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FOODS AND FEEDING OF THE WRYBILL (*Anarhynchus frontalis*) ON ITS RIVERBED BREEDING GROUNDS

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ABSTRACT

The feeding ecology of the Wrybill was compared between two sites — a flood-prone riverbed and a stable riverbed. Larvae of aquatic insects, particularly mayfly (*Deleatidium* spp.), were the main prey of Wrybills, which captured them by a variety of methods. The sideways-bent bill was useful in capturing insects from the undersurface of stones where they would normally have been inaccessible to birds with shorter, straight, or even upcurved bills. The evolutionary significance of the bent bill is discussed with reference to climatic trends during and since the Pleistocene period. During floods, aquatic prey was relatively unavailable to Wrybills, causing them to switch to riparian foraging.

INTRODUCTION

The shingle riverbeds of the eastern South Island provide breeding grounds for a variety of New Zealand birds, particularly members of the order Charadriiformes. One species, the Wrybill *(Anarhynchus frontalis)*, breeds entirely within these habitats (Falla *et al.* 1970), occurring on the riverbeds from late winter (August) until mid-summer with comparatively few remaining from February to April (pers. obs.). From late summer until mid-winter the bulk of the population occurs on extensive tidal mudflats in Auckland province (Sibson 1963).

Few studies have been made of the feeding behaviour of the Wrybill since the early twentieth century. This is surprising considering that it is the only living species with a sideways bent bill. Oliver (1955) records the 28-30 mm long bill as being bent to the right by up to 12°. However, bill angles of eight Canterbury Museum specimens range from 14-23° (R. Hay, pers. comm.). Wrybill feeding techniques on North Island mudflats have been described recently by Turbott (1970) who found that tilting of the head to the left followed by a sideways sweep of the bill from right to left was a common feeding movement on mudflats. Like other riverbed birds, the Wrybill has been little studied on the breeding grounds and some aspects of their feeding ecology have been left for speculation only. Potts (1871) saw the value of the curved bill in fitting close to a stone. He wrote " . . . the bird is enabled to follow up retreating insects by making the circuit of a water-worn stone with far greater ease than if it had been furnished with the straight bill of the plover or the long flexible scoop of the avocet." Potts' account was quoted again by Buller (1873 and 1882). The value of the curvature of the bill for feeding was disputed by some later authors (Stead, 1932; Soper, 1963 and 1972; Turbott, 1970). Stead wrote of the bent bill that " . . . there can be very few occasions when the peculiarity is of any decided benefit to its possessor for over nearly all the riverbeds on which the bird feeds, the stones are so much buried in sand as to make the bent bill quite unnecessary."

The above accounts showed that there are gaps and contradictions in the knowledge of Wrybill feeding on riverbeds, largely because authors have formed impressions rather than made quantitative measurements. The purpose of the present paper is to present some general patterns of the riverbed feeding of adult Wrybills, with particular reference to how the bent bill is used.

STUDY AREAS

Most field work was carried out from 5 October 1975 until 23 August 1976 in two study areas, on the Rakaia River and on the Cass River delta (Fig. 1). These riverbeds were chosen because they presented contrasting habitats as well as having relatively high concentrations of Wrybills.

The Rakaia River study area was situated about 70 km inland and 340-370 m above sea-level. The four kilometres of riverbed studied consists of flat expanses of shingle and sand, dissected by streams and old streambeds. Patches of sand are sometimes extensive at the edges of streams. Silt commonly settles on the streambeds in areas of quieter water, but is generally absent from the riffles or rapids. Stones in the river channels and on the shingle-banks are typically smoothly rounded. Floods were frequent during the study period and the streams altered their courses by continually eroding one bank and depositing on the other. Only the more stable shingle-banks were vegetated, the largest plants being lupins *(Lupinus arboreus)*, gorse *(Ulex europeus)* and tussocks (*Poa* spp.). Within the study area, ten

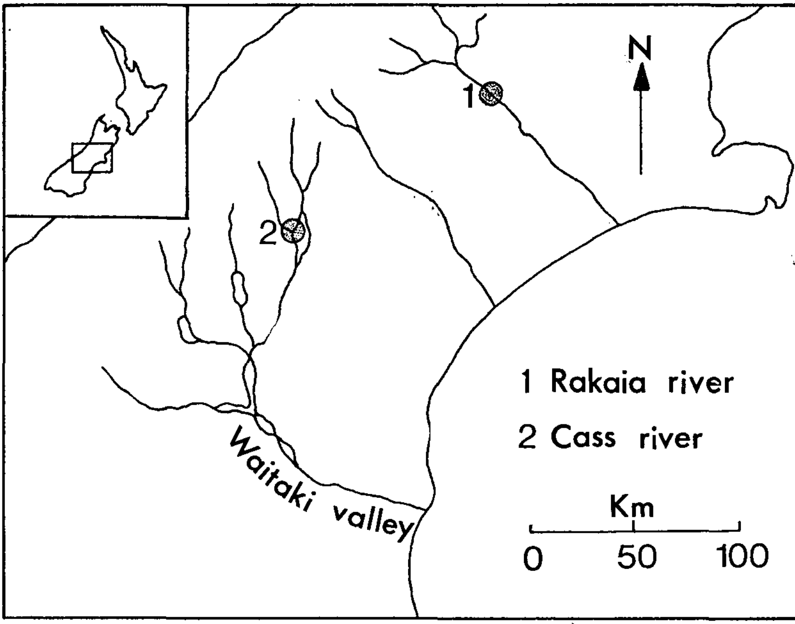

FIGURE 1 — Map of study areas.

Wrybill pairs were located on or near the south bank, and these were regularly visited.

The second study area was situated on the delta of the Cass River where it flows into Lake Tekapo at about 700 m above sea-level. The two-kilometre-wide delta consists of two distinct areas of shingle riverbed separated by tussock grassland and muddy ponds or mudflats (Fig. 2). Since 1973 the river has flowed along the narrow southern bed which is poorly braided and subject to flooding. The northern bed, which had been the main river course before 1973, is wider. Several small streams, which are fed by seepage from the main river and from swampland, dissect this northern bed and they remained clear and at a fairly constant level throughout the study period. Average stone-size in these streams is much less than in the Rakaia River, and mud forms on the beds of some of the pools. Shallow pools comprised a greater surface area of the streams than did riffles. Small plants (including tussocks) have proliferated on this old riverbed since 1973, but lupins and gorse are absent from the entire delta. During the study period, at least seven pairs of Wrybills nested on the shingle-banks of the northern bed and their feeding was studied and compared with that of Rakaia River Wrybills. No feeding data were collected from the southern bed of the delta.

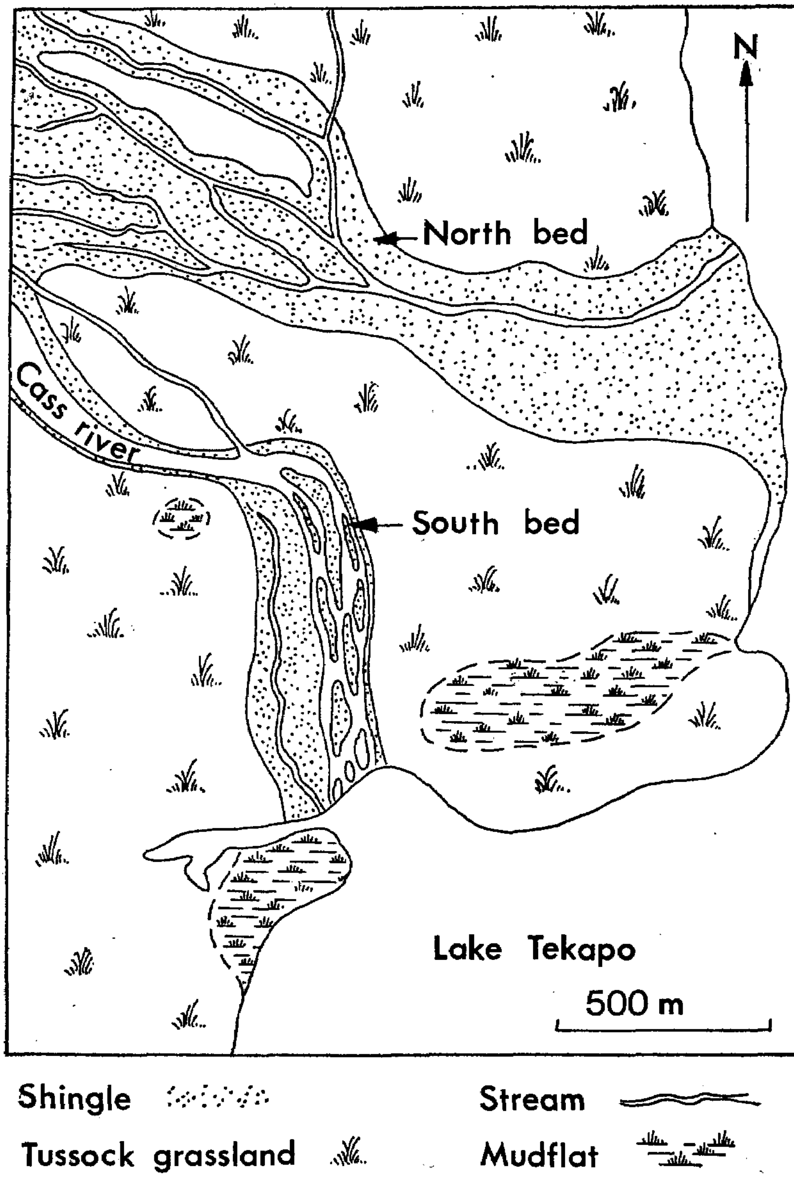

FIGURE 2 — Cass River delta.

METHODS

Field observations were made from elevated shingle-banks, using 8 x 40 binoculars and a 13-40 x telescope. Because they were very active and quite tame, the birds were more easily viewed through binoculars. Sexes were differentiated by the black forehead line of the males (absent in females) and juveniles by the lack of a black pectoral band. Each non-incubating bird was watched either for an hour or, more often, until it was lost from view. Notes were made on habitats, sub-habitats, feeding methods, peck rate, feeding success and search rate.

Habitats

Two habitats were distinguished — aquatic (shallow water) and riparian (shingled river-edge). The aquatic habitat was sub-divided into riffles (broken water), pools (unbroken water), backwashes and transitional areas. Backwashes were defined as pools separated from the main flow of river water. Transitional areas were used for indeterminable situations, particularly where backwashes merged with pools. The riparian habitat was readily sub-divided into shingle-banks and the water-edge. Shingle-banks consisted of elevated areas of stones, shingle and sand, not immediately influenced by river water. The water-edge consisted of the edges of streams where debris collected, and the damp area immediately above.

Feeding methods

Feeding methods in the aquatic habitat were classified according to whether they were ' direct pecks,' ' clockwise movements ' or ' probes.' Direct pecks were very rapid movements after each of which the bill was quickly withdrawn. Clockwise movements involved tilting of the head to the left followed by a left to right movement of the bill. Probing was a prolonged action in which the bill was pushed at a steep angle into the streambed.

Direct pecks and clockwise movements were subdivided according to where the bill was directed. These subdivisions were ' water-surface,' ' in-water ' and ' around-stones.' Water-surface feeding was defined as pecking to a depth not greater than one third bill-length, while in-water feeding was at greater depths. Although these divisions possibly led to some interpretative error, water-surface pecks were generally directed at floating insects, with the bill held at a distinctly shallower angle to the water surface than when pecking at submerged prey. In-water pecks, in contrast, were almost always directed at benthic animals, with the bill held at a steep angle and plunged well into the water. Around-stone feeding was directed at the base of, or under, a partly submerged stone. Clearly many of the in-water movements would have been around-stone movements around sub-merged stones. Feeding methods in the riparian habitat were recorded similarly but fewer categories were required.

Peck rate in both habitats was measured as the number of feeding actions per minute. Peck rate and feeding methods could often be recorded concurrently, particularly when feeding methods were fairly stereotyped. Success rate (percent successful pecks) could be recorded for Wrybills at close quarters only, because small prey items were mandibulated to a very small extent. Several of the larger prey types could be identified in the bills of Wrybills. The search rate (distance travelled per minute) was estimated in metres. This proved more practical than counting the steps taken by birds, and could be recorded concurrently with peck rate.

Collection of prey samples

Samples of the riverbed fauna were collected where Wrybills had been observed foraging for ten or more minutes, and later identified and counted. As Wrybills took relatively few prey from the sample areas, the faunal composition and numbers would not have been significantly changed by the foraging birds. In the aquatic habitat these samples covered 0.5 m^2. A square wooden-framed Surber sampler with a 0.5 mm mesh net was operated for two minutes during which time the surface layer of shingle was stirred by hand. In some situations currents also had to be created by hand. In the riparian habitat, the quadrat samples covered 1.0 m^2, and all invertebrates were collected by hand. All aquatic and riparian samples intended for weighing were preserved in 10% formalin and later dried to constant weight at 80°C. Average dry weights of animals per 1.0 m^2 were then calculated. It was not possible to use fresh material for weighing because many aquatic insects emerged soon after collection.

RESULTS

Aquatic Foraging

INVERTEBRATE FAUNA

The aquatic fauna at Wrybill feeding stations on the Rakaia River is summarised in Appendix 1. The dominant animals were mayfly larvae of the genus *Deleatidium,* with densities ranging 0-775 per m^2 (average 85 per m^2). Any seasonal changes in mayfly numbers and biomass were obscured by river condition, which had a marked effect on mayfly abundance. Floods caused temporary but spectacular declines in the numbers of mayflies in shallow water with an average of only 2 per m^2 at those times. As the river subsided, densities of 200-775 per m^2 were recorded, and even greater densities sometimes occurred in landlocked pools (R. Hay, pers. comm.). Free-living (uncased) caddisfly larvae of the families Hydrobiosinae and Hydropsychidae were the second most common animal group of the Rakaia River aquatic fauna and their total biomass per m^2 approached that of mayflies. Floods made caddisflies as well as mayflies much less available to Wrybills.

The aquatic fauna was more varied in the Cass River streams (Appendix 2) than in the Rakaia River, with many additional invertebrate groups being recorded. Cased caddisfly larvae of the families Leptoceridae and Sericostomatidae, and mayfly *(Deleatidium)* larvae were the most numerous animals. Numbers of cased caddisflies ranged approximately 66-1000 per m^2, with an approximate average of 560 per m^2, while numbers of mayflies ranged 114-310 per m^2 with an average of 176 per m^2. As on the Rakaia River, free-living caddisfly larvae were an important group in terms of biomass. Numbers of invertebrates in the stable Cass River streams fluctuated much less than in shallow water situations on the flood-prone Rakaia River, and densities of mayflies, for example, never approached the extremes for Rakaia River.

In both study areas mayfly larvae were found to be negatively phototactic, clinging to the undersurface of stones during the day. Stones that were free of silt, and were partly covered in algae, normally supported mayflies. These conditions were characteristic of the riffles and it was here that mayflies were most abundant and Wrybills most frequent. Mayfly larvae moult to a sub-imago phase, which flies from the water and shelters in a damp terrestrial site where it completes a final moult to the imago (adult) phase within three days and flies away (Penniket 1969). Both mayfly and stonefly larvae were seen to emerge in the early afternoon at both study areas.

Free-living and cased forms of caddisfly larvae were also usually found on the undersurface of stones. McFarlane (1969) reported caddisflies emerging from the water in the evening or at night and this was confirmed for at least the Cass River study area.

FOOD TAKEN

Mayfly larvae appeared to be the staple diet of Wrybills at each river, despite diverse aquatic faunas, particularly on the Cass. Mayfly sub-imagos floating on the water surface were also taken, as were drifting mayfly larvae. On both riverbeds, Wrybills were occasionally seen mandibulating large free-living caddisfly larvae. No cased caddisfly larvae were seen being mandibulated by Wrybills and none was eaten when large numbers of cased larvae were provided experimentally at the edge of a Cass stream. Wrybills may not eat cased caddisflies because of a low energy return. I extracted 300 caddisfly larvae from their cases, dried them and the cases at 80°C, and then calculated their dry weights. The average dry weight of the extracted larva was only 0.7 mg compared with 2.9 mg for mayfly larvae (Appendix 2). Caddisflies and mayflies were recorded by Cummins & Wuycheck (1971) as having relatively similar energy values per gram of dry weight, hence the average energy intake per individual caddisfly was probably much lower than per individual mayfly on the Cass River streams. Moreover, the dry weight of extracted caddisfly larvae averaged only 17% of the total dry weight of extracted caddisfly larvae plus case, the remaining 83% consisting of a sand and/or silt case which would have been largely unpalatable to Wrybills. However, it is possible that Wrybills take some cased caddisflies when tactile feeding.

On the Rakaia River, when ten dead bullies *(Gobiomorphus cotidianus)* averaging 3.0 cm long were provided at the river edge, one was eaten. On another occasion, one bird was seen attempting unsuccessfully to eat whole a dead 7.0 cm long bully at the water-edge. Wrybills were sometimes seen with fish eggs on their mandibles at the Cass River, and it is possible that eggs of aquatic insects, as well as those of fish, were an additional food at both rivers.

SUB-HABITATS FREQUENTED

On the Rakaia and Cass Rivers, the riffles had highest mayfly densities and were the preferred aquatic sub-habitat of Wrybills (Fig. 3). This was contrary to Turbott's (1970) observation that Wrybills on the riverbeds obtained most of their food from the " . . . soft muddy drifts on the riverbeds and the softer interstices between shingle . . ." On the Rakaia River " muddy interstices " were in the form of silt and occurred only along the quieter stretches of water. These quieter stretches (pools) had low mayfly densities and were not favoured by Wrybills (Fig. 3a). Muddy pools were common on the Cass River streams, but they also had low mayfly densities and were less often frequented by Wrybills than were the silt-free and mud-free riffles (Fig. 3b). Similarly, backwashes and transitional areas had lower mayfly densities than the riffles and were not favoured by Wrybills.

FEEDING METHODS

In aquatic feeding, Wrybills walked moderately fast through shallow water, maintaining an on-going search path and seldom retracing their steps. The relative frequencies of the different bill movements that birds used when feeding are given as percentages in Figure 4. These frequencies were not found to differ significantly between sexes, nor with time of day and season, although comparatively few observations were made in August and none in September.

Direct pecks were the main bill movements, accounting for 59.5% of Rakaia River observations and 54.1% of Cass observations. Most of these direct pecks were of the ' in-water ' category and were probably directed mainly at benthic prey, because the bottom-dwelling mayfly and caddisfly larvae were frequently seen to be captured. Wrybills were often seen to alter the direction of the chase, suggesting that moving prey was the target or at least that the prey had moved. It is likely that direct pecks to the base of stones may have been directed at mayfly larvae which, having detected the approaching bird, were seeking the shelter of the stones. Surface pecking was used to capture floating insects and was also used at some land-locked pools where mayfly larvae often swam to the water surface.

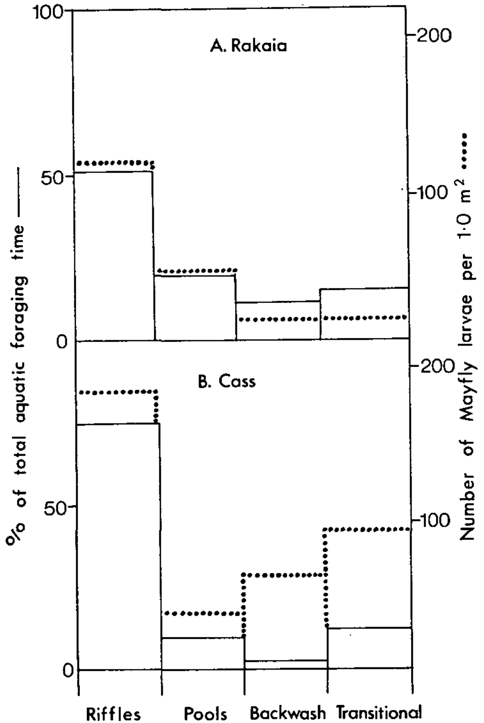

FIGURE 3 — The relationship between preferred aquatic subhabitats of Wrybills and the abundance of mayfly larvae.

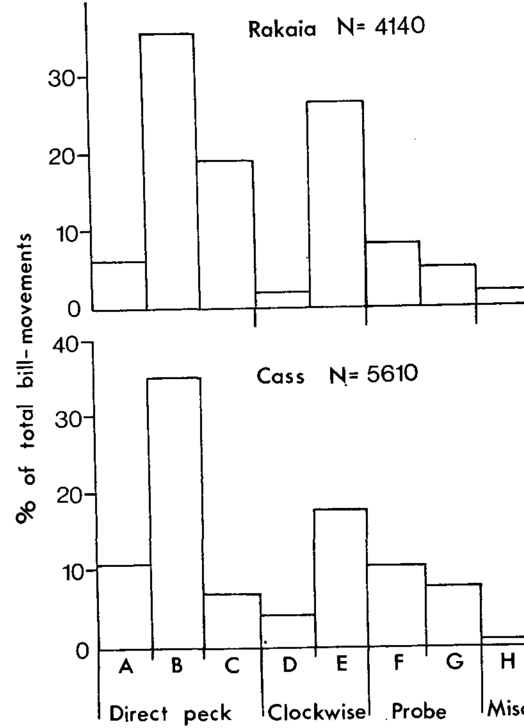

FIGURE 4 — Frequency of bill-movements in aquatic feeding. A: surface. B: in water. C: around stone: D: in water. E: around stone. F: direct. G: clockwise. H: miscellaneous.

Clockwise bill movements accounted for 27.1% of Rakaia observations and 22.4% of Cass observations. These movements involved the head being tilted to the left side and the bill being pushed forward and/or to the right. In most clockwise bill movements the bill was pushed under a stone where prey appeared to be felt for and not necessarily seen first. It is well known that sensory nerve endings are numerous in the bills of birds (e.g. Heather 1966) and they are particularly important in waders that probe for their food (Heppleston 1971). As mayfly larvae typically cling to the undersurface of stones, they would not be easily accessible to birds with short, straight bills such as the Banded Dotterel *(Charadrius bicinctus)*. The long, sideways bent bill of the Wrybill, by contrast, appears effective in capturing these mayflies but, for this to be so, the head needs to be tilted to the left so that the curvature of the bill more closely fits the undersurface of a stone (Fig. 5). Wrybills always employed

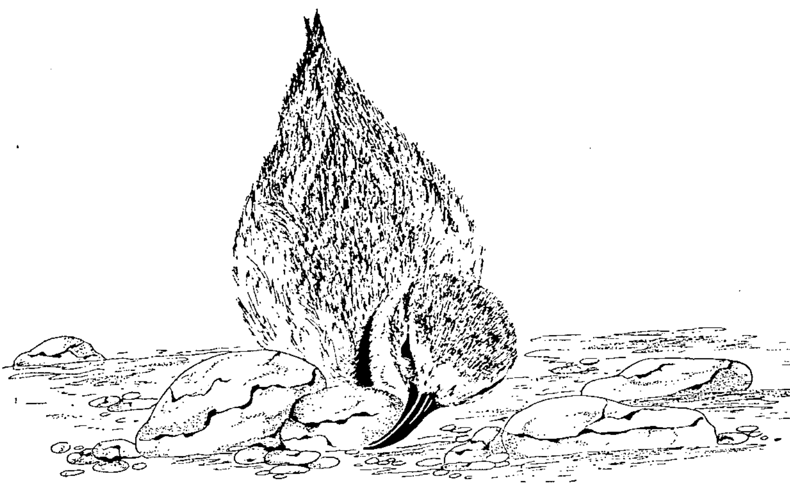

FIGURE 5 — Clockwise feeding around a stone. Mrs J. Clough, del.

this head tilting when feeding by clockwise bill movements. An up-curved bill like that of the Terek Sandpiper *(Xenus cinereus)* would be unsuited to feeding under stones, because the mandibles cannot be opened between the undersurface of a stone and the stones beneath, except very clumsily. The mandibles of the Wrybill are not so restricted because they open sideways to a stone's surface with ample freedom of movement to capture large or small prey.

Soper (1963 and 1972) suggested that clockwise bill movements could only help to capture insects if the bird circled each stone in a clockwise direction. On the Rakaia and Cass, Wrybills were seldom seen circling individual stones in that manner, and even then they were often merely following up prey which had escaped an initial direct peck. Clockwise circling of stones is unnecessary because a Wrybill is highly manoeuvrable and can swing its body around more than 90° in a single step. Thus, all the stones to the right of a bird's path of movement are accessible to clockwise bill movements and, if the body is swung to the left, further stones (formerly to the left of the bird) are made accessible. In some cases, clockwise bill movements were used exclusively throughout a period of observation, but it was more usual for this method to be interchanged with direct pecks.

The third most common bill movement was probing but accounted for comparatively few observations at each river (Fig. 4), and was usually restricted to areas of small stones. Miscellaneous bill movements included direct pecks at insects on emergent stones and in algae, anticlockwise movements (from right to left) and aerial insect-catching. Foot-trembling, used by some other New Zealand plovers (Heather, 1977; Phillips, 1977), was not seen to be used by Wrybills.

PECK RATE AND SUCCESS RATE

Peck rates for the Cass River and under three river conditions for the Rakaia River are given in Table 1. Highest peck rates occurred on the Cass River and on the Rakaia during low or dropping water levels, that is, in conditions of high prey densities. During floods or rising water levels on the Rakaia, when prey densities in shallow water were low, peck rate was significantly lower as birds had to forage more widely for their food.

TABLE 1 — PECK RATES AT CASS AND RAKAIA RIVERS COMPARED

River	River condition	Minutes of observation	Range of pecks per min.	Mean pecks per min.	Statistical significance between Rakaia and Cass (t-test)
Cass	stable streams	550	12 - 56	30	—
Rakaia	very low	55	14 - 53	26	N.S.
Rakaia	moderate	350	2 - 42	18	S.
Rakaia	flood	242	3 - 42	13	H.S.

N.S. = not significant
S. = significantly different (at $p = 0.01$ level)
H.S. = highly significantly different (at $p = 0.001$ level)

When clockwise feeding movements were used exclusively, peck rates were higher than in normal feeding in the same sub-habitat, but success rate was considerably less (Table 2). As a result, prey intake per minute of clockwise feeding was only half that for normal feeding. This does not mean that biomass ingested was only half that for direct pecking, because clockwise feeding may have obtained, on average, larger prey such as free-living caddisfly larvae normally found only under stones and less accessible to direct pecks.

TABLE 2 — FEEDING SUCCESS AT CASS RIVER

Bill-movement	Minutes of observation	Range of pecks per min.	Mean pecks per min.	Successful pecks (%)	Prey intake per min. (nos.)
Mixed (= normal feeding)	195	12 - 42	26	81%	21.1
Clockwise	24	27 - 46	39	26%	10.1

SEARCH RATE

On both the Rakaia and Cass Rivers, the distance walked by Wrybills in search of food corresponded closely with peck rate, as expected (Fig. 6). The higher the peck rate, indicating abundant prey, the less the distance walked; conversely, the lower the peck rate, indicating low prey density such as during floods, the greater the distance walked.

Riparian foraging — the effects of floods

Because the Cass River streams remained at fairly constant levels throughout the study, mayfly larvae and other aquatic prey were always available to Wrybills. Consequently, Cass Wrybills did almost all of their foraging in the streams (Fig. 7). On the Rakaia River in contrast, rising water levels and floods following the rapid onset of snow melt in October caused Wrybills to spend a higher proportion of their foraging time searching for riparian rather than aquatic prey (Fig. 7). Riparian-foraging birds on the Rakaia spent, on average, about equal proportions of time in the shingle-bank and water-edge sub-habitats, although observations may have been biased against birds on shingle-banks where they were difficult to locate.

SHINGLE-BANKS

The shingle-bank invertebrate fauna is summarised by season and presented in Appendix 3. Unlike the aquatic fauna (Appendix 1), total numbers and biomass of invertebrates remained low throughout the sampling period. Carabid beetles and spiders were the most regularly recorded animals, but by December these were outnumbered by the several families of dipteran flies. Carabid beetles and spiders were usually beneath stones and were not easily found by Wrybills. Mayfly sub-imagos and some dipteran flies e.g. *Anabarhynchus* sp. were fairly inactive, did not penetrate far under stones, and were presumably more readily found by Wrybills.

Wrybills were observed feeding on all of the larger, more common invertebrates — beetles, flies, mayflies and spiders. Although spiders were not seen to be eaten in normal feeding, at least four out of twenty small, live spiders provided experimentally near a foraging Wrybill were found and eaten. Very small insects (about the size of sand-

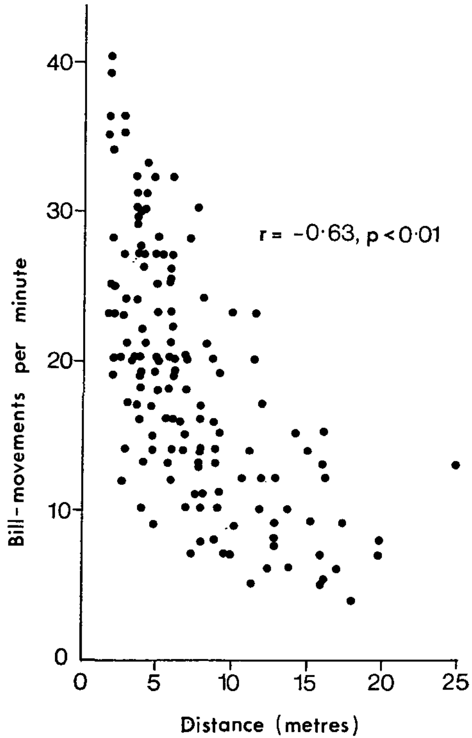

FIGURE 6 — The relationship between distance walked and feeding rate of aquatic-foraging Wrybills on the Rakaia and Cass Rivers, October 1975. Each dot represents observations of one bird for one minute.

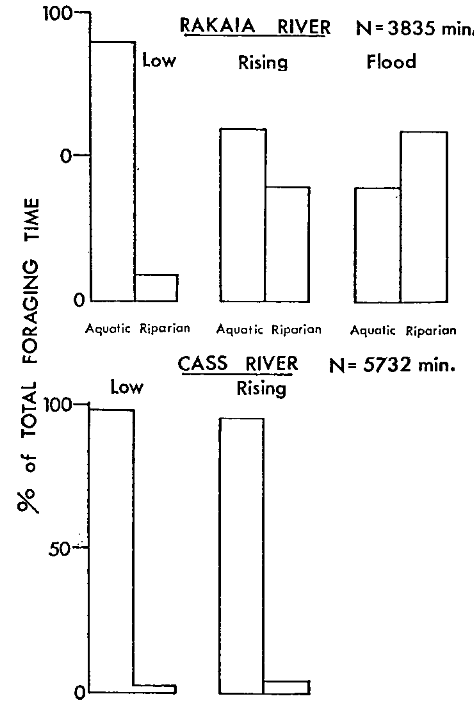

FIGURE 7 — The foraging habitats preferred by Wrybills at different water levels.

flies or newly hatched spiders) were common prey, but their identity was not established. When foraging for sheltering insects, Wrybills typically probed beneath stones (in the manner of clockwise feeding in the aquatic habitat), although prey was more often captured by a direct peck, after it had been first located by the clockwise movement. Prey in more open situations were taken by direct pecks only.

Peck rates in the shingle-bank sub-habitat ranged from 6-28 bill movements per minute with an average of 14, based on 190 minutes of observation. However, most of these bill movements were clockwise sweeps, very few of which resulted in the capture of prey. On average, only five captures were made per minute and Wrybills were often seen foraging for two or three minutes without consuming any large prey, such as *Anabarhynchus*, or mature spiders. Average dry weights of these animals were nevertheless high, some individuals weighing as much as 30-40 mg, nearly twenty times the average dry weight of mayflies. If Wrybills ate one of these large animals about every 90 seconds, then that biomass alone would probably exceed biomass eaten in the aquatic habitat during floods.

Search rates in the shingle-bank sub-habitat averaged 20.0 m per minute compared with 7.2 m per minute in the aquatic habitat ($t = 23.47$, 148 df, $P < 0.001$) during December. This high search rate correlated with the low density of prey on shingle-banks, similar to aquatic situations during floods so that, on shingle-banks, more ground had to be covered (and therefore more energy expended) in order to gain sufficient food.

WATER-EDGE

Invertebrate numbers and biomass of the water-edge are given by seasons in Appendix 4. Sandflies, cyclorraphan flies, hemipteran bugs and mayflies (dead and alive) were the dominant animals, but a variety of others occurred in smaller numbers. Total numbers were low in August (0.7 per m^2) but were significantly higher in October-November (3.2 per m^2) and December-January (4.5 per m^2). Total biomass was also low in August, the bulk being made up of mayflies. From October to January, cyclorraphans comprised more of the water-edge fauna than any other invertebrate group, except on occasions when mayfly larvae became stranded as the river dropped, and at times of mayfly emergence. As no samples could be taken in September, the peak period of mayfly and stonefly emergence was probably missed. Subsequent observations on other rivers at that time of year, suggested that emerged mayflies and stoneflies were regular in the Wrybill diet. These also formed an important part of the diet of chicks (Pierce, 1976), the slow movements of these insects making them an ideal prey.

Food was normally obtained by direct pecks only, although clockwise feeding was sometimes employed at the stony edge of the river. As well as taking mayflies and stoneflies, adult Wrybills preyed on cyclorraphans, but these highly active flies were difficult to catch.

Hemipterans could not be identified for sure in the bills of Wrybills, but much of the smaller prey was probably of this sort. Some birds specialised for several minutes in catching small flies (probably sandflies) which were common on the sandy and silty stretches of the water-edge.

Peck rates in the water-edge sub-habitat ranged from 5-21 bill movements per minute with an average of 10 per minute, based on 115 minutes of observation. Success rate was about 90% for mayfly prey, but observations of Wrybill behaviour following pecks, suggested that it was comparatively low for sandfly and cyclorraphan prey.

Search rates during water-edge foraging averaged 12 m per minute, based on 84 minutes of observation, and was intermediate between shingle-bank search rates (20 m per minute) and aquatic search rates (6 m per minute). This probably reflected the average density of the water-edge prey which was intermediate between shingle-bank prey and aquatic prey.

DISCUSSION

Apart from those of Potts (1871) and Buller (1873 and 1882), published accounts of Wrybill feeding behaviour have suggested that the bent bill has little or no significance on riverbeds (e.g. Stead, 1932; Turbott 1970). However, in the Rakaia and Cass River study areas the feeding repertoire of Wrybills included a significant percentage of tactile bill movements (particularly clockwise bill movements) in which the curvature of the bill assisted prey capture. The bill appears to be pre-adapted for obtaining mayfly and caddisfly larvae from their inactive diurnal positions on the undersurface of submerged stones, where they are normally not visible to Wrybills. Larvae that are visible to Wrybills may also be gleaned from the curved surfaces of stones more readily by a bent bill than by a straight bill.

It is possible that birds are forced to feed by clockwise movements in late winter and early spring when aquatic prey is inactive during the morning because of low water temperatures. This trend was noted at Cass River in August and early September 1977, when almost all feeding movements were tactile. At this time also, other riverbed birds, notably Black Stilt *(Himantopus novaezealandiae)* and Pied Oystercatchers *(Haematopus ostralegus finschi)* were, like Wrybills, probing under stones, and Black-billed Gulls *(Larus bulleri)* were foot-paddling to stir up benthic insects. With their prey inactive, these four birds could not feed by sight alone, except late in the day. Any behavioural or morphological modification that increases the ability of these birds to capture prey during this potentially difficult time, clearly has survival value. Such adaptations are probably more important to the Wrybill than to the other three species, since its shorter legs prevent it from foraging in deeper water where prey density is often high. As Wrybills are small birds, they are probably susceptible to heat loss in very cold conditions (e.g. Kendeigh 1970). A combination of subzero blizzard conditions, which frequently occur in late winter and spring, and a low intake of food, could result in their death. One can speculate that a bent bill had even more survival value during the glacial epochs of the Pleistocene Period, when many New Zealand bird species probably became extinct (Fleming 1962), and the suggested climatic deteriorations since then (Fleming 1963; Molloy 1969). Because of high mortality rates, evolutionary forces are strongest during bad years (MacArthur 1972), in the case of the Wrybill, such forces may have been particularly strong during prolonged cool periods. A scarcity of riparian insects and comparatively stable river levels (both results of a cold climate), coupled with heat-loss problems, would have selected for improved feeding techniques in the aquatic habitat. The bent bill may have permitted an efficient food intake, allowing the species to persist through adverse climatic conditions, such as occurred during glacial epochs. The winter-spring feeding methods of Wrybills on riverbeds are currently being investigated to elucidate the significance of clockwise feeding at that time of year.

It is interesting that on North Island mudflats, Wrybills sweep their bills through the mud from right to left (Turbott 1970), the opposite direction to clockwise feeding on riverbeds. On mudflats and the muddy edges to tarns at the Cass River delta, Wrybills sometimes fed from right to left, although from left to right more commonly; direct pecking and probing also occurred. Clearly, the long curved bill of the Wrybill has different uses and suits different habitats.

The specialised feeding niche (mayflies in riffles) occupied by Wrybills when river levels were low and/or stable, supported the MacArthur & Pianka (1966) time-energy model which predicts that " . . . a more productive environment should lead to a more restricted diet in the numbers of different species eaten." Conversely, as water level rose on the Rakaia, Wrybills changed from a relatively narrow (stenophagous) to a broad (euryphagous) diet, with many species of shingle-bank and water-edge invertebrates being taken, as well as aquatic invertebrates.

The switch to riparian feeding can be explained in terms of " profitability " which Royama (1970) defined as " the amount of food a predator can collect for a given amount of hunting effort." Clearly, at low water levels it was more profitable for Wrybills to forage in aquatic situations, where the biomass of food and the search rate could be low. At flood levels, however, the average numbers of mayflies (2.0) and caddisflies (0.1) per m^2 in shallow water were very low, representing only 4.9 mg per m^2, and the search rates of birds needed to be high. On the other hand, average prey biomass per m^2 in riparian areas exceeded 4.9 mg, except for the water-edge in August (Appendix 3 and 4). Assuming that prey species were equally available in all months, it was therefore more profitable during floods for Wrybills to forage for riparian prey than for aquatic prey. That many birds continued to forage aquatically during floods may have been because they were feeding on drifting mayflies — particularly evident at the beginning of the spring thaw in October — or because the margin of difference between the total prey biomass of the two habitats may have fluctuated from time to time as physical conditions such as weather and water clarity changed.

The bent bill and flexible diet of the Wrybill adapt it to its specialised breeding environment on shingle riverbeds. In favourable conditions, mayfly larvae, its preferred prey, are obtained by direct pecking and by clockwise sweeps beneath the stones of riffles. In localities where river levels rise from time to time, it often shifts to shingle flats where it feeds on varied prey, where the bent bill is of no particular advantage.

APPENDIX 1 — Aquatic fauna in the Rakaia River study area. (N = 160 x 0.5 m^2, each taken where Wrybills had foraged for ten minutes).

Animal Group	Life Form	Abundance August-January				
		Average numbers per m^2	Average dry weight per animal (mg)	Weight range of animals (mg)	Number weigh-ed	Average dry weight per m^2 (mg)
OLIGOCHAETA						
Lumbricidae						
Eiseniella tetraedra	adult	0.12	1.2	0.8 - 1.9	3	0.1
INSECTA						
Ephemeroptera						
Deleatidium sp.	eggs	x100	?	-	-	?
	larvae	85.00	2.1	0.1 - 6.8	500	178.5
	imagos & sub-imagos	0.52	2.5	2.4 -2.8	12	1.3
Plecoptera						
Aucklandobius sp.	larvae	0.63	1.1	0.3 - 2.3	25	0.7
Neuroptera						
Archichauliodes diversum	larvae	0.20	35	27 - 42	20	7.0
Trichoptera						
Hydrobiosinae & Hydropsychidae	larvae	14.88	7.5	0.2 - 18.0	210	111.6
	pupae	2.00	1.8	?	5	3.6
PISCES						
Gobiomorphus cotidianus	eggs	10	0.3	?	100	3.0
TOTAL FAUNA						305.8

APPENDIX 2 — Aquatic fauna in the Cass River study area. (N = 70 x 0.5 m^2, each taken where Wrybills had foraged for ten minutes).

Animal Group	Life Form	Abundance August-January				
		Average numbers per m^2	Average dry weight per animal (mg)	Weight range of animals	Number weigh-ed	Average dry weight per m^2 (mg)
TURBELLARIA						
Tricladida						
Dugesia montana	adult	0.11	2.3	-	2	0.3
OLIGOCHAETA						
Lumbricidae						
Eiseniella tetraedra	adult	0.29	5.0	3.2 - 6.0	8	1.5
HIRUDINEA						
Glossiphoniidae						
Glossiphonia heteroclita	adult	0.14	3.1	?	4	0.4
GASTROPODA						
Potamopyrgus antipodarum	adult	0.26	1.3	0.5 - 1.5	17	0.3
INSECTA						
Ephemeroptera	eggs	x 100	?			
Deleatidium sp.	larvae	176.01	2.9	0.1 - 7.2	500	510.4
	imagos & sub-imagos	0.37	2.5	2.1 - 2.7	17	0.9
Nesamaletus sp.	larvae	0.08	7.1	4.5 -12.1	3	0.6
Plecoptera						
Aucklandobius sp.	larvae	0.37	1.3	0.5 - 1.7	11	0.5
Stenoperla prasina	larvae	0.11	52.0	43.6-60.4	4	5.7
Hymenoptera						
Salius sp.	adult	0.08	1.5	1.3 - 1.6	4	0.1
Coleoptera						
Hydora sp.	adult	0.91	2.1	1.5 - 3.1	20	1.9
Trichoptera						
Leptoceridae & Sericostomatidae	larvae	560.00	0.7	0.1 - 3.9	300	390.32 [1]
Hydrobiosinae & Hydropsychidae	larvae	25.11	7.5	1.5 -24.0	110	188.3
Diptera						
Australosimulium sp.	larvae	0.37	0.5	?	11	0.2
Tipulidae	pupae	6.11	1.5	?	24	9.2
PISCES						
Gobiomorphus breviceps	eggs	40	0.3	?	100	12.0
	fish	0.23	35.0	25.0-47.5	4	8.1
TOTAL FAUNA						1130.7

[1] Excludes larval cases

APPENDIX 3 — Shingle-bank fauna in the Rakaia River study area.

Animal Group	Abundance: August N=100 m²				October - November N=140 m²				December - January N 105 m²			
	Average Nos per m²	Average dry weight per animal (mg)	Number weighed	Average dry weight per m² (mg)	Average Nos per m²	Average dry weight per animal (mg)	Number weighed	Average dry weight per m² (mg)	Average Nos per m²	Average dry weight per animal (mg)	Number weighed	Average dry weight per m² (mg)
ARACHNIDA												
Aranaeida 2-3 spp.	.17	18.0	10	3.1	.13	31.0	25	4.0	.22	28.4	12	6.2
Acarina 1 sp.	.10	1.0	4	0.1	0	-	-	0	0	-	-	0
INSECTA												
Ephemeroptera *Deleatidium* sp.	0	-	-	0	.14	2.6	10	0.4	.10	2.1	20	0.2
Dermaptera *Forficula auricularia*	0	-	-	0	.10	1.6	4	0.2	0	-	-	0
Hemiptera Cicadidae	0	-	-	0	0	-	-	0	.04	52.5	2	2.1
Lepidoptera 2 - 3 spp	0	-	-	0	.10	6.3	5	0.6	.04	5.0	5	0.2
Hymenoptera Formicidae	.04	0.5	5	<0.1	.12	0.5	10	0.1	0	-	-	0
Coleoptera Carabidae	.37	5.6	20	2.1	.65	5.9	30	3.8	.44	5.5	10	2.4
Trichoptera Hydrobiosinae	0	-	-	0	.02	3.0	5	0.1	-	-	-	-
Diptera *Australosimulium* sp.	.02	<1.0	2	<0.1	.11	<1.0	5	0.1	.14	0.3	10	<0.1
Therevidae *Anabarhynchus*	0	-	-	0	.05	26.5	2	1.3	.46	24.0	20	11.0
Tachinidae & Muscidae	0	-	-	0	.10	4.8	5	0.5	.10	4.3	15	0.4
TOTAL FAUNA	.70			5.4	1.52			11.1	1.54			22.5

APPENDIX 4 — Water-edge fauna in the Rakaia River study area.

Animal Group	Abundance: August N = 50 m^2				October - November N = 65 m^2				December-January N = 45 m^2			
	Average Nos. per m^2	Average dry weight per animal (mg)	Number weighed	Average dry weight per m^2 (mg)	Average Nos per m^2	Average dry weight per animal (mg)	Number weighed	Average dry weight per m^2 (mg)	Average Nos per m^2	Average dry weight per animal (mg)	Number weighed	Average dry weight per m^2 (mg)
OLIGOCHAETA												
Tubificidae	0	-	-	0	0	-	-	0	.04	1.3	3	0.1
INSECTA												
Ephemeroptera												
Deleatidium sp,	.30	2.4	10	0.7	.40	1.9	20	0.8	.62	1.5	18	0.9
Hemiptera												
Saldidae & Pentamidae	0	-	-	0	.52	1.4	10	0.7	1.40	1.1	15	1.5
Lepidoptera 2-3 spp.	.16	2.9	6	0.5	.19	7.1	10	1.4	.11	6.9	10	0.8
Hymenoptera												
Salius sp.	0	-	-	0	.38	1.5	4	0.6	.09	1.6	5	0.1
Coleoptera												
Carabidae	.06	5.6	1	0.3	0	-	-	0	.04	5.9	1	0.2
Hydora sp.	0	-	-	0	.17	1.7	5	0.3	.31	1.3	5	0.4
Trichoptera												
Hydrobiosinae	0	-	-	0	0	-	-	0	.07	1.3	4	0.1
Diptera												
Australosimulium sp	.18	<0.5	3	0.1	.95	0.4	10	0.4	1.00	0.4	10	0.4
Tachinidae & Muscidae	0	-	-	0	.62	3.2	10	2.0	.80	4.5	10	3.6
TOTAL FAUNA	.70			1.6	3.23			6.2	4.48			8.1

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