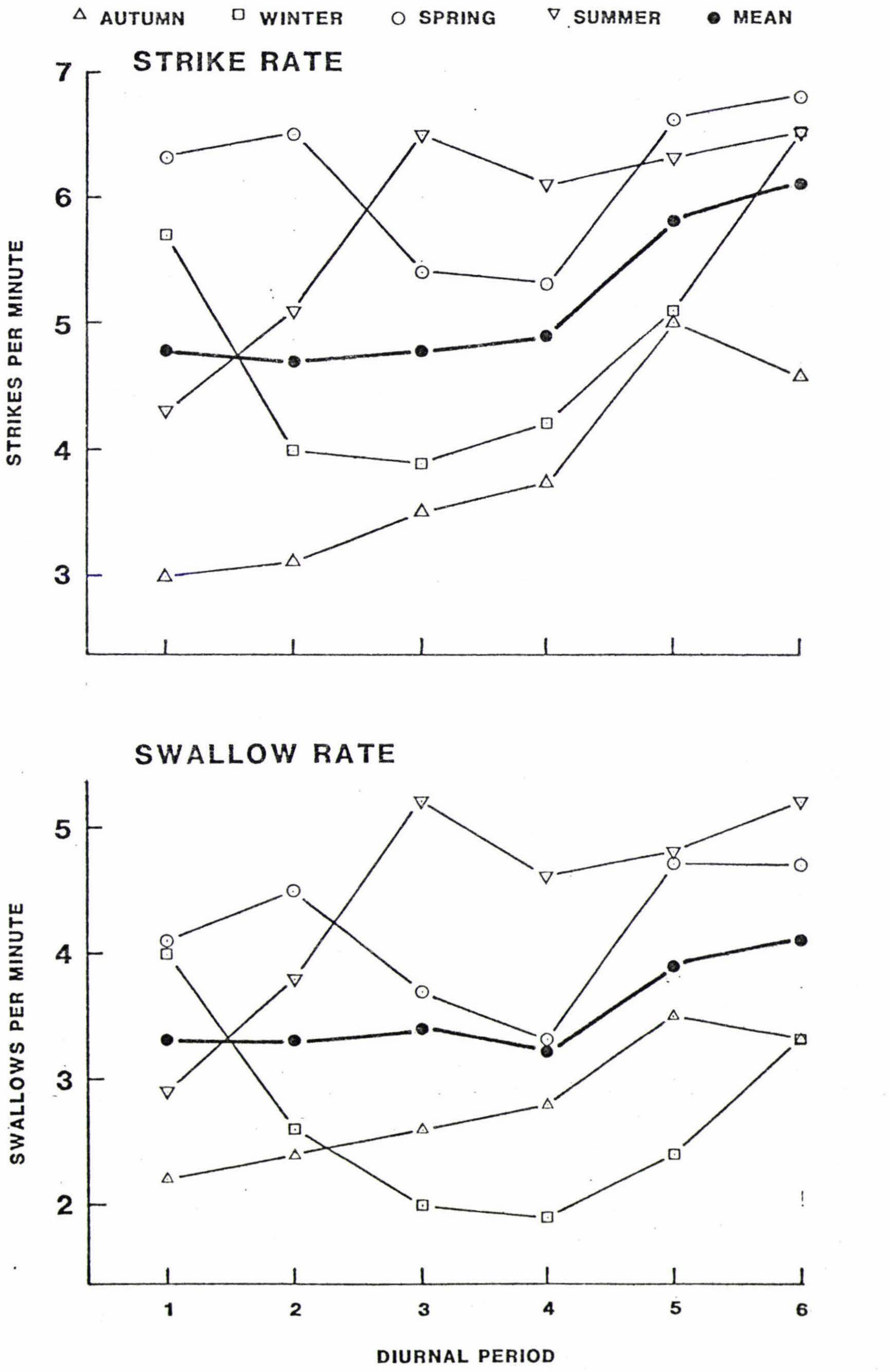
Other activities remained at a similar low level during the day with slightly higher percentages in the first and last periods, so there was a quadratic trend ($P < 0.01$) but no increasing or decreasing linear one. Flying, which accounted for most of these observations, followed the same pattern, while the little agonistic behaviour observed was evenly distributed over the day. Other activities occupied less than 0.4% of each period. The seasonal patterns were similar to the overall one.

4.3.2 Feeding ecology

A total of 4813 feeding rates were recorded including 104 from juvenile herons (see section 5.3.2) (Appendix 6). Over the year, herons averaged 5.2 strikes and 3.5 swallows/minute, which was equivalent to successful capture of prey on 68.2% of strikes. The overall hourly strike index was 218 strikes/hour, the hourly catch index was 147 swallows/hour, and the strikes were in the proportions of 24% horizontal and 76% vertical. There was an average of 38.8 steps/minute and a significant negative correlation between strikes and steps ($P < 0.001$).

Strike rates did not have a significant diurnal variation, but there was an increasing linear trend ($P < 0.01$) although not a quadratic one during the day (Figure 4.3). Summer and autumn had similar patterns as did winter and spring. In autumn the strike rate was significantly lower in the morning than in the afternoon ($P < 0.001$), and similarly in summer the rate was low early in the day and significantly higher from period three onwards ($P < 0.001$). Winter and spring both had bimodal patterns with significantly higher strike

FIGURE 4.3 DIURNAL STRIKE AND SWALLOW RATES



rates at the beginning and end of the day (both $P < 0.001$). Swallow rates had a similar diurnal pattern to that for strikes (Figure 4.3), although they varied less over the day and there was no significant linear increase. Seasonal variations were also similar, differing mainly in the relative position of the winter curve. The proportion of vertical strikes was highest early and late in the day and more strikes were horizontal in the four middle periods. This was the pattern seen in summer and autumn, whereas in winter and spring the percentage of horizontal strikes stayed low over the whole day.

Overall, the percentage of successful strikes was similar throughout the day, and the tests for linear and quadratic trends were not significant (Figure 4.4). In winter however, herons were significantly more successful in the first two periods than during the other four ($P < 0.001$), whereas in the other seasons they were equally successful over the day.

The hourly strike index showed significant variation over the day ($P < 0.01$), with peaks in the early morning and evening which resulted in there being an increasing linear trend ($P < 0.001$) and a quadratic trend ($P < 0.01$) to the data (Figure 4.5). The diurnal patterns in autumn and winter were similar to the overall one, whereas in summer the feeding intensity tended to increase over the day. Herons fed with the greatest intensity throughout the day in spring, but there was a marked drop in the index for the middle two periods compared with the earlier and later ones ($P < 0.01$). Differences in the hourly catch index over the day were also significant ($P < 0.05$), and there were linear ($P < 0.01$) and quadratic ($P < 0.05$) trends. Seasonal variations were similar to those for the strike index, differing in the relative positions of the curves (Figure 4.5).

Unlike the other variables, the step rate was highest in period one and did not increase during the afternoon (Figure 4.6). The data had a significant linear decrease ($P < 0.001$) and a quadratic trend ($P < 0.01$). In summer the step rate decreased throughout the day, while in the other seasons it increased slightly towards evening. The

FIGURE 4.4

DIURNAL PERCENTAGE OF SUCCESSFUL STRIKES

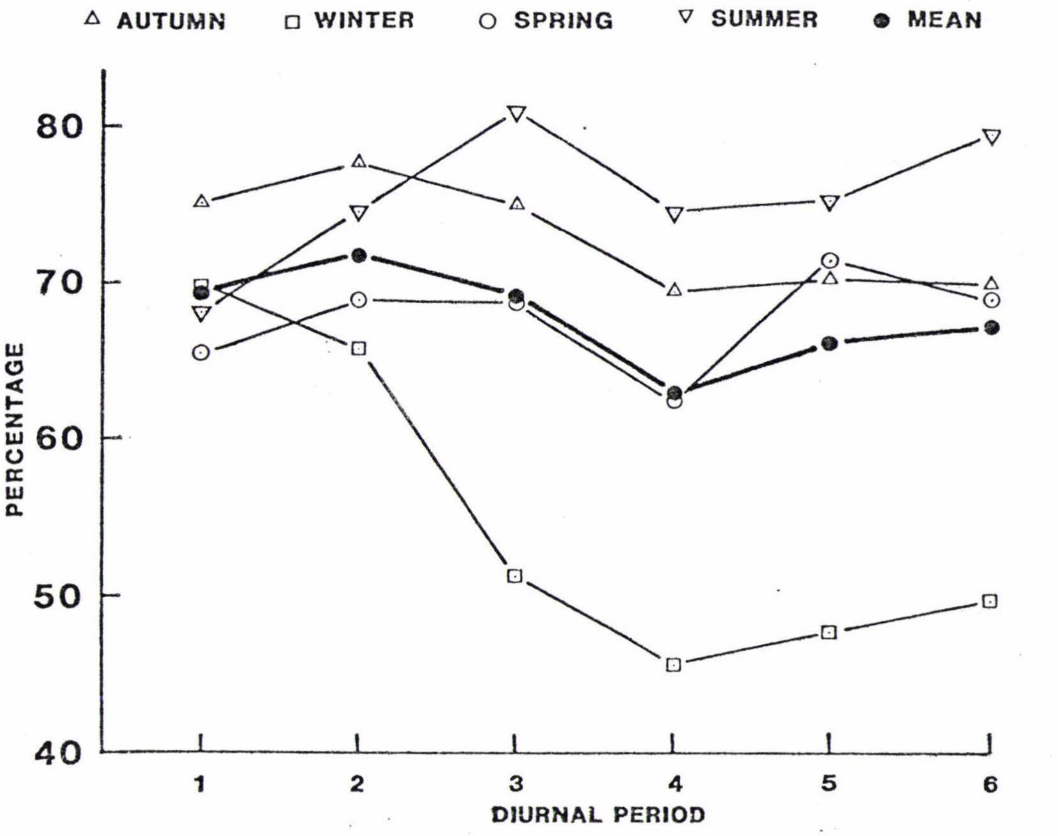


FIGURE 4.6 DIURNAL STEP RATE

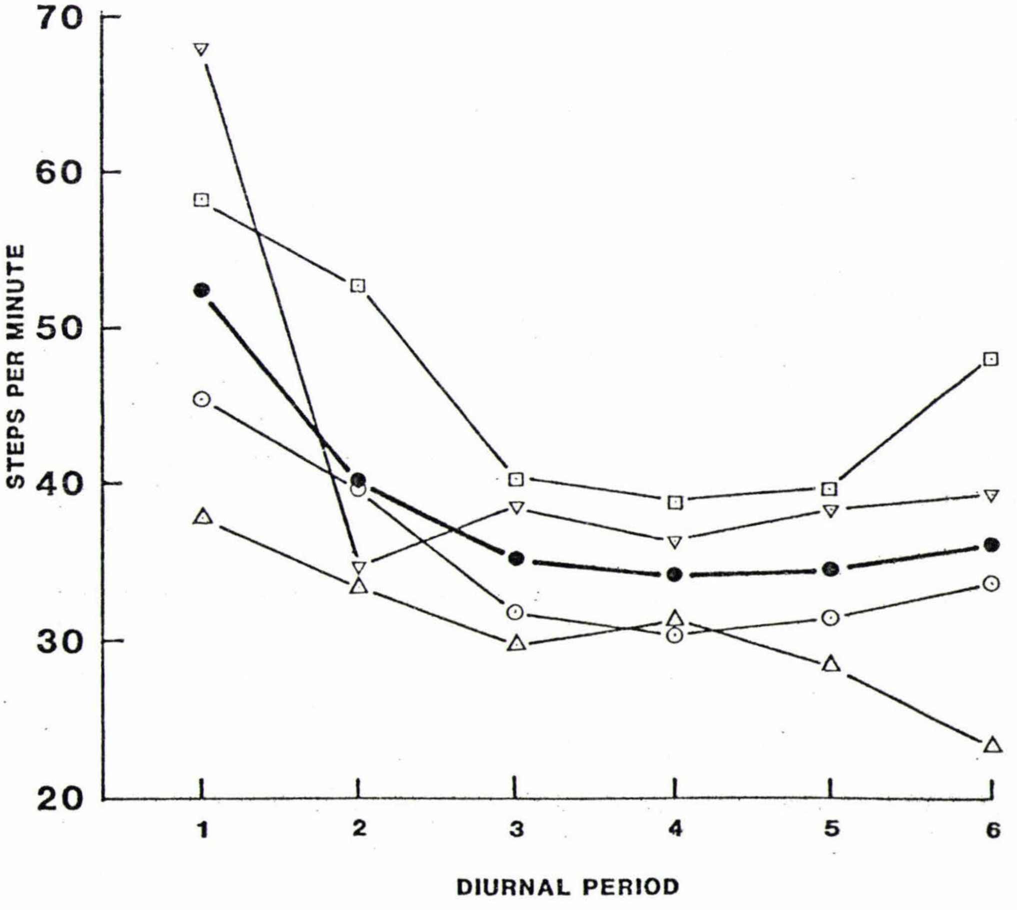
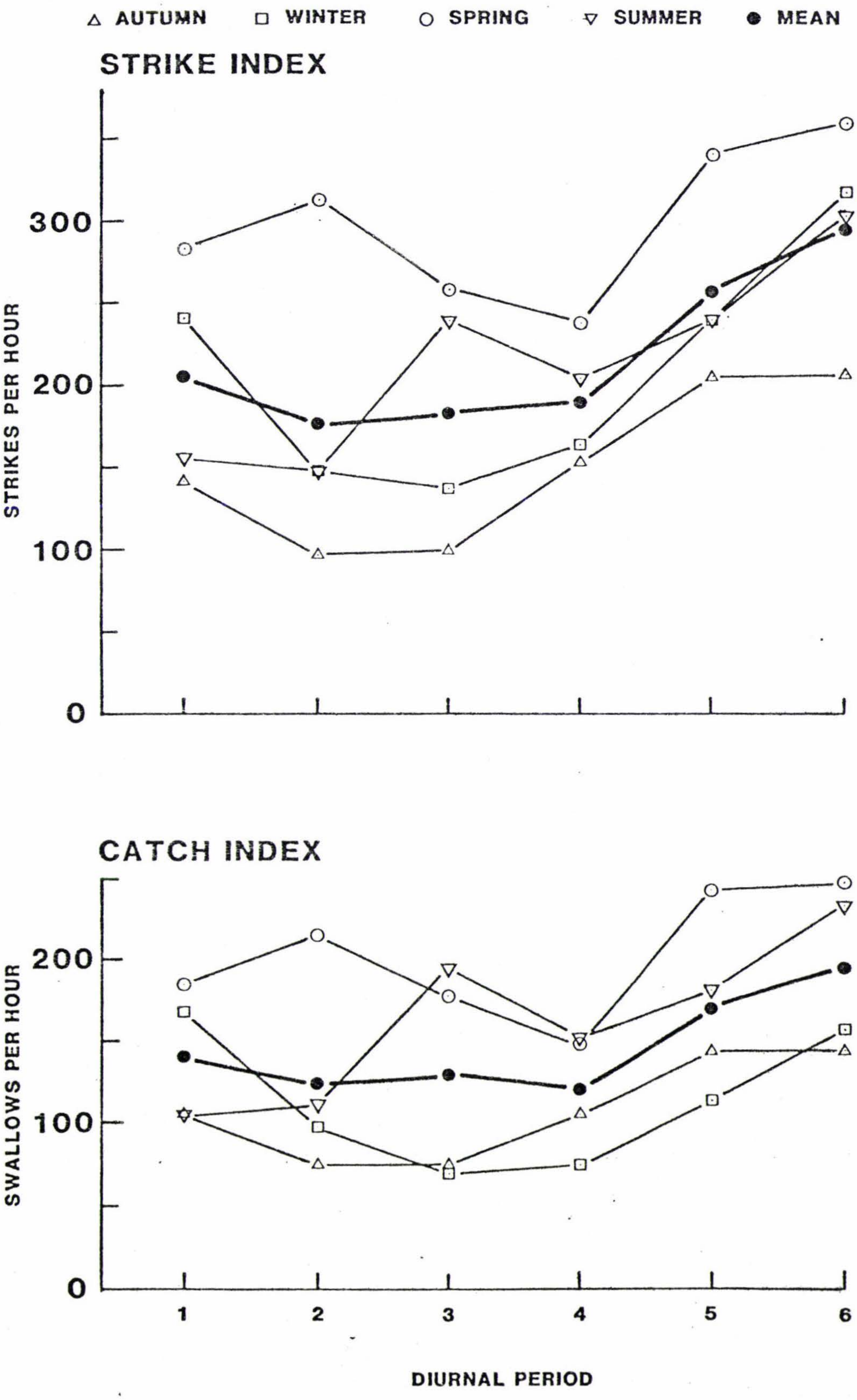


FIGURE 4.5 DIURNAL FEEDING INTENSITY INDICES



correlations between strikes and steps were negative in each period and significant at the 0.001 level.

4.4 Discussion

4.4.1 Time budget

The daily and annual rhythms of behaviour characteristic of most animals are not simple passive responses to periodically changing environmental conditions. They depend partly on endogenous rhythms with periods of approximately 24 hours and 12 months respectively, and which are then synchronized by environmental rhythms (Enright 1966, Gwinner 1981). There are four main environmental rhythms; tidal, daily, lunar, and annual; but lunar rhythms are of minor significance in birds (Gwinner 1975) and tidal rhythms were not important for herons at Pukepuke.

Feeding has a regular daily periodicity in birds, usually with morning and evening maxima, although the pattern can be modified by many factors including availability of food, air temperature, photoperiod, and reproductive status (Morton 1967). The early morning peak of foraging seen in herons probably indicates a greater need for food following the nightly fast and while ambient temperatures are low. Gibson (1978) and Wright (1978) reached the same conclusion for American avocets (Recurvirostra americana) and Pukekos respectively. The energy debt incurred during the night appears to have been met by mid-morning, and between then and early afternoon is an interval when the need to feed is reduced and more time is devoted to other activities. The increase in foraging time over the afternoon may anticipate the need to store energy before nightfall, and reflect the falling temperature.

Birds demonstrate an inverse relationship between food (or energy) intake and ambient temperature (King and Farner 1961), so more energy is needed in the cooler conditions of morning and evening, partially accounting for the higher proportion of time spent foraging these periods. Warmer air temperatures are probably a major factor contributing to the reduced time spent feeding around midday.

Another factor contributing to the unequal distribution of feeding may be food availability. Verner (1965) states that, "If food can be more readily obtained at one time of the day than another, selection should favour those individuals that forage at the better time, since an equivalent amount of food could be acquired in less time, leaving more time for other activities." As discussed in sections 4.4.2 and 7.4.1, earthworms are likely to be most readily available to herons in the morning, and insects, in summer and autumn, during the afternoon.

Seasonal differences in foraging are discussed in Chapter 5, and it is sufficient to say here that spring was the only season to differ greatly from the overall diurnal pattern. The extra activities and demands of breeding meant that a high level of foraging activity was necessary throughout the day.

Changes in the time spent on looking largely complemented changes in foraging. Looking, which included many observations of resting birds, occupied the largest proportion of the time budget between mid-morning and early afternoon. A resting or comparatively inactive period occurs sometime during the day in most birds, and according to Palmgren (1949) for most species it occurs in the afternoon, slightly later in the day compared with White-faced Herons. For herons, a late-morning peak of looking was seen most clearly in autumn and winter. During spring and summer the time spent on looking was relatively constant over the day except period four in spring. During spring the large proportion of time allocated to foraging throughout the day leaves little time for resting. The diurnal pattern of looking in summer was influenced by the moult and the consequent rise in importance of body care activities. These occupied more of the time budget in the second and third periods, which was when looking peaked in autumn and winter. Gibson (1978) suggested for American avocets that, "By resting in mid-morning the birds did not interfere with times when feeding was necessary or when environmental conditions were optimal for foraging", and this could also apply to herons.

Time allocated to body care activities also complemented that spent on foraging. Having a lower priority than feeding, they must be fitted into the time budget whenever time allows, and it appears that the most convenient time of day for herons to preen was just after the morning peak of feeding. The afternoons were progressively taken up by foraging so that by evening little time was available to spend on body care.

Other activities occupied a small proportion of the time budget. The main activity in this category was flying, which included herons moving between feeding areas, flying to and from roosts and nests, or after being disturbed. The most frequent cause of disturbance was Harriers flying nearby. Herons would stop any activity and watch the Harrier, and if it flew too close the herons would take off and circle around until it left. No feeding territories were defended and few agonistic interactions were observed. Most of these were quickly settled although occasionally the aggressor would persistently drive away another bird.

Orians (1961) suggested that the amount of time and energy devoted to different activities must inevitably influence an animal's survival and reproductive rates. Consequently, for a species in a particular environment there must be an optimum time and energy budget, and natural selection will favour those individuals whose budgets most closely approach this optimum. The most important activity of any organism is the accumulation of sufficient energy to exist (Verner 1965), but the intake of energy (which requires time) to maintain other essential activities, and the allocation of time to these activities cannot be simultaneously maximized (Wolf and Hainsworth 1971). Thus the optimum time budget must be a balance between obtaining energy and performing other activities associated with survival and reproduction (Schoener 1971).

4.4.2 Feeding ecology

The amount of food that can be collected per unit time depends on its availability, which includes the location, distribution, density, size and habits of prey species (Murton *et al*. 1963, King 1974). Feeding rates (i.e. strike and swallow rates) depend on the availability of food and on how much food the bird must collect. They can be expected to increase when there is more food available, and/or when the birds need more food, because they might be less selective in their choice of prey and take items that they would leave at other times (Emlen 1966).

Over summer and autumn the feeding rate appears to be influenced mainly by food availability. Herons capture many insects in these seasons, especially summer (see sections 5.4.2 and 7.4.2), and the feeding rates which tended to be low in the morning and considerably higher during the afternoon, may primarily follow the diurnal pattern of insect activity. Verner (1965) states, "For an insectivorous species ... food species would be less active, hence less conspicuous at lower temperatures ... Consequently, the most efficient period ... to forage is probably during the afternoon, when ambient temperature reaches a maximum."

Probably both availability and amount of food needed affect the diurnal feeding rates in winter, when earthworms are a major food (see Chapter 7). The high feeding rate and high feeding intensity indices in period one may indicate both compararively easily available prey and a high energy demand, while the increase over the afternoon suggests that herons were storing energy for the long cold winter nights. The lower percentage of successful strikes from late-morning onwards was possibly due to a change in the availability of worms.

In spring, changes in the feeding rate may be mainly due to the amount of food that must be collected. The drop in feeding rates and feeding intensity indices around midday suggests that this was a period of reduced feeding activity. But herons were not spending much more time resting because there was only a small decrease in time spent foraging in the same periods. Owen (1955) observed that Grey Herons (Ardea cinerea) arrived at the nest with food most often early in the morning and about sunset. This also occurs with White-faced Herons (Moon 1967). Gathering food for chicks is probably the most time consuming part of breeding, and if adults concentrate on this early and late in the day then they could attend to their own needs in-between. Less food would then need to be collected around midday and so feeding rates drop accordingly.

Few horizontal strikes were made in winter and spring, but during summer and autumn more above ground prey was captured in the middle of the day. This diurnal variation probably resulted from changes in the relative availability of prey species, especially insects.

The step rate (or area searched) tended to decrease over the day whereas prey were captured at a greater rate towards evening, indicating that herons searched a progressively smaller area per prey item over the day. Either herons became less selective in choosing prey or more food became available. The former probably had the greater significance with the birds storing food to last the night. Murton et al. (1963) found that Woodpigeons (Columba palumbus), which had a constant food supply, fed less selectively from mid-morning onwards and were gradually storing food before roosting.

The negative strike-step correlation suggests that when herons were finding few prey they searched a larger area and vice versa. The correlation was strongest in the first, and last two diurnal periods which were likely to be when the most food must be collected, so herons may have been searching hardest for prey at these times.

To summarize, at Pukepuke the "effort" that herons put into feeding as indicated by a combination of time spent foraging, feeding rates, feeding intensity indices, and step rates; tended to be lower around late-morning than earlier in the day, and it increased over the afternoon to a maximum in the evening. Feeding intensity indices showed that generally, fewest prey were obtained around midday, and the concentration of feeding early and late in the day is probably due to higher energy demands at these times. There may also tend to be less food available around midday, so the early morning and mid to late afternoon periods might also be better times of the day to forage.

CHAPTER FIVE

SEASONAL TIME BUDGET AND FEEDING ECOLOGY

5.1 Introduction

The annual cycle of the seasons is one of the two main environmental rhythms (the other is the daily day-night cycle) important to herons at Pukepuke. Activities such as breeding, moult, and migration that have a long term influence on a bird's selective fitness should be spread over the year and performed at the optimal stage of the annual cycle. The timing of these activities is coordinated by the changing photoperiod (Gwinner 1981), and birds must adjust their seasonal time budget and feeding ecology to take account of any extra activities as well as different environmental conditions.

The methods described in section 4.2 also apply to this chapter, plus a section on the positions of herons within feeding areas. Periodically I plotted the location of herons at the time of the five minute scan sample, on maps of the feeding area. Also included here are the data from herons at Palmerston North.

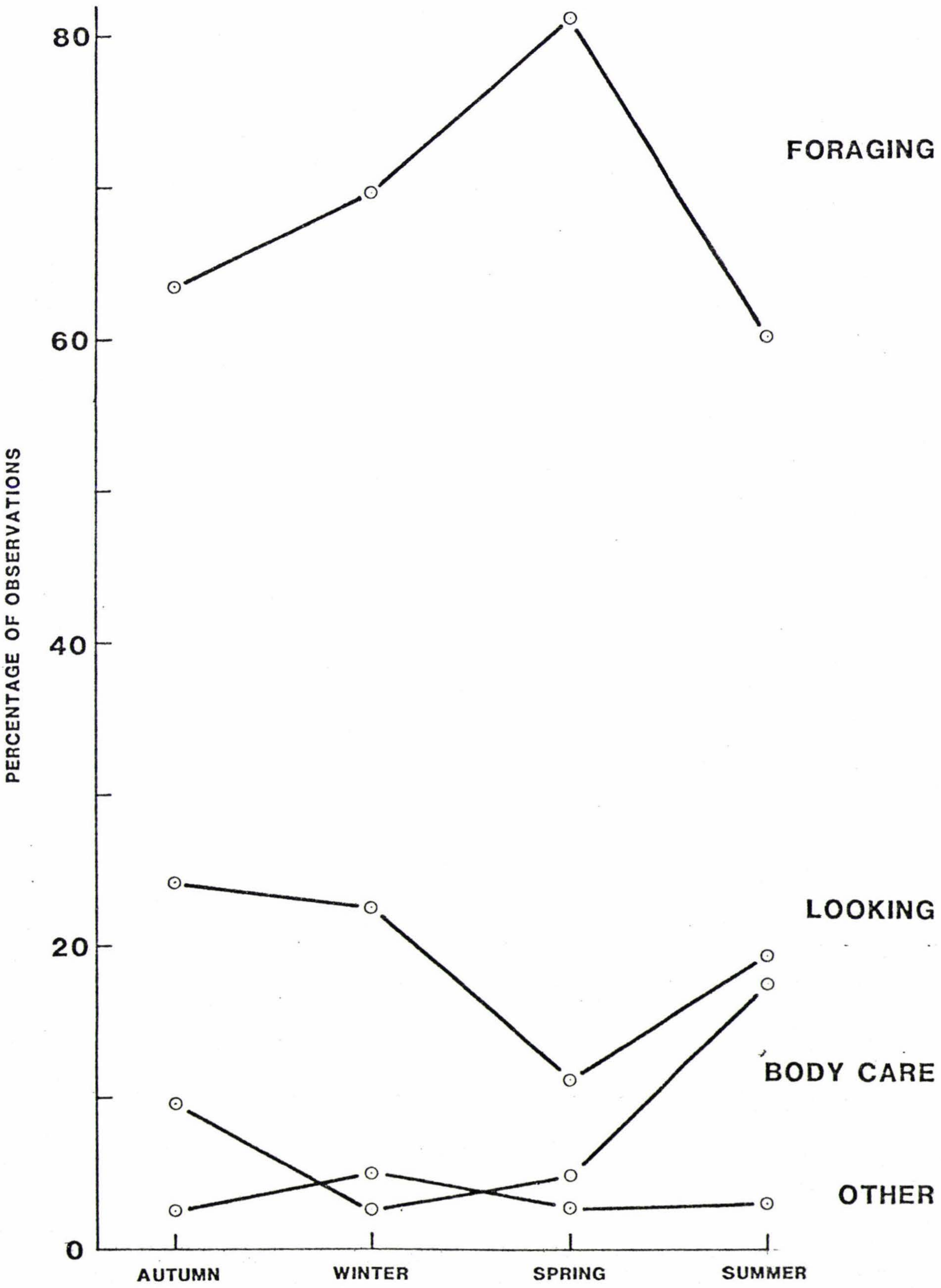
5.2 Results

5.2.1 Time budget

There was a significant annual variation in the proportion of time spent on each of the four main activity categories ($P < 0.001$, $P < 0.01$ for other activities) (Figure 5.1). Foraging occupied over 60% of the herons' time in all seasons, and the proportion increased from summer through to spring with significant differences between each season ($P < 0.001$). The monthly percentage of foraging time peaked in October (86.3%) and was at a minimum during January (54.2%).

Looking was the second most frequently observed activity in each season and accounted for the largest proportion of time in autumn.

FIGURE 5.1 SEASONAL TIME BUDGET



The least time was spent on looking in spring with just 7.8% in October. Differences between seasons were significant at the 0.001 level except between autumn and winter ($P < 0.05$).

Body care activities occupied less than 10% of the birds' time except in summer, when they were the second most frequently recorded category in December and January (maximum 23.0%). The least time was spent preening during winter and spring, and in August occupied only 1.6% of the day. The seasonal percentages were significantly different ($P < 0.001$). Much less time was spent on body care than looking during autumn and winter, the gap narrowed in spring and was negligible over summer.

Other activities comprised less than 5% of the time budget over the year, with a significantly higher percentage in winter than in the other seasons ($P < 0.001$) which all had similar percentages. The highest percentage of flying was in winter and most of the agonistic behaviour occurred in May, June, and July. Virtually no courtship behaviour was observed, although a greeting ceremony was recorded on nine occasions, six in August which is the start of the breeding season at Pukepuke.

Table 5.1 : Time budget of herons at Pukepuke and Palmerston North between April and June.

Activity	Pukepuke	Palmerston North
Foraging	61.9	55.6
Looking	25.3	24.9
Body care	9.1	16.3
Other	3.7	3.2
TOTAL	100.0	100.0

An additional 23 hours of observation were made on herons at the DSIR, Palmerston North, and 1570 bird observations were recorded (Appendix 5). Compared with data from Pukepuke during the same months (Table 5.1), herons at Palmerston North foraged significantly less and spent significantly more time on body care activities ($P < 0.001$), while the percentages of looking and other activities were similar for both groups.

5.2.2 Feeding ecology

The strike rate of herons was lowest in autumn and highest during spring, with significant differences between seasons ($P < 0.001$, $P < 0.05$ between spring and summer) (Figure 5.2). April had the lowest monthly rate (3.3/minute) compared with the maximum of 7.0/minute in October. Less than 3% of the strikes in winter and spring were horizontal, compared with 21% in autumn and 69% during summer. The swallow rate was lowest in winter (Figure 5.2), which was significantly lower than autumn ($P < 0.05$) and both rates were lower than those for spring and summer ($P < 0.001$). Summer had the highest rate but it was statistically similar to the spring rate. The monthly rates varied between 2.2/minute in June and 5.2/minute in October and February.

The percentage of successful strikes was considerably lower in winter than in the other seasons (Figure 5.3), and each season had a significantly different percentage ($P < 0.001$). The monthly percentages followed a sinusoidal shaped curve, oscillating between 84.9% in March and 5.1% during July.

The two feeding intensity indices had similar seasonal patterns (Figure 5.4), being low in autumn and highest in spring, except that winter had an intermediate strike index but was low for the catch index. The strike index was significantly different between successive seasons ($P < 0.001$), as was the catch index ($P < 0.05$) except between autumn and winter. It is notable that the hourly catch indices

FIGURE 5.2 SEASONAL STRIKE AND SWALLOW RATE

FIGURE 5.3

SEASONAL PERCENTAGE OF SUCCESSFUL STRIKES

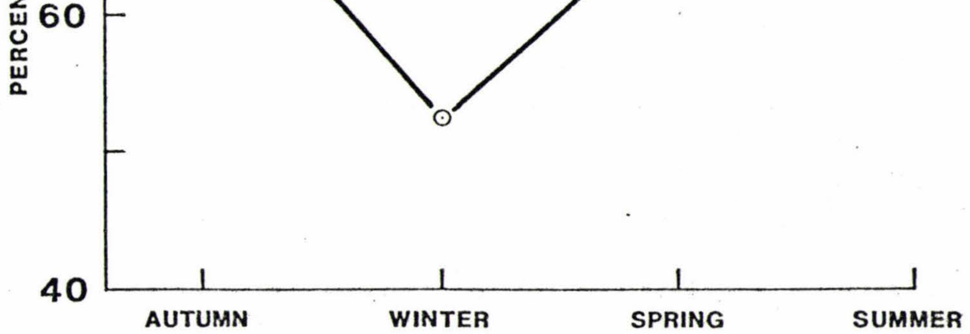


FIGURE 5.4 SEASONAL FEEDING INTENSITY INDICES

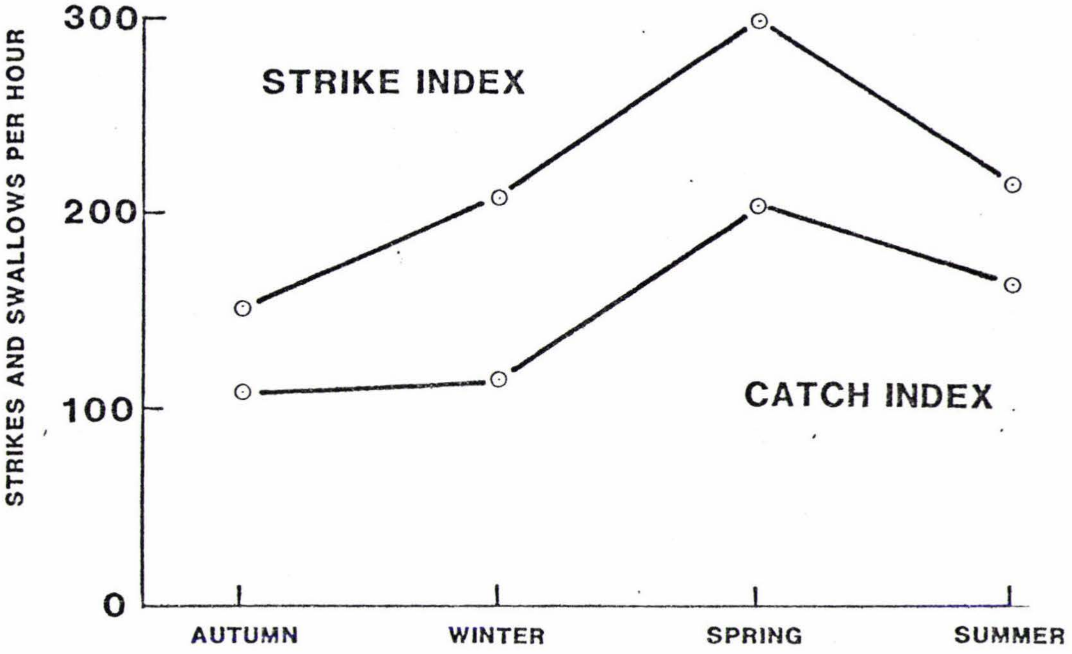
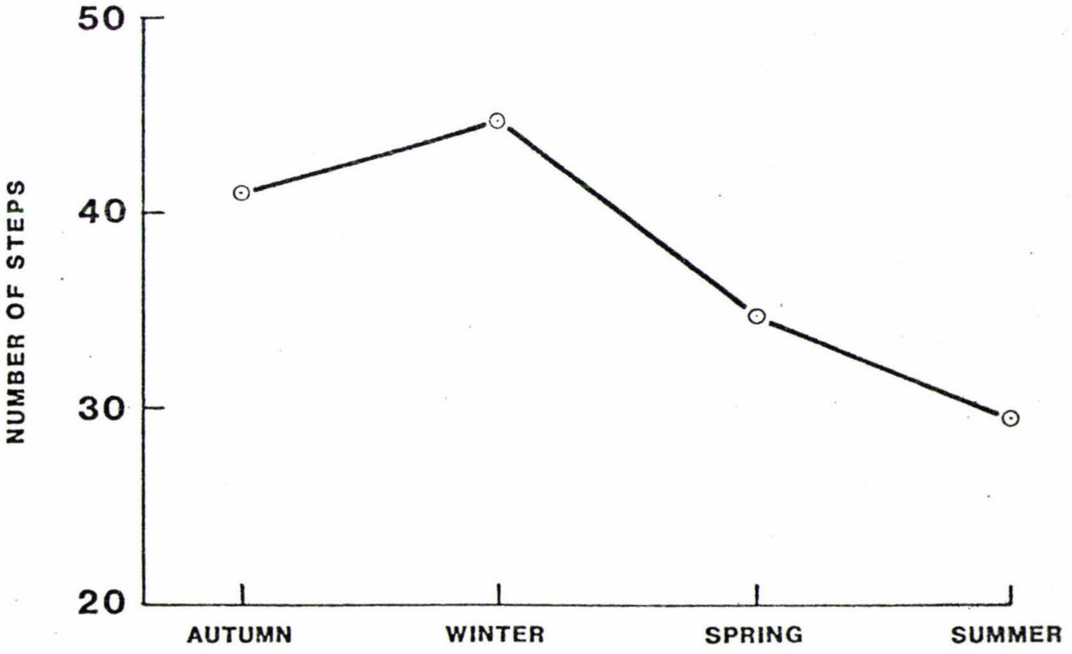


FIGURE 5.5 SEASONAL STEP RATE



in October and November were double the value for the respective adjoining months of September and December.

The step rate was highest in winter and lowest in summer (Figure 5.5), and each season had a significantly different rate ($P < 0.001$). The number of steps per minute in August (49.8) was almost double that in January (25.4). The correlation between strikes and steps was negative in each season but was not significant in autumn, significant at the 0.01 level for winter, and highly significant in spring and summer ($P < 0.001$).

Feeding rates of juvenile herons were recorded in all months except between April and July, and are compared with data from adults recorded during the same months in Table 5.2. Adult and juvenile strike and step rates were not significantly different, but juveniles had a significantly lower swallow rate and percentage of successful strikes ($P < 0.001$ for both tests).

Table 5.2 : Feeding rates per minute of adults and juveniles between August and March

Feeding measure	Adults	Juveniles
Strikes	5.8	5.1
Swallows	4.0	2.8
% successful strikes	69.5	53.9
Steps	37.3	41.5

Compared with herons at Pukepuke, those at Palmerston North had significantly higher strike ($P < 0.05$) and step ($P < 0.001$) rates, and a lower percentage of successful strikes ($P < 0.001$), while both groups had similar swallow rates (Table 5.3).

Plots of herons at Area 2 (Figure 2.2) in winter are shown in Figure 5.6, and at Area 1 over summer in Figure 5.1. Figure 5.6

FIGURE 5.6

DISTRIBUTION OF HERONS AT AREA 2 DURING JUNE AND JULY

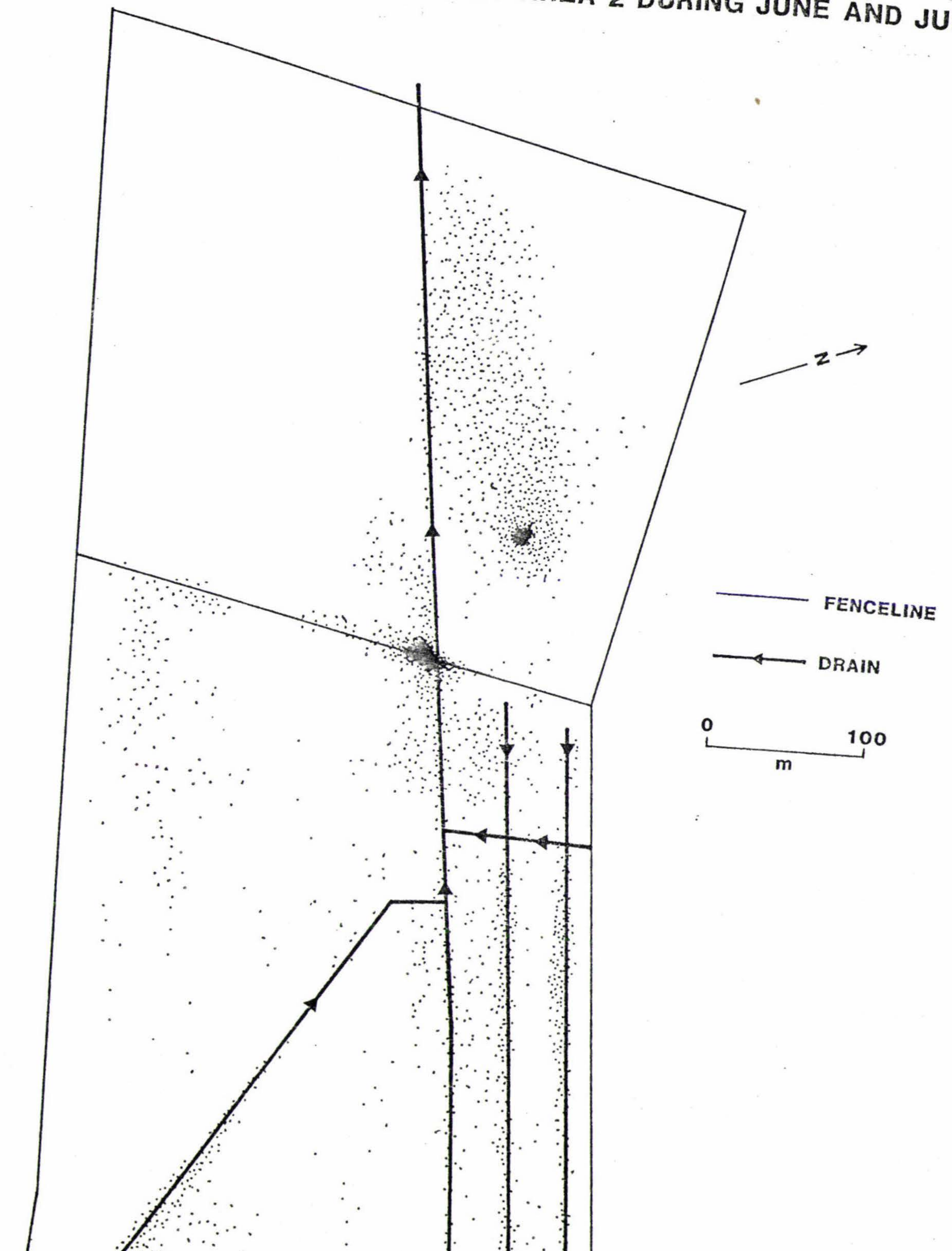
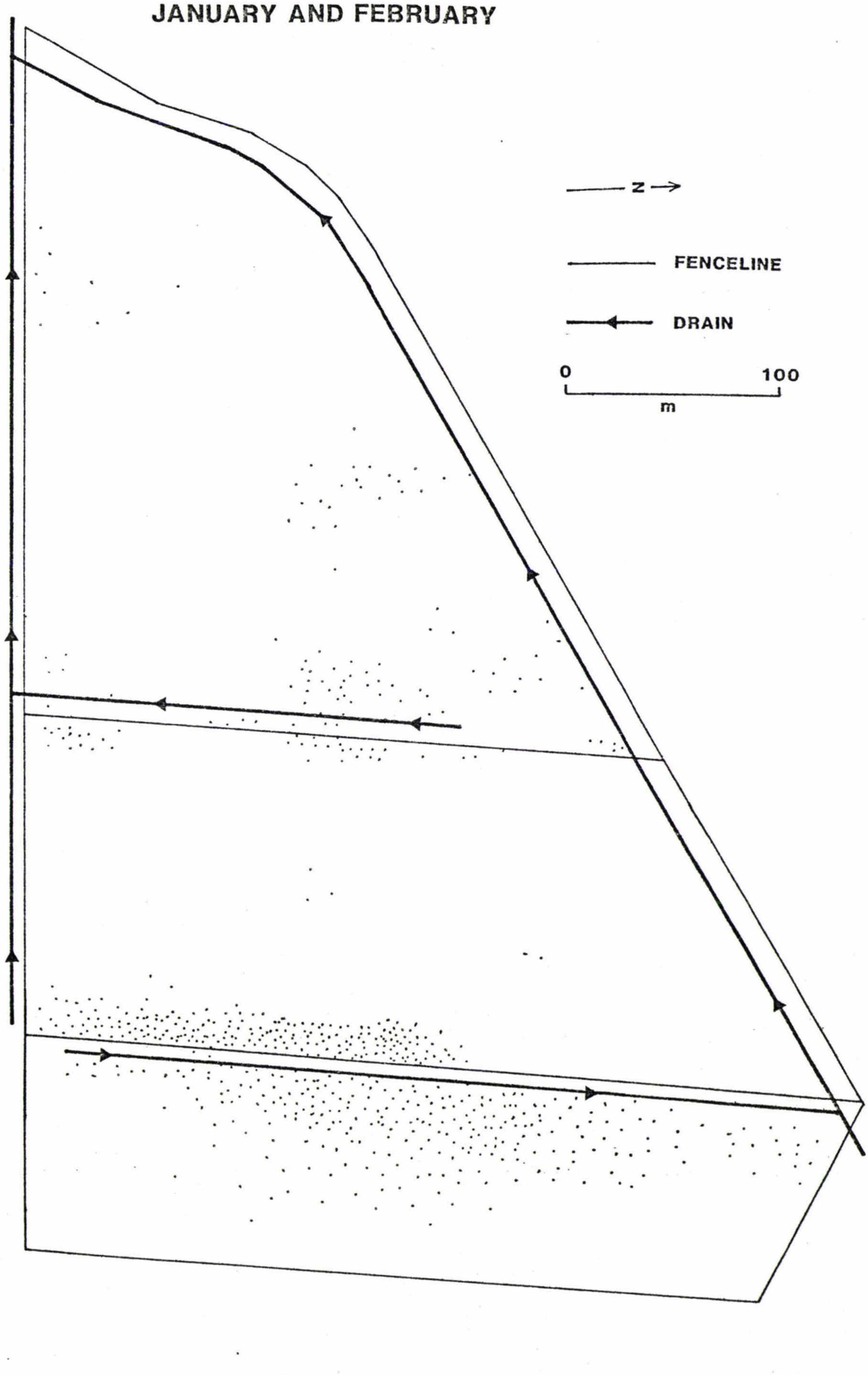


FIGURE 5.7 DISTRIBUTION OF HERONS AT AREA 1 DURING JANUARY AND FEBRUARY



illustrates the herons' preference for wetter areas especially around drains, in contrast to their distribution in summer when the pasture was dry and there was no concentration of feeding at drains.

Table 5.3 : Feeding rates per minute of herons at Pukepuke and Palmerston North between April and June.

Feeding measure	Pukepuke	Palmerston North
Strikes	3.8	4.2
Swallows	2.4	2.3
% successful strikes	63.8	53.6
Steps	40.4	55.1

5.3 Discussion

5.3.1 Time budget

Foraging dominated the time budget but compared with winter and spring, a small proportion of time was spent foraging in summer and autumn. This was probably due to the favourable environmental conditions. Summer is the warmest season so birds can survive on less food than in other seasons, and it has the longest days during which birds can feed and the shortest time at night when they are without food. Also the young have fledged by December, relieving parents of the need to feed them. Autumn is also comparatively warm and without extra demands on the birds like reproduction, migration, or moult, is probably the most "relaxed" time of year for herons at Pukepuke.

Winter has the most unfavourable environmental conditions with low temperatures, short days, and long nights, so birds have the highest metabolic demands in this season. A greater proportion of time was spent foraging than in autumn and summer but herons still spent almost a third of the day not feeding, which suggests that they had plenty of time to gather sufficient food. If herons had difficulty obtaining enough food, feeding could be expected to be maximized and other activities minimized, but this did not occur in winter because they spent more time foraging in spring. Goss-Custard (1969) found that Redshanks (Tringa totanus) devoted a very high proportion of the winter day to feeding, feeding at high tide and at night whereas in spring and autumn they stopped feeding at dusk and high tide.

The proportion of time spent foraging during spring was substantially higher than in winter. Self-maintenance demands should be lower due to improved weather conditions, but this feeding peak coincides with the breeding season at Pukepuke. Egg production, incubation and feeding chicks are energy demanding and time-consuming activities so that in spring a high proportion of the time spent at feeding areas must be devoted to foraging.

When maintenance demands were met in less time, as in summer and autumn, more time could be spent on looking and body care activities. Looking occupied the largest part of the day in autumn, supporting the suggestion that autumn is a period of reduced stress for herons. Only slightly less of the day was spent on looking in winter which further indicates that herons had ample time to gather sufficient energy. In contrast, the peak of foraging in spring was largely at the expense of time spent looking.

The most notable feature of the seasonal distribution of body care activities was the large increase between spring and summer. Increased preening at this time is probably associated with a post-nuptial moult. Moulting is an energetically expensive process so it occurs when warm conditions allow plenty of time for resting and preening (Verbeek 1972). Presumably apart from in summer, only a small amount of time needs to be spent preening to keep the plumage in good condition.

Other activities occupied a minor proportion of time in each season, only exceeding body care in winter. The concentration of agonistic interactions into three months may have been a preliminary to breeding, or perhaps there was greater competition for food during those months. Alternatively this could have been an artificial situation if most of the interactions were started by one or two aggressive birds. Courtship behaviour was conspicuously absent from the time budget, but Moon (1967) observed courtship displays between a pair of White-faced Herons in a tree, so it may occur away from feeding areas.

Herons at Palmerston North presumably satisfied their self-maintenance requirements in less time than those at Pukepuke since they spent less time feeding. Differences in the time budgets for the two groups may be due to differences in their diets, especially the proportion of earthworms (see section 7.3.1). Herons in both areas captured prey at similar rates and since worms were the only prey large enough to be seen being eaten, presumably Palmerston North birds, which captured a much higher percentage of worms, were ingesting more food per unit time than those at Pukepuke. This can explain how they could afford to spend less time foraging and devote more attention to body care activities.

5.3.2 Feeding ecology

Measures of the feeding ecology were combined to determine the overall feeding "effort" for each season (Table 5.4, from data presented in Figures 5.1 to 5.5). The seasonal value of each measure was categorized as low, medium, or high in relation to the other seasons to simplify the seasonal comparisons.

Two factors principally determine the feeding effort in each season, the amount of food required and the availability of food. Food requirements vary inversely with temperature, and increase as birds undergo the energy demanding functions of moult, reproduction, and migration. Season and weather affect the numbers and behaviour, and hence the availability, of prey species (King 1974), so at different times of the year food may be easier or harder to obtain. It appears that herons captured prey more easily in summer than in winter. As the proportion of vertical strikes increased in each season, the percentage of successful strikes decreased while the step rate increased. In other words, when herons were obtaining most of their food from the ground, as in winter and spring, they made more strikes and searched a larger area per item caught than when more of their food was above ground prey as in summer and autumn. This suggests that ground prey such as worms may be less readily available than above ground prey such as insects, and would require a greater feeding effort to obtain.

Table 5.4 : Synthesis of the seasonal feeding ecology

Feeding measure	Autumn	Winter	Spring	Summer
% time foraging	Low	Medium	High	Low
Strike rate	Low	Medium	High	High
Swallow rate	Low	Low	High	High
% successful strikes	High	Low	Medium	High
Hourly strike index	Low	Medium	High	Medium
Hourly catch index	Low	Low	High	Medium
Index of area searched	Medium	High	Medium	Low
OVERALL FEEDING EFFORT	Low	Medium	High	Medium

Autumn had a low value for each of the feeding measures except the area searched (there was a low percentage of unsuccessful strikes). This was probably due to a lack of extra demands on the herons' time and energy above their self maintenance requirements, since they were apparently not involved with reproduction, moult, or migration at this time of year. Energy demands were low and could be met relatively easily so a low feeding effort was sufficient.

The most food for self maintenance was probably needed in winter but herons appeared to expend the most energy to obtain their food. A low percentage of successful strikes and high step rate meant that in winter, herons made the highest number of strikes and steps per prey caught, which suggests that they also expended the most energy while foraging. The catch index was low, so with the short days it is likely that herons caught the fewest prey per day in winter. However, this could be offset if they received a higher energy return per prey, which is possible since they captured more large earthworms than in other seasons (see section 7.3.1). Self-maintenance demands were high in winter and food appeared relatively hard to obtain, so a fairly high feeding effort was necessary.

The greatest feeding effort occurred during spring, when every feeding measure had high values, except the step rate and percentage of successful strikes. Many more prey were captured than during the rest of the year as shown by the catch index. The high feeding effort was almost certainly due to breeding, when less time is available to forage because of other activities, but more food must be collected than in other seasons. In spring the high feeding effort reflects the extra food needed to raise chicks.

Herons had a feeding effort in summer intermediate between the extremes of spring and autumn. The strikes were predominantly horizintal suggesting that their prey were mainly insects, which are probably relatively easily captured as indicated by the low number of strikes and step per prey. But the net energy gain per item may be less than in other seasons so herons had to catch large numbers of insects, hence the high strike rate. Herons probably met their self maintenance requirements with less effort than in winter since they needed less energy and insects were readily available. Self maintenance demands may have been lowest in summer but the catch index was still higher than in autumn. It is unlikely that this extra food was needed for breeding (which was completed by December) or to build up reserves before migrating. The extra energy was probably needed for the post-nuptial moult.

Efficiency in collecting food presumably increases with experience, so adult birds should be more efficient than juveniles (Lack 1954). Among ardeids this has been demonstrated in the Grey Heron (Cook 1978b), Little Blue Heron (Florida caerula) (Recher and Recher 1969), and Cattle Egret(Siegfried 1971b, 1972). Spurr (1967b) recorded that juvenile White-faced Herons had a greater feeding rate and about the same success as adults, but his results were from only 17 observations. I found that adults and juveniles had similar strike rates, but adults caught more prey. The relative inefficiency of juveniles at capturing prey indicates that they must forage for longer and expend more energy than adults to obtain an equal quantity of food, and presumably this has unfavourable implications for their survival (see section 3.4).

Differences in the feeding ecology of herons at Pukepuke and at Palmerston North can also be explained by the higher proportion of earthworms eaten at the latter locality. Worms appear to be relatively hard to obtain because herons generally took more strikes to capture a worm than other prey such as flies (pers. obs.), and the lowest percentage of successful strikes and the largest area searched occurred in winter when herons ate the most worms. Herons at Palmerston North appeared to expend more energy when foraging than herons at Pukepuke, and this was possibly because worms comprised more of the diet.

It was clear from the positions of herons on maps and from casual observations, that herons did not forage over all the pasture but concentrated on low lying wet areas such as near surface water and drains. In summer the drains were dry, and presumably no better than the surrounding pasture with regard to food availability because they were not favoured as foraging sites. The two especially dense areas of dots in Figure 5.5 represent herons that were mainly resting and preening. The drain running through area two was deep enough to obscure the birds so the number of herons feeding there was underestimated. When wetter areas of pasture existed they were preferred by herons probably because more food was available (see section 6.4.1).

CHAPTER SIX

SAMPLING FOR POTENTIAL PREY

6.1 Introduction

The sampling of feeding areas for potential prey is an indirect method of determining the diet of a predator. It is a useful and sometimes essential supplement to direct observation of feeding, and analysis of regurgitated food and pellets, gut contents, and faeces (Goss-Custard 1973). A sampling programme was undertaken in pasture at Pukepuke to determine seasonal changes in the number and dry weight of animals that were potentially available as prey for herons.

6.2 Methods

Weekly sweep net, and soil and turf samples were taken from the same area as that week's observations on herons. Consequently they came from the five areas described in section 2.2. A sweep net sample consisted of 100 sweeps with a long handled dip net brushing the pasture while walking around the sampling area (Plate 7). All insects caught were counted, and identified according to Harrison (1959) and Colless and McAlpine (1970), while P. McGregor (DSIR) and J. Esson (MAF) also identified some of the insects.

Invertebrates on and in the ground were sampled each week with five 0.05 m^2 x 7.5 cm quadrats which comprised the turf and underlying soil (Plate 8). Although herons were never seen probing the ground to the full depth of their bill (about 7 cm), quadrats were taken to a depth of 7.5 cm to ensure that all potential prey were collected. The samples were handsorted, because this is one of the most accurate methods for extracting large animals such as worms (Edwards and Lofty 1977). I was not concerned with very small animals. These samples were examined either in the field or in the laboratory, and any

Plate 7 : Sampling for insects with a sweep net. Photo Dr R. Fordham.

Plate 8 : Sampling for soil and turf animals with a quadrat which is in the ground and partially exposed. Photo Dr R. Fordham.

animals were identified, counted, and their dry weight obtained by heating at 80° C to a constant weight. Earthworms were identified according to Martin (1977) and by Dr J. Springett (MAF). Barker (1977) was used to identify slugs.

In addition to these weekly samples, on 16 July, 18 September and 28 November 1980, and on 14 January 1981, four sweep net and four soil and turf samples were taken, one in the middle of each quarter of the daylight period, to investigate whether invertebrate numbers changed during the day. Sweep net and soil and turf samples were also taken from places within the study area that herons continually avoided, as a comparison with the areas in which they did feed. From July 1980 to February 1981 (except December), a monthly sweep net and soil and turf sample was taken from a non-feeding area close to where I took that week's feeding area sample.

Mann-Whitney tests were used for all of the statistical analyses except to compare the samples taken in each quarter of the day when Chi square tests were performed. Significance was set at the 0.05 level, and the seasons comprise the same months as in Chapters four and five.

6.3 Results

6.3.1 Soil and Turf samples

Earthworms comprised 98% of the animals collected. A few slugs were present in most months, and the larvae of three Costelytra zealandica, seven Tipulidae, 80 unidentified Scarabaeidae, and one other larva were the only other animals found (Appendix 7). Details of the earthworms and slugs collected from the 56 feeding area samples are given in Table 6.1.

Four species comprised 89.6% of the worms and 98.6% of the dry weight, and the remainder were unidentified small immature worms. The species in order of decreasing total numbers were: A. caliginosa,

L. rubellus, E. tetraedra, and A. longa. The dry weights were calculated from 48 samples, and here the species in decreasing order were: A. longa, L. rubellus, A. caliginosa, E. tetraedra; and this order was the same for the average weight per worm of each species.

Table 6.1 : Total number and dry weight of earthworms and slugs from feeding area samples.

Species	Number	Dry weight (g)
Allolobophora caliginosa	2646	53.01 (1869 worms)
Allolobophora longa	1116	69.64 (1042 ")
Lumbricus rubellus	1843	67.45 (1493 ")
Eiseniella tetraedra	1395	13.07 (1268 ")
Unidentified	816	2.85 (549 ")
Total earthworms	7816	206.02 (6214 ")
Deraceros reticulatum	80	0.52 (27 slugs)
Deraceros panormitanum	16	0.24 (15 ")
Total slugs	96	0.76 (42 ")

Table 6.2 : Seasonal number and dry weight of earthworms and slugs per m^2 from feeding area samples.

Season	Earthworms		Slugs	
	Number	Dry weight (g)	Number	Dry weight (g)
Autumn	786.6	14.64*	22.8	0.17*
Winter	875.5	21.92	6.3	0.09
Spring	380.2	19.90	1.9	0.06
Summer	196.0	6.01	1.8	0.01

* Calculated from only two samples.

The largest number and dry weight of worms was collected in winter (Table 6.2).

In spring, the number of worms was significantly lower than in winter ($P < 0.001$), but the dry weight was not. The number of worms in autumn was high and not significantly different from that in winter, but the dry weight was considerably less than in winter and spring. The autumn dry weight was not significantly different from the other seasons, but was calculated from comparatively few data. Significantly fewer worms were found in summer compared with the other seasons ($P < 0.01$), and the dry weight was significantly less than in winter and spring at the 0.001 level.

A. caliginosa and L. rubellus comprised most of the weight of worms in winter, while A. longa and L. rubellus were the main species collected in spring. About half of the worms in autumn were A. caliginosa, but in summer no single species was prominent numerically, although A. longa comprised about half the dry weight. E. tetraedra comprised 20-22% of the seasonal total numbers except in autumn, but being much smaller than the other species, it accounted for less than 7% of the dry weight in each season.

The two slug species (Table 6.1) were most abundant in autumn and scarce in spring and summer (Table 6.2), but seasonal differences in both number and dry weight were not significant.

The results from the four occasions on which four samples were taken over a day are given in Table 6.3. The number of worms varied significantly between periods, but the dry weight did not. Significantly fewer worms were collected in the early morning than in the other periods ($P < 0.001$), and late morning samples also had more worms than samples from the late afternoon ($P < 0.01$).

In the seven non-feeding area samples A. caliginosa, A. longa, and L. rubellus comprised 94.9% of the number of worms and 99.2% of the dry weight, with L. rubellus the main contributor (Table 6.4). The proportion of E. tetraedra was much lower than in feeding area samples. Also found were two D. panormitanum, 78 Scarabaeidae larvae and one unidentified larva.

Table 6.3 : Number and dry weight per m^2 of earthworms over the day.

Period	Number	Dry weight (g)
Early morning	322	12.76
Late morning	480	16.84
Early afternoon	456	15.00
Late afternoon	403	13.81

Table 6.4 : Total number and dry weight of earthworms from non-feeding area samples.

Species	Number	Dry weight (g)
A. caliginosa	166	3.64
A. longa	74	4.46
L. rubellus	242	10.71
E. tetraedra	14	0.14
Unidentified	12	0.01
TOTAL	508	18.96

Feeding areas had a higher number and dry weight of worms than non-feeding areas (Table 6.5), but the differences were marginally not significant for both tests.

Table 6.5 : Number and dry weight of earthworms per m^2 in feeding and non-feeding areas from July to February.

Area	Number	Dry weight (g)
Feeding	463.9	16.77
Non-feeding	290.3	10.84

6.3.2 Sweep net samples

Sweep net samples from feeding areas contained insects from seven orders and spiders (Table 6.6).

Table 6.6 : Seasonal sweep net catches per sample from feeding areas.

Order		Autumn	Winter	Spring	Summer
Odonata	(damselflies)	0.1	-	0.2	0.1
Hemiptera	(bugs)	7.7	1.4	1.8	0.4
Neuroptera	(lacewings)	0.3	-	-	0.1
Coleoptera	(beetles)	4.9	1.6	0.3	1.2
Diptera	(flies)	449.6	168.5	265.0	623.2
Lepidoptera	(moths)	1.7	0.1	0.1	0.2
Hymenoptera	(bees and wasps)	51.4	1.4	1.3	19.3
Araneae	(spiders)	17.7	5.2	0.5	2.2
Unidentified		6.2	1.6	1.1	2.9
TOTAL		539.6	179.8	270.3	649.6

The insects were usually identified to family and in some cases to species (Appendix 8). Diptera, mainly small acalypterate flies, comprised over 90% of the animals collected. Hymenoptera were the second most numerous insects and consisted mainly of small wasps. Aphids and shield bugs were the Hemipterans while the Coleoptera were all small and included a few weevils. Spiders were found in all months, but few insects of other orders were collected.

The number of insects per sample in summer and autumn were not significantly different, but they were both significantly higher than winter and spring ($P < 0.05$). The most numerous insects were acalypterate flies, particularly Hydrellia spp. and Scatella spp. (both Ephydridae), Leptocera spp. (Sphaeroceridae), and Cerodontha spp. (Agromyzidae), which were very common at various times.

The insects from feeding area samples that were larger than 4 mm are listed in Table 6.7. Common larger flies were *Delia* spp. (Anthomyiidae), various Muscidae, and *Hybopygia varia* (Sarcophagidae). The latter was the largest fly caught and was collected only in summer and autumn. The other insects included damselflies (Coenagrionidae), shield bugs (Pentatomidae), and honey bees (Apidae).

Table 6.7 : Seasonal number per sample of insects larger than 4 mm.

		Autumn	Winter	Spring	Summer
Family	Coenagrionidae	0.1	-	0.2	0.1
	Pentatomidae	0.1	-	-	0.4
	Tipulidae	0.1	-	0.6	-
	Chironomidae	1.2	0.6	0.3	0.4
	Bibionidae	-	-	0.1	-
	Syrphidae	0.6	-	-	0.2
	Anthomyiidae	16.5	14.7	1.5	3.6
	Muscidae	14.5	1.5	16.1	32.7
	Sarcophagidae	9.4	-	-	6.8
	Ichneumonidae	0.2	-	-	-
	Apidae	-	-	-	0.8
Order	Lepidoptera	1.6	0.1	0.1	0.2
TOTAL		44.3	16.9	18.9	45.2

The samples taken at four times of the day had no distinct variation in insect numbers (Table 6.8), and the numbers in each period were not significantly different. Most insects were collected in the last period but this was due to one sample with a large number of *Hydrellia* spp.

Similar numbers of insects per sample were collected in feeding and non-feeding areas (Table 6.8). Ephydridae (Diptera) were more numerous in feeding areas, while other families were generally as, or more common in non-feeding areas. For the larger insects, both areas had similar numbers of Sarcophagidae and Muscidae (both Diptera), while non-feeding areas had more Anthomyiidae (Diptera) and Orthoptera (grasshoppers).

Table 6.8 : Sweep net catches per sample over the day, and in feeding and non-feeding area samples from July to February.

	Period				Area	
	Early Morning	Late Morning	Early Afternoon	Late Afternoon	Feeding	Non-feeding
Odonata	-	-	-	-	0.1	-
Orthoptera	-	-	-	-	-	2.1
Hemiptera	0.5	1.3	-	0.3	1.1	0.4
Coleoptera	0.3	-	0.8	1.3	0.7	1.0
Diptera	175.5	196.8	115.8	608.5	289.1	226.0
Lepidoptera	-	-	0.3	-	0.1	-
Hymenoptera	3.0	1.0	5.0	2.3	5.8	8.7
Araneae	-	-	0.8	-	1.0	1.7
Unidentified	1.8	-	0.3	2.3	1.4	4.4
TOTAL	181.1	199.1	123.0	614.7	299.3	244.3

6.4 Discussion

6.4.1 Soil and turf animals

The changes of sampling area and the accuracy of handsorting the quadrats were possible sources of bias in soil and turf samples. Ideally all samples should have come from the same place, but this was not possible because the herons periodically switched feeding areas. Faunas differed between sampling areas, so seasonal differences in the abundance of each species were partly due to changing the sampling area and not just to season. Despite this, my results are still valid because they still estimated what was available to herons.

The accuracy of handsorting for recovering earthworms was tested by Nelson and Satchell (1962) who found that numerically 93% were recovered (99% by weight), but a greater proportion of medium to large worms were recovered than small ones. E. tetraedra is small (30-58 mm, Martin 1977), dark coloured, and appears to live in the turf rather than the soil, which are all factors that hinder its detection, so it was more likely to be missed than the other three species which are all large enough to be easily detected.

Many species of earthworms have a diurnal pattern of activity (Edwards and Lofty 1977) and this could influence their availability to herons during the day. A. caliginosa feeds just below the surface where it can be found throughout the day, while L. rubellus also lives near the surface and under the right conditions it is active on the surface early in the morning (Dr J. Springett pers. comm.). A. longa inhabits a greater range of soil depth than these two species, and is found on the surface at night. E. tetraedra is probably also a superficial feeder although little is known of its ecology (Dr J. Springett pers. comm.). All four species should be available to herons throughout the day, but earthworms should be more readily available in the morning when L. rubellus and possibly A. longa tend to be on the surface. My direct observations of the prey confirms that herons did capture more worms in the morning than in the afternoon (see Chapter 7).

In my samples however, the fewest worms were found in the early morning (although the dry weight was not significantly less than in other periods), which contradicts what is expected from the worms' behaviour and from my observations of herons feeding on them. The number of worms in each quadrat was quite variable however, and the four samples might have been unduly subject to sampling error. More samples may have given a closer agreement to the expected pattern.

Evans and Guild (1947) stated that temperature and moisture are the two main soil conditions determining seasonal earthworm activity. They found an inverse relationship between temperature and the number of active worms, while soil moisture and activity were positively correlated. Gerard (1967) found that more worms are inactive during summer than in winter, presumably because they tolerate cold wet conditions better than hot dry ones. Earthworms avoid adverse conditions at the surface by migrating to deeper soil layers and aestivating (Edwards and Lofty 1977). Aestivating worms presumably cannot be detected by herons, and those deeper than 7.5 cm are almost certainly beyond their reach even if detected. Therefore soil conditions of high temperature and/or low moisture tend to make earthworms unavailable as prey for herons.

High soil temperature and low soil moisture are most likely to occur in summer, which is the season when earthworms are least available to herons. The number and dry weight of worms near the surface was considerably lower than in other seasons and more of the population was likely to be aestivating. Worms were most readily available to herons in winter when the greatest numbers and mass were recorded at the soil surface. The availability of worms in autumn and spring was intermediate, but probably more like winter than summer because the autumn numbers and spring dry weights were not significantly different from the respective winter figures. This changing seasonal availability of worms was confirmed by direct observation of the prey (Chapter 7).

The reduction in earthworm numbers near the soil surface over summer seems to be a general phenomenon in New Zealand pastures (Lee 1951). Waters (1955) at Palmerston North, found that the total number and weight of worms was lowest in summer, increased rapidly in autumn, and reached a maximum in winter, then declined over spring. Moeed (1980) and Purchas (1980) both working near Hastings, Hawkes Bay, also found a similar pattern. Since my results from Pukepuke agree with these authors, it is likely that the seasonal differences in the numbers and weights of worms that I recorded were due mainly to seasonal fluctuations rather than to changes in sampling area.

Herons preferred to forage in the wettest areas of pasture (section 5.3.2). Since birds could be expected to forage where they can gather food most efficiently, it was likely that such areas either had more food or that it was easier to obtain. Both factors probably applied to herons. Feeding areas had considerably more earthworms than non-feeding areas, and the difference may have proved significant if more samples had been taken from the latter. Food was probably easier to obtain from wet areas because a high water table forces worms right to the surface (Lee 1959). Also probing into soil to extract worms would be easier in soft wet ground than in drier harder areas.

Slugs prefer damp conditions and they were more common in feeding area samples, whereas beetle larvae were more abundant in drier non-feeding areas. Moeed (1980) and Purchas (1980) both collected beetles from pasture throughout the year, either as larvae in soil samples or as adults in pitfall traps. Their samples may have been from drier ground than my feeding area ones where only five beetle larvae were collected.

To summarize, earthworms were the main animals found in soil and turf samples. Diurnally they are probably most readily available in the morning, while seasonally they are comparatively unobtainable in summer and most readily available in winter. Samples were taken over the day but the results were inconclusive. Herons fed mainly in wetter parts of the pasture, and these places had more worms available than in drier non-feeding areas which presumably accounts for their attractiveness.

6.4.2 Sweep net animals

The size range of prey taken by White-faced Herons, particularly the lower size limit, is unknown, but Cattle Egrets which are mainly insectivorous take prey 2 mm and larger (Siegfried 1972). Rooks (Corvus frugilegus) feeding on farmland took invertebrates larger than about 4 mm (R. Porter in Purchas 1980). Both these species are smaller than White-faced Herons so I considered it unlikely that herons would often take prey smaller than 4 mm. This view is supported by the size of prey in regurgitated pellets (see section 7.4.2).

Insects collected by sweep netting ranged in size from tiny flies to bees and damselflies, and it was highly unlikely for them all to be eaten by herons. Most of the insects were very small and only those larger than 4 mm were considered as potential prey. In this group H. varia (striped dungfly) was the most likely prey due to its comparatively large size and numbers, and it was numerous in pellets collected in summer (Chapter 7). Damselflies and bees were also recorded in pellets and their size and hovering flight appear to make them relatively attractive prey for herons. Delia spp. and the various Muscidae were the most numerous insects larger than 4 mm, but they were much smaller than striped dungflies and may have little potential as prey for herons.

The number of insects collected depended greatly on the weather at the time of sampling, so for the samples taken over the day, like the soil and turf quadrats, four samples were probably too few to be able to portray the changing diurnal availability of insects. The strike rates in summer and autumn (section 4.4.2) suggested that more insects are active and hence available to herons in the afternoon compared with the morning. Seasonally, the most insects were collected in summer and autumn, and during winter and spring almost no insects likely to be prey were found.

My samples suggested that insect populations in feeding and non-feeding areas were similar. Although flies are highly mobile and can potentially range widely over pasture this does not necessarily occur. Dennison(1979) found that blowflies were not randomly distributed in fields but were heavily clumped even in apparently "homogeneous" pasture. When feeding on insects, herons are likely to forage where they can be gathered most efficiently, so my sampling may have been inadequate to detect differences between feeding and non-feeding areas. This is illustrated by the presence of grasshoppers only in non-feeding area samples although they were recorded as prey in pellets.

To summarize, insects were numerous in summer and autumn, and scarce in winter and spring. The great majority of them were almost certainly too small to be eaten by herons, and of the larger insects striped dungflies were the most likely prey. Insufficient samples were taken to be able to properly compare insect numbers between periods of the day and between feeding and non-feeding areas. Because pitfall traps were not used some animals, such as ground-living beetles, grasshoppers, crickets, and spiders were underestimated by my sampling methods. Therefore the range of potential prey in pasture at Pukepuke was greater than what I recorded, as shown by the insects found in pellets.

CHAPTER SEVEN

DIET

7.1 Introduction

Herons are opportunistic predators and feed on a variety of animals. Although most species are primarily piscivorous, the diet may also include molluscs, annelids, crustaceans, spiders, insects, reptiles, amphibians, birds and mammals (Hancock and Elliott 1978). Some species are quite specialized feeders while others, such as White-faced Herons, have catholic diets which may encompass many animal groups. The food habits of the White-faced Heron have only previously been studied by Carroll (1967), who investigated their impact on the trout population by collecting 93 birds from within feeding range of trout-stocked waters. This study followed a different approach with the emphasis on determining the diet by methods that did not require killing birds.

7.2 Methods

It is important that if possible, a number of methods are used to assess the diet since they are all subject to some detree of bias (Hartley 1948, Goss-Custard 1973). My main methods were direct observation of prey and analysis of regurgitated pellets, supplemented by sampling feeding areas (Chapter 6). Direct observation of the diet was made while recording feeding rates, when any prey large enough to be identified was noted. Differences between diurnal periods and seasons were compared by Chi square tests with a significance level of 0.05.

Regurgitated pellets and two masses of regurgitated food were gathered from under roosts and nests. I tied a sack just below one nest to catch pellets as they fell (Plate 4). Complete pellets whose shape had not been deformed upon hitting the ground were measured with vernier calipers. All pellet material was dried at 80°C to a constant weight, and the volume of complete pellets was measured in a graduated cylinder. Pellets and food were examined under a dissecting microscope and recognizable parts of the prey such as heads, mandibles, thoraxes and elytra were extracted from the debris (Plates 9 and 10). Mr J. Esson initially identified many of the fragments, after which I built up my own reference collection. Winterbourn and Gregson (1981) was used to identify a few aquatic insects. For each species only one fragment was counted to avoid the possibility of recording an individual more than once. Chi square tests with significance set at 0.05 were used to compare the monthly percentages of the most numerous orders. It was not possible to determine the volumetric proportions of each group from pellets, but live specimens of the three most numerous species were obtained by sampling aquatic areas at Pukepuke during October to give an indication of the fresh weight of food that the pellets represented.

Originally I planned to collect some birds to examine their gut contents, and a permit to do this was obtained. But herons were difficult targets, being wary birds which feed in open areas. The collection of a shot sample of herons was abandoned after one bird was taken, when it proved extremely difficult and time consuming to get close enough for an accurate shot.

7.3 Results

7.3.1 Direct observation

The only prey identified by direct observation of feeding were earthworms (Table 7.1) (Appendix 9), and nine Golden Bell frogs, six in September, two in October and one in February.

Earthworms were identified as the prey on a decreasing percentage of the successful strikes over the day. The percentage was significantly higher in period one than in the other periods ($P < 0.01$), and in the morning compared with the afternoon ($P < 0.001$). The

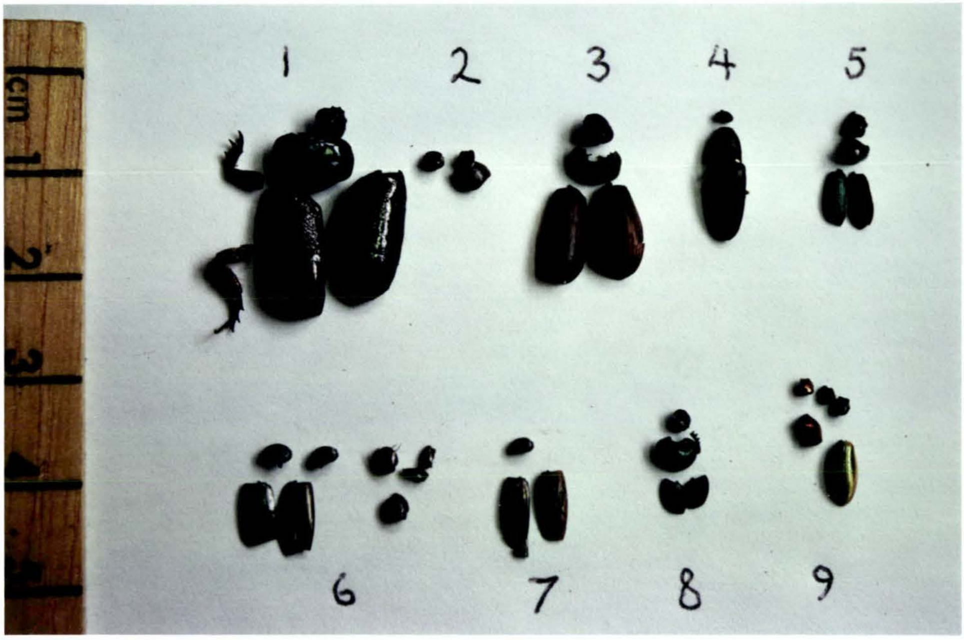
Plates 9 and 10 : Fragments of prey from pellets that were used for identification.

Plate 9 : Various Coleoptera

1. *Pericoptus truncatus* : head, thorax, elytra, legs
2. *Costelytra zealandica* : " "
3. *Odontria* spp. : " " "
4. *Lonoderus exsul* : " " "
5. *Harpalus aeneus* : " " "
6. *Rhantus pulverosus* : left - adult ; head, elytra
   right - larvae ; heads
7. *Lancetes lanceolatus* : head, elytra
8. *Onthophagus posticus* : " , thorax, elytra
9. *Pyronota festiva* : " " "

Plate 10 : Other orders

1. Stratiomyidae larvae (Diptera)
2. *Hybopygia varia* (Diptera) : heads
3. *Eristalis tenax* (Diptera) : "
4. Left - *Xanthocnemis zealandica* (Odonata) : head
   Right - *Austrolestes colensonis* (Odonata) : head
5. *Wiseana* spp. larvae (Lepidoptera) : left - head
   right - mandibles
6. *Phaulacridium marginale* (Orthoptera) : head, hind femur
7. *Anisops* spp. (Hemiptera) : left - complete
   right - heads
8. Araneae : mandibles
9. *Lepidurus apus viridus* (Notostraca) : mandibles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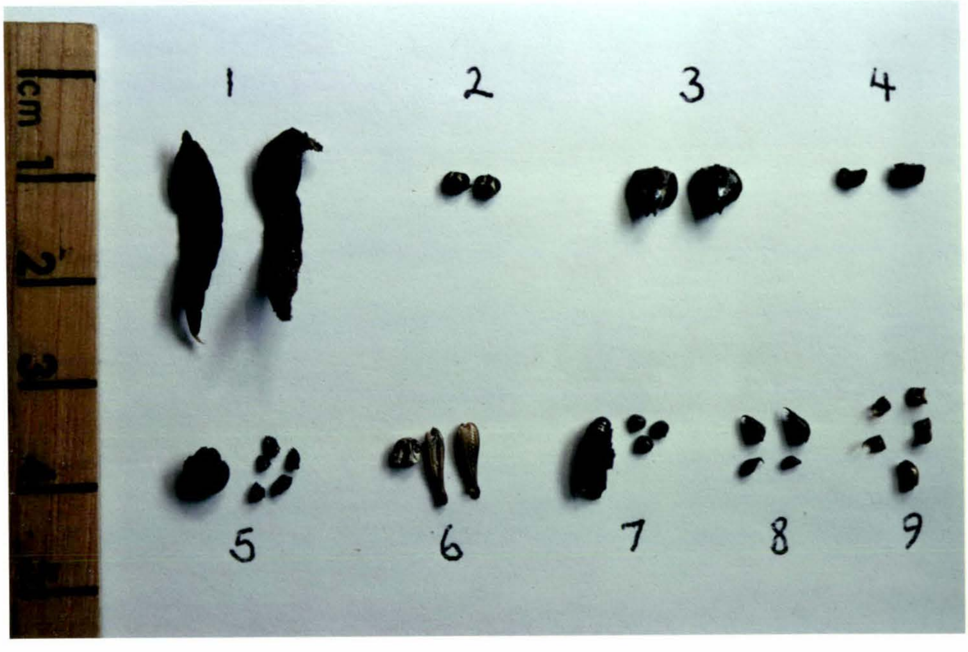
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Table 7.1 : Number and percentage of prey captured during feeding rate recordings that were identified as earthworms

Season	Diurnal Period												Total	
	1		2		3		4		5		6			
	n	%	n	%	n	%	n	%	n	%	n	%	n	%
Autumn	37	10.6	29	5.0	13	2.4	26	5.2	31	3.7	13	1.6	149	4.1
Winter	83	17.7	140	22.8	141	26.1	94	18.3	143	18.0	135	13.1	736	18.5
Spring	72	12.2	42	4.5	59	6.9	54	9.2	39	3.3	19	1.4	285	5.1
Summer	3	1.4	13	3.2	2	0.5	8	1.0	0	0	7	0.8	33	1.0
TOTAL	195	12.0	224	8.8	215	9.2	182	7.6	213	6.3	174	4.3	1203	7.4

percentage of worms taken was significantly higher in winter than in the other seasons ($P < 0.001$), and significantly higher in autumn and spring than in summer ($P < 0.001$).

Herons at Palmerston North were observed to capture worms on a significantly higher percentage of successful strikes ($P < 0.001$) than did Pukepuke herons during the same months (Table 7.2).

Table 7.2 : Number and percentage of earthworms observed to be captured at Pukepuke and Palmerston North during feeding rate recordings.

Month	Pukepuke		Palmerston North	
	Number	%	Number	%
April	34	3.0	66	34.2
May	114	8.2	41	30.1
June	120	13.5	30	29.7
TOTAL	268	7.9	137	31.9

7.3.2 Pellets

Pellets were collected from August to April, but at Pukepuke they were mostly taken between September and November. A total of 805.02 g dry weight of pellet material was examined, comprising 95 complete pellets weighing 415.83 g dry weight (average 4.38 g) and a further 389.19 g dry weight of broken material. Thrity-eight pellets averaged 38.7 x 23.0 mm, and the mean volume of 63 pellets was 3.0 cc. In total 29 153 animals were recorded (Table 7.3), averaging 171 per complete pellet. In all 36 genera were identified, including 28 species (Appendix 10), and these identifications are of adults unless specifically noted as larvae.

Table 7.3 : Orders of prey recorded in pellets

Order		Number	%
Coleoptera	(beetles)	14354	49.2
Notostraca	(shield shrimps)	8684	29.8
Diptera	(flies)	2118	7.3
Hemiptera	(bugs)	1959	6.7
Lepidoptera	(moths and butterflies)	656	2.3
Odonata	(damselflies)	241	0.8
Araneae	(spiders)	211	0.7
Orthoptera	(grasshoppers and crickets)	201	0.7
Hymenoptera	(bees and wasps)	47	0.2
Decapoda	(crabs)	7	<0.1
Unidentified		675	2.3
TOTAL		29153	100.0

No vertebrates were recorded in pellets and approximately 70% of the items were insects. About half of the animals were Coleoptera, and while 23 beetle genera were recorded, over 90% of the beetles were larval and adult *Rhantus pulverosus* (Cosmopolitan diving beetle) which comprised 45.5% of the total number and was by far the most common species. Two other water beetles *Lancetes lanceolatus* and *Homeodytes hookeri* were the next most abundant coleopterans, but both comprised less than 1% of the total number.

Tadpole shrimps (*Lepidurus apus viridus*) were the second most abundant species in pellets (29.8% of the total), and the only major non-insect component. Diptera were represented mainly by *Hybopygia varia* which was the fourth most numerous species (4.5%), and by Stratiomyiidae larvae. The common pond insects backswimmers (*Anisops* spp.) and waterboatmen (*Sigara* spp.) comprised the great majority of the Hemiptera, and backswimmers were the third most common species (5.6%). The Lepidoptera were virtually all caterpillars and about half were Porina (*Wiseana* spp.). Animals from each of the other orders comprised less than 1% of the total number.

Monthly changes in the proportions of the main orders and species found in pellets are shown in Figure 7.1 A and B. Insufficient data were available for April. Tadpole shrimps were the main component of pellets collected in August and September, and they still formed a substantial proportion of the prey until early November, occurring in three-quarters of the pellets up to this time. But from mid-November, onwards they were recorded only rarely. The percentage in August and September was significantly higher than in the other months ($P < 0.001$). Significantly more beetles occurred in pellets between October and December than at other times ($P < 0.001$), although they continued to contribute a large portion of the prey until February. Cosmopolitan diving beetle larvae were mainly responsible for this pattern and they were absent from only 12 pellets. Adults of this species were present in all but two pellets, and comprised a similar proportion of the animals in each month except December.

There was little evidence of Diptera being taken until November when Stratiomyiidae larvae began appearing. Diptera comprised a significantly higher proportion of the prey from December onwards ($P< 0.001$). H. varia did not occur in great numbers until December, but by January it had superseded R. pulverosus as the main component of pellets, and this situation continued until March. Striped dungflies occurred in only 5% of pellets before December, but in 79% from then on. Hemiptera contributed a contributed a consistent proportion of animals to pellets from August to January, and this was mainly due to backswimmers which occurred in almost two-thirds of the pellets. Some of the less numerous groups were seasonally abundant. Porina larvae were not recorded after mid-November, while virtually all the grass grubs were eaten in October and November. Adult damselflies occurred mainly from February to March, and grasshoppers from February to April. A few spiders were taken in each month.

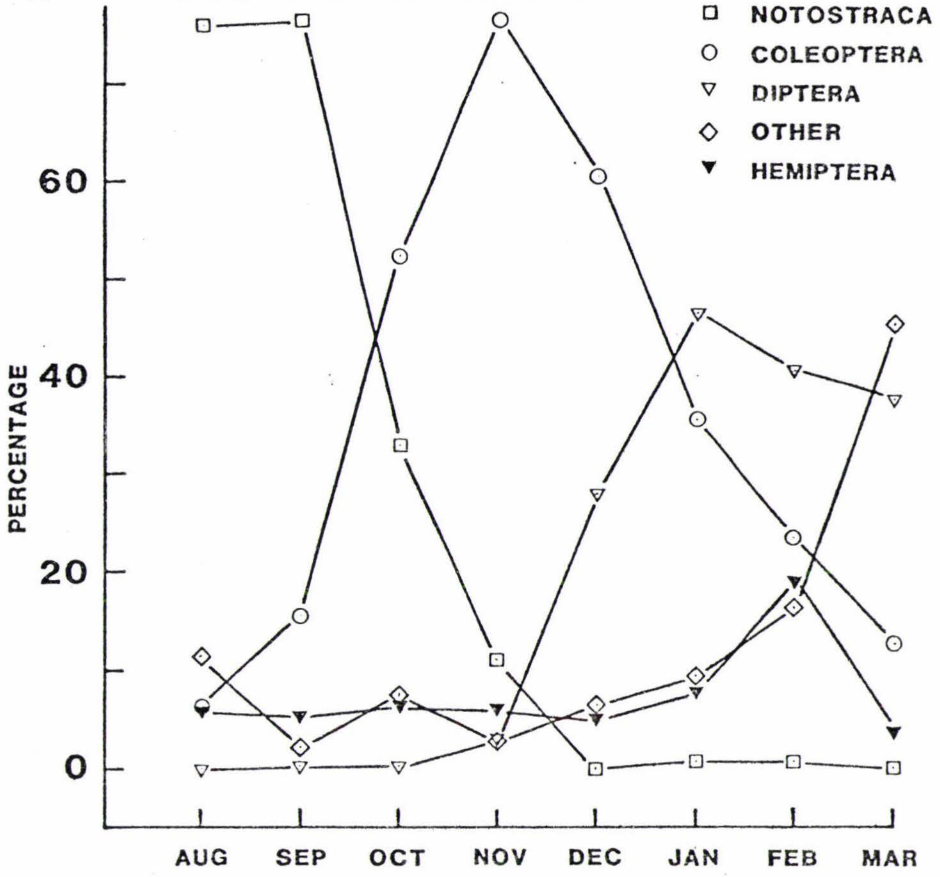
7.3.3 Fresh weights

Tadpole shrimps were considerably larger than the other two species in Table 7.4. Pellets collected in August and September had

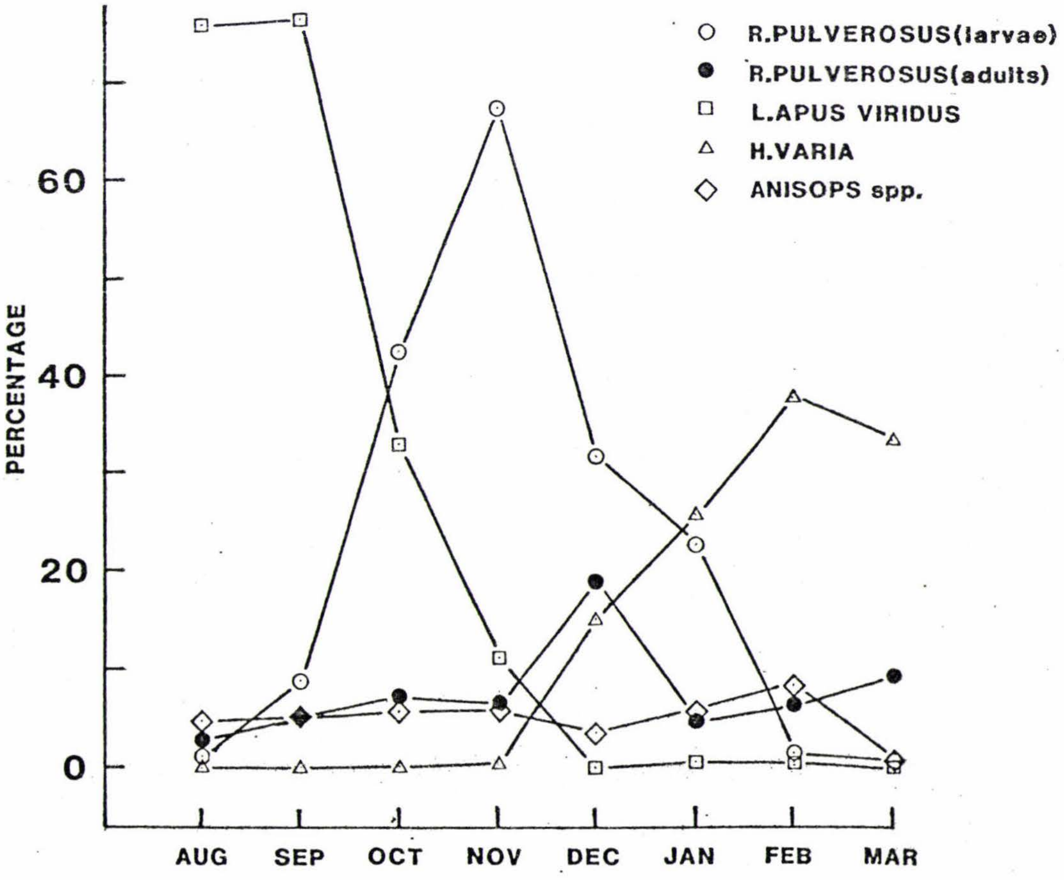
FIGURE 7.1

MONTHLY CHANGES OF PREY IN HERON PELLETS SHOWN AS PERCENTAGES OF THE TOTAL NUMBER OF PREY

A THE MOST NUMEROUS ORDERS



B THE MOST NUMEROUS SPECIES



higher numbers of Tadpole shrimps than those from October and November, and therefore represented a much larger fresh weight of animals (Table 7.5).

Table 7.4 : Fresh weight of live specimens of the three most common species in pellets.

Species	Number	Fresh weight (g) Total	Fresh weight (g) Per animal
R. pulverosus (larvae)	90	2.28	0.025
" (adults)	17	1.56	0.092
Anisops spp.	200	4.13	0.021
L. apus viridus	14	4.66	0.333

Table 7.5 : Average number per pellet of the three most common species and the equivalent fresh weight of live animals.

Species	August-September Number	August-September Weight (g)	October-November Number	October-November Weight (g)
R. pulverosus (larvae)	11	0.3	85	2.1
" (adults)	8	0.8	11	1.0
Anisops spp.	12	0.3	8	0.2
L. apus viridus	177	58.9	38	12.6
Other prey	14	*	21	*
TOTAL	222	60.3	163	15.9

* Weight unknown

7.3.4 Regurgitated food and stomach contents

A further 243 animals were identified from the regurgitated food and from the one bird collected in December (Plate 11) (Table 7.6).

The most numerous animals were Whistling frogs, damselflies (Zygoptera, all or mostly Austrolestes colensonis), Cosmopolitan diving beetles, and earthworms (Lumbricidae). Also on 23 October I found a dried-up Whistling frog on a branch beneath a nest, while under another nest on 30 October were two half digested Golden Bell frogs (Plate 12).

Table 7.6 : Prey identified from regurgitated food and stomach contents.

Prey	Regurgitated food 21 November	Regurgitated food 11 December	Stomach contents 11 December
Zygoptera (nymphs)	60	16	–
Anisops spp.	–	–	3
Sigara spp.	–	–	1
R. pulverosus (larvae)	10	12	15
" (adults)	1	5	8
H. hookeri (larvae)	2	–	–
Odontria spp.	1	–	–
Stratiomyiidae (larva)	1	–	–
Calliphoridae	–	1	1
Unidentified insect larvae	–	3	–
Araneae	–	1	–
Lumbricidae	–	20	2
L. ewingi (tadpoles)	38	–	32
" (adults)	–	8	–
Unidentified	2	–	–
TOTAL	115	66	62

7.4 Discussion

7.4.1 Direct observation

Direct observation for determining the diet has the advantage of avoiding the problems arising from the different rates of digestion of

Plate 11 : Prey in the regurgitated food and stomach. Clockwise from the top : *R. pulverosus* larvae
" adults
Homeodytes hookeri larvae
Austrolestes colensonis nymphs
Litoria ewingi tadpoles

Plate 12 : *Litoria raniformis* (body about 6 cm long) which were probably regurgitated as food for the young. Digestion had already started on the anterior portion of the body while the rest was still unaffected.


cm 1 2 3 4 5 6 7 8 9 10 11 12

the various prey, and data can be obtained without disturbing the birds. In this study however, its usefulness was limited because most of the prey were too small to be seen clearly. Only frogs and earthworms could be identified. Golden Bell frogs were the largest prey that I recorded, and in spring and summer are likely to be an important source of food for herons hunting around ponds and drains.

Only large earthworms (about bill length or longer) could be identified by direct observation, because herons often paused briefly with a large worm in their bill whereas smaller items were swallowed immediately after capture. Therefore the percentage of worms in the diet was undoubtedly higher than what I recorded. I was unable to identify the species captured, but from samples taken in feeding areas they could only have been *Allolobophora caliginosa*, *A. longa*, and *Lumbricus rubellus*. The other worm present, *Eiseniella tetraedra*, was too small to be observed as prey, but it was quite likely to be eaten since many of the animals represented in pellets were much smaller than these worms.

Herons took a decreasing proportion of worms over the day which could suggest that they were actively searching for worms to a greater degree in the morning than in the afternoon. However, it is more likely that they feed on worms in proportion to their availability, since the activity cycles of the worms should make them more readily available early in the day (section 6.4.1). Siegfried (1971a, 1972) found that Cattle Egrets consumed more earthworms in the morning than in the afternoon, and he considered that this was due to the relative availability of prey species.

Changes in the seasonal percentage of worms observed as prey corresponded to changes in the amount of worms present in feeding areas, further supporting the contention that herons fed on worms in relation to their availability. Worms were eaten all year round, but particularly from June to September, and comparatively rarely between January and March. Cattle Egrets (Siegfried 1972), Rooks (Porter 1979, Purchas 1980), and Starlings (Moeed 1980), also eat most earthworms during the wetter winter months and least in summer.

I was slightly closer to the herons at Palmerston North than at Pukepuke, but the marginally better viewing position was insufficient to account for the much higher percentage of prey identified as earthworms at Palmerston North. I do not have comparative data on the number of worms in both areas, but there may have been more available at Palmerston North and consequently they comprised a larger portion of the food than at Pukepuke.

7.4.2 Pellets

Bird pellets consist of the indigestible portion of food items, which are accumulated in the stomach and regurgitated through the mouth in compact masses instead of being defaecated. They may be composed of bones, claws, beaks, teeth, mandibles, insect exoskeleton, fur, feathers, and plant matter (Glue 1970). Such pellets are produced by at least 329 species of birds from 68 families and 18 orders (Below 1979), and the habit is strongly developed among the Ardeidae and birds of prey.

Pellets provide an extremely valuable source of dietary information, again without having to kill or disturb birds, and a large sample of pellets can be easily collected from under roosts and nests. The items are usually broken up and only some parts of an animal may be present, but the larger fragments can usually be identified with experience. The major problem with pellets however, is that they may provide a biased sample of the prey since they contain only the indigestible parts of animals (Goss-Custard 1973). Fragments from some prey species may be more likely to be incorporated in pellets than those from others, while certain prey may not have any indigestible parts and therefore leave no evidence of their having been eaten. The highly acidic gastric juices of herons readily dissolves vertebrate bones, and evidence of fish and amphibians especially, is usually almost entirely lacking in heron pellets (Hibbert-Ware 1940, Lowe 1954). It is important to keep these sources of error in mind when discussing data obtained from pellets.

White-faced Heron pellets differed greatly in size and weight, but there was little relationship between the two because the denisty was quite variable. Density depended on the proportion of sand in the pellet, and those collected from October to December generally had the most sand. The colour of pellets depended on their composition (Plate 13). Those collected in August and September were fawn coloured because the main component was Tadpole shrimps. Later pellets, composed mostly of Cosmopolitan diving beetle larvae were a darker brown, while summer and autumn pellets were black due to the predominance of flies.

At Pukepuke, herons evidently rarely produce pellets away from roosts and nests because I observed only one pellet being regurgitated at a feeding area. The frequency of pellet production probably depends mainly on the digestibility of the prey, and therefore could easily change from month to month. My only evidence on this subject came from visits to the roost at Sexton's farm on 14 and 15 February 1980. Overnight 12 pellets were produced by an estimated nine herons, and their position on the ground suggested that three birds produced two pellets each and the others one each.

In terms of the total number, 87% of the prey in pellets were aquatic, almost half were one species of beetle, and a further 30% were Tadpole shrimps. This apparently limited range of food is not an accurate description of the diet, but instead reflects the unequal quantity of pellets available from each month, and the biased nature of pellet contents. There was a predominance of pellets collected between September and November, when Cosmopolitan diving beetle larvae and Tadpole shrimps (both aquatic) were by far the largest components of pellets. Earthworms and anurans comprised a large portion of the prey but they do not have indigestible parts large enough to be seen in pellets so not surprisingly their importance was overlooked altogether by pellet analysis.

The diet can be more accurately described by examining the monthly changes of the main orders and species. A major switch in prey

Plate 13 : Variation in pellet appearance. The main component from left to right is as follows : Tadpole shrimps, adult Cosmopolitan diving beetles, sand, larval Cosmopolitan diving beetles, grasshoppers and flies.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occurred between September and October. Tadpole shrimps had begun to decline in importance and were replaced by R. pulverosus larvae as the main component of pellets. The proportion of tadpole shrimps in pellets corresponds with the annual cycle of the species, which is common in temporary ponds at Pukepuke during winter and spring, and dying out as the ponds dry up (Dr I. Stringer pers. comm.). These animals are considerably larger than other common prey, and presumably are a highly favoured food. Therefore as they decrease in numbers, herons are forced to switch to other prey such as the larvae of Cosmopolitan diving beetles, but whether this change also coincides with increasing numbers of these larvae is unknown.

The decline of R. pulverosus after the peak in November coincides with the rise of Diptera and in particular H. varia, so that between December and January flies superseded beetles as the most numerous animals in pellets. The low rainfall over summer meant that surface water and drains dried up while ponds shrank, greatly reducing the extent of aquatic habitats and presumably the availability of aquatic prey. As this occurred more terrestrial prey such as flies, grasshoppers, damselflies, and terrestrial beetles appeared in pellets. Between August and December 92% of the animals in pellets were aquatic, whereas from January onwards terrestrial species comprised 72% of the items. Pellets collected in summer contained a greater diversity of prey than those from earlier months.

The absence of any data on pellets between May and July is because I did not have permission to visit the roost at Sexton's during the duck-shooting season, and because I was unable to find any at Pukepuke. Herons at Pukepuke did not roost in the same trees each night, a habit also observed by Spurr (1967a), and this made finding roosts difficult. Even when I did locate a roost I still did not find any pellets. This gap in pellets is unfortunate because there was probably another major change of diet between autumn and winter, from insects to earthworms. Possibly fewer pellets are produced in winter since worms have fewer indigestible parts. Captive Cattle Egrets fed on minced beef rarely regurgitated pellets (Siegfried 1969).

Virtually all of the animals in pellets were 6 mm or larger, and they ranged in size up to H. hookeri larvae about 6 cm in length. Waterboatmen and backswimmers inhabit similar aquatic environments and both were abundant at Pukepuke, but backswimmers outnumbered waterboatmen in pellets by almost 8:1. The latter might be less readily incorporated in pellets, but it is more likely that the larger backswimmer (8 mm long) was preferred as prey. Waterboatmen (6 mm long) may be near the lower size limit of prey taken by White-faced Herons.

In addition to animal fragments, most pellets contained some plant material and sand. Usually there were minor amounts compared with the animal debris, but some pellets were composed almost entirely of sand while a few had comparatively large amounts of plants. The sand was probably ingested with the prey and not swallowed purposely for grit since herons digest their food chemically not mechanically. Vegetable matter however, is ingested often enough to suggest that it serves a purpose. Carroll (1967) found plant material in 65 out of 93 White-faced Heron stomachs although 35 of them were only traces. Although herons may obtain some nutrients from plants, Hibbert-Ware (1940) and Lowe (1954) suggest that vegetable matter acts as roughage to facilitate pellet formation.

7.4.3 Fresh weights

Tadpole shrimps were easily the largest of the animals common in pellets, and from August to November their proportion of the fresh weight of food that these pellets represented far outweighed that of the other species. Tadpole shrimps were only weighed in October, and this figure was also used to calculate the fresh weight of August and September specimens which were probably smaller. Therefore the difference between the fresh weight of food represented by August-September pellets and those from October and November, was less than my figures suggest.

There were too many unknown factors to try and estimate the total food intake by means of pellets, or to compare this in August and September with October and November. I did not know what proportion of a day's food each pellet represented, and there is the problem of pellets being biased towards prey with indigestible parts.

7.4.4 Regurgitated food and stomach contents

The different rates of digestion of various prey is also a source of error in the analysis of regurgitated food and gut contents (Goss-Custard 1973), but depending on the degree of digestion, this material is generally not biased to the same extent as are pellets. Tadpoles, frogs, earthworms, and damselfly nymphs comprised numerically, about 70% of the items and an estimated 90-95% of the volume of the regurgitated food and stomach contents. These animals were not recorded in pellets except for damselfly nymphs on three occasions. Cosmopolitan diving beetles comprised a minor portion of the prey in the regurgitated food and in the stomach, but they were the main component of pellets collected in the same months. These differences between regurgitated food and stomach contents, and pellets, illustrates the danger of relying solely on pellets to determine the diet.

The two Golden Bell frogs were found under a nest containing half grown chicks. They had probably been brought as food for the young, and presumably were rejected as being too large. Lowe (1954) noted that Grey Herons also do this occasionally, and items that are too big for their chicks may be re-swallowed to be digested further before being presented again.

7.4.5 Synthesis

White-faced Herons will feed on fish, eels, crabs, shrimps, earthworms, insects, tadpoles, and frogs depending on what is available (Oliver 1955, Moon 1967). The fish eaten include trout, but the impact of White-faced Herons on the trout population is at worst neutral and probably often beneficial, because they also eat many more bullies and smelts which are competitors and predators of trout fry (Carroll 1967). Small reptiles, birds, and mammals are also eaten occasionally when the opportunity arises (Reader's Digest 1976).

The major prey recorded in this study were earthworms, Tadpole shrimps, larval and adult Cosmopolitan diving beetles, Striped dungflies, backswimmers, tadpoles and frogs. Also important as prey were other beetles and flies both larval and adult, caterpillars, nymphal and adult damselflies, grasshoppers, waterboatmen, and spiders. Slugs were present in feeding areas but there was no direct evidence that they were eaten. The main foods in each season were : Winter - worms and Tadpole shrimps; Spring - worms, Tadpole shrimps, Cosmopolitan diving beetles, damselfly nymphs, tadpoles and frogs; Summer - larvae and adults of flies and beetles, tadpoles and frogs; Autumn - adult flies, grasshoppers, and worms.

In Carroll's (1967) analysis of White-faced Heron stomachs, invertebrates formed about 40% by weight of the food and vertebrates (mainly fish) about 60%. The main invertebrates in decreasing order of weight were crustaceans, earthworms, larval moths and beetles, grasshoppers and crickets, and adult beetles and flies. Among insects the most consistently occurring were flies and beetles, as both larvae and adults. The Coleoptera were mainly water beetles which Carroll called Dytiscus spp., but they may actually have been R. pulverosus (Carroll pers. comm.). The genus Dytiscus has been recorded only once in New Zealand and no larvae have been found here (Winterbourn and Gregson 1981).

Apart from fish, there were several differences between the prey recorded by Carroll (1967) and myself. The flies in White-faced Heron stomachs were predominantly Calliphora spp., whereas few of these blowflies were recorded in this study. Waterboatmen were present in a third of Carroll's specimens but no backswimmers were found. In contrast backswimmers greatly outnumbered waterboatmen in pellets from

Pukepuke. Carroll did not find any frogs and recorded only three tadpoles from one stomach, which was surprising since these animals are often quoted as being common prey of White-faced Herons (e.g. Oliver 1955, Moon 1967, Hancock and Elliott 1978). Tadpoles and frogs were both present in the small amount of regurgitated food and single stomach that I collected. Presumably these dissimilarities were due to habitat differences between Pukepuke and locations where Carroll's herons were collected. Trout inhabit rivers and streams, whereas water bodies at Pukepuke are mainly small ponds and drains, and ephemeral surface water.

CHAPTER EIGHT

DISCUSSION AND CONCLUSIONS

The White-faced Heron is a highly successful immigrant to New Zealand. Forty years ago it was just establishing itself here, and now it is the most common heron in this country having spread to all districts. Why has it been so successful? The bird itself is highly versatile and is able to exploit a wide range of food from a variety of habitats. It is well adapted to take advantage of European land "development" practices, particularly the conversion of forest and scrub to pasture and the clearing of river and stream banks, which have greatly increased the extent of suitable habitats. Pastoral areas are poorly utilized by indigenous birds, so White-faced Herons face competition for pasture invertebrates mainly from other introduced species such as Starlings, Magpies, and Spur-winged Plovers. At Pukepuke these three species avoided the wettest areas, while White-faced Herons, which are primarily wetland birds, favoured flooded pasture, ponds and drains.

White-faced Herons exploit habitats and foods that may fluctuate greatly in extent and abundance respectively, and as predicted by optimal foraging theory (Morse 1971, Schoener 1971) the species has a generalized feeding strategy. At Pukepuke, herons fed extensively on pasture and their preferred wet areas varied considerably in extent over the year as the water table fluctuated. Consequently food abundance in a particular area was also likely to vary which was probably the reason why herons switched feeding grounds periodically. Since animals should maximize their net energy intake while foraging (Emlen 1966, 1968; Pyke et al. 1977) the herons' foraging strategy and diet should change readily and appropriately to environmental changes (Emlen 1966).

A heron's primary requirement is to satisfy its self-maintenance demands, and therefore its time is organized around the need to gather food. White-faced Herons tended to concentrate on foraging early and late in the day and spend more of the middle periods resting. In the terminology of Schoener (1971) they tend to be "time minimizers", and the optimization of their time budget may be the most important consideration so that the time required to obtain their necessary energy is minimized and some time is available to perform other activities.

Birds can accommodate increased seasonal demands by either increasing their total energy budget, or by changing the allocation of time and energy to different activities (Orians 1961). It is not known whether the White-faced Heron's energy budget altered with season, but there were large seasonal differences in their time budgets. The time budget in spring differed the most from the other seasons because of the particularly heavy demands of breeding. Here the time spent foraging was expanded into the midday rest period at the expense of time spent resting.

The main prey for herons feeding in pasture were likely to be earthworms and flies, whose availability depended on the water table and presumably the ambient temperature respectively. The relative seasonal availability of these animals was reflected in the type of prey captured. Herons took prey mostly from the ground and in the soil during winter and spring, but this changed in summer when predominantly above ground animals were eaten. Direct observation of the prey confirmed that worms were a major food item in winter, while many fewer worms were eaten in summer. Analysis of pellets demonstrated that in summer the largest proportion of flies was consumed. As well as feeding in pasture, herons took large numbers of aquatic animals especially in winter and spring, and changes in the proportions of these groups in pellets probably corresponded with their relative availability.

At Pukepuke in areas outside the lagoon, there may have been less food available for herons in summer and autumn when earthworms and aquatic prey were comparatively unavailable, than during winter and spring when they were readily obtained. Although the heron population at Pukepuke peaked in summer, the birds were utilizing the edge of the lagoon to a much greater extent than in other seasons. It seems likely that the movement of White-faced Herons in summer to estuaries and harbours around New Zealand may be in response to a general decrease of food in pasture at this time of year. Siegfried (1971b, 1972), Purchas (1980), and Verbeek (1972) found that Cattle Egrets, Rooks, and Yellow-billed Magpies (Pica nuttalli) respectively, had the hardest time finding food during late summer when pasture invertebrates were least available.

Today, the main threat to herons in New Zealand and throughout the world is the modification, drainage, and pollution of freshwater and marine wetlands (Curry-Lindahl 1978). While the destruction of wetland habitats must be detrimental to the White-faced Heron population, this is offset by the species' ability to utilize other habitats such as pasture. But this does not remove herons from the risk of poisoning by toxic chemicals, although this is probably less of a problem than in many other countries. Three White-faced Herons analysed by Lock and Solly (1976) had moderate levels of organochlorine pesticides compared with other birds from New Zealand, and since the use of DDT has been phased out, the level of organochlorine residues in New Zealand wildlife is probably declining.

In conclusion, at Pukepuke White-faced Herons adjusted readily to changes in their environment, particularly the fluctuating water table, by utilizing a wide range of foods from both pastoral and aquatic habitats. This adaptability augers well for the species' continued prosperity.

In the future, White-faced Herons may face competition from Cattle Egrets which, unusually for herons, generally feed away from water and are primarily insectivorous. Cattle Egrets take a wide range of prey with grasshoppers being perhaps the most important, but earthworms, caterpillars, flies, crickets, and beetles are also major food items (Jenni 1969, Siegfried 1971a, Fogarty and Hetrick 1973 and references cited therein). These animals are also important foods of White-faced Herons at Pukepuke, and since the Cattle Egret is presently becoming established in this country it will be interesting to see how much ecological overlap develops between the two species.

SUMMARY

1. This study investigated the time budget and feeding ecology of White-faced herons feeding in pasture. Feeding areas were sampled to determine potential prey. The diet was assessed through direct observation, and analysis of pellets, regurgitated food and stomach contents.

2. The White-faced Heron's standard method of hunting on pasture is a steady walk while methodically searching for prey.

3. Herons spent more time foraging early in the morning and towards evening, than from mid-morning to early afternoon when more time was allocated to looking and body care. The peaks of foraging were probably mainly due to a greater need for food at those times.

4. Feeding rates increased over the afternoon and were lowest either in the morning or around midday depending on the season, and usually the fewest prey were captured in the middle periods. This pattern reflects energy demands and food availability.

5. Herons were equally successful at capturing prey over the day except in winter.

6. The proportion of time spent foraging was greatest in spring and least in summer. Much less time was taken up by looking in winter than in other seasons, while considerably more time was devoted to body care activities in summer than during the rest of the year.

7. Breeding in spring and the moult in summer were the main extra activities performed by herons. These activities and the changing environmental conditions determined the feeding effort, which appeared to be highest in spring and lowest in autumn. The most prey were collected in spring and the fewest in winter when the proportion of successful strikes was much lower than in other seasons.

8. Juveniles were less successful than adults at capturing prey.

9. Compared with herons at Pukepuke, those at Palmerston North spent less time foraging and more time preening, and they took more strikes and steps per prey captured. These differences may result from the higher proportion of worms eaten by the latter, which might have obtained more food per unit time while foraging.

10. Except in summer when the pasture was dry, herons concentrated on foraging at the wetter areas such as near surface water and drains, presumably because more food was available in such places.

11. The most earthworms were available to herons in winter and the fewest in summer, while insects were numerous in summer and autumn, but comparatively scarce in the other two seasons when virtually no insects likely to be prey were collected.

12. The herons' diet appeared to change readily according to relative prey availability. Major foods were earthworms, Tadpole shrimps, Cosmopolitan diving beetles, Striped dungflies, backswimmers, caterpillars, damselflies, grasshoppers, tadpoles and frogs.

13. Herons ate a decreasing proportion of worms over the day, and a much higher proportion in winter than in other seasons, especially summer. This pattern corresponded with the seasonal availability of worms, and probably also to diurnal changes.

14. Pellets contained predominantly aquatic prey between August and December, and as aquatic habitats became less extensive the prey changed to terrestrial insects over summer and autumn.

15. The majority of the prey in the regurgitated food and stomach were absent from pellets or only occurred rarely, which reflects the strong chemical digestion of herons and the biased nature of pellets.

16. The White-faced Heron is a generalist in its feeding habits, and at Pukepuke they utilized similar foods to Cattle Egrets, which is likely to lead to competition between the two species in the future.

APPENDIX 1

WEATHER DATA OVER THE STUDY PERIOD

		OHAKEA		PUKEPUKE
		Mean temperature (°C)	Total rainfall (mm)	Level of Pukepuke Lagoon (metres above sea level)
1980	March	15.3	139	6.31
	April	12.6	55	6.44
	May	10.6	37	6.43
	June	7.1	62	6.45
	July	6.7	64	6.41
	August	8.6	87	6.44
	September	11.6	115	6.47
	October	13.7	75	6.49
	November	12.8	120	6.43
	December	15.9	33	6.38
1981	January	19.0	20	6.20
	February	18.7	74	6.15

APPENIDX 2

EGG MEASUREMENTS

	Length (mm)	Width (mm)
	47.1	34.3
	47.8	34.6
	48.6	33.6
	48.8	33.4
	43.7	31.8
	44.6	31.2
	43.5	32.4
	47.1	32.8
	46.3	34.3
	41.2	34.1
	47.1	37.5
	42.0	32.3
	41.8	31.3
	46.5	33.7
	44.8	33.8
	45.9	31.8
	47.1	34.5
	46.9	34.0
	44.0	33.5
	42.9	33.5
	47.0	33.9
Mean	45.5	33.4
Standard deviation	± 2.3	± 1.4

APPENDIX 3

SHORT NOTES

WHITE-FACED HERON FLEDGLING WITH A DEFORMED BILL

On 30 October 1980, during routine observations as part of a study of the White-faced Heron *(Ardea novaehollandiae)* near Tangimoana, Manawatu, I found a heron nest containing two live young and an infertile egg. Judging by the growth rates of chicks in other nests I estimated these birds to be about 4 weeks old; the fledging period is about 6 weeks (Falla *et al.* 1979, *A new guide to the birds of New Zealand*). One chick appeared to be normal, but the less well-developed chick had a distinctively deformed bill (Fig. 1). As far as I know, this has not previously been recorded for the species in New Zealand. On a second visit to the nest (6 November 1980), both chicks were still present, although the more advanced bird flew away quite strongly as I approached. This bird was not seen on 13 November, when the deformed chick was found dead beneath the nest. Neither parent was seen on any visit, although one or both presumably were attending the nest up to at least 6 November.

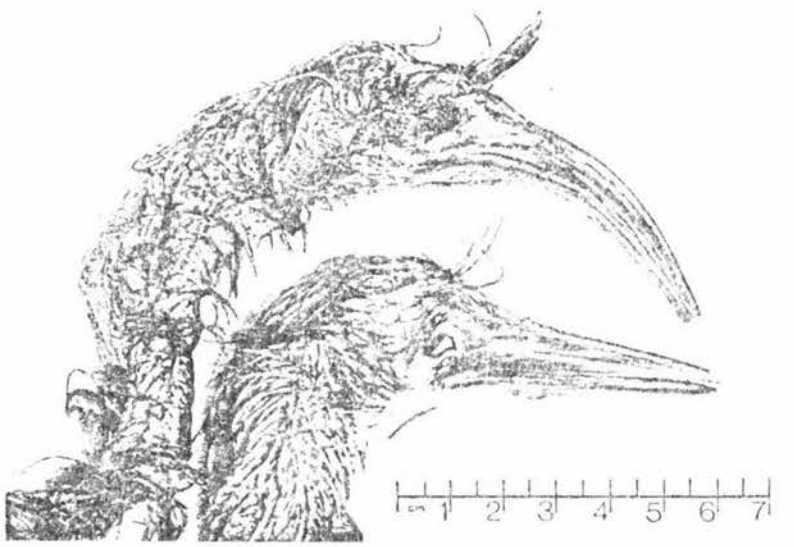

FIGURE 1 — Comparison of a normal White-faced Heron chick, about 3 weeks old, with the deformed chick.

Photo: B A. Campbell

It is interesting to speculate to what extent (if any), the misshapen bill retarded growth in the deformed chick. Although both chicks appeared similar in size, the plumage of the normal chick was further advanced than that of the deformed chick. From observations of other White-faced Heron nests, siblings from about 2 weeks of age onwards appear to be equally developed. This suggests that the bill deformity did have a detrimental influence upon the chick, perhaps in the success with which food was transferred from parent to young.

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Notornis 28 : 133-134 (1981)

APPENDIX 4

BEHAVIOURAL CATEGORIES

FORAGING

Walk Look Down : Heron walks while looking downwards searching for food.

Stand Look Down : Bird is stationary and looks downwards, after presumably detecting some prey.

Prepare to Strike : Bird is stationary and about to make a horizontal or a vertical strike.

Strike : The action of directing the bill at prey.

Swallow : Immediately after a successful strike the head is jerked sharply backwards to swallow the prey.

Foot Shake : One leg is extended forwards and the foot is shaken, presumably to disturb hidden prey. Occasionally seen when feeding in shallow water.

LOOKING

Stand Look Round : Bird stands with its body upright and neck partly extended or fully withdrawn onto its shoulders. Heron either resting or pausing between another activity.

Upright : Heron showing signs of alarm with its body upright and neck fully extended, and the bird watches the source of disturbance.

Walk Look Round : Heron walking but not looking at the ground.

BODY CARE

Preen : Manipulating feathers with the bill.

Scratch : Underside of the head scratched with the foot.

Ruffle feathers : The body is shaken vigorously to ruffle the plumage.

Stretch : Either a leg is extended backwards or a wing is extended sideways.

Bathe : Heron sits and splashes water over itself.

FLYING

Fly : All flying except aerial chases between herons.

AGONISTIC

Chase : Chase between two or more herons, on the ground or more often, in the air.

Head Up Bill Up : An aggressive behaviour with the neck fully extended and bill pointed upwards, wings folded but held away from the body as the bird runs towards another heron.

Run : Heron runs away from a threatening bird.

Jump Up and Down : Two herons jump in the air while appearing to spar. Only observed once.

OTHER

Circle Head to Tail : Greeting ceremony between a pair. With their bodies lowered and horizontal the pair circle

	each other, and direct their bills at the partner's tail.
Drink :	Drinking.
Defaecate :	Defaecating.
Run :	Heron runs without another heron apparently involved.
Erect Plumage :	Body feathers raised in response to Magpies flying past closely.

APPENDIX 5

TIME BUDGET DATA FROM PUKEPUKE

DIURNAL PERIOD 1

		Mar	Apr	May	Autumn	Jun	Jul	Aug	Winter	Sep	Oct	Nov	Spring	Dec	Jan	Feb	Summer
Foraging	N	50	148	141	339	81	160	109	350	122	154	365	641	232	199	623	1054
	%				79.9				70.0				74.5				60.2
Looking	N	4	27	22	53	13	46	28	87	31	22	52	105	49	34	243	326
	%				12.5				17.4				12.2				18.6
Body care	N	0	6	4	10	0	5	6	11	11	13	64	88	81	31	183	295
	%				2.4				2.2				10.2				16.8
Flying	N	0	3	17	20	16	28	7	51	8	6	12	26	14	11	48	73
	%				4.7				10.2				3.0				4.2
Agonistic	N	0	0	2	2	0	0	1	1	1	0	0	1	2	0	1	3
	%				0.5				0.2				0.1				0.2
Other	N	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	%				0				0				0				0
TOTAL	N	54	184	186	424	110	239	151	500	173	195	493	861	378	275	1098	1751
	%				100.0				100.0				100.0				100.0
Hours of Observation		2.45	7.10	7.05	17.00	4.30	8.15	5.30	18.15	5.15	8.05	9.20	22.40	4.55	4.30	11.30	20.55

DIURNAL PERIOD 2

		Mar	Apr	May	Autumn	Jun	Jul	Aug	Winter	Sep	Oct	Nov	Spring	Dec	Jan	Feb	Summer
Foraging	N	39	211	115	365	142	249	286	677	212	401	651	1264	103	255	881	1239
	%				52.2				61.4				80.5				48.8
Looking	N	5	78	104	187	54	137	138	229	79	22	72	173	74	105	369	548
	%				26.7				29.9				11.0				21.5
Body care	N	7	56	68	131	12	10	10	32	19	7	74	100	84	150	469	703
	%				18.7				2.9				6.4				27.7
Flying	N	1	3	5	9	12	27	17	56	5	5	22	32	14	10	26	50
	%				1.3				5.1				2.0				2.0
Agonistic	N	0	0	8	8	2	4	1	7	0	1	0	1	0	0	0	0
	%				1.1				0.6				0.1				0
Other	N	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0
	%				0				0.1				0				0
TOTAL	N	52	348	300	700	222	427	453	1102	315	436	819	1570	275	520	1745	2540
	%				100.0				100.0				100.0				100.0
Hours of Observation		3.10	13.50	8.55	25.55	9.50	10.45	11.35	32.10	9.30	10.50	11.30	31.50	5.05	7.35	15.35	28.15

DIURNAL PERIOD 3

		Mar	Apr	May	Autumn	Jun	Jul	Aug	Winter	Sep	Oct	Nov	Spring	Dec	Jan	Feb	Summer
Foraging	N	47	145	131	323	165	332	431	928	328	551	758	1637	507	305	1190	2002
	%				47.8				58.6				79.4				62.1
Looking	N	14	108	102	224	96	197	218	511	68	53	80	201	116	132	342	590
	%				33.2				32.2				9.8				18.3
Body care	N	0	42	83	125	32	18	18	68	35	25	84	144	71	228	258	557
	%				18.5				4.3				7.0				17.3
Flying	N	0	0	2	2	11	33	21	65	4	16	59	79	21	11	35	67
	%				0.3				4.1				3.8				2.1
Agonistic	N	0	0	1	1	3	2	3	8	0	0	0	0	0	1	3	4
	%				0.2				0.5				0				0.1
Other	N	0	0	1	1	0	0	4	4	0	0	0	0	1	2	2	5
	%				0.2				0.3				0				0.1
TOTAL	N	61	295	320	676	307	582	695	1584	435	645	981	2061	716	679	1830	3225
	%				100.0				100.0				100.0				100.0
Hours of Observation		3.00	12.05	9.15	24.20	10.15	12.25	12.50	35.30	9.45	12.20	11.15	33.20	6.30	6.50	13.10	26.30

DIURNAL PERIOD 4

		Mar	Apr	May	Autumn	Jun	Jul	Aug	Winter	Sep	Oct	Nov	Spring	Dec	Jan	Feb	Summer
Foraging	N	65	98	225	388	191	452	636	1279	467	196	605	1268	444	369	894	1707
	%				62.5				65.8				75.7				55.6
Looking	N	46	50	72	168	133	214	166	513	113	56	120	289	137	203	327	667
	%				27.1				26.3				17.3				21.7
Body care	N	14	19	24	57	41	21	27	89	44	17	35	96	180	270	120	570
	%				9.2				4.6				5.7				18.5
Flying	N	1	2	4	7	8	12	22	42	6	3	12	21	37	32	54	123
	%				1.1				2.2				1.3				4.0
Agonistic	N	0	0	0	0	5	8	0	13	0	0	0	0	0	0	4	4
	%				0				0.7				0				0.1
Other	N	0	0	1	1	0	1	6	7	0	0	0	0	0	1	1	2
	%				0.1				0.4				0				0.1
Total	N	126	169	326	621	378	708	857	1943	630	272	772	1674	798	875	1400	3073
	%				100.0				100.0				100.0				100.0
Hours of Observation		3.35	6.55	10.25	20.55	12.35	12.45	9.35	34.55	13.10	9.45	10.40	33.35	7.40	9.15	10.30	27.25

DIURNAL PERIOD 5

		Mar	Apr	May	Autumn	Jun	Jul	Aug	Winter	Sep	Oct	Nov	Spring	Dec	Jan	Feb	Summer
Foraging	N	141	223	232	596	195	444	973	1612	683	479	692	1854	469	502	854	1825
	%				68.0				77.9				86.7				63.2
Looking	N	37	52	112	201	86	118	151	355	112	27	64	203	137	241	180	558
	%				22.9				17.1				9.5				19.3
Body care	N	5	22	28	55	12	10	3	25	16	2	10	28	215	169	49	433
	%				6.3				1.2				1.3				15.0
Flying	N	3	6	4	13	10	25	27	62	25	15	9	49	23	22	22	67
	%				1.5				3.0				2.2				2.3
Agonistic	N	2	0	5	7	4	2	0	6	0	0	2	2	0	0	1	1
	%				0.8				0.3				0.1				0
Other	N	0	1	3	4	0	1	9	10	4	0	0	4	0	3	1	4
	%				0.5				0.5				0.2				0.2
TOTAL	N	188	304	384	876	307	600	1163	2070	840	523	777	2140	844	937	1107	2888
	%				100.0				100.0				100.0				100.0
Hours of Observation		6.55	9.40	10.25	27.00	9.40	12.55	11.40	34.15	16.05	10.00	9.30	35.35	9.50	8.45	10.20	28.55

DIURNAL PERIOD 6

		Mar	Apr	May	Autumn	Jun	Jul	Aug	Winter	Sep	Oct	Nov	Spring	Dec	Jan	Feb	Summer
Foraging	N	180	181	263	624	264	311	730	1305	345	394	469	1208	447	467	502	1416
	%				73.2				80.9				87.6				75.0
Looking	N	50	60	62	172	57	62	79	198	39	17	45	101	75	65	141	281
	%				20.2				12.2				7.3				14.9
Body care	N	11	8	5	24	1	3	2	6	1	14	4	19	53	43	35	131
	%				2.8				0.4				1.4				6.9
Flying	N	2	12	9	23	15	40	29	84	13	25	12	50	26	7	15	48
	%				2.7				5.2				3.6				2.6
Agonistic	N	0	2	4	6	6	6	5	17	0	0	0	0	3	0	6	9
	%				0.7				1.1				0				0.5
Other	N	2	0	1	3	0	2	2	4	0	1	0	1	0	1	1	2
	%				0.4				0.2				0.1				0.1
TOTAL	N	245	263	344	852	343	424	847	1614	398	451	530	1379	604	583	700	1887
	%				100.0				100.0				100.0				100.0
Hours of Observation		7.15	7.35	9.55	24.45	9.55	9.35	10.40	30.10	11.00	10.40	8.25	30.05	6.40	6.10	10.45	23.35

TOTAL NUMBER OF OBSERVATIONS FOR EACH DIURNAL PERIOD

ACTIVITY		1	2	3	4	5	6	TOTAL
Foraging	n	2384	3545	4890	4642	5887	4553	25 901
	* %	71.2	60.7	62.0	64.9	74.0	79.2	68.7
Looking	n	571	1237	1526	1637	1317	752	7 040
	* %	15.2	22.3	23.4	23.1	17.2	13.7	19.1
Body care	n	404	966	894	812	541	180	3 797
	* %	7.9	13.9	11.8	9.5	6.0	2.9	8.7
Flying	n	170	147	213	193	191	205	1 119
	* %	5.5	2.6	2.6	2.2	2.2	3.5	3.1
Agonistic	n	7	16	13	17	16	32	101
	* %	0.2	0.5	0.1	0.2	0.3	0.5	0.3
Other	n	0	1	10	10	22	10	53
	* %	0	0	0.1	0.1	0.3	0.2	0.1
Total	n	3536	5912	7546	7311	7974	5732	38 011
	* %	100.0	100.0	100.0	100.0	100.0	100.0	100.0
Hours of Observation		78.50	118.10	119.40	116.50	125.45	108.35	667.50

* Mean seasonal percentage

MONTHLY AND SEASONAL TOTALS

		Mar	Apr	May	Autumn	Jun	Jul	Aug	Winter	Sep	Oct	Nov	Spring	Dec	Jan	Feb	Summer
Foraging	N	522	1006	1107	2635	1038	1948	3165	6151	2157	2175	3540	7872	2202	2097	4944	9243
	%				63.5				69.8				81.3				60.2
Looking	N	156	375	474	1005	439	774	780	1993	442	197	433	1072	588	780	1602	2970
	%				24.2				22.6				11.1				19.3
Body care	N	37	153	212	402	98	67	66	231	126	78	271	475	684	891	1114	2689
	%				9.7				2.6				4.9				17.5
Flying	N	7	26	41	74	72	165	123	360	61	70	126	257	135	93	200	428
	%				1.8				4.1				2.7				2.8
Agonistic	N	2	2	20	24	20	22	10	52	1	1	2	4	5	1	15	21
	%				0.6				0.6				0				0.1
Other	N	2	1	6	9	0	4	22	26	4	1	0	5	1	7	5	13
	%				0.2				0.3				0				0.1
TOTAL	N	726	1563	1860	4149	1667	2980	4166	8813	2791	2522	4372	9685	3615	3869	7880	15364
	%				100.0				100.0				100.0				100.0
Hours of Observation		26.40	57.15	56.00	139.55	56.45	66.40	61.50	185.15	64.45	61.40	60.40	187.05	40.40	43.05	71.50	155.35

APPENDIX 5A

TIME BUDGET DATA FROM PALMERSTON NORTH

Activity		April	May	June	TOTAL
Foraging	n	482	329	61	872
	%				55.6
Looking	n	270	90	31	391
	%				24.9
Body care	n	220	36	0	256
	%				16.3
Flying	n	21	22	1	44
	%				2.8
Agonistic	n	2	0	0	2
	%				0.1
Other	n	4	1	0	5
	%				0.3
TOTAL	n	999	478	93	1570
	%				100.0
Hours of Observation		11.00	7.40	4.20	23.00

APPENDIX 5B

TEST STATISTICS FOR THE TIME BUDGET ANALYSES

Significance level : NS not significant * P<0.05 ** P<0.01 *** P<0.001

F ratio values for the main activities over the day and year

Variation		Foraging	Looking	Body care	Other
Daily	$F_{5,15}$	5.42 **	3.94 *	5.62 **	3.44 *
Linear	$F_{1,15}$	10.35 **	1.79 NS	13.55 **	1.31 NS
Quadratic	$F_{1,15}$	14.40 **	16.66 ***	12.62 **	15.14 **
Seasonal	$F_{3,15}$	12.18 ***	11.27 ***	18.69 ***	7.19 **

Chi^2 values with 1 degree of freedom

Foraging

	Autumn	Winter	Spring
Winter	50.7***		
Spring	502.2***	331.3***	
Summer	15.2***	224.7***	1222.4***

Looking

	Autumn	Winter	Spring
Winter	4.0*		
Spring	392.9***	444.1***	
Summer	47.9***	36.8***	299.1***

Body care

	Autumn	Winter	Spring
Winter	301.9***		
Spring	111.2***	64.9***	
Summer	149.0***	1166.5***	853.1***

Other

	Autumn	Winter	Spring
Winter	39.4***		
Spring	0.3 NS	61.7***	
Summer	2.0 NS	59.7***	1.3 NS

Chi^2 values between data from Pukepuke and Palmerston North

Foraging	20.1 ***
Looking	0.1 NS
Body care	64.0 ***
Other	0.6 NS

APPENDIX 6

FEEDING ECOLOGY DATA FROM PUKEPUKE

DIURNAL PERIOD 1

MONTH	N	STRIKES TOTAL	MEAN	N	HORIZONTAL TOTAL	%	VERTICAL TOTAL	%	SWALLOWS TOTAL	MEAN	% SUCCESSFUL STRIKES	N	STEPS TOTAL	MEAN
March	22	35	1.6	7	2		5		31	1.4	88.6	-	-	-
April	69	167	2.4	56	32		78		135	2.0	80.8	20	1091	54.6
May	66	263	4.0	66	0		263		183	2.8	69.6	47	3453	73.5
AUTUMN	157	465	3.0	129	34	9	346	91	349	2.2	75.1	67	4544	67.8
June	25	159	6.4	25	0		159		101	4.0	63.5	22	1029	46.8
July	39	229	5.9	39	3		226		154	3.9	67.2	39	2593	66.5
August	53	283	5.3	53	0		283		214	4.0	75.6	52	2970	57.1
WINTER	117	671	5.7	117	3	0	668	100	469	4.0	69.9	113	6592	58.3
September	30	165	5.5	30	0		165		98	3.3	59.4	30	1579	52.6
October	67	505	7.5	67	3		502		342	5.1	67.7	67	3260	48.7
November	46	235	5.1	46	1		234		152	3.3	64.7	42	1477	35.2
SPRING	143	905	6.3	143	4	0	901	100	592	4.1	65.4	139	6316	45.4
December	14	85	6.1	14	0		85		46	3.3	54.1	11	381	34.6
January	22	74	3.4	22	29		45		52	2.4	70.3	20	829	41.5
February	35	148	4.2	15	98		9		111	3.2	75.0	15	535	35.7
SUMMER	71	307	4.3	51	127	48	139	52	209	2.9	68.1	46	1745	37.9

DIURNAL PERIOD 2

				STRIKES					SWALLOWS				STEPS	
MONTH	N	TOTAL	MEAN	N	HORIZONTAL TOTAL	%	VERTICAL TOTAL	%	TOTAL	MEAN	% SUCCESSFUL STRIKES	N	TOTAL	MEAN
March	24	135	5.6	7	1		18		122	5.1	90.4	-	-	-
April	125	327	2.6	106	120		128		273	2.2	83.5	37	828	22.4
May	91	283	3.1	88	41		210		183	2.0	64.7	75	3082	41.1
AUTUMN	240	745	3.1	201	162	31	356	69	578	2.4	77.6	112	3910	34.9
June	65	178	2.7	64	1		170		115	1.8	64.6	56	2790	49.8
July	63	344	5.5	63	2		342		241	3.8	70.1	60	2904	48.4
August	104	413	4.0	104	14		398		258	2.5	62.5	104	5911	56.8
WINTER	232	935	4.0	231	17	2	910	98	614	2.6	65.7	220	11605	52.8
September	48	223	4.6	48	2		221		140	2.9	62.8	47	2143	45.6
October	105	727	6.9	105	16		711		527	5.0	72.5	105	3850	36.7
November	58	415	7.2	58	16		399		274	4.7	66.0	47	1947	41.4
SPRING	211	1365	6.5	211	34	2	1331	98	941	4.5	68.9	199	7940	39.9
December	27	127	4.7	26	18		108		75	2.8	59.1	27	939	34.8
January	18	104	5.8	10	68		13		81	4.5	77.9	1	32	32.0
February	61	306	5.0	40	217		31		245	4.0	80.0	38	1236	32.5
SUMMER	106	537	5.1	76	303	67	152	33	401	3.8	74.7	66	2207	33.4

DIURNAL PERIOD 3

MONTH	STRIKES								SWALLOWS		% SUCCESSFUL STRIKES	STEPS		
	N	TOTAL	MEAN	N	HORIZONTAL TOTAL	%	VERTICAL TOTAL	%	TOTAL	MEAN		N	TOTAL	MEAN
March	27	137	5.1	5	29		0		118	4.4	86.1	-	-	-
April	88	254	2.9	73	148		62		213	2.4	83.9	19	592	31.2
May	91	322	3.5	88	41		251		204	2.2	63.4	68	2790	41.0
AUTUMN	206	713	3.5	166	218	41	313	59	535	2.6	75.0	87	3382	38.9
June	90	265	2.9	90	4		259		148	1.6	55.8	78	2446	31.4
July	87	392	4.5	87	6		386		193	2.2	49.2	83	3028	36.5
August	97	420	4.3	97	12		408		210	2.2	50.0	95	4787	50.4
WINTER	274	1077	3.9	274	22	2	1053	98	551	2.0	51.2	256	10261	40.1
September	81	345	4.3	81	29		316		188	2.3	54.5	80	2978	37.2
October	111	655	5.9	111	26		629		484	4.4	73.9	110	3071	27.9
November	38	252	6.6	38	6		246		188	4.9	74.6	30	920	30.7
SPRING	230	1252	5.4	230	61	5	1191	95	860	3.7	68.7	220	6969	31.7
December	7	21	3.0	7	6		15		12	1.7	57.1	7	418	59.7
January	13	86	6.6	7	42		6		61	4.7	70.9	7	165	23.6
February	55	377	6.9	51	303		47		319	5.8	84.6	51	1357	26.6
SUMMER	75	484	6.5	65	351	84	68	16	392	5.2	81.0	65	1940	29.8

DIURNAL PERIOD 4

MONTH	N	TOTAL	MEAN	STRIKES N	HORIZONTAL TOTAL	%	VERTICAL TOTAL	%	SWALLOWS TOTAL	MEAN	% SUCCESSFUL STRIKES	N	STEPS TOTAL	MEAN
March	32	175	5.5	5	0		21		149	4.7	85.1	-	-	-
April	32	139	4.3	26	45		59		104	3.3	74.8	3	106	35.3
May	112	404	3.6	108	28		359		246	2.2	60.9	103	3742	36.3
AUTUMN	176	718	4.1	139	73	14	439	86	499	2.8	69.5	106	3848	36.3
June	69	247	3.6	69	6		241		122	1.8	49.4	53	1791	33.8
July	124	563	4.5	124	5		556		235	1.9	41.7	121	4606	58.3
August	78	317	4.1	78	4		313		156	2.0	49.2	77	3372	43.8
WINTER	271	1127	4.2	271	15	1	1110	99	513	1.9	45.5	251	9769	38.9
September	89	449	5.0	89	9		440		233	2.6	51.9	89	2992	33.6
October	54	290	5.4	54	19		271		215	4.0	74.1	46	1136	24.7
November	36	204	5.7	36	4		200		139	3.9	68.1	31	886	28.6
SPRING	179	943	5.3	179	32	3	911	97	587	3.3	62.2	166	5014	30.2
December	33	120	3.6	32	9		104		67	2.0	55.8	26	1169	45.0
January	74	516	7.0	39	279		42		387	5.2	75.0	32	762	23.8
February	64	412	6.4	63	332		60		327	5.1	79.4	63	1842	29.2
SUMMER	171	1048	6.1	134	620	75	206	25	781	4.6	74.5	121	3773	31.2

DIURNAL PERIOD 5

MONTH	STRIKES								SWALLOWS		% SUCCESSFUL STRIKES	STEPS		
	N	TOTAL	MEAN	N	HORIZONTAL TOTAL	%	VERTICAL TOTAL	%	TOTAL	MEAN		N	TOTAL	MEAN
March	66	397	6.0	9	34		29		337	5.1	84.9	-	-	-
April	74	360	4.9	62	120		161		243	3.3	67.5	33	1019	30.9
May	96	426	4.4	94	10		406		251	2.6	58.9	81	3367	41.6
AUTUMN	236	1183	5.0	165	164	22	596	78	831	3.5	70.2	114	4386	38.5
June	64	270	4.2	63	9		257		132	2.1	48.9	53	1719	32.4
July	131	787	6.0	131	15		770		360	2.7	45.7	126	5192	41.2
August	131	615	4.7	131	11		603		304	2.3	49.4	129	5333	41.3
WINTER	326	1672	5.1	325	35	2	1630	98	796	2.4	47.6	308	12244	39.8
September	105	499	4.8	104	4		492		290	2.8	58.1	104	4008	38.5
October	122	995	8.2	122	39		955		775	6.4	77.9	95	2326	24.5
November	24	152	6.3	24	1		151		105	4.4	69.1	14	307	21.9
SPRING	251	1646	6.6	250	44	3	1598	97	1170	4.7	71.1	213	6641	31.2
December	18	98	5.4	16	2		86		47	2.6	48.0	14	310	22.1
January	39	308	7.9	35	225		58		232	5.9	75.3	28	515	18.4
February	61	341	5.6	61	277		64		283	4.6	83.0	61	2112	34.6
SUMMER	118	747	6.3	112	504	71	208	29	562	4.8	75.2	103	2937	28.5

DIURNAL PERIOD 6

				STRIKES					SWALLOWS		% SUCCESSFUL STRIKES		STEPS	
MONTH	N	TOTAL	MEAN	N	HORIZONTAL TOTAL	%	VERTICAL TOTAL	%	TOTAL	MEAN		N	TOTAL	MEAN
March	83	408	4.9	15	18		21		336	4.0	82.4	-	-	-
April	60	221	3.7	47	17		126		153	2.6	69.2	27	974	36.1
May	101	522	5.2	100	21		495		316	3.1	60.5	87	3537	40.7
AUTUMN	244	1151	4.7	162	56	8	642	92	805	3.3	69.9	114	4511	39.6
June	94	508	5.4	94	8		500		270	2.9	53.1	78	3623	46.4
July	91	804	8.8	91	14		790		410	4.5	51.0	88	3750	42.6
August	132	764	5.8	132	5		759		354	2.7	46.3	132	6953	52.7
WINTER	317	2076	6.5	317	27	1	2049	99	1034	3.3	49.8	298	14326	48.1
September	106	662	6.2	106	7		655		391	3.7	59.1	102	4367	42.8
October	132	991	7.5	132	26		964		759	5.8	76.6	128	3758	29.4
November	58	373	6.4	58	5		368		243	4.2	65.1	47	1205	25.6
SPRING	296	2026	6.8	296	38	2	1987	98	1393	4.7	68.8	277	9330	33.7
December	34	217	6.4	34	3		214		123	3.6	56.7	27	784	29.0
January	39	128	3.3	39	54		72		84	2.2	65.6	17	362	21.3
February	93	735	7.9	72	506		40		652	7.0	88.7	73	1560	21.4
SUMMER	166	1080	6.5	145	563	63	326	37	859	5.2	79.5	117	2706	23.1

TOTALS FOR EACH DIURNAL PERIOD

				STRIKES					SWALLOWS				STEPS	
PERIOD	N	TOTAL	MEAN*	N	HORIZONTAL TOTAL	%*	VERTICAL TOTAL	%*	TOTAL	MEAN*	% SUCCESSFUL STRIKES*	N	TOTAL	MEAN*
1	488	2348	4.8	440	168	14	2054	86	1619	3.3	69.6	365	19197	52.4
2	789	3582	4.7	719	516	26	2749	74	2534	3.3	71.7	597	25662	40.3
3	785	3526	4.8	735	652	33	2625	67	2338	3.4	69.0	628	22552	35.1
4	797	3836	4.9	723	740	23	2666	77	2380	3.2	62.9	644	22404	34.2
5	931	5248	5.8	852	747	25	4032	75	3359	3.9	66.0	738	26208	34.5
6	1023	6333	6.1	920	684	19	5004	81	4091	4.1	67.0	806	30873	36.1
TOTAL	4813	24873	5.2	4389	3507	23	19130	77	16321	3.5	67.7	3778	146896	38.8

* Mean seasonal value

MONTHLY TOTALS

MONTH	N	STRIKES TOTAL	MEAN	N	HORIZONTAL TOTAL	%	VERTICAL TOTAL	%	SWALLOWS TOTAL	MEAN	% SUCCESSFUL STRIKES	N	STEPS TOTAL	MEAN
March	254	1287	5.1	48	84		94		1093	4.3	84.9	–	–	–
April	448	1468	3.3	370	482		614		1121	2.5	76.4	139	4610	33.2
May	557	2220	4.0	544	141		1984		1383	2.5	62.3	461	19971	43.3
AUTUMN	1259	4975	4.0	962	707	21	2692	79	3597	2.9	72.3	600	24581	41.0
June	407	1627	4.0	405	28		1586		888	2.2	54.6	340	13398	39.4
July	535	3119	5.8	535	45		3070		1593	3.0	51.1	517	22073	42.7
August	595	2812	4.7	595	46		2764		1496	2.5	53.2	589	29326	49.8
WINTER	1537	7558	4.9	1535	119	2	7420	98	3977	2.6	52.6	1446	64797	44.8
September	459	2343	5.1	458	51		2289		1340	2.9	57.2	452	18067	40.0
October	591	4163	7.0	591	129		4032		3102	5.2	74.5	551	17401	31.6
November	260	1631	6.3	260	33		1598		1101	4.2	67.5	211	6742	32.0
SPRING	1310	8137	6.2	1309	213	3	7919	97	5543	4.2	68.1	1214	42210	34.8
December	133	668	5.0	129	38		612		370	2.8	55.4	112	4001	35.7
January	205	1216	5.9	152	697		236		897	4.4	73.8	105	2665	25.4
February	369	2319	6.3	302	1733		251		1937	5.2	83.5	301	8642	28.7
SUMMER	707	4203	5.9	583	2468	69	1099	31	3204	4.5	76.2	518	15308	29.6

APPENDIX 6 continued

FEEDING INTENSITY INDICES

PERIOD		AUTUMN	WINTER	SPRING	SUMMER	MEAN
1	SI	142	241	283	156	206
	CI	107	168	185	106	142
2	SI	97	149	313	148	177
	CI	75	98	215	111	125
3	SI	99	138	259	240	184
	CI	75	70	178	195	130
4	SI	153	164	239	204	190
	CI	106	75	149	152	121
5	SI	205	240	341	240	257
	CI	144	114	242	181	170
6	SI	207	318	360	293	295
	CI	145	158	247	233	196
Mean	SI	151	208	299	214	218
	CI	109	114	203	163	147

SI Strike index (strikes/hour)   CI Catch index (swallows/hour)

APPENDIX 6A

DATA FROM PALMERSTON NORTH

				STRIKES					SWALLOWS				STEPS	
MONTH	N	TOTAL	MEAN	N	HORIZONTAL TOTAL	%	VERTICAL TOTAL	%	TOTAL	MEAN	% SUCCESSFUL STRIKES	N	TOTAL	MEAN
APRIL	87	364	4.2	79	28		277		193	2.2	53.0	40	1314	32.9
MAY	63	257	4.1	63	22		235		136	2.2	52.9	57	2852	50.0
JUNE	41	181	4.4	41	0		181		101	2.5	55.8	41	3436	83.8
TOTAL	191	802	4.2	183	50	7	693	93	430	2.3	53.6	138	7602	55.1

APPENDIX 6B

TEST STATISTICS FOR FEEDING ECOLOGY DATA

Significance level : NS not significant *$P<0.05$ **$P<0.01$ ***$P<0.001$

F ratio for measures of the feeding ecology over the day and year

Variation		Strike rate	Swallow rate	% successful strikes	Strike index	Catch index	Step rate
Daily	$F_{5,15}$	2.69 NS	1.16 NS	1.03 NS	7.31**	3.47*	7.10**
Linear	$F_{1,15}$	10.35**	3.45 NS	1.91 NS	22.39***	8.85**	20.37***
Quadratic	$F_{1,15}$	2.53 NS	1.42 NS	0.36 NS	12.70**	7.12*	14.02**
Seasonal	$F_{3,15}$	11.41***	9.72***	13.80***	18.54***	11.56***	10.86***

Mann-Whitney U statistic and equivalent Z score for measures between seasons

Strike rate

	Autumn		Winter		Spring	
Winter	785608.5	-8.57***				
Spring	508611	-16.82***	781077.5	-10.32***		
Summer	306410	-11.48***	460375	-5.82***	435921	-2.18*

Swallow rate

	Autumn		Winter		Spring	
Winter	920213	2.23*				
Spring	591928.5	-12.38***	663968	-15.68***		
Summer	311781	-11.03***	351293.5	-13.47***	447648.5	-1.24 NS

Step rate

	Autumn		Winter		Spring	
Winter	367926.5	-5.41***				
Spring	301292.5	-5.99***	584504	-14.86***		
Summer	106971	-9.00***	216758.5	-14.24***	262335.5	-5.47***

Spearman correlation coefficient between strikes and steps

Period	1	2	3	4	5	6	Overall
	-0.252	-0.189	-0.169	-0.174	-0.210	-0.214	-0.189
	***	***	***	***	***	***	***

Season	Autumn	Winter	Spring	Summer
	-0.056	-0.071	-0.121	-0.351
	NS	**	***	***

Chi^2 values for diurnal variation within seasons (5 degrees of freedom) and between seasons (1 degree of freedom)

Percentage of successful strikes

Autumn	0.58 NS
Winter	8.63 NS
Spring	0.55 NS
Summer	1.12 NS

Periods 1 and 2 v.3-6 of winter

Chi^2 1 d.f. = 178.8***

	Autumn		
Winter	485.2***	Winter	
Spring	25.4***	393.9***	Spring
Summer	18.1***	632.3***	87.9***

Strike index

	Autumn		
Winter	8.73**	Winter	
Spring	48.02***	15.97***	Spring
Summer	10.53**	0.05 NS	13.75***

Spring periods 3 and 4 v. rest

Chi^2 1 d.f. = 9.54**

Catch index

	Autumn		
Winter	0.07 NS	Winter	
Spring	27.72***	24.42***	Spring
Summer	10.32**	8.31**	4.15*

Adults v. Juveniles

Strikes U = 158701 Z = -1.82*
Swallows U = 104460 Z = -5.19***
Steps U = 88410.5 Z = -1.60 NS
% successful strikes Chi^2 1 d.f. = 57.9***

APPENDIX 7

DATA FROM SOIL AND TURF SAMPLES

	AUTUMN (10 samples)		WINTER (16 samples)		SPRING (19 samples)		SUMMER (11 samples)		TOTAL (56 samples)	
	No.	Dry wt. (g)	No.	Dry wt. (g)	No.	Dry wt. (g)	No.	Dry wt. (g)	No.	Dry wt. (g)
_A_. _caliginosa_	971	3.87 (187 worms)	1356	36.40	191	9.14	128	3.60	2646	53.01 (1862 worms)
_A_. _longa_	92	0.80 (18 worms)	272	14.48	602	46.52	150	7.84	1116	69.64 (1042 worms)
_L_. _rubellus_	467	2.35 (117 worms)	933	30.69	387	31.12	56	3.29	1843	67.45 (1493 worms)
_E_. _tetraedra_	165	0.30 (38 worms)	716	5.33	397	6.34	117	1.10	1395	13.07 (1268 worms)
Unidentified	274	0.01 (7 worms)	225	0.77	229	1.39	88	0.68	816	2.85 (549 worms)
TOTAL EARTHWORMS	1969	7.33 (367 worms)	3502	87.67	1806	94.51	539	16.51	7816	206.02 (6214 worms)
_D_. _reticulatum_	54	0.02 (1 slug)	16	0.25	6	0.22	4	0.02	80	0.51 (27 slugs)
_D_. _panormitanum_	3	0.06 (2 slugs)	9	0.12	3	0.06	1	0	16	0.24 (15 slugs)
TOTAL SLUGS	57	0.08 (3 slugs)	25	0.37	9	0.28	5	0.02	96	0.75 (42 slugs)
Other	_C_. _zealandica_ larvae (3)		Tipulidae larvae (7)		-		Scarabaeidae larvae (2)			

APPENDIX 7 continued

	Early morning		Late morning		Early afternoon		Late afternoon		Non-feeding area	
	No.	Dry wt. (g)	No.	Dry wt. (g)	No.	Dry wt. (g)	No.	Dry wt. (g)	No.	Dry wt. (g)
A. caliginosa	115	4.18	143	4.14	165	5.39	152	4.38	166	3.64
A. longa	50	3.92	67	4.80	70	4.00	45	2.96	74	4.46
L. rubellus	66	3.98	160	7.11	89	4.40	92	5.76	242	10.71
E. tetraedra	80	0.64	106	0.78	120	1.16	105	0.68	14	0.14
Unidentified	11	0.04	4	0.01	12	0.05	9	0.03	12	0.01
TOTAL	322	12.76	480	16.84	456	15.00	403	13.81	508	18.96

APPENDIX 7A

TEST STATISTICS ON DATA FROM SOIL AND TURF SAMPLES

Significance level : NS not significant *$P<0.05$ **$P<0.01$ ***$P<0.001$

Mann-Whitney U statistic (sample sizes less than 20)

Number of worms

	Autumn	Winter	Spring
Winter	68 NS		
Spring	77 NS	18***	
Summer	14**	4.5***	37**

Dry weight of worms

	Autumn	Winter	Spring
Winter	8 NS		
Spring	13 NS	124 NS	
Summer	4 NS	14***	22.5***

Number of slugs

	Autumn	Winter	Spring
Winter	61.5 NS		
Spring	52.5 NS	106.5 NS	
Summer	30.5 NS	61.5 NS	104 NS

Chi^2 values (1 degree of freedom)

Number of worms

	Early morning	Late morning	Early afternoon
Late morning	30.7***		
Early afternoon	22.7***	0.6 NS	
Late afternoon	8.8**	6.5**	3.1 NS

Dry weight of worms

	Early morning	Late morning	Early afternoon
Late morning	0.3 NS		
Early afternoon	0.1 NS	0 NS	
Late afternoon	0 NS	0.1 NS	0 NS

APPENDIX 8

SWEEP NET SAMPLE DATA

	Autumn 10 samples	Winter 16 samples	Spring 19 samples	Summer 11 samples	Total 56 samples	Early Morning	Late Morning	Early Afternoon	Late Afternoon	Non-feeding area 7 samples
Order Odonata										
Family Coenagrionidae	1	–	3	1	5	–	–	–	–	–
Order Orthoptera (unid.)	–	–	–	–	–	–	–	–	–	15
Order Hemiptera										
Family Aphididae	76	23	34	–	133	–	5	–	1	1
" Pentatomidae	1	–	–	4	5	2	–	–	–	2
Order Neuroptera (unid)	3	–	–	1	4	–	–	–	–	–
Order Coleoptera (unid.)	43	25	5	6	79	–	–	1	5	5
Family Coccinellidae	–	–	–	3	3	1	–	–	–	–
" Curculionidae	6	1	1	4	12	–	–	2	–	2
Order Diptera (unid.)	686	94	188	1163	2131	105	38	71	130	386
Family Tipulidae	1	–	11	–	12	–	–	–	–	–
" Psychodidae	1	–	–	–	1	–	–	–	–	–
" Chironomidae	13	9	5	4	31	2	1	3	–	–
" Scatopsidae	–	1	–	–	1	–	–	–	–	–
" Bibionidae	–	–	2	–	2	–	–	–	–	–
" Cecidomyiidae	4	13	479	–	496	–	3	–	–	–
" Sciaridae	43	31	43	3	120	1	–	–	5	5
" Dolichopodidae	532	312	118	33	995	6	2	11	2	25
" Lonchopteridae	144	12	1	93	250	1	–	3	7	44
" Phoridae	38	–	–	–	38	–	–	–	–	–
" Syrphidae	7	–	–	2	9	–	1	–	–	–
" Sphaeroceridae*	769	48	164	569	1550	42	143	13	257	9
" Agromyzidae*	561	316	176	541	1594	44	13	42	18	434
" Ephydridae*	1254	1576	3495	3970	10295	368	498	243	1913	400
" Drosophilidae*	–	25	10	2	37	–	–	–	–	–
" Chloropidae*	–	–	9	–	9	–	–	–	–	104
" Anthomyiidae	181	235	29	40	485	2	2	4	9	80
" Muscidae	159	24	305	360	848	127	85	64	93	85
" Sarcophagidae	103	–	–	75	178	4	1	9	–	9
Order Lepidoptera (adult)	14	1	2	2	19	–	–	1	–	–
" " (larvae)	3	–	–	–	3	–	–	–	–	–
Order Hymenoptera (unid.)	512	22	25	203	762	11	4	18	9	54
Family Ichneumonidae	2	–	–	–	2	–	–	–	–	–
" Apidae	–	–	–	9	9	1	–	2	–	7
Order Araneae	177	83	9	24	293	–	–	3	–	12
Unidentified	62	26	21	32	141	7	–	1	9	32
TOTAL	5396	2877	5135	7144	20552	724	796	491	2458	1711

* acalypterate families

APPENDIX 8A

MANN-WHITNEY U STATISTIC FOR INSECT NUMBERS BETWEEN SEASONS AND PERIODS

Significance level : NS not significant * $P<0.05$ ** $P<0.01$

	Autumn		
Winter	34 *	Winter	
Spring	57.5 *	101 NS	Spring
Summer	55 NS	34 **	56 *

Early afternoon v. Late afternoon

U = 7 NS

APPENDIX 9

NUMBER OF EARTHWORMS DIRECTLY OBSERVED AS PREY DURING FEEDING RATE RECORDINGS

	DIURNAL PERIOD						Total worms	% of swallows
	1	2	3	4	5	6		
March	0	0	0	0	1	0	1	0.1
April	3	10	0	2	15	4	34	3.0
May	34	19	13	24	15	9	114	8.2
AUTUMN	37	29	13	26	31	13	149	4.1
June	4	21	32	15	24	24	120	13.5
July	6	40	75	50	52	39	262	16.4
August	73	79	34	29	67	72	354	23.7
WINTER	83	140	141	94	143	135	736	18.5
September	48	33	36	51	39	19	226	16.9
October	19	3	13	1	0	0	36	1.2
November	5	6	10	2	0	0	23	2.1
SPRING	72	42	59	54	39	19	285	5.1
December	3	12	2	7	0	3	27	7.3
January	0	1	0	1	0	4	6	0.7
February	0	0	0	0	0	0	0	0
SUMMER	3	13	2	8	0	7	33	1.0
TOTAL	195	224	215	182	213	174	1203	7.4
% of swallows	12.0	8.8	9.2	7.6	6.3	4.3	7.4	

APPENDIX 9A

CHI SQUARE TESTS ON THE PROPORTIONS OF WORMS

Significance level : * P<0.05 ** P<0.01 *** P<0.001

Period 1 v Period	2	3	4	5	6
Chi^2 1 d.f.	8.7**	6.5*	17.5***	38.7***	98.1***

Morning v Afternoon 77.1***

APPENDIX 10

PELLET DATA

Prey	August	September	October	November	December	January	February	March	April	TOTAL
Order Coleoptera										
Rhantus pulverosus (larvae)	19	433	3601	6055	842	111	22	5	5	11093
" " (adults)	44	258	629	566	501	24	85	59	5	2171
Lancetes Lanceolatus	18	56	79	33	7	2	1	2	-	198
Homeodytes hookeri (larvae/adult)	-	-	1	15	12	5	129/1	-	-	163
Enochrus tritus	-	-	8	3	2	3	33	-	1	50
Antiporus spp.	-	-	-	-	-	-	5	-	-	5
Pyronota festiva	-	1	4	5	75	-	-	-	-	85
Costelytra zealandica	-	1	12	53	5	-	1	-	-	72
Pericoptus truncatus	-	4	19	5	1	1	-	-	-	30
Odontria spp.	-	-	14	8	3	-	-	-	-	25
Onthophagus posticus	-	-	21	1	1	-	-	3	-	26
" *granulatus*	-	-	1	-	-	-	1	-	-	2
Notagonum *submetallicum*	-	2	18	9	4	-	9	1	-	43
Harpalus arneus	-	-	5	6	25	-	1	-	-	37
Clivina rugithorax	-	-	-	13	-	-	-	-	-	13
Carabidae	-	1	1	4	7	2	4	-	-	19
Lonoderus exsul	-	1	-	1	27	2	3	-	-	34
Elateridae (larvae)	1	1	-	8	2	-	-	-	-	12
Graphognathus leucoloma	-	-	-	-	-	-	1	3	-	4
Irenimus spp.	1	-	-	-	-	-	-	-	-	1
Cecyropa spp.	-	-	1	-	-	-	-	-	-	1
Curculionidae	2	1	4	3	1	5	5	-	-	21
Coccinella undecimpunctata	-	-	-	-	-	1	2	-	-	3
Saprosites communis	1	-	-	15	1	-	-	-	-	17
Neocicindela tuberculata	-	-	-	-	-	-	1	-	-	1
Thelyphassa spp.	-	-	-	-	4	-	-	-	-	4
Xylotoles spp.	-	-	-	-	1	-	-	-	-	1
Tenebrionidae	-	-	8	3	1	-	-	-	-	12
Unidentified	5	15	42	39	70	17	17	5	1	211
TOTAL	91	774	4468	6845	1592	173	321	78	12	14354
%	6.3	15.7	52.5	76.4	60.3	35.6	23.6	12.8	5.8	49.2

APPENDIX 10 Continued

Prey	August	September	October	November	December	January	February	March	April	TOTAL
Order Diptera										
Hybopygia varia	-	-	3	22	403	126	514	206	26	1300
Lucilia sericata	-	-	1	1	2	-	1	-	-	5
Muscoidea	-	-	1	17	47	-	11	-	-	76
Calliphoridae	-	-	-	-	5	-	-	-	-	5
Stratiomyiidae (larvae)	-	-	-	190	269	-	1	-	-	460
Eristalis tenax	-	-	3	1	8	95	9	1	-	117
Unidentified	-	7	10	73	6	4	14	25	16	155
TOTAL	0	7	18	304	740	225	550	232	42	2118
%	0	0.2	0.2	3.4	28.0	46.3	40.5	37.9	20.3	7.3
Order Hemiptera										
Anisops spp.	70	255	505	525	103	28	113	5	21	1625
Sigara spp.	16	22	49	30	32	11	29	19	3	211
Cermatulus nasalis	-	-	-	-	1	-	-	-	-	1
Pentatomidae	-	-	-	1	1	-	1	-	1	4
Lygaeidae	-	-	-	-	-	-	112	-	-	112
Unidentified	-	-	-	-	-	-	6	-	-	6
TOTAL	86	277	554	556	137	39	261	24	25	1959
%	6.0	5.6	6.5	6.2	5.2	8.0	19.2	3.9	12.1	6.7
Order Lepidoptera										
Wiseana spp. (larvae/adults)	165	17	130/29	9	-	-	-	-	-	350
Unidentified larvae	-	2	189	22	3	5	24	60	1	306
TOTAL	165	19	348	31	3	5	24	60	1	656
%	11.4	0.4	4.1	0.4	0.1	1.0	1.8	9.8	0.5	2.3
Order Odonata										
Austrolestes colensonis	-	-	-	-	2	1	11	111	-	125
Xanthocnemis zealandica	-	-	-	1	-	4	40	14	-	59
Zygoptera (nymphs)	-	-	-	57	-	-	-	-	-	57
TOTAL	0	0	0	58	2	5	51	125	0	241
%	0	0	0	0.7	0	1.0	3.8	20.4	0	0.8

APPENDIX 10 Continued

Prey	August	September	October	November	December	January	February	March	April	TOTAL
Order Orthoptera										
Phaulacridium marginale	-	-	-	2	6	-	66	33	62	169
Metioche maoricum	-	-	-	-	-	-	6	11	15	32
TOTAL	0	0	0	2	6	0	72	44	77	201
%	0	0	0	0	0.2	0	5.3	7.2	37.2	0.7
Order Hymenoptera										
Apis mellifera	-	-	-	-	2	-	-	-	-	2
Epipompilus spp.	-	-	-	-	1	-	-	-	-	1
Unidentified	-	-	2	19	2	8	5	7	1	44
TOTAL	0	0	2	19	5	8	5	7	1	47
%	0	0	0	0.2	0.2	1.6	0.4	1.1	0.5	0.2
Order Notostraca										
Lepidurus apus viridus	1097	3758	2812	1007	-	3	7	-	-	8684
%	76.0	76.4	33.0	11.2	0	0.6	0.5	0	0	29.8
Order Araneae										
Unidentified	-	3	80	42	69	4	12	1	-	211
%	0	0.1	0.9	0.5	2.6	0.8	0.9	0.2	0	0.7
Order Decapoda										
Unidentified	-	-	7	-	-	-	-	-	-	7
%	0	0	0.1	0	0	0	0	0	0	0
Unidentified	5	81	229	102	88	24	56	41	49	675
%	0.3	1.6	2.7	1.1	3.3	4.9	4.1	6.7	23.7	2.3
TOTAL	1444	4919	8518	8966	2642	486	1359	612	207	29153
%	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0
Weight of pellets (g)	34.91	119.72	261.35	199.52	103.06	17.80	29.64	34.26	4.76	805.02

APPENDIX 10A

CHI SQUARE TESTS ON THE PELLET DATA

Significance level : NS not significant * $P < 0.001$

Proportion of : Coleoptera from October - December v. other months Chi^2 1 d.f. = 5610*
Notostraca from August - September v. " " " = 8323*
Diptera from December - March v. " " " = 6822*
Other orders from February - March v. " " " = 1325*

Monthly proportion of Hemiptera between August and January 5 d.f. = 10.85 NS

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