

Hydrological factors influencing the ecology of riverbed breeding
birds on the plains' reaches of Canterbury's braided rivers

A thesis

Submitted in fulfilment
of the requirements for the degree

of

Doctor of Philosophy
in the
University of Canterbury

by

K.F.D. Hughey

Lincoln College

1985

Abstract of a thesis submitted in partial fulfilment of the requirements for the degree of Ph.D.

HYDROLOGICAL FACTORS INFLUENCING THE ECOLOGY OF RIVERBED BREEDING BIRDS ON THE PLAINS' REACHES OF CANTERBURY'S BRAIDED RIVERS.

by

K.F.D. Hughey

The wide, unstable, braided riverbeds of the eastern South Island, New Zealand, have been inhabited by a diverse avifauna. Several species including the wrybill breed only on these rivers. Use is restricted mainly to the breeding season from September to December, so this was the critical study period. Previous, behaviourally oriented studies have occurred mainly in the high country catchments where habitat modification is slight. However, substantial bird numbers also occur on lowland riverbeds. These areas are subject to existing or planned water developments which may have negative impacts on the conservation of these habitats and bird species. The principal goal of this study was to add to the information necessary to conserve lowland riverbed habitat within multiple use planning strategies. Specific objectives associated with assessing breeding and feeding requirements were therefore hydrologically oriented.

Study areas were chosen on the lower Rakaia and lower Ashley rivers. Both are braided but have markedly different flow regimes. The Rakaia is snowfed and has peak flows occurring during the breeding season. The Ashley is primarily rainfed and has a declining breeding season flow regime. Wrybills, black-fronted terns, banded dotterels, South Island pied oystercatchers, and pied stilts breed in these areas. The first two of these were selected as indicator species. It was assumed that because of their restricted habitat needs, flow requirements recommended to meet their needs would also meet those of most other species. Banded dotterels were also studied because of their close taxonomic relationship and overlapping distribution with wrybills. South Island pied oystercatchers and pied stilts were chosen to check the validity of the approach.

Breeding, nest site requirements, microhabitat preferences for foraging, diets, home ranges and food supply were studied. Wrybill time-budgets were examined, and the incremental approach to impact assessment was applied to wrybill foraging needs.

Breeding success for all species was dependent on the flow regime. In 1982 wrybill fledging success was moderate on the Rakaia, whereas in 1983 it was very low. Conversely, in both years fledging success was very high on the Ashley. This variability resulted from serious flooding on the Rakaia in 1983 which effected all species. Wrybills have nest site characteristics most closely approximating a habitat specialist, while the other species should be considered habitat generalists. Nests are generally close to water, near minor braids, and on non-vegetated shingle substrates. On average there is a higher chance of nests being flooded on the Rakaia than on the Ashley where predation is more likely to reduce nesting success. Vegetation encroachment threatens nest site provision and floods are presently the only natural regulator of exotic plants such as lupin.

Banded dotterel home ranges were significantly smaller than wrybills, and on an intra-specific basis were smaller on the Ashley. A correlation existed between home range size and habitat quality, so that small wrybill home ranges were dominated by the occurrence of productive minor braids, and larger ones by less productive major channels.

Time-budgets provided further insights into the influence of hydrological factors on wrybill ecology. Wrybill time-budgets appear to be inflexible because a high proportion of time is devoted to foraging, with relatively little time available for other activities. Resource depression on the Rakaia in 1983 lessened the chances for wrybills to breed successfully because sufficient food could not be gathered to provide for breeding energy needs. This did not occur on the Ashley river where flows were generally more stable. From a management viewpoint, development strategies which lead to greater flow fluctuations will have a detrimental impact on wrybills.

The foraging patterns for all species except black-fronted terns were examined. There was a general preference for aquatic habitats, particularly those associated with minor braids and disconnected pools. Depth and substrate use were studied in detail for wrybills and banded dotterels. Wrybills displayed consistent use patterns between rivers,

which reflected specialisation in habitat use. Banded dotterel habitat use varied considerably. Diet was studied by faecal analysis. Both wrybills and banded dotterels fed on invertebrates of aquatic and terrestrial origin. For wrybills it was noticeable that Ephemeroptera larvae did not dominate the diet as had previously been reported for high country catchments. Coleoptera, Hemiptera, and Ephemeroptera were important on the Rakaia with Trichoptera replacing Ephemeroptera larvae on the Ashley. Banded dotterels were more reliant on Coleoptera and Hemiptera on both rivers. Pitfall trapping results showed that terrestrial invertebrate availability was dependent on the proximity of water. Fewer floods on the Ashley led to a more consistent food supply on that river. This helps explain the greater bird density on this river. Severe flooding in 1983 appeared to seriously depress aquatic invertebrate densities on the Rakaia.

The incremental approach to impact assessment was applied to wrybill foraging requirements. Depth, substrate, and water velocity preferences were included within a weighted usable area model already developed for fisheries use on the Rakaia river. Over the range of median to low flows studied, weighted usable area increased with declining discharge. A simplified usable width approach was applied to a highly braided section of the Ashley river. Here, usable width declined with falling discharges. This inter-basin difference could be explained with reference to the braiding pattern of each river.

The main study objectives were achieved, but the indicator species management approach was of limited value in areas other than nest site requirements. Pied stilts and South Island pied oystercatchers fed at greater depths than wrybills, and often used different microhabitats. However, for foraging, wrybills need appeared adequate indicators of banded dotterel requirements.

KEYWORDS: Canterbury; braided riverbeds; Ashley and Rakaia rivers; birds - wrybills especially; hydrology; breeding; feeding; home ranges; time-budgets; habitat requirements; impact assessment; management.

TABLE OF CONTENTS

Chapter	Page
1. INTRODUCTION.....	1
1.1. Background.....	1
1.2. Study approach.....	3
1.2.1. Determining instream flow needs.....	3
1.2.2. Study priorities.....	6
1.2.3. Thesis format.....	8
1.3. Objectives.....	8
2. STUDY AREA.....	10
2.1. Introduction.....	10
2.2. Study area selection criteria.....	10
2.3. The Ashley river study area.....	13
2.3.1. Location.....	13
2.3.2. River hydrology.....	13
2.3.3. Braiding hydrology.....	17
2.3.4. Riverbed vegetation.....	17
2.3.5. Riverbed fauna.....	18
2.3.6. Recreational use of the riverbed.....	19
2.3.7. Riverbed management.....	19
2.4. The Rakaia river study area.....	19
2.4.1. Location.....	19
2.4.2. Hydrology.....	19
2.4.3. Braiding hydrology.....	20
2.4.4. Riverbed vegetation.....	20
2.4.5. Riverbed fauna.....	21
2.4.6. Recreational use of the riverbed.....	22
2.4.7. Riverbed management.....	23
2.5. Summary.....	23
3. BREEDING ECOLOGY.....	24
✓3.1. Introduction.....	24
3.2. Literature review.....	24
3.2.1. Breeding success.....	24
3.2.2. Bias in breeding studies.....	25
3.2.3. Previous ground-nesting bird breeding studies.....	26
3.2.4. Nest site selection.....	27
✓3.2.4.1. The influence of vegetation on breeding.....	29
3.3. Methods.....	30

3.3.1. Breeding success.....	30
3.3.2. Nest site characterisation.....	31
3.3.2.1. Nest site selection, vegetation tolerance, and the flood regime.....	32
3.4. Results.....	35
3.4.1. Breeding success.....	35
3.4.1.1. Wrybill.....	35
3.4.1.2. Banded dotterel.....	39
3.4.1.3. Black-fronted tern.....	43
3.4.1.4. Pied stilt.....	46
3.4.1.5. South Island pied oystercatcher.....	46
3.4.2. Causes of nest failure.....	46
3.4.3. Species-specific susceptibility to nest destruction by flooding.....	51
3.4.3.1. Flood size and nest loss.....	51
3.4.3.2. Nest height selection.....	55
3.4.3.3. Flood size and the probability of nest loss.....	55
3.4.4. Nest site characterisation.....	62
3.4.4.1. Proximity of nests to water.....	62
3.4.4.2. Nest location in relation to channel form.....	64
3.4.4.3. Distance of nests from dense and mature stands of exotic vegetation.....	64
3.4.4.4. Nest site vegetation tolerance.....	66
3.4.4.5. Nest site substrate character.....	69
3.5. Discussion.....	72
3.5.1. Breeding.....	72
3.5.2. Inter-specific aspects of nest site selection.....	79
3.5.3. Vegetation tolerances and the flow regime.....	83
3.5.4. Management considerations.....	86
3.6. Summary and conclusions.....	89
4. BIRD DENSITY IN RELATION TO BRAIDED RIVER HYDROLOGY.....	91
4.1. Introduction.....	91
4.2. Developing a model to measure home range size on riverbeds....	92
4.3. Methods.....	93
4.4. Results.....	94
4.4.1. Density considerations.....	94
4.4.2. Home range sizes.....	99
4.4.3. Home range site tenacity.....	100

4.4.4. Space use in relation to inter-specific considerations.....	100
4.5. Discussion.....	102
4.6. Summary and conclusions.....	108
 5. WRYBILL TIME-BUDGETS.....	109
5.1. Introduction.....	109
5.2. Methods.....	109
5.3. Results.....	112
5.3.1. Breeding season time-budgets classified by flow.....	112
5.3.2. Bi-monthly breeding season time-budgets.....	112
5.3.3. Breeding season time-budgets.....	115
5.4. Discussion.....	117
5.5. Summary and conclusions.....	124
 6. FORAGING AND FOOD IN RELATION TO MICROHABITAT USE.....	125
6.1. Introduction.....	125
6.2. Literature review.....	125
6.3. Methods.....	134
6.3.1. Microhabitat use and preference measurements.....	134
6.3.2. Diets of wrybills and banded dotterels.....	136
6.3.3. Food resource availability.....	138
6.4. Results.....	139
6.4.1. Microhabitat use.....	139
6.4.1.1. Wrybill and banded dotterel microhabitat use.....	139
6.4.1.2. Pied stilt and South Island pied oystercatcher microhabitat use.....	144
6.4.1.3. Depth and substrate requirements.....	146
6.4.2. Diets of wrybills and banded dotterels.....	149
6.4.3. Terrestrial invertebrate productivity.....	153
6.4.4. Wrybill feeding behaviour.....	155
6.5. Discussion.....	157
6.5.1. Microhabitat use and preferences.....	157
6.5.2. Overlap in microhabitat use.....	160
6.5.3. Diet composition and overlap.....	160
6.5.4. Food resource provision and availability.....	162
6.5.5. The impact of fluctuating flows on patterns of resource use.....	165

6.6. Summary and conclusions.....	168
7. THE INCREMENTAL APPROACH TO IMPACT ASSESSMENT.....	170
7.1. Introduction.....	170
7.2. Literature review.....	170
7.3. Methods.....	172
7.3.1. Stream simulation.....	173
7.3.2. Habitat use measurements.....	175
7.3.3. Probability of use curves.....	176
7.3.4. Hydrological sampling.....	176
7.3.5. A simplified approach for smaller rivers.....	177
7.4. Results.....	177
7.4.1. Probability of use and weighting factor calculations.....	177
7.4.2. The discharge-width relationship.....	181
7.4.3. The discharge-weighted usable area relationship.....	183
7.4.4. Usable width on the Ashley river.....	185
7.5. Discussion.....	189
7.6. Summary and conclusions.....	196
8. CONCLUSIONS AND MANAGEMENT IMPLICATIONS.....	198
8.1. Summary.....	198
8.1.1. The study approach.....	198
8.1.2. The study findings.....	200
8.2. Management recommendations.....	203
8.3. Conclusions.....	206
ACKNOWLEDGEMENTS.....	208
REFERENCES.....	210
APPENDIX 1: The braided river environment.....	222
APPENDIX 2: The relationship between riverbed flooding and non-breeding wrybills on northern feeding grounds in summer.....	239
APPENDIX 3: Composition of wrybill and banded dotterel faeces collected on the Ashley and Rakaia study areas.....	248
APPENDIX 4: Numbers of invertebrates caught in pitfall traps located at three sites (4 traps per site) on the Ashley and Rakaia rivers.....	250
APPENDIX 5: Wrybill weighted usable area, channel width, and	

channel discharge data for individual channels on
the Rakaia river.....252

LIST OF FIGURES

FIGURE	Page
1-1: Thesis format and content.....	9
2-1: Location map and study areas.....	15
2-2: Flow regime variability of a snowfed, mountain catchment braided river (the Rakaia) compared to a foothill catchment river (the Ashley).....	16
3-1: Periods of nest initiation and incubation for wrybills on the Rakaia (1982 and 1983) and Ashley (1983) rivers.....	38
3-2: Periods of nest initiation and incubation of banded dotterels on the Rakaia (1982 and 1983) and Ashley (1983) rivers.....	41
3-3: Periods of nest initiation and incubation of black-fronted terns on the Rakaia (1982 and 1983) and Ashley (1983) rivers...	45
3-4: Periods of nest initiation and incubation for pied stilts on the Rakaia (1982) and Ashley (1983) rivers.....	47
3-5: Periods of nest initiation and incubation for South Island pied oystercatchers on the Rakaia (1982 and 1983) and Ashley (1983) rivers.....	48
3-6: The relationship between flood peaks and nest losses of wrybills and banded dotterels on the Rakaia river.....	54
3-7: Partial duration and annual flood series for the Rakaia river - peak instantaneous discharges (1957 - 1982).....	58
3-8: Daily flow pattern of the Rakaia river during three breeding seasons: 1981-83 inclusive.....	59
3-9: Daily mean flow pattern of the Ashley river during the 1982 and 1983 breeding seasons.....	60
3-10: Partial duration and annual flood series for the Ashley river - mean daily flows (1966 - 1983).....	61

3-11: The distance of nests from water for riverbed bird species nesting on the Rakaia and Ashley rivers.....	63
3-12: The aquatic microhabitats closest to the nests of five riverbed nesting bird species on the Rakaia and Ashley rivers..	65
3-13: The location of wrybill and banded dotterel nests in relation to the dominant plant species of the nearest dense and mature stand of exotic vegetation on the Ashley and Rakaia rivers.....	67
3-14: Changes in percentage of vegetative ground cover within one metre of wrybill nests on the Rakaia river in 1982.....	68
3-15: The availability of nest sites with lower plant densities and percent ground cover at the same or higher levels along the surveyed cross-sections of wrybill, banded dotterel, and black-fronted tern nests on the Rakaia river.....	70
3-16: Dominant substrate size classes within one metre of wrybill, banded dotterel, and black-fronted tern nests on the Rakaia and Ashley rivers.....	71
3-17: Monthly high and low flows for the Rakaia and Ashley rivers....	73
4-1: Nest site locations and home ranges of riverbed bird species on the Rakaia river in 1982.....	96
4-2: Nest site locations and home ranges of riverbed bird species on the Rakaia river in 1983.....	97
4-3: Nest site locations and home ranges of riverbed bird species on the Ashley river in 1983.....	98
4-4: Home range movements of wrybill pairs on the Rakaia study area from 1982 to 1983.....	101
4-5: Pattern of space use for breeding pairs of wrybills and banded dotterels on the Ashley river in 1983.....	103
5-1: Time-budgets by river condition for adult wrybills on the Rakaia river in the 1982 and 1983 breeding seasons.....	113

5-2:	Bi-monthly time-budgets for adult wrybills on the Ashley and Rakaia rivers for the 1983 breeding season.....	114
5-3:	Breeding season time-budgets for adult wrybills on the Rakaia river, 1982 and 1983, and Ashley river, 1983.....	116
6-1:	Foraging microhabitat use comparisons for wrybills and banded dotterels on the Ashley and Rakaia rivers - spot observations - three seasons.....	140
6-2:	Foraging time-budgets of wrybills classified by river conditions on the Rakaia in the 1982 and 1983 breeding seasons.....	143
6-3:	Foraging microhabitat use comparisons for South Island pied oystercatchers and pied stilts on the Ashley and Rakaia rivers - spot observations - three seasons.....	145
6-4:	Foraging depths of aquatically feeding wrybills and banded dotterels on the Ashley and Rakaia rivers - spot observations.	147
6-5:	Dominant substrates used by foraging wrybills and banded dotterels on the Ashley and Rakaia rivers - spot observations.	148
6-6:	Combination substrate-water depth use by foraging wrybills and banded dotterels on the Ashley and Rakaia rivers - spot observations.....	150
6-7:	Percent occurrence of food items in wrybill and banded dotterel faeces collected from the Ashley and Rakaia rivers...	151
6-8:	Relative abundance of different food items in wrybill and banded dotterel faeces collected from the Ashley and Rakaia rivers.....	152
6-9:	Total invertebrate numbers per pitfall trap in three sampling locations on the Ashley and Rakaia rivers in 1983....	154
6-10:	Numbers of <i>Actenonyx bembidoides</i> and <i>Bembidion</i> spp. (Order Coleoptera) per pitfall trap in three different micro-habitats on the Ashley and Rakaia rivers in 1983.....	156
6-11:	Proposed invertebrate availability index for the Rakaia river over the period August 1981 - January 1984.....	159

7-1:	Probability of use weighting factors for adult wrybills on the Rakaia river.....	180
7-2:	Discharge-channel width relationships for the Rakaia river....	182
7-3:	Discharge-weighted usable area relationships for two study cross-sections and two sets of declining flows on the Rakaia river.....	184
7-4:	Number of channels-total discharge relationships for two cross-sections on the Ashley river.....	187
7-5:	Total usable width-discharge relationships for two cross- sections on the Ashley river.....	188
7-6:	Total usable width-number of channels relationships for two cross-sections on the Ashley river.....	190
7-7:	Total width-usable width relationships for two cross- sections on the Ashley river.....	191
7-8:	Total width-discharge relationships for two cross-sections on the Ashley river.....	192

LIST OF TABLES

TABLE	Page
2-1: Numbers of black-fronted terns and wrybills on braided riverbeds of the Canterbury Plains.....	12
3-1: Breeding success of wrybills nesting on the Ashley and Rakaia rivers during 1982 and 1983.....	36
3-2: Breeding success of banded dotterels nesting on the Ashley (1983) and Rakaia (1982 and 1983) rivers.....	40
3-3: Breeding success of black-fronted terns, pied stilts, and South Island pied oystercatchers nesting on the Ashley (1983) and Rakaia (1982 and 1983) rivers.....	44
3-4: The causes of nest losses for riverbed birds on the Rakaia (1982 and 1983) and Ashley (1983) rivers.....	49
3-5: The effects of floods on the nests of five riverbed bird species on the Rakaia river.....	53
3-6: Survey results for cross-sectional nest heights for wrybills, banded dotterels, and black-fronted terns nesting on the Rakaia river.....	56
4-1: Densities of solitary breeding bird species on the Ashley and Rakaia study areas in 1983.....	95
4-2: Variability in wrybill home range sizes on the Rakaia river according to microhabitat character.....	100
6-1: A comparison of aquatic invertebrate studies on East Coast South Island braided rivers in view of sample size considerations identified by Downing (1979) and Resh (1979).....	132
6-2: Wrybill feeding methods on the lower Ashley and Rakaia rivers combined, compared with those determined on the upper Rakaia by Pierce (1976).....	157

7-1: Probability of use and weighting factor calculations for depth, velocity, and substrate requirements of wrybills on the Rakaia river.....	178
7-2: Weighted usable area and channel width values for two cross-sections and two flow sets on the Rakaia river.....	181
7-3: Rates of decline in channel width with falling discharges over two flow ranges on the Rakaia river.....	183
7-4: Rates of increase in weighted usable area with declining discharges over two flow ranges on the Rakaia river.....	185
7-5: Usable width and other cross-sectional data collected at a range of flows on the Ashley river in 1983.....	186

LIST OF PLATES

Page

1. Study areas.....	14
2. Cross-sectional surveying of a wrybill nest site.....	34
3. A colour-banded wrybill on nest and eggs on the Ashley river during the 1983 breeding season.....	37
4. A banded dotterel on nest and eggs before being trapped on the Rakaia river during the 1982 breeding season.....	42
5. A bankful discharge in the Rakaia study area during 1983.....	50
6. An outstanding area of wrybill foraging and breeding habitat in the Rakaia river study area.....	141
7. Approximate locations of surveyed cross-sections for the incremental analysis on the Rakaia and Ashley study areas.....	174

1. INTRODUCTION

1.1. Background

The broad, open, shingle riverbed of the Rakaia and other eastern South Island rivers is the main or exclusive breeding habitat of four bird species: the black-billed gull (Larus bulleri Hutton), black-fronted tern (Sterna albostriata Grey), South Island pied oystercatcher (Haematopus ostralegus finschi Martens) and the wrybill (Anarhynchus frontalis Quoy and Gaimard) (Turbott, 1969). Several of the braided riverbeds inhabited by these and other species have recently been classified as nationally important wildlife habitats (O'Donnell and Moore, 1983). These rivers also have recreational value, particularly for fishing and boating. Competing demands for water also include irrigation and hydro-electric storage. From the Waiau in the north, to the Waitaki in the south, no major river system has escaped the impact of development. Early schemes such as the Rangitata Diversion Race incorporated two uses, namely hydro electricity and irrigation. Hydro dams on the Waitaki, and irrigation schemes taking water from the Ashburton, Opihi and Waiau rivers, are single purpose developments. However, some rivers, including the Rakaia and sections of the upper Rangitata and Ahuriri, remain substantially undeveloped. Yet even on these the threat of development exists, and partial modification associated with land use and the encroachment of exotic plants has occurred.

Until recently, research into the streamflow needs of salmonids and native fish in New Zealand had been negligible (Hughey, 1980), but acceleration of water resource development and the associated conflicts with recreational groups have improved this situation. Although proven methods now exist for assessing fish habitat needs, no studies in New Zealand or overseas have established the habitat needs of riverbed birds. Indeed, few studies have evaluated the effects of river development on even the riparian wildlife (Swales, 1982). Internationally, this is partly caused by the scarcity of braided rivers in western nations where most such research occurs. In North America this is attributable to the lack of colonial species exploiting this habitat (Weseloh, pers. comm.) and to the lack of suitable habitats. Aleutian terns, Sterna aleutica Baird, breed on the Copper river delta in Alaska, either monospecifically or in association with Arctic terns,

Sterna paradisea Pontoppidan, (Buckley and Buckley, 1979). Although braided, the Copper river delta is regarded as a marsh, rather than a series of bare shingle islands as commonly found in New Zealand braided rivers. The creation of 'dredge-spoil islands' on the Mississippi river has created artificial braiding, but these islands have become heavily vegetated and investigations into their use by birds have just begun (Weseloh, pers. comm.).

The neglect of wildlife in the evaluation of river development proposals in New Zealand is largely attributable to two assumptions previously inherent in water use planning:

- (1) that 'improved conditions for wildlife are related to... new stable water bodies' (Anon., 1976); and
- (2) 'the provision of a sufficient residual flow to maintain the fishery would accommodate most other recreational and ecological requirements' (North Canterbury Catchment Board, 1974).

Neither assumption is based on any known research.

A primary function of water management agencies in New Zealand is the promotion of multiple use water development while protecting the natural characteristics of the resource. Inherent in this process, and where the resource is scarce, is the need to allocate water according to established priorities and the proven needs of particular users. Whereas wildlife requirements used to be unquantified and provided for by a 'rule of thumb' approach, the responsibility now exists to examine these needs in greater detail. This position has resulted in the completion of a study to assess the habitat needs of wetland birds in the Ahuriri river catchment (Robertson *et al.*, 1983). The study concluded that the Ahuriri bird community totally relies on the existing flow regime and channel morphology of the river. However, where competition for water makes it likely that multiple use development will occur, an approach based on the determination of habitat needs which are compatible with development must be used. In multiple use developments, which are characteristic of braided rivers flowing across the Canterbury Plains, an acceptable flow regime for 'desirable' species must be defined. To date such an approach has not been developed.

1.2. Study approach

1.2.1. Determining instream flow needs

Because so little work has been done to quantify the habitat needs of riverbed nesting birds, it is necessary to evaluate fisheries' methodology and identify those aspects appropriate to this study. Two general approaches are used to evaluate the effect of flow manipulations on a fishery: the basically subjective recommendations of experienced fisheries managers; and those based on quantifying a number of physical variables related to the ecological needs of fish (Jowett and Wing, 1980). Unfortunately, the subjective evaluations of fisheries experts lack field quantification and are difficult to defend during water allocation hearings. Field investigations, which cost more in time and money, can nevertheless provide the objective information required by water management agencies.

Most quantitative instream studies have occurred in North America. This is partly explained by the presence of a broad range of recreational fisheries, the values of which frequently conflict with water developments. The continued degradation of river fisheries has led to demands for compensatory measures based on the proven ecological needs of these fisheries. Managers have responded by developing a number of techniques for recommending minimum flows. The 'Montana Method' (Tennant, 1972) was based on variable proportions of the mean annual flow being retained, depending on the season in question. If applied to New Zealand, this translates to 30% of the April to September mean annual flow, and 60% for the October to March period. The differences in river character between North America and New Zealand are so great that this method is considered inappropriate for our rivers (Mosley and Glova, 1983). Furthermore, there is no evidence that this method would satisfy the habitat needs of riverbed birds.

A new approach, termed the incremental method of assessing habitat potential for coolwater species, has been developed in North America (Bovee and Cochnauer, 1977; Bovee, 1978). The method was designed to evaluate changes in the standing crop and species composition caused by changes in the flow regime. In New Zealand, the method was first applied to a study of the flow requirements of trout in the Tekapo river (Jowett and Wing, 1980). The Tekapo flow (average 16.6 cumecs (cubic metres per second)) was considered large in comparison to studies of

smaller rivers in the United States. Another complication was the braided nature of the Tekapo compared with the single channel rivers studied in North America. Braiding increases the amount of field work and complicates use of the model (Cowie, 1983), particularly with regard to the statistical reliability of quantitative findings. Without major modification it is doubtful whether the model can be used for anything more detailed in wildlife investigations than some aspects of aquatic habitat use related to species-specific feeding behaviour. Even with this constraint, the model remains one way of quantitatively predicting the impacts of water development on certain aspects of bird habitat needs.

Continuing fisheries assessment studies under New Zealand conditions have concentrated on the collection of specific habitat use data and relating this to critical hydrological parameters (Glova, pers. comm.). Because of problems encountered with the statistical reliability of the incremental method when applied to braided rivers, it seemed appropriate to identify a number of critical wildlife parameters for further research, and to use these findings to supplement the incremental method. Quantifying bird habitat needs on braided riverbeds involves assessing both the aquatic and terrestrial habitat components. Fisheries research deals primarily with the former, and only occasionally with the latter. Determination of the complex patterns of riverbed use by birds, and the relationship between the occurrence and exploitation of aquatic and terrestrial habitats, makes the evaluation of habitat needs for birds more difficult to assess than those for fish.

When compared to the fisheries techniques it is clear that the criteria needed to evaluate the impacts of water developments on wildlife are inadequate. Possardt and Dodge (1978) recognised this problem and concluded that most channelisation studies, until recently, have focused only on the fisheries resource. Impact studies have particularly neglected non-game wildlife. This non-recognition of the value of streams and rivers as wildlife habitats is also a problem in the British Isles where Smith (1975, p253) noted that 'the practical problems of ensuring adequate conservation management of even a part of a river system are formidable'. A similar situation exists along the eastern South Island where the wildlife values of several river systems have only recently been classified (O'Donnell and Moore, 1983). An example of this non-recognition can be cited from Dingwall (1982), who,

in a review of New Zealand's conservation record, did not even mention rivers as important wildlife habitats.

Although no evaluative tool for assessing development impacts on riverbed bird communities has been developed, a range of techniques exists in other ornithological fields. Considerable research concerning the relationships between nest site selection in members of Family Laridae and vegetation have been undertaken, e.g., Burger (1976), Blokpoel *et al.* (1978), and Winnett-Murray (1979). The wrybill displays an aversion to vegetation cover when nesting (Hay, 1984). Methods for determining tolerances can be established from the literature, while the relationship between the extent of vegetation cover and flooding may be determined from aerial photo interpretation, associated with an examination of flood flow data. Studies of larid site tenacity (McNicholl, 1975) and nest site selection in herring gulls, Larus argentatus Pontoppidan, provide an insight into possible research areas. Both parameters may be important when assessing the habitat needs of riverbed birds. For instance, minor braids are more productive for aquatic invertebrates than major channels (Sagar, 1983a), but minor channels are the first to dry up when flows decline (see Bowden *et al.*, 1982). Some species may show a preference for nesting close to these productive small braids. If so, this can be determined by a study of the physical characteristics of the nest site, and then related to the possible impact of changes in flow. Thus, a study of the physical and botanical aspects of nest sites and home ranges was required.

The effects of floods and other flow conditions have been examined for their impact on the feeding behaviour of dippers, Cinclus cinclus L., (da Prato, 1981), wrybills (Pierce, 1979), and black stilts, Himantopus novaezelandiae Gould, and pied stilts, Himantopus himantopus leucocephalus L., (Pierce, 1982a). However, no study has examined the precise use of aquatic microhabitats according to standard hydrological classifications. Until this has been done it is difficult to evaluate the results of hydrological studies in terms of the habitat requirements of riverbed birds. Furthermore, time-budget studies, which may indicate the impact of flow regime or habitat quality variation, have not been done for riverbed nesting species. These studies can be used to identify trends which may assist in water management. Detailed measurements of water depth, velocity, and bird substrate preferences

have also been neglected. All of these parameters were measured in this study and incorporated within an overall decision-making framework to arrive at flow recommendations designed to meet the habitat needs of riverbed nesting birds.

Breeding studies also indicate habitat suitability, particularly when the research results can be compared to studies of the same species carried out on habitats of different quality. With the lower Rakaia affected by exotic plant encroachment, full breeding studies of wrybills and banded dotterels on this habitat, compared with those already undertaken on the upper Rakaia (Hay, 1979, 1984) and Cass (Bomford, 1978) rivers respectively, where habitat modification is slight, could be beneficial. Studies on a river with a very different annual flow regime to that of the Rakaia could also provide habitat recommendations. The Ashley river in North Canterbury, which is characterised by a declining spring to summer discharge pattern, provides such a contrast to the flood-dominated breeding season flows of rivers like the Rakaia.

1.2.2. Study priorities

A large and diverse bird fauna inhabits New Zealand's braided rivers but it was not possible, because of time and logistical constraints, to study all species. Clearly, a set of criteria was needed to identify appropriate study species and priorities. Recourse was made to fisheries research where biological criteria have been developed for fish species (Bovee and Cochnauer, 1977). These criteria can be used to meet other wildlife requirements and enable the identification of five classes of species:

(1) Management-objective species, commercial birds and birds considered important and desirable by the public for sport, and are important to the objectives of management agencies, e.g., paradise shelducks, Tadorna variegata Gmelin, which commonly breed on riparian margins and occasionally on riverbeds;

(2) Indicator species, those with narrow habitat tolerances inhabiting areas of streams and riverbeds that are particularly sensitive to changes in flow, e.g., wrybills and black-fronted terns. It is assumed that if conditions remain suitable for the indicator species, all other resident species will continue to find suitable habitat there, and species composition will remain constant;

(3) Endangered or threatened species, which include those which may be locally abundant but with highly restricted distribution, or those which occupy much of their former range but in greatly reduced numbers, e.g., black stilts (Williams and Given, 1981);

(4) Non-game species, especially those which may act in direct competition with any of the desirable species, e.g., southern black-backed gulls, Larus dominicanus Lichtenstein;

(5) Forage species, which are those organisms occupying intermediate positions in the food chain, including both forage fish and aquatic invertebrates, e.g., mayflies as wrybill food.

Wrybills and black-fronted terns occupy riverbeds used by most of the riverbed nesting species. Their representativeness and reliance on riverbeds for breeding and feeding make them suitable indicator species. This study therefore tries to quantify critical aspects of the habitat needs of wrybills and black-fronted terns in relation to braided river hydrology. Information on the habitat needs of banded dotterels, Charadrius bicinctus Jardine and Selby, pied stilts and South Island pied oystercatchers was also collected to assess the applicability of the approach. Banded dotterels were chosen to assess inter-specific compatibility with wrybills, while the other two species, which commonly nest on riverbeds, provided a check on the methodology. Colonial species, like southern black-backed and black-billed gulls, were only briefly studied. Black stilts were ignored because they no longer breed on the rivers flowing over the Canterbury Plains, and because a full-time conservation programme is already underway in the MacKenzie Basin (Pierce, 1982b).

So far, little mention has been made of the hydrological components of this study. Since the project was begun in 1981 considerable research directed toward obtaining an understanding of braiding hydrology has occurred. The work of Mosley (1982a,b,c; 1983a,b) on East Coast braided rivers has added greatly to this understanding. These findings and those of Glova and Duncan (1985), along with the limited research concerning the braiding pattern undertaken in this study, have provided the basis for many of the management conclusions drawn in Section 8.2. Statistical analysis of discharge data has satisfied the other research needs.

1.2.3. Thesis format

The study approach combines two disciplines: ornithology and hydrology. This presents difficulties in interpreting previous research, selecting appropriate combinations of techniques and communicating results to scientists in either discipline and to other interested parties, such as those involved in water resource management.

The lack of an established technique for evaluating the habitat needs of riverbed nesting birds was a major difficulty. The thesis format (Figure 1-1) therefore reflects a largely empirical approach. Field results and the management implications of these results will test the procedure and its applicability for future use and refinement. Chapters 1 and 2 establish research criteria and priorities, and describe the study areas. The relationships between hydrology, and breeding and nest site selection are examined in chapter 3. Density considerations are examined in chapter 4, providing a link with chapter 6 which deals principally with the foraging-hydrology relationship. Chapter 5 deals with wrybill time-budgets. A quantitative approach toward impact assessment is presented in chapter 7 with the discussion also drawing on the results of earlier chapters. Finally, chapter 8 summarises and concludes the thesis by examining the results in terms of their contribution to an understanding of the hydrological factors influencing birds nesting on Canterbury braided rivers.

1.3. Objectives

The principal goal of this study was to add to the knowledge necessary to provide for the conservation of important riverbed bird habitats in New Zealand. The three specific objectives were:

- (1) to describe the relationship between riverbed nesting birds and the physical characteristics of braided riverbed breeding habitats;
- (2) to quantify the nesting and feeding habitat requirements of these birds and to assess the impact of water resource developments on these needs; and
- (3) to develop predictive tools for the assessment of impacts which planned water resource developments may have on the survival of these birds.

FIGURE 1-1: Thesis format and content

Chapter headings	Content
1. Introduction -----	Background, the problem, approach and research priorities, study aims
2. Study areas -----	Selection criteria, physical overview of Ashley and Rakaia areas
3. Breeding ecology -----	Literature, breeding success, nest site character, vegetation tolerance and flow
4. Bird density in relation --	Literature, home range size in relation to braided river hydrology to habitat, densities
5. Wrybill time-budgets -----	Literature, Ashley-Rakaia and inter-seasonal comparisons
6. Foraging and food in relation to microhabitat --	Literature, habitat preference, pitfall trapping, faecal analysis, inter-specific comparisons, overlaps
7. The incremental approach --	Literature, weighted usable area applied to impact assessment to feeding microhabitat use, management
8. Conclusions and -----	Overall findings and implications for the recommendations conservation of riverbed nesting birds

2. STUDY AREA

2.1. Introduction

It seems likely that major differences between habitat types and bird use characteristics will appear when comparisons are made between braided rivers. These variations relate to a number of factors including the flow regime, channel form, vegetation status, and various water management programmes. To best utilise the indicator species approach it is important to choose representative study areas which may themselves be used as indicators of within, and between-river habitat requirements. This chapter outlines the study area selection criteria, and describes the chosen areas in terms of their physical and biotic habitat characteristics, while Appendix 1 gives a background to braided river hydrology, physical habitat definitions and the birds of braided rivers.

2.2. Study area selection criteria

Previous studies have been on high country catchments where habitat modification is normally slight, and where populations of the selected study species are usually greatest. These areas are generally above the main gorges on rivers flowing from the mountains to the sea, or on rivers flowing into high country lakes. Thus, Hay (1984) and Pierce (1979) studied wrybills on the upper Rakaia river, Lala (1977) black-fronted terns on the Ahuriri, and Pierce (1982a) black and pied stilts in the MacKenzie Basin. While these areas often have exceptional wildlife values, the plains sections of rivers such as the Rakaia, Ashley, and Ashburton are considered to have values of almost equal importance (O'Donnell and Moore, 1983). These waterways are most immediately threatened by development proposals, and have been most affected by existing management practices. They are therefore particularly appropriate for the study of habitat needs, where such needs are likely to be frustrated by multiple use development.

Species composition and community structure are other factors which must be considered in study area selection. Black-fronted terns breed on most of the Canterbury Plains riverbeds, but wrybills are sparsely distributed or absent from several of the same rivers. Riverbed surveys carried out by the Wildlife Service Fauna Survey Unit (O'Donnell and Moore, 1983) helped to isolate potential study areas. Survey results

(Table 2-1) indicate the patterns of lowland braided riverbed use for both species. These surveys seriously underestimate wrybill numbers (O'Donnell and Moore, 1983). Where wrybill numbers are highest, the degree of underestimation is likely to be greatest. This is because:

- (1) The wrybill is a unique species generating a great deal of ornithological interest. Consequently, on rivers with few wrybills, researchers tend to keep a special watch for their presence. In these situations it is likely that a high proportion of a small population will be observed. Conversely, on rivers such as the Rakaia, where the population is greatest, the relatively common occurrence makes them very easy to bypass as other species are spotted and recorded.
- (2) Rivers with low wrybill numbers are often narrower than the larger and more heavily populated waterways. Surveyors are generally closer together and are consequently more likely to find the well-camouflaged bird in its natural surroundings. On wide riverbeds such as the Rakaia, the same number of surveyors are spread over much wider distances, leading to an underestimation of the total population.

Allowing for the unsurveyed areas, the Rakaia stands out as the river of greatest importance to wrybills.

TABLE 2-1: Numbers of black-fronted terns and wrybills on braided riverbeds of the Canterbury Plains.

RIVER	SPECIES	
	Black-fronted Tern	Wrybill
Waiau	Not counted	Not counted
Hurunui	338	0
Ashley	194	6
Waimakariri	74	45
Rakaia*	167	82
Ashburton	762	5
Rangitata	284	13

*Approximately half the river section was not surveyed because of adverse river conditions.

Data source: O'Donnell and Moore (1983)
and Moore (pers. comm.).

This combination of factors makes the lower Rakaia an obvious study area. The riverbed is under threat of large-scale water resource development and is a habitat which has already suffered from the effects of development. Selecting a contrasting habitat for comparative study, and which also includes the range of study species, is more difficult. This is because most of the rivers have either high numbers of black-fronted terns and very few wrybills, e.g., the Hurunui, Ashley, Ashburton, and Rangitata rivers, or medium numbers of wrybills and low black-fronted tern numbers, e.g., the Waimakariri river. An additional consideration was the need to study a river with a markedly different flow regime from the Rakaia to enable an evaluation to be made of the effect of different flow regimes on overall community structure and species population dynamics. Of the potential choices, the Ashburton and the Ashley fulfill this role but contain very few wrybills. However, the concentration of wrybills on the Ashley is considerably closer to the coast than on the Ashburton (Moore, pers. comm.), where the five birds recorded were located just above the gorge on the South Branch of the river. Furthermore, the wrybills seen on the Ashley were recorded in an area which has ready access.

Having selected two study rivers, it then became important to choose particular reaches for detailed research. Apart from the need to include representative study areas, the task on the Rakaia was simplified by the nature and extent of concurrent research concerning other aspects of river hydrology and ecology. The Fisheries Research Division of the Ministry of Agriculture and Fisheries had established study cross-sections on the Rakaia river in the 10km reach above the State Highway One bridge, an area also being intensively studied by hydrologists from the Ministry of Works and Development. Research involved invertebrate sampling, studies of fish stocks, and weighted usable area as a function of discharge. This river section was considered representative of the Rakaia below the Gorge; and with the additional advantage of ready access to both banks, became an obvious choice as the Rakaia study area. Results from related research were expected to help fill gaps in this study. Selection of the Ashley study area was based on the known distribution of wrybills on that river.

2.3. The Ashley river study area

2.3.1. Location

The 4km long Ashley river study area is located approximately 1.5km upstream of the Ashley river bridge near Rangiora (Plate 1 and Figure 2-1). The study area is 14km from the coast at the eastern (downstream) margin, and 30km from the Gorge at the western (upstream) boundary.

2.3.2. River hydrology

A water level recorder and gauging station were installed at the Ashley Gorge in 1938 but, because of blockages and inadequate gaugings, only records obtained from the recorder installed on the gorge bridge in 1972 have been used in flow analyses (Bowden, *et al.*, 1982). The pattern of Gorge flows (Figure 2-2) is a modification of those at other gorge sites of major eastern South Island rivers from the Waimakariri, north (Bowden, *et al.*, 1982). Thus, the lowest flows occur in February and the highest in September. At Gorge flows of 1.69 cumecs and less (compared to a mean flow of 14.62 cumecs) there is no surface flow at the Rangiora traffic bridge (Bowden, *et al.*, 1982). Based on 15 sets of concurrent gaugings Bowden *et al.* (1982) demonstrated that the Gorge flow could be related to the Rangiora Traffic Bridge discharge by the equation:

PLATE 1: Study areas. (Note, both photos were taken toward the end of the 1983 breeding season. Also note the different scales.)

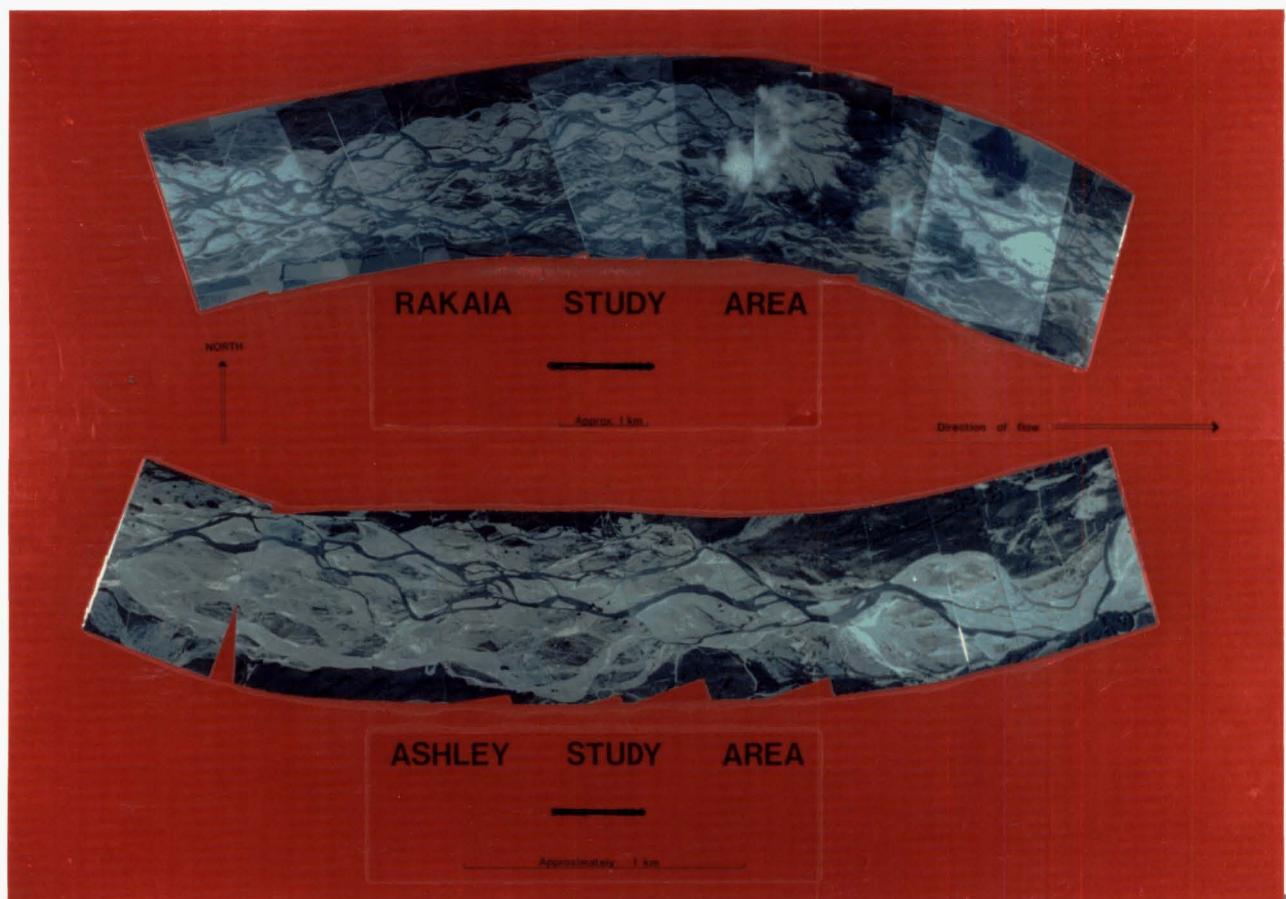


FIGURE 2-1: Location map and study areas.

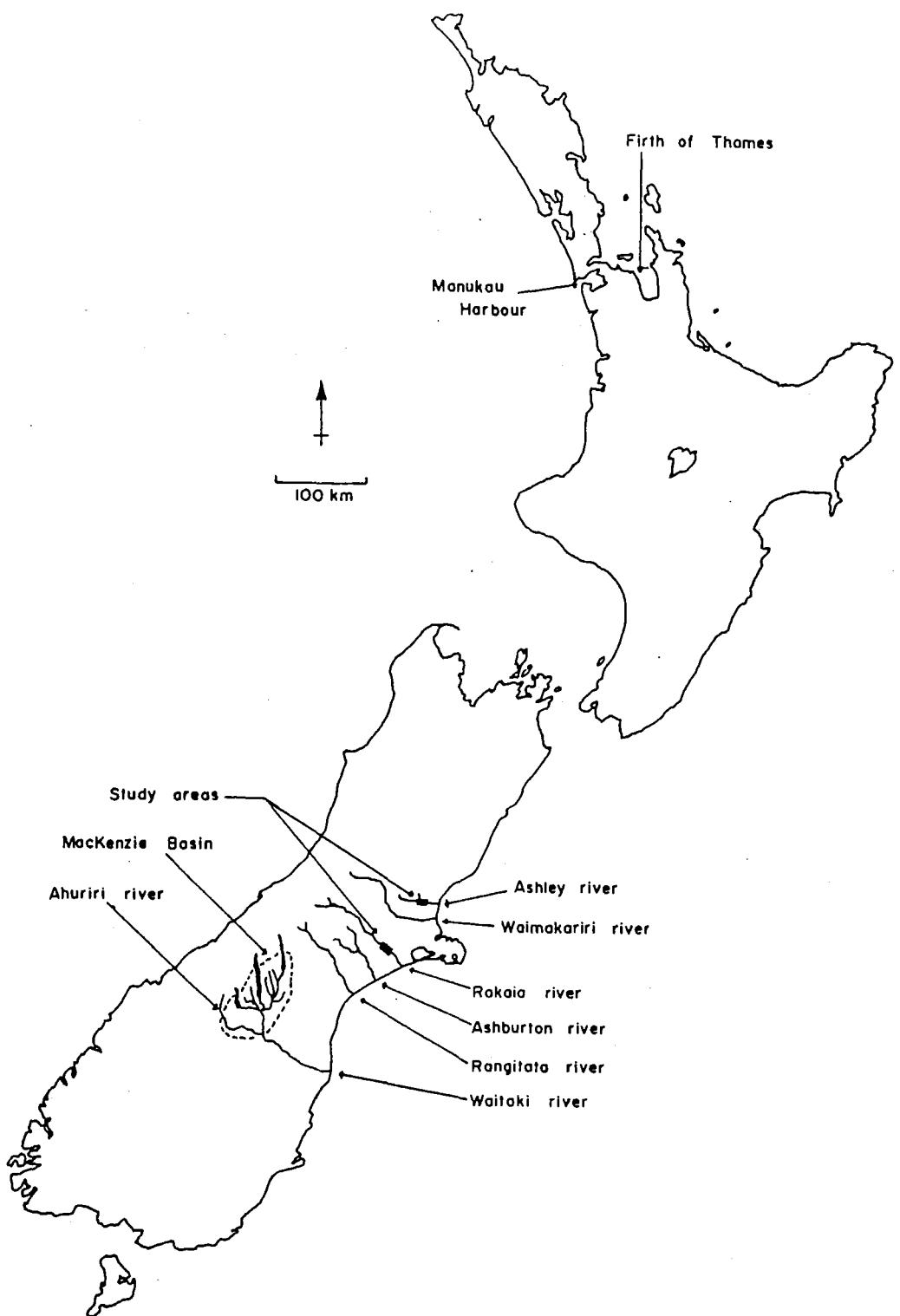
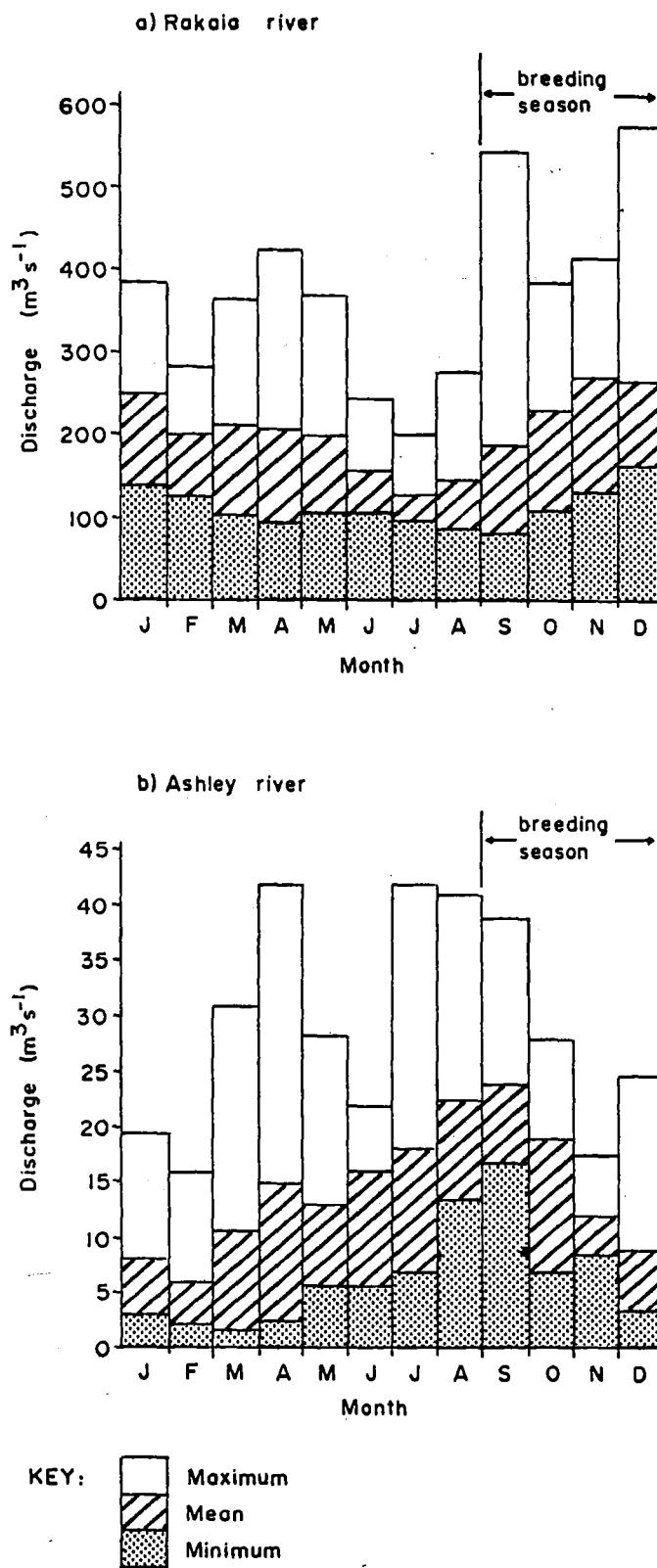


FIGURE 2-2 : Flow regime variability of a snowfed, mountain catchment braided river (the Rakaia) compared to a foothill catchment river (the Ashley).



$$y=1.42x - 2.232$$

where; y =Rangiora traffic bridge discharge
 x =Gorge discharge.

Using the Gorge mean flow of 14.62 cumecs gives a calculated discharge of 18.53 cumecs at the Rangiora bridge. Conversely, at very low flows, when other inputs are small and groundwater recharge is proportionately very high, there may be no surface flow occurring at the bridge.

2.3.3. Braiding hydrology

From the Gorge to the sea the Ashley is a shingle-bedded braided river. A study of the braiding pattern near the airfield (3km west of the Rangiora traffic bridge) for one representative cross-section indicated that the number of channels is a function of discharge. The study also showed that as flow decreases the percentage in the main braid increases (Bowden, *et al.*, 1982). This shows that minor braids are overflow channels, so that, at a certain threshold low flow value, there will be a reduction in the number of channels. Griffiths (pers. comm.) has concluded, from studies of outwash gravels on the Plains, that braided rivers similar in form to those existing today have been present since at least the last glaciation and probably before.

2.3.4. Riverbed vegetation

Prior to European colonisation, lowland sections of braided rivers probably resembled present-day conditions on the upper reaches of rivers such as the Rakaia and Waimakariri, where the landscape is dominated by bare shingle areas and low mat plant vegetation. Since the turn of the century when lupins (Lupinus arboreus and Lupinus polyphyllus) were introduced to maintain sand dune stability (Stead, 1932), there has been a dramatic change to the vegetation of lowland rivers. Lupins spread rapidly and grow extremely quickly. Following the colonisation of temporarily stable islands, the vegetation succession involves invasion by broom (Cytisus scoparius), gorse (Ulex europaeus), and finally, willow (Salix spp.). On the Ashley broom and gorse dominate over lupin indicating the relative stability of the bed of the river.

2.3.5. Riverbed fauna

The fauna of the Ashley can be divided into three main groups; fish, invertebrates, and birds. Mammals, including mustelids and lagomorphs also occurred on the riverbed but in widely varying densities.

a) Fish

The fish of the Ashley river are comparable to those in the Rakaia on the basis of species occurrence and diversity. However, on a unit area basis the Ashley has approximately 20 times the fish population of the Rakaia (Glova, pers. comm.). Summer low flows, which result in periodic drying up of the middle reaches, are a serious constraint on the fishery.

b) Invertebrates

There has been little or no study of the invertebrate fauna of the Ashley river, although it is likely to be similar to other Canterbury braided rivers. The increased spring and summer flow stability, compared with the Rakaia, and the higher relative fish population lead to the conclusion that invertebrate productivity would also be higher. The ability of many aquatic insects to survive in the substrate means that periods of low flow or no-surface-flow do not have the same disastrous effects on invertebrates that they do on fish. Terrestrial insect productivity should also be considerably higher because of the improved stability of the Ashley.

c) Birds

A bird survey of the Ashley river was carried out by the Wildlife Service (Moore, 1981). Bird numbers were generally highest in the upstream section (which included the study area). The comparatively low numbers in the downstream reach (immediately above the estuary and upstream for approximately 10km) are probably attributable to the highly variable nature of the flow regime, especially during periods of low flow and to the increased impact of vegetation encroachment. It is noteworthy that, when occurrence on the upper section is compared with downstream, banded dotterels and South Island pied oystercatchers were recorded with a 2:1 ratio, pied stilts at 3:1, black-fronted terns 1:1, and wrybills present to zero (the survey distances were approximately

the same).

2.3.6. Recreational use of the riverbed

Apart from bird-watching, a number of other recreational activities are regularly undertaken on the riverbed during the breeding season. The Ashley is a popular trout fishery, and many people visit the river to picnic and swim. Off-road trail-biking and four-wheel drive visits are common, and appear to be becoming more popular. Both have the potential to disturb bird habitat seriously.

2.3.7. Riverbed management

Flood control work by stopbanking is the dominant management impact in the study area. Planned and constructed by the North Canterbury Catchment Board, these works line the southern margins and much of the north bank of the study area. In addition, they tend to stabilise and confine the active riverbed. The extraction of shingle from the riverbed is also supervised by the Catchment Board but is largely undertaken by private contracting firms. The practice is widespread and has a range of potential impacts for riverbed birds.

2.4. The Rakaia river study area

2.4.1. Location

Located immediately upstream of the State Highway One bridge at Rakaia township, this study area is 10km long and approximately 1.5km wide (Plate 1 and Figure 2-1). At the downstream end the study area is approximately 22km from the coast, and at the upstream limit is approximately 30km from the Rakaia Gorge.

2.4.2. Hydrology

A flow recorder operated at the Gorge bridge over the period 1957-1978. In 1978, the recorder was moved to a site 3km upstream where the collection of more accurate recordings was possible. The mean daily flow for the period 1959-1981 was 200 cumecs (Bowden, 1983), with the pattern of Gorge flows reflecting the geographical and climatological influence of the Southern Alps (see Figure 2-2). Thus, the mean daily flow of 127 cumecs in July results from the high proportion of precipitation retained in snow and ice storage. Conversely, high flows occurring from September to January result from warm north-westerly

airflows and rainfall releasing large volumes of water from ice and snow melt.

The lowest minimum daily recorded flow is 79 cumecs, although an instantaneous low flow of 68.7 cumecs was experimentally induced during 1982. An examination of the pattern of low flows indicates the same general trends observed for mean and maximum discharges. Low flows are therefore highest during the October-January period, and lowest during July and August.

The largest flood recorded in the Rakaia had an instantaneous peak flow of 4330 cumecs and occurred on 3, December, 1979. This flow corresponded to a maximum daily discharge of 2317 cumecs. Flood damage was minimal and generally confined to fences (Bowden, 1983). Peak discharges occur most frequently and are highest during the September-December period.

Losses of water from surface flow are small between the Gorge and State Highway One bridge, though there is considerable loss to underflow and groundwater immediately downstream from the bridge (Bowden, 1983). These losses do not affect the hydrology of the study area.

2.4.3. Braiding hydrology

The Rakaia is highly braided in all reaches excepting the Gorge area. The number of channels per cross-section increases downstream, so that in the study area the number varies from 3 to 20 depending on the cross-section and the discharge at survey time. Flows are accommodated to channel shapes formed by preceding higher flows, so that the shape of the water body becomes increasingly independent of discharge as flow declines (Mosley, 1982a). This indicates that the number of channels does not decline in relation to flow. Bowden *et al.* (1982) found that on the Ashley the number of channels in a cross-section tended to decline with discharge. This aspect of braiding hydrology may therefore require more research.

2.4.4. Riverbed vegetation

Stead (1932) was the first to assess the impact of vegetation encroachment on riverbed birds. Following the introduction of lupins, the riverbed landscape had changed from a vast open area of bare shingle islands to a bed of vegetated islands interspersed with areas of open

shingle. Stead (1932) concluded that this change was having a substantial impact on bird use of the Rakaia.

The dominant plant in the Rakaia study area is lupin. However, after colonisation and stabilisation, lupins are replaced by gorse and broom, and then often by willows. On heavily vegetated islands, with their dense plant growth, mustelids and lagomorphs are frequently seen.

2.4.5. Riverbed fauna

a) Fish

Introduced salmonids (quinnat salmon, Onchorhynchus tshawytscha Walbaum and brown trout, Salmo trutta L.) are the dominant fish species inhabiting the study area. However, several native fish species, including the torrent fish (Cheimarrichthys fosteri Haast) and the bluegilled bully (Gobiomorphus hubbsi Stokell), are present and are of considerable scientific interest. While both species are widely distributed throughout New Zealand, most research concerning their life histories and habitat requirements has been on the Rakaia river.

The quinnat salmon life cycle involves the upstream migration of mature adults and subsequent spawning in stable high country tributaries. After the eggs hatch, the young fry move downstream to the sea where they remain to grow for a number of years. This downstream migration may involve 10-20 million fry, and is a food resource used by several avian feeders, including shags (Phalacrocorax spp.) and terns.

b) Invertebrates

Riverbed invertebrates can be broadly classified into aquatic and terrestrial groups. Both contribute to the diet of birds and fish. Aquatic invertebrate communities are dominated by members of several insect orders, along with animals such as flatworms, worms, and snails (Cowie, 1983). Sagar (1983a) found that riffles in the Rakaia are dominated by Deleatidium spp. mayflies. He also showed that the average number of species collected per sample dropped from 8.3 (Range=3-13) near the mouth to 6.7 (Range=3-12) at the State Highway One bridge. Invertebrate densities fluctuate greatly but species diversity and abundance were only marginally higher in minor braid riffles than in a major braid.

Among terrestrial invertebrates living on braided riverbeds, spiders (Arachnida) and insects are important bird foods. Ground beetles of the genus Bembidion, which are confined to the banks of running water (Lindroth, 1976) and separated ecologically according to substrate character and distance from water (Herron, 1981), may also be important bird foods. Captures of Bembidion spp. were most numerous in January, with the spring months from September onwards being more rewarding than autumn (Lindroth, 1976).

c) Birds

The Rakaia river was surveyed by the Wildlife Service in the period 1975-1979 (O'Donnell and Moore, 1983). Although some sections were not covered because of adverse river conditions, the study area selected for this research was completed. Survey results indicate that the important riverbed nesting birds (except for black-fronted dotterels, Charadrius melanops Vieillot, and black stilts) were well distributed over the river system. Numbers of wrybills, black-fronted terns and banded dotterels, were generally greater in the areas above the gorge, while many more black-billed gulls, black-backed gulls and pied stilts were recorded downstream. Apart from the riverbed nesting birds, other species commonly frequenting the area were black shags (Phalacrocorax carbo novaehollandiae Stephens), Australasian harriers (Circus approximans gouldi Bonaparte), welcome swallows (Hirundo tahitica neoxena Gould), grey ducks (Anas s. superciliosa Gmelin) and paradise shelducks (Tadorna variegata Gmelin) among native birds; and introduced game birds including mallard ducks (Anas d. platyrhynchos L.), Canada geese (Branta canadensis L.) and Californian quail (Lophortyx californica brunnescens Ridgway).

2.4.6. Recreational use of the riverbed

During breeding the river is used extensively by anglers, jetboaters and shooters. The Rakaia is regarded as one of the best salmon rivers in New Zealand, with the period of most intense angling use being from January to April. The river is also of national importance to jetboaters; and in September 1983 a leg of the world jetboat marathon was held on the river. There is some trail-bike riding and four-wheel drive use which has the potential to affect birds during breeding.

2.4.7. Riverbed management

There are two irrigation race intakes in the study area. On the north bank the diversion occurs approximately 1.5km upstream of the bridge. Water flows into a channel which follows the river downstream for a distance of 2km before being diverted north to irrigate farmland. The south side intake structure is located just downstream of the bridge, but water diversion begins 8km upstream through an existing, and partially controlled, side braid. Periodically, both diversions require repair work after floods. As floods occur most frequently during the breeding season, and repairs involve bulldozer and grader work, this can seriously affect breeding birds. There are no major stopbanks within the study area but cattle graze on the south side of the riverbed. Cattle stray over large areas causing isolated, but significant, damage to individual breeding pairs.

2.5. Summary

Study areas on the Ashley and Rakaia rivers were chosen as representative of braided river bird habitats on the Canterbury Plains. Both areas are occupied by the typical Canterbury riverbed bird community, including populations of black-fronted terns and wrybills. However, the study areas contrast markedly with regard to flow regime character. The Ashley has summer low flows which can lead to a no-surface-flow condition, while flows in the Rakaia are lowest during the winter and highest in the breeding season. These contrasts were chosen for their possible impact on population ecology of riverbed birds.

3. BREEDING ECOLOGY

3.1. Introduction

Several studies of breeding riverbed birds have recently been undertaken in New Zealand, e.g., McConkey (1971), Bomford (1978), Phillips (1980), Pierce (1982a), and Hay (1984). However, the use of a broad range of habitats by several species has influenced the choice of study areas for two of these projects. Thus, the McConkey (1971) pied stilt study was carried out on wetland pasture in Manawatu in the North Island, and the banded dotterel study of Bomford (1978) was on stabilised bermland bordering the Cass river in the MacKenzie Basin. These studies provide data which can be compared with later riverbed studies, i.e., Pierce's (1982a) study of pied and black stilts, and the wrybill research of Hay (1984). This study, and the findings of Hay (1984) and Pierce (1982a), may make it possible to identify flow characteristics which are critically related to breeding and to aspects of the population biology. Some of these factors may be crucial when defining management strategies for birds relying on braided rivers.

Previous studies of riverbed birds have used well-established methods of determining breeding success. However, there are several flow-related physical and biological parameters previously neglected which may have important direct and indirect impacts on, and relationships with, breeding and population biology. The lack of previous research concerning these parameters, which relate specifically to the hydrology of braided rivers, means there is almost no relevant literature from which to establish a methodology. This chapter reviews the literature on breeding ecology, details the method used in the study, and discusses the results.

3.2. Literature review

3.2.1. Breeding success

Three related parameters can be used to determine breeding success:

- (1) Hatching success, which is defined as the proportion of eggs laid that finally hatches (Holland *et al.*, 1982);

(2) Nesting success, which is the percentage of successful nests, i.e., those where at least one egg hatches (Miller and Johnson, 1978); and

(3) Fledging success, which for this study, is the proportion of eggs laid which ultimately produces flying juveniles.

Most studies have concentrated on determining hatching and fledging success, e.g., Soikkeli (1967), Jackson and Jackson (1980), Ratcliffe (1976), Holland *et al.* (1982), with very few examining all three parameters. Some have recorded hatching success only, e.g., Ratcliffe (1976), and while this information is of some value, it may be impractical or impossible to obtain further data, as for example in some nidifugous birds. Since wrybill and banded dotterel chicks are nidifugous (Bomford, 1978), and braided rivers are particularly unstable, this problem is relevant.

3.2.2. Bias in breeding studies

Bias associated with breeding studies is closely related to the time span of nest observation, and the method of determining nest location (Mayfield, 1961). If nest location depends on flushing birds, it is possible that the nest will not be detected if it is not attended by a bird at the time of search, or if the bird failed to flush (Higgins *et al.*, 1969). Potential problems caused by predatory nest loss as a result of surveyor presence (MacInnes, 1980; Strang, 1980), and nest desertion caused by repeated surveys, may preclude a continual search programme of a study area. Repetitious programmes can have logistical problems in large areas and when working within a limited time-budget. It follows that the higher the proportion of nests found in the later stages of incubation, the more the composite hatch rate will be biased upwards (Miller and Johnson, 1978). Furthermore, as the proportion of unsuccessful nests which are not found increases, so the nesting density will be biased further downward (Miller and Johnson, 1978).

Hensler and Nichols (1981) claim the Mayfield method of estimating nesting success (Mayfield, 1961, 1975) removes the time-span-associated sources of bias. An important assumption of the method is that the daily nest survival rate is constant among nests (Green, 1977), and throughout the laying and incubation periods (Miller and Johnson, 1978). Johnson (1979) developed a technique to test for heterogeneity in daily

mortality rates, and the effect it has on the usefulness of the Mayfield method. This led to the conclusion that 'unless a large proportion of nests have appreciably higher daily mortality rates than the others, the actual bias in the Mayfield estimator is slight' (Johnson, 1979; p661). Breeding season flows in the Rakaia river are characterised by periodic and highly variable floods. Nests are located at a range of levels on island cross-sections. At discharges of less than bankful flow (approximately 2200 cumecs), various areas remain clear of water, and some nests remain unflooded, with this proportion increasing as these flood levels become smaller. No one has yet measured species-specific nest losses caused by different flood levels, and whether such differences are large enough to affect the usefulness of the method. This information would allow a more thorough evaluation of the Mayfield estimator in riverbed bird breeding studies.

3.2.3. Previous ground-nesting bird breeding studies

The global scarcity of braided riverbeds, and of birds which use these habitats for breeding, explains the lack of research into breeding success and population dynamics. Hay's (1984) wrybill study was completed on the upper reaches of the Rakaia river where the habitat is relatively unaffected by man. His findings provide data for comparison with breeding success on the modified habitat downstream of the Rakaia Gorge. During the three years of his study, Hay (1979), when using traditional measures of breeding success, found that hatching success varied annually between 68.3 and 81.8%, and fledging success varied between 21.9 and 28.2%. He also noted that a single flood on 7 December, 1976, washed out almost every nest in his study area.

In a study of pied stilts breeding in Manawatu, McConkey (1971) reported a nesting success rate of 48%, and a hatching success rate of 46.6%. Pierce (1982a) recorded an overall hatching success rate of 61% for pied stilts breeding on a variety of habitats in the MacKenzie Basin. However, riverbed nesting pied stilts had a hatching success rate of 29%. This large difference in success rates was due mainly to the impact of flooding on riverbed nesters (Pierce, 1982a). Bomford (1978) reported rates of hatching and nesting success of 44.4% for banded dotterels nesting on stabilised berm land adjacent to the Cass river in the MacKenzie Basin, while Phillips (1980) recorded rates of 10.3% and 20.0% respectively, in addition to a fledging success rate of

0.9% on the Tukituki river in Hawke's Bay. The relative severity of predation and flooding for these single season studies is not known.

Bomford (1978) concluded that predators caused most nest failures, while Phillips (1980) and Hay (1984) found flooding to be the chief cause of failure. Bomford (1978) worked on stable berm land while the latter two studies referred to flood-prone, unstable riverbeds. Where a species is breeding on a braided riverbed the influence of predators may be reduced by the 'moat effect' of river braids.

Despite this ~~effect~~, Hay's (1979) high hatching success rates are surprising. Two factors may help to explain his results:

- (a) During the three year study, flood peaks were smaller, and flood return periods greater than for 'typical' years. This would increase hatching success;
- (b) Wrybills have breeding adaptations which reduce the risk of flooding losses, and result in high hatching success rates over a range of flooding conditions.

Hay (1984) did not examine either factor in any detail but if the latter is correct then his results may be considered representative of all years. However, even from the limited data presented above, probability analysis of flow data may make it possible to determine whether the findings are representative of a typical time period and, if not, then by how much. It is also important to quantify any physical parameters associated with behaviour which diminish the potential impacts of flooding, because these may be directly related to man-made changes in habitat.

3.2.4. Nest site selection

The range of microhabitats occupied by a species is modified by population density, so that where density is low, only optimal microhabitat is exploited. Conversely, with increasing density less suitable microhabitat will also be accepted, in order of decreasing acceptability (Hilden, 1965). Previous wrybill studies have assumed that the braided riverbeds above the main gorges are the most densely populated breeding areas (Pierce, 1976; Hay, 1979). Recent surveys have confirmed this, but have also shown that large numbers of birds, especially on the Rakaia, do nest below the Gorge (O'Donnell and Moore,

1983). Similar patterns also exist for banded dotterels and black-fronted terns. Riverbed habitat above the Rakaia Gorge is relatively unmodified, but there have been no comparative studies to assess the effect of downstream modifications on breeding densities and community structure.

Many workers, e.g., Lack (1949), Svardson (1949), Hilden (1965), have proposed that birds select habitats on the basis of 'sign stimuli' that convey information about ultimate factors such as food, protection and availability of nest sites. Wiens (1969) further hypothesised that birds actively select habitat according to such proximate factors as features of the landscape, substrate, or vegetation. Hilden (1965) argued that the choice of breeding station is released by certain proximate factors as soon as the sum of the stimuli exceeds the threshold of the reaction (depending on the motivation of the bird). This site selection mechanism guides birds to an environment meeting their ecological requirements (ultimate factors). He further proposed that the combined effect of these positive characteristics may be diminished by habitat negatives which repel. Therefore, where several territories release similar settling reactions, the bird will choose the one where the threshold is exceeded by the greatest margin. Multivariate analysis has been used to identify the habitat relations of bird communities while focusing on the identification of habitat variables that elicit measured species responses. Many of these studies have occurred in forest habitats, e.g., Anderson and Shugart (1974), James (1971).

Studies of a similar nature have not been undertaken for riverbed birds. Although considerable knowledge regarding behavioural aspects of breeding has been obtained, the potentially more important tasks of collecting detailed data on nest site selection have been largely ignored. Pierce (1982a), for pied and black stilt nests, kept records of the distance birds nested from water, the vertical height of nests above water, the general microhabitats selected by birds, generalised substrate preferences, and the land configuration around nests. Inter-specific differences were obvious enough to negate the need for anything more complicated than tabular analysis. Considering the habitat restrictions of black-fronted terns and wrybills, detailed information is required to define the relationship between physical nest site needs and the flow regime. Furthermore, the sympatric distribution

of wrybills and banded dotterels (pers. obs.), their possible overlap in microhabitat nest site requirements, and the possible modification of preferred microhabitats as a result of flow modification, provide sufficient cause to extend this study further. Multivariate analysis requires quantification of all microhabitats so that their use can be rigorously compared with occurrence. Braided river instability extends beyond flows, to large scale changes in the proportion of riverbed occupied by different microhabitats, e.g., vegetation and areas of bare shingle. An additional complication arises because of shifts in the location of different microhabitats. Together, these facts meant that there were continued major changes in the amount and distribution of various microhabitat types. Multivariate measures of nest site selection were therefore abandoned in favour of the simpler, but rewarding methods used by Pierce (1982a).

3.2.4.1. The influence of vegetation on breeding

Birds are generally believed to select their habitat according to visual aspects of the vegetation configuration (Shugart and Patten, 1972; Smith, 1977). Northern Hemisphere studies of gull and tern species have indicated a general preference for nest sites near vegetation. Blokpoel et al. (1978) showed that common terns (Sterna striata L.) locate nests near plants or other objects. The recent establishment of the studied tern colony led to the conclusion that the results would be more likely to reflect true habitat preferences than the results of studies in well-established or crowded colonies. Herring gulls (Burger and Lesser, 1980) and western gulls, Larus occidentalis Audubon, (Winnett-Murray, 1979) select territories according to the amount of cover, but while common terns prefer to nest near low vegetation, tall vegetation can negatively affect breeding success (Morris et al., 1980).

On Canterbury riverbeds the encroachment of vegetation is believed to have reduced wrybill numbers on downstream reaches (Stead, 1932; Pierce, 1976). Other species in New Zealand may have low tolerances toward vegetation encroachment, although this suggestion has received only limited study. [For these birds, vegetation may act as a habitat-negative in selecting a nest site.] This has been demonstrated for black-billed gulls where site tenacity of colonies is influenced by vegetation to the extent that a site will be abandoned if it becomes

overgrown (Beer, 1966). Black-fronted terns and wrybills have been recorded nesting on open gravel riverbeds mainly clear of vegetation growth (Lalas, 1977; Pierce, 1976; Hay, 1984). However, most previous wrybill research has been on little modified riverbeds with little exotic vegetation, e.g., Pierce (1976), Hay (1984). These studies were carried out above the main gorges, or in high country catchments. In downstream areas a mixture of open shingle and exotic vegetation at various stages of development provides the chance to examine nest site needs in relation to a range of physical and biological parameters.

3.3. Methods

3.3.1. Breeding

For wrybills and banded dotterels, success rates through to fledging stage were obtained on both the Ashley and Rakaia study areas for the 1983 season. A colour banding permit was obtained from the New Zealand Wildlife Service and young birds were ringed before they could fly. Adults were trapped at the nest by using a drop trap, while chicks were caught by hand after leaving the nest. A colour banding permit was not obtained for banded dotterels until 1983, hence only nesting and hatching success were measured in 1982. The breeding studies were extended to the Ashley river in 1983, because more field assistance was available. A full breeding study of black-fronted terns was planned, but the possibility of desertion caused by observers was too high to warrant further recordings other than clutch size, and rates of nesting success and hatching success. Time constraints meant studies of pied stilts and South Island pied oystercatchers were also limited.

Nest searches were undertaken on foot using a zig-zag ground coverage which ignored areas of dense-mature exotic vegetation growth (lupin, broom, gorse and willow). Although time-consuming and laborious, this was the only method which provided complete ground coverage, and maximised the likelihood of eliciting flight from a 'sitting' individual. Wrybill nests were quickly identified as the most difficult to find because the adults were well camouflaged and did not flush easily. Because the survey coverage was so comprehensive it was considered that the nests of other species would be found while concentrating on the search for wrybill nests. Nests of wrybills, banded dotterels, pied stilts and South Island pied oystercatchers were located by flushing the sitting birds, walking away, and then watching

them return to the nest. For black-fronted terns, the colony signs were obvious and nests were located when birds landed, or during general searching where the defensive attacks of breeding adults peaked. Both study areas were searched at least fortnightly, where possible, during the breeding season. The much smaller area and lower flows of the Ashley meant it could be done in two days. However, for the Rakaia, a period of 4-6 days was required, and this was influenced by the flow, with floods and freshes often restricting the area surveyed.

Nests were monitored until hatching or until nest failure. Following each fresh or flood, nest sites (with and without eggs) were checked to determine whether or not they had been flooded. Mean daily and peak instantaneous discharge data for the Rakaia river were obtained from the Ministry of Works and Development, and used to determine the proportion of nests flooded by a range of high flows. Nest losses on the Rakaia in 1982 and 1983 were calculated for each species over a range of discharges. These figures were then plotted to assess the extent of inter-specific differences in site selection and the impact of various sized floods.

3.3.2. Nest site characterisation

For all species in both study areas the following nest site information was recorded:

- (1) The location, mapped on an aerial photograph;
- (2) Number of eggs or chicks in the nest;
- (3) The horizontal distance and direction from the nest of all plants within one metre, including species and height;
- (4) Visual estimates of percent vegetative ground cover within one metre of the nest, recorded as: 0, <1, 1-5, 5.1-10, >10%;
- (5) Estimates of plant density and percent ground cover were made to determine the availability of alternative sites with greater than, less than, or equivalent, vegetated percentage ground cover to the nest site, at changes in the cross-section profile which were determined during levelling surveys, e.g., ridge tops;
- (6) The horizontal distance from, and description of, the water body closest to the nest according to the microhabitat classifications defined in Section 6.3.1;
- (7) Type of substrate within one metre of the nest, including a visual estimate of the dominant substrate according to the following

size ranges:

- sand; < 2mm
- shingle; 2 - 32mm
- stones; 32 - 64mm
- small cobbles; 64 - 128mm
- large cobbles; 128 - 256mm
- boulders; > 256mm;

(8) Distance of the nest from the nearest medium-dense stand of mature exotic vegetation, e.g., willow, lupin, broom or gorse. Only the dominant species of the plant association was recorded.

All results were expressed in proportional values and graphed, and where appropriate the significance of inter-specific and other comparisons were determined by the 'G test for heterogeneity' and the 'G test for goodness of fit' (Sokal and Rohlf, 1981). Substrate type and vegetation density were analysed for overlap by the Morisita (1959)-Horn (1966) method (see Section 6.3.2), while variations in mean vegetation densities and the distance of nests from water were tested for significance by the Mann-Whitney U test.

3.3.2.1. Nest site selection, vegetation tolerance, and the flow regime

Data on nest site selection, vegetation encroachment and the cross-sectional characteristics of site selection were analysed to test the hypothesis that wrybills are restricted in their nest site requirements and that these restrictions are influenced by the flood regime. On the Rakaia, the original vegetation survey (Section 3.3.2) was followed by subsequent visits to measure changes in percentage ground cover over time. Observations were continued after hatching and nest abandonment, assuming that the nest could have been used at any time during the breeding season, so that it was important to ascertain whether vegetational character would remain suitable throughout this period. Data on vegetation encroachment were tested for species-specific tolerances and the potential impact on site selection and nest site tenacity of modifications to the natural flows. Flooding is considered to be the dominant limiting factor to further vegetation encroachment. The same information was also used to examine inter-specific tolerances and differences between wrybills and banded dotterels. Aerial photos of the Rakaia study area were used to examine

changes in the area of dense and mature vegetation between 1982 and 1983.

To further evaluate nest site selection in relation to vegetation and flooding, cross-sectional transects through the nest perpendicular to the principal river form (or flood plain direction) were marked out. This line was surveyed over the width of some wrybill and banded dotterel home ranges by using an Abney level (mounted on a tripod) and a survey staff (Plate 2). The vertical height of the nest above all water bodies was recorded, as was the height of the nest from the maximum cross-sectional height. Because two people are needed for surveying, and because of flooding, all nests were not surveyed. River width in the study area varied from 1.5-2km, so it was unrealistic to survey the total cross-section. Wrybill and banded dotterel nests were surveyed on the Rakaia in 1982 and 1983, while black-fronted tern nests were surveyed only on the Rakaia in 1983. From the raw data three mean values were calculated for each species:

- (1) The vertical height of each nest above the closest water body along the cross-section;
- (2) The minimum vertical height of each nest above any water body in the surveyed cross-section; and
- (3) The height of each nest from the maximum cross-sectional height.

As flood levels rise, so the range of water level heights of each braid in a cross-section of the river declines. Consequently, at flows of bankful or greater, the cross-sectional water level will be horizontal. Because of these changes it was essential to measure all three parameters. The significance of differences between means was determined by using the Student's t-test after the data were transformed by the square root transformation.

PLATE 2: Cross-sectional surveying of a wrybill nest site.

(Note the dense-mature lupin at a higher riverbed level than the nest which is below the tripod. The cattle in the background were considered responsible for nest trampling.)



3.4. Results

TO TSP

3.4.1. Breeding success

3.4.1.1. Wrybill

On the Rakaia, breeding was confirmed for 21 wrybill pairs in 1982 and 26 pairs in 1983 (Table 3-1). However, in both years, several pairs (including four colour-banded pairs in 1983) occupied home ranges, but no nests were found, almost certainly because floods destroyed all attempts. Plate 3 shows a colour-banded wrybill on the nest.

Only 19 first clutch nests were located in 1982 and all were observed to hatching or nest loss. One other pair was found on an isolated island with two very young chicks, and another pair with at least one older chick (approximately two weeks old) was found at another site with restricted access. It was assumed, on the ground that all other 1982 nests had clutch sizes of two, that these pairs also had two eggs. A further nest with one egg was found during the rising stage of a large flood, but it was soon destroyed. Thus, while it has been included in the analysis, it is not known whether it was a first clutch or a repeat clutch nest, and because it was flooded within hours of finding, it was excluded from the calculation of mean clutch size.

Breeding success was, therefore, obtained from 21 nests, whose locations are shown in Figure 4-1, representing 20 confirmed 1982 breeding pairs. The laying of most pairs commenced in early to mid September with October the month of greatest first clutch incubation overlap (Figure 3-1a). Hatching success was 78.0%, nesting success 76.2% and fledging success 29.3%.

In 1983, 30 nests were found on the Rakaia, but the frequent floods made it difficult to assess whether some October nests were for first or repeat clutches. Most nests found in the 1983 season were initiated during October (Figure 3-1b). Therefore, on the basis of the 1982 season, all September and October nests were assumed to be first clutches. Three nests found in late November and December, for which corresponding first clutches had not been located, were considered to be repeat attempts, as were those of four other known pairs found during November. Therefore, in 1983, 23 first clutch and seven second (repeat) clutch nests, whose locations are shown in Figure 4-2, were identified on the Rakaia, representing 26 breeding pairs. Overall mean clutch size

TABLE 3-1 : Breeding success of wrybills nesting on the Ashley and Rakaia rivers during 1982 and 1983.

Breeding parameter	RAKAIA		ASHLEY	
	1982	1983	1982 ^a	1983
Number of confirmed breeding pairs.	21	27	?6	6
Number of pairs with unconfirmed breeding status.	1	4	?	0
Overall:	- mean clutch size (N=20)	2.0 (N=30)	NA	2.0 (N=7)
	- hatching success (%)	78.0	22.6	NA
	- nesting success (%)	76.2	20.0	NA
	- fledging success (%)	29.3	3.8	40
Number of confirmed first clutch nests.	21	23	NA	6
First clutch:	- mean clutch size (N=20)	2.0 (N=23)	NA	2.0 (N=6)
	- hatching success (%)	80.0	23.3	NA
	- nesting success (%)	85.0	21.7	NA
	- fledging success (%)	30.0	2.3	NA
Number of confirmed second clutches.	0	4	NA	1
Number of assumed second clutches for which no first clutch had been found.	0	3	NA	0
Second clutch:	- mean clutch size -	1.4 (N=7)	NA	2.0 (N=1)
	- hatching success (%)	-	20.0	NA
	- nesting success (%)	-	14.3	NA
	- fledging success (%)	-	10.0	NA
Proportion of unsuccessful first clutch pairs laying second clutches(%)	0	28.0 (N=7)	NA	100.0 (N=1)

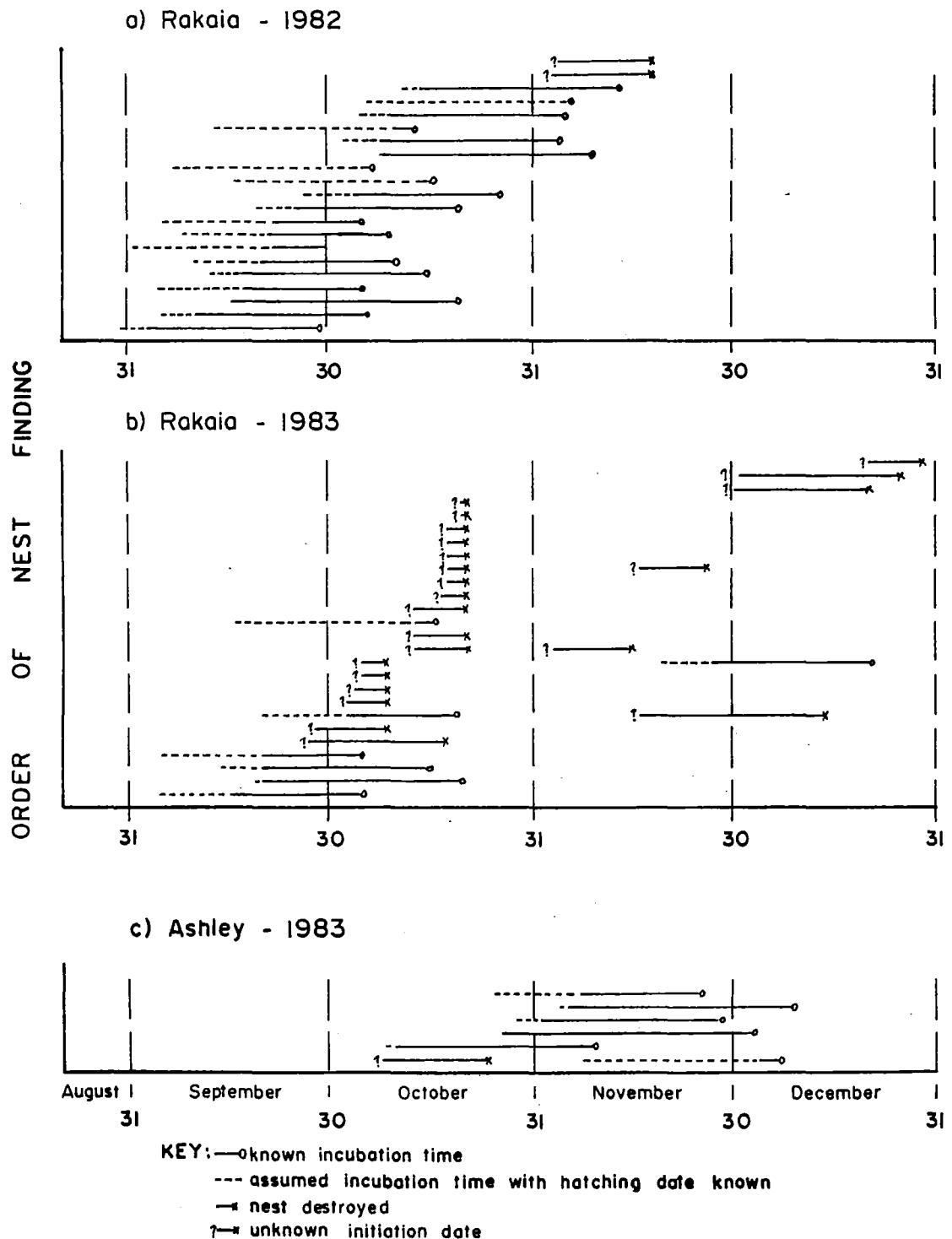
^a = Ashley fledging rate for 1982 estimated on the basis of a December survey.

NA= Not assessed in the study.

PLATE 3: A colour-banded wrybill on nest and eggs on the Ashley river during the 1983 breeding season.



FIGURE 3-1 : Periods of nest initiation and incubation for wrybills on the Rakaia (1982 and 1983) and Ashley (1983) rivers.¹



¹Horizontally adjacent lines represent repeat clutches.

was 1.8, hatching success was 22.6%, nesting success was 20% and fledgling success was 3.8%. Of the 26 breeding pairs only one successfully reared a chick to fledgling from the first clutches. Of the remaining 25 unsuccessful pairs, 28% (7/25) laid repeat clutches, but only one of these reared a further fledgling.

Six breeding pairs of wrybills were located on the Ashley river in 1983 and their locations are shown in Figure 4-3. As with the Rakaia, most nests were occupied in October and November (Figure 3-1c). Mean clutch size was two, hatching and nesting success were both 85.7%, and fledgling success was 42.9%. Only one first clutch nest failed, and this pair successfully re-nested. Time constraints meant it was not possible to undertake a full breeding study on the Ashley in 1982. However, five fledglings were found in the study area during December. Including a further fledgling which did not fly until late January 1983, and assuming six pairs were breeding, fledgling success in the order of 40% was estimated for 1982.

3.4.1.2. Banded dotterel

Table 3-2 summarises the breeding success of banded dotterels in the two study areas. In 1982 breeding was confirmed for 25 pairs on the Rakaia, with nest locations shown on Figure 4-1. Two confirmed, and one probable, repeat clutches were found. The peak laying and incubation period occurred from mid September to early October (Figure 3-2a), although the first nests were found in late August.. Mean clutch size for all nests was 2.7, hatching success 64.9% and nesting success 70.4%. One pair re-nested in the same bowl as for the first nest. Plate 4 shows a banded dotterel on the nest.

During the 1983 season, at least 32 pairs bred on the Rakaia river, as shown in Figure 4-2, building a total of 42 nests. Patterns of laying and incubation in 1983 (Figure 3-2b) were similar to the 1982 season. Mean clutch size was 2.8, hatching success 40.2%, nesting success 38.1%, and fledgling success 15.4%. Nests found after the end of October were considered to be repeat clutches, although one confirmed second clutch was found in mid October. Of 24 confirmed first clutch nests, 19 were unsuccessful, and in addition to eight second clutch nests for which a corresponding first clutch had not been found, a potential 27 second clutch nests could have been attempted. However, only 18 nests were located, showing that at least 66.7% of pairs which

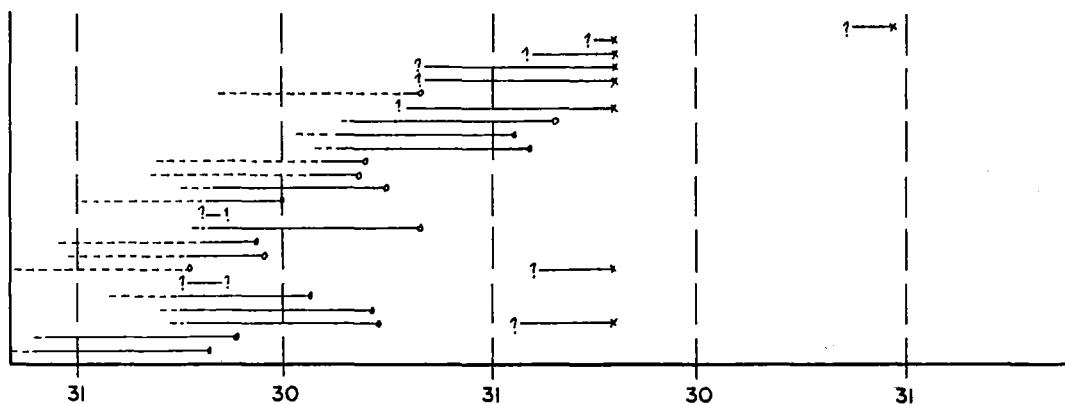
TABLE 3-2 : Breeding success of banded dotterels nesting on the Ashley (1983) and Rakaia (1982 and 1983) rivers.

Breeding parameter	RAKAIA		ASHLEY
	1982	1983	1983
Number of confirmed breeding pairs.	25	32	40
Overall:			
- mean clutch size	2.7 (N=27)	2.8 (N=42)	2.8 (N=58)
- hatching success (%)	64.9	40.2	51.9
- nesting success (%)	70.4	38.1	50.0
- fledging success (%)	NA	15.4	15.6
Number of confirmed first clutch nests.	22	24	28
First clutch:			
- mean clutch size	2.7 (N=22)	2.8 (N=24)	2.7 (N=28)
- hatching success (%)	80.0	40.3	52.0
- nesting success (%)	86.4	37.5	50.0
- fledging success (%)	NA	14.9	13.3
Number of confirmed second clutches.	2	10	14
Number of assumed second clutches for which no first clutch had been found.	3	8	12
Second clutch:			
- mean clutch size	2.8 (N=5)	2.8 (N=18)	2.8 (N=26)
- hatching success (%)	0	40.0	52.1
- nesting success (%)	0	38.9	50.0
- fledging success (%)	0	16.0	17.8
Proportion of unsuccessful first clutch pairs laying second clutches. (%)	NA	66.7	NA
Number of confirmed and assumed third clutches	0	0	3+1
Third clutch:			
- mean clutch size	0	0	3.0 (N=4)
- hatching success (%)	0	0	50.0
- nesting success (%)	0	0	50.0
- fledging success (%)	0	0	16.7

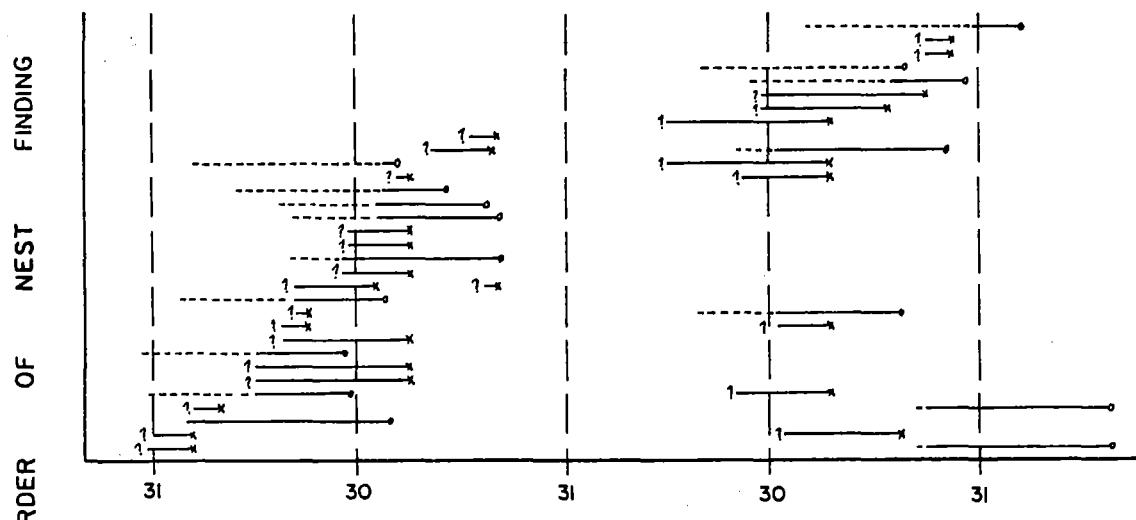
NA = not assessed.

FIGURE 3-2 : Periods of nest initiation and incubation of banded dotterels on the Rakaia (1982 and 1983) and Ashley (1983) rivers.¹

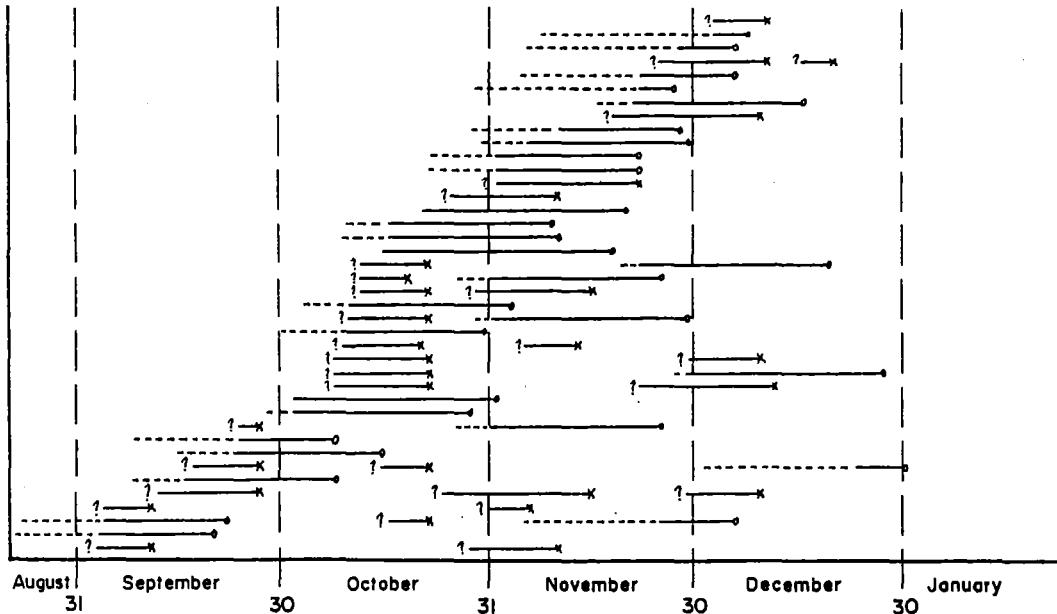
a) Rakaia - 1982



b) Rakaia - 1983



c) Ashley - 1983



KEY : — known incubation time

---- assumed incubation time with hatching date known

— nest destroyed

?— unknown initiation date

¹Horizontally adjacent lines represent repeat clutches.

PLATE 4: A banded dotterel on nest and eggs before being trapped on the Rakaia river during the 1982 breeding season.



were unsuccessful with a first clutch attempted a second.

During the 1983 breeding season the nesting of 40 pairs on the Ashley river study area was confirmed. Laying and incubation patterns are shown in Figure 3-2c. Overall mean clutch size was 2.8, hatching success 51.9%, nesting success 50%, and fledging success 15.6%. As for the Rakaia, nests found after the end of October were considered to be repeat clutches. In all, 30 repeat clutches were found, of which 14 were confirmed and 12 assumed to be second clutches, and three were confirmed and another assumed to be a third clutch. At least 81.3% (26/32) of unsuccessful first clutch pairs attempted to re-nest. Nest locations are shown in Figure 4-3.

3.4.1.3. Black-fronted tern

Nesting success and hatching success were measured for black-fronted terns, pied stilts, and South Island pied oystercatchers (Table 3-3). In 1981, no black-fronted terns nested on the Rakaia study area, but three breeding colonies, with a total of 23 nests, were located in 1982, and are shown in Figure 4-1. Laying and incubation occurred mainly in October and early November (Figure 3-3a), and were characterised by a colony-by-colony initiation sequence. Clutch size averaged 2.0, but hatching and nesting success rates were much more difficult to quantify because of the effects of observer disturbance on breeding. Hatching success of 20% and nesting success of 21.7% were recorded.

During 1983, only one colony (19 nests) was occupied in the Rakaia study area, as shown in Figure 4-2. Laying and incubation occurred mainly in December (Figure 3-3b). Average clutch size was 1.9, hatching success was 91.2%, and nesting success was 89.5%. No estimate of fledging success was made in either 1982 or 1983.

In 1983 one tern colony was established on the Ashley study area. Laying started in early December (Figure 3-3c), but all 11 nests were either destroyed or abandoned as a result of human interference associated with gravel extraction. Mean clutch size at the time of the first survey was 1.7. One nest contained a clutch of four eggs. After their nests were destroyed, the terns left the area without re-laying. Colony and nest locations are mapped in Figure 4-3.

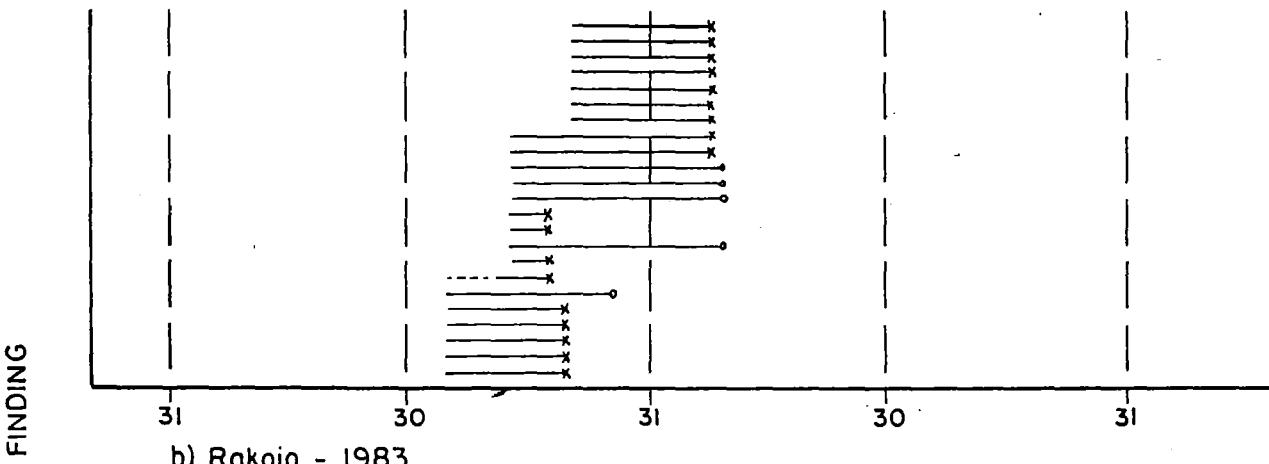
Table 3-3 : Breeding success of black-fronted terns, pied stilts, and South Island pied oystercatchers nesting on the Ashley (1983) and Rakaia (1982 and 1983) rivers.

Species	Breeding Parameter	RAKAIA		ASHLEY
		1982	1983	1983
Black-fronted tern	Number of confirmed nesting pairs	23	19	11
	Overall : - mean clutch size	2.0 (N=23; Range=1-3)	1.9 (N=19; Range=1-2)	1.7 (N=11; Range=1-4)
	- hatching success (%)	20.0	91.2	0.0
	- nesting success (%)	21.7	89.5	0.0
	- fledging success (%)	NA	NA	NA
Pied stilt	Number of confirmed nesting pairs	5		7
	Overall: - mean clutch size	3.6 (N=5; Range=3-4)	NO NESTING	3.1 (N=8; Range=2-4)
	- hatching success (%)	16.7		36.0
	- nesting success (%)	20.0		37.5
	- fledging success (%)	NA		NA
South Island pied oystercatcher	Number of confirmed nesting pairs	6	2	5
	Overall: - mean clutch size	2.2 (N=6; Range=1-3)	2.0 (N=2; Range=2)	1.8 (N=5; Range=1-2)
	- hatching success (%)	61.5	50.0	66.7
	- nesting success (%)	66.7	50.0	60.0
	- fledging success (%)	NA	NA	33.3

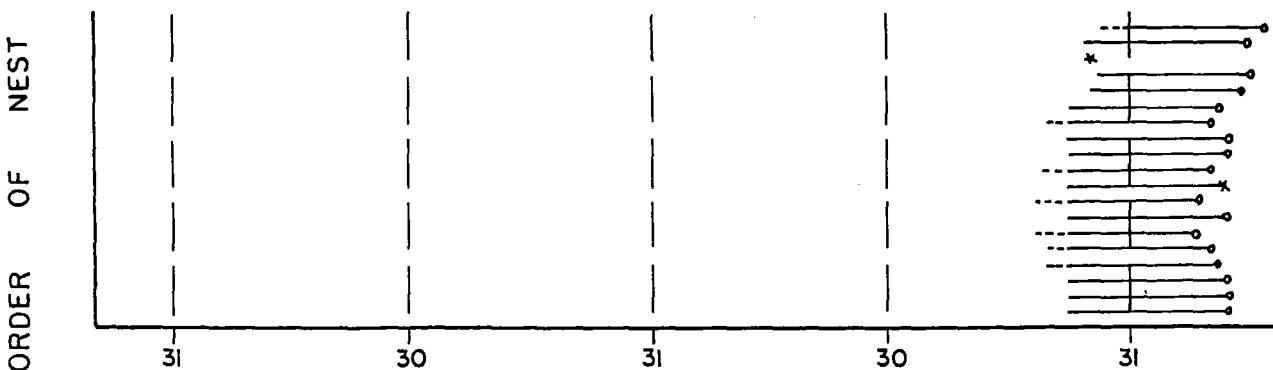
NA = not assessed.

FIGURE 3-3 : Periods of nest initiation and incubation of black-fronted terns on the Rakaia (1982 and 1983) and Ashley (1983) rivers.

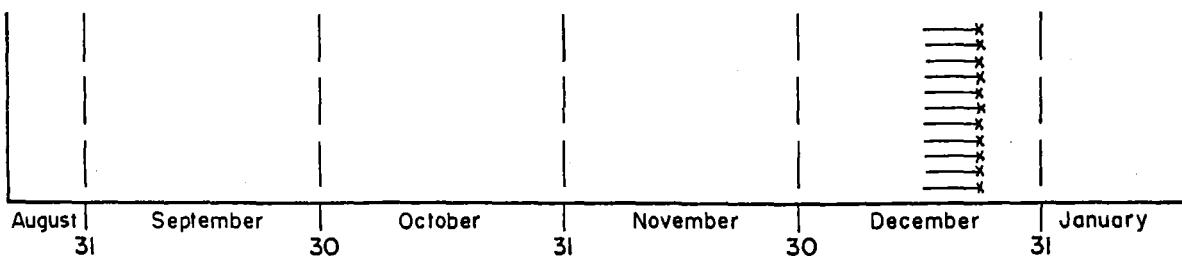
a) Rakaia - 1982



b) Rakaia - 1983



c) Ashley - 1983



KEY: — known incubation time

--- assumed incubation time with hatching date known

→ nest destroyed

3.4.1.4. Pied stilt

Although 50-60 pied stilts were recorded in the Rakaia study area during 1982 (compared with <10 in 1981 and none in 1983), only five nests were found, as shown in Figure 4-1. Laying and incubation began in mid October and continued into November (Figure 3-4a). Clutch size averaged 3.6, while hatching success was 16.7%, and nesting success 20%. No fledglings were seen and no repeat nests were found.

In 1983 eight nests were found on the Ashley study area, and their locations are shown in Figure 4-3. Peak laying and incubation occurred from mid October to early November (Figure 3-4b). Overall mean clutch size was 3.1, hatching success 36.0% and nesting success 37.5%. One pair laid a second clutch after losing their first.

3.4.1.5. South Island pied oystercatcher

The six nests found in the Rakaia study area in 1982 had a mean clutch size of 2.2, a hatching success rate of 61.5% and a nesting success of 66.7%. Nesting occurred from mid August to mid November (Figure 3-5a), after which breeding was completed. Only two nests with clutch sizes of two were found on the Rakaia during 1983; both hatched one egg (Figure 3-5b). The locations of nests for both years on the Rakaia are mapped in Figures 4-1 and 4-2.

During 1983, five nests were found in the Ashley study area, as shown in Figure 4-3. Laying and incubation were confined mainly to the months of September and October (Figure 3-5c). Mean clutch size was 1.8, hatching success 66.7%, nesting success 60%, and fledgling success 33.3%. No confirmed second clutch nests were found.

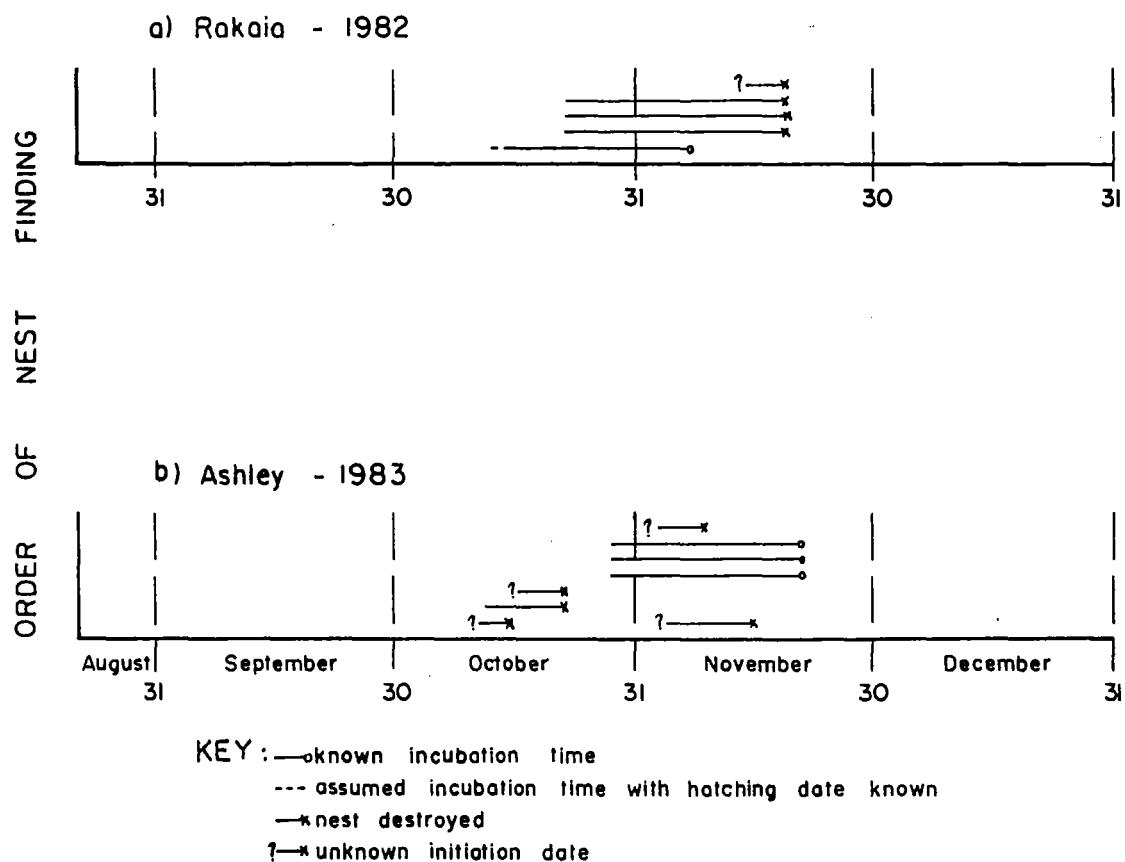
3.4.2. Causes of nest failure

Table 3-4 summarises the causes of nest failure for all species.

(a) Wrybill:

During the study 50% of all wrybill nests were destroyed, mostly by floods (72.4%; See plate 5) or by predators (24.1%). Although flooding caused 75% of nest losses in 1982 and 1983 on the Rakaia, predation was recorded only during 1983. Trampling by cattle resulted in the loss of at least one nest in 1982 (See plate 2).

FIGURE 3-4 : Periods of nest initiation and incubation of pied stilts on the Rakaia (1982) and Ashley (1983) rivers.¹



¹Horizontally adjacent lines represent repeat clutches.

FIGURE 3-5 : Periods of nest initiation and incubation of South Island pied oystercatchers on the Rakaia (1982 and 1983) and Ashley (1983) rivers.

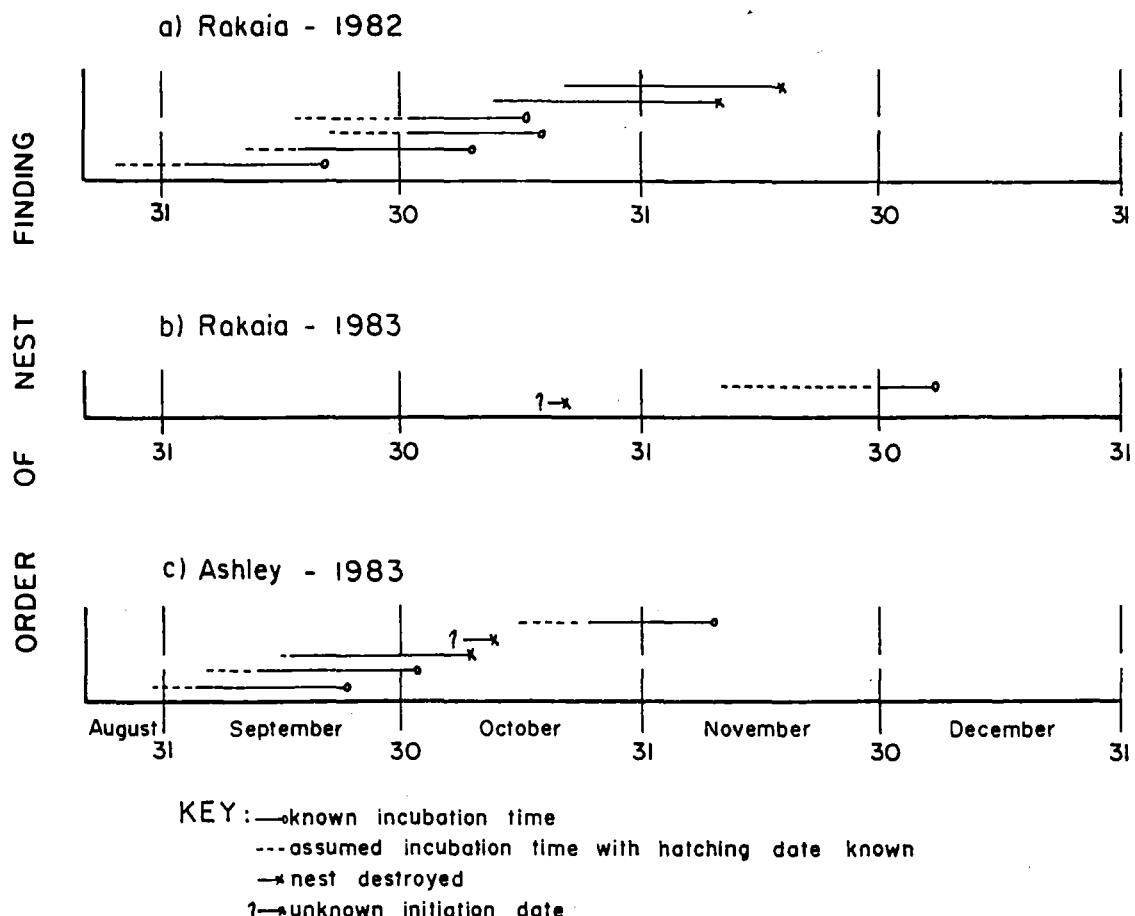


TABLE 3-4 : The causes of nest loss for riverbed birds on the Rakaia (1982 and 1983) and Ashley rivers (1983).

SPECIES	CAUSE	RAKAIA		ASHLEY 1983 N %	ALL RIVER TOTALS N %	PROPORTION OF ALL NESTS FOUND N %	
		1982 N	1983 %			N	%
Wrybill	Floods	3	75	18	75	-	72.4
	Predators ^a	-	-	6	25	1	100
	Trampling ^a	1	25	-	-	-	-
Banded dotterel	Floods	5	100	18	72	14	48.3
	Predators	-	-	7	28	14	48.3
	Trampling ^b	-	-	-	-	1	3.4
Pied stilt	Floods	4	100	NO NESTING		4	80
	Predators	-	-			1	20
						8	88.9
South Island pied oystercatcher	Floods	2	100	1	100	-	-
	Predators	-	-	-	-	2	100
						3	60
Black-fronted tern	Floods	9	50	-	-	2	40
	Desertion ^c	9	50	1	100	11	100
						9	30
						21	70
						9/53	17.0
						21/53	39.6

^a Trampled by cattle

^b Trampled by assistant

^c Human induced desertion : Rakaia by researcher and Ashley by contractors.

PLATE 5: A bankful discharge in the Rakaia study area during 1983.



(b) Banded dotterel:

Over both seasons and rivers, 46.4% of nests were destroyed. Floods (62.7%) were the main cause of nest loss, again followed by predators (35.6%). On the Rakaia, floods caused 76.7% of nest losses, but only 48.3% on the Ashley. In contrast, predators caused 48.3% of nest losses on the Ashley and 23.3% on the Rakaia.

(c) Black-fronted tern:

Overall, 56.6% of nests failed during the period of the study. Floods caused 30% and deserting 70% of these failures. Only Rakaia nests were affected by floods, but observer-induced desertion and desertion caused by gravel extractors occurred on the Rakaia and Ashley rivers respectively.

(d) Pied stilt:

In all, 69.2% of nests failed during the study. Floods caused 88.9% and predators the remaining loss.

(e) South Island pied oystercatcher:

Overall 38.5% of nests were destroyed. Floods caused 60% and predators 40% of these losses. All losses to floods occurred on the Rakaia, while predatory losses occurred only on the Ashley.

3.4.3. Species-specific susceptibility to nest destruction by flooding

The proportion of occupied nests destroyed by flooding shows the relationship between floods and nesting success. The length of the laying and incubation period, the size and recurrence interval of floods at different times of the breeding season, and the vertical height above water of the nest are all parameters which must be analysed to assess the relationship between flooding and nesting success.

3.4.3.1. Flood size and nest loss

Theoretically, only the bankful discharge will flood every nest site. However, because plant encroachment usually reaches its greatest height and density on high ground, and the study species will not nest in these habitats, floods of less than bankful discharge can flood all nests. As the peak flows decline below this level, smaller

species-specific nest losses will occur, according to a predictable shift from specialist to generalist patterns of site selection.

During two floods in 1982 and three floods in 1983, the proportion of all nests (occupied or unoccupied) destroyed on the Rakaia was recorded. In both years further often large floods occurred but, as a result of changes in bed morphology and a lack of repeat nesting, these floods were not included in the analysis.

Data on the susceptibility of wrybill and banded dotterel nests were collected for all five floods, but for black-fronted terns, pied stilts, and South Island pied oystercatchers, only the two 1982 floods provided sufficient data (Table 3-5). The impact of the flood on 11 November, 1982, (peak instantaneous discharge of 784 cumecs) showed a progression from wrybills with 31.6% of nests affected, through South Island pied oystercatchers (33.3%), banded dotterels (43.5%), black-fronted terns (47.8%) to pied stilts (60%). The flood of 19 November, 1982, (peak instantaneous discharge 2290 cumecs) destroyed all nests. This flow is slightly higher than the estimated bankful discharge of 2200 cumecs (See Section 3.4.3.3).

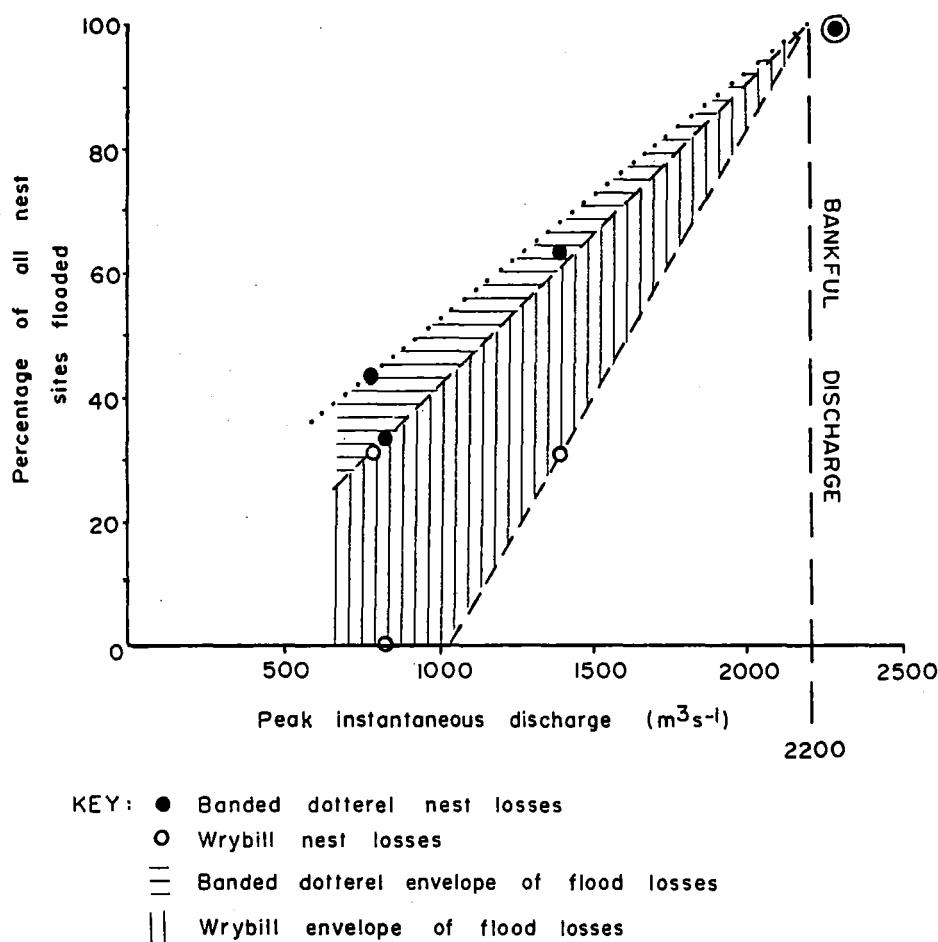
In 1983, three floods within the space of 30 days provided the opportunity to examine the progressive impact of increasingly larger floods. The first flood of 824 cumecs on 22 September, 1983, had no effect on wrybill nests, but covered 33.3% of banded dotterel nests. A flood peak of 1390 cumecs on 9 October, 1983, covered 31.3% of wrybill and 63.6% of banded dotterel nests. Finally, on 21 October, a flood of 2795 cumecs destroyed all nests.

The relationship between floods of various sizes and wrybill and banded dotterel nest survival (Figure 3-6) can be used to predict the proportion of nests likely to be destroyed by floods. However, because of the wide scatter of points at small to medium sized floods, it was considered more appropriate to fit, visually, a regression envelope encompassing the range of losses, rather than to calculate a simple linear regression. As expected, the range of species-specific nest losses narrows as the flood peaks and associated proportion of nest losses increase. While there is some overlap, wrybills are less affected than banded dotterels by all floods other than bankful flows.

TABLE 3-5 : The effects of floods on the nests of five riverbed bird species on the Rakaia river.

Date	Peak instantaneous discharge (m^3s^{-1})	Mean daily discharge (m^3s^{-1})	Species	Proportion of all nest sites flooded		Proportion of occupied nest sites flooded	
				Number	%	Number	%
11 November 1982	784	501	Wrybill	6/19	31.6	1/4	25.0
			South Island pied oystercatcher	2/6	33.3	2/2	100.0
			Banded dotterel	10/23	43.5	0/5	0.0
			Black-fronted tern	11/23	47.8	5/17	29.4
			Pied stilt	3/5	60.0	3/5	60.0
19 November 1982	2290	1340	ALL SPECIES	ALL NESTS	100.0	ALL NESTS	100.0
22 September 1983	824	422	Wrybill	0/4	0.0	0/4	0.0
			Banded dotterel	4/12	33.3	4/10	40.0
9 October 1983	1390	1118	Wrybill	5/16	31.3	4/14	28.6
			Banded dotterel	14/22	63.6	8/14	57.1
21 October 1983	2795	2045	ALL SPECIES	ALL NESTS	100.0	ALL NESTS	100.0

FIGURE 3-6 : The relationship between flood peaks and nest losses of wrybills and banded dotterels on the Rakaia river.



3.4.3.2. Nest height selection

The Rakaia cross-sectional surveys (Table 3-6) showed the relationship between nest site selection and a range of physical parameters associated with the cross-section. Wrybill nests were higher above the horizontally closest moving water body than banded dotterel nests which in turn were higher than black-fronted tern nests. The difference between wrybills and black-fronted terns was significant ($P<0.01$). The average minimum height of nests above water, regardless of the horizontal distance away from the nest, indicated that wrybill nests were again higher than banded dotterel nests but the latter were lower than black-fronted tern nests. The difference between wrybills and banded dotterels was significant ($P<0.05$). The average height of nests below the top of the surveyed cross-section showed that wrybill nests were closer to the top than banded dotterel nests which were closer than black-fronted tern nests. Wrybills nested significantly closer to the cross-sectional peak than did banded dotterels ($P<0.05$) and highly significantly closer than did black-fronted terns ($P<0.001$). There were no significant differences between black-fronted terns and banded dotterels for any of these relationships.

3.4.3.3. Flood size and the probability of nest loss

Analysis of Rakaia river flood flows can be used to determine the probability of nesting success being affected in any breeding season. Peak instantaneous flows have been used here, rather than mean daily flows, because it is the former which result in nest loss. However, medium sized floods may have longer term, less immediate effects on breeding success. In particular, after the flood peak has passed, there may be localised erosion and deposition resulting in nest site destruction, and also a decline in invertebrate productivity which may have a negative effect on chick survival.

Two methods, the annual flood series, and the partial duration flood series, are used for flood probability analysis. For the annual flood series the largest flood in each year or time segment under analysis is recorded and ranked according to the plotting formula:

Table 3-6 : Survey results for cross-sectional nest heights for wrybills, banded dotterels and black-fronted terns nesting on the Rakaia River.

Cross-sectional parameter	Wrybill (N=27)	Banded dotterel (N=22)	Black-fronted tern (N=8)
A) Average height of nests above the horizontally closest moving water body in the cross-section (m)	$\bar{x} = 0.87$ Range = 0.49-1.34 SD = 0.24	$\bar{x} = 0.75$ Range = -0.17-1.39 SD = 0.36	$\bar{x} = 0.55$ Range = 0.10-0.87 SD = 0.21
B) Average minimum height of nests above water regardless of the horizontal distance from the nest (m)	$\bar{x} = 0.72$ Range = 0.09-1.24 SD = 0.31	$\bar{x} = 0.48$ Range = -0.17-1.15 SD = 0.32	$\bar{x} = 0.55$ Range = 0.10-0.87 SD = 0.21
C) Average height of nests from the top of the surveyed cross-section (m)	$\bar{x} = 0.11$ Range = 0.0-0.28 SD = 0.13	$\bar{x} = 0.22$ Range = 0.00-0.53 SD = 0.16	$\bar{x} = 0.32$ Range = 0.05-0.53 SD = 0.16

Students t-test for the significance of differences between means

A)	Banded dotterel ($\bar{x}=0.75$)	Black-fronted tern ($\bar{x}=0.55$)
	Wrybill ($\bar{x}=0.87$)	t=1.30 NS
	Banded dotterel ($\bar{x}=0.75$)	- t=1.33 NS
B)	Banded dotterel ($\bar{x}=0.48$)	Black-fronted tern ($\bar{x}=0.55$)
	Wrybill ($\bar{x}=0.72$)	t=2.54 P<0.05
	Banded dotterel ($\bar{x}=0.48$)	- t=0.54 NS
C)	Banded dotterel ($\bar{x}=0.22$)	Black-fronted tern ($\bar{x}=0.32$)
	Wrybill ($\bar{x}=0.11$)	t=2.64 P<0.05
	Banded dotterel ($\bar{x}=0.22$)	- t=1.57 NS

NS = Not significant, i.e. P>0.05.

$$T = n + 0.12/m - 0.44$$

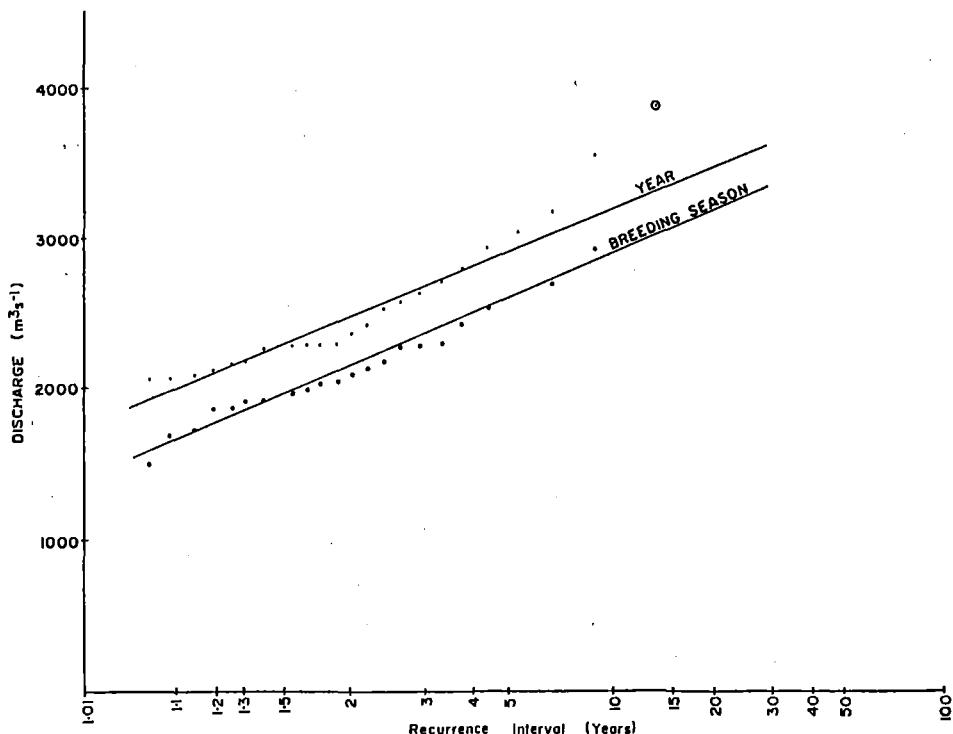
where T = recurrence interval;
 n = number of items in a record;
 m = rank of an event according to its size.

This is the most commonly used method in New Zealand (Duncan, pers. comm.), but when applied to the annual flood series it does not take account of other large events occurring in the same year or time segment. Such events may be bigger than annual floods recorded in other years of the analysis. The partial duration series which contains as many floods as there are years of record, but records the largest events regardless of the time of occurrence, is a means of overcoming this problem. Results are recorded by using the same plotting formula and are then evaluated on Gumbel probability paper (Figure 3-7a).

A flow with a recurrence interval of 1.5 years in the annual flood series (the bankful discharge) theoretically has a recurrence interval of 0.9 years in the partial duration series (Dunne and Leopold, 1978). The bankful stage will therefore be equalled or exceeded once a year in the partial duration series. The annual flood series for the Rakaia river (Figure 3-7b) indicates a bankful discharge of approximately 2200 cumecs. Taking this flow for the September-December breeding period indicates that this sized flood would occur about once in every 2.7 nesting seasons. By contrast, applying the partial duration series to the nesting season shows that, on average, the bankful discharge occurs approximately every 2.2 seasons. Peak instantaneous discharge plots for the Rakaia during the 1981 to 1983 study seasons (Figure 3-8a,b,c) show that flows for this period exceeded those predicted. Conversely, Ashley river flow plots (Figure 3-9a,b) for the same period (using daily mean flows only) show that the floods which did occur were all lower than the predicted bankful discharge (Figure 3-10a,b). (The Ashley bankful discharge has a breeding season recurrence interval of 3.4 seasons. Convergence between annual and breeding season plots happens as recurrence intervals become larger on the Rakaia because of the large contribution to extreme flood events made in the 4-month breeding period. In contrast, divergence on the Ashley resulted from the relatively smaller flood input on that river during the breeding season. Therefore nest sites are less likely to be affected by floods on the Ashley than on the Rakaia.)

FIGURE 3-7 : Partial duration and annual flood series for the Rakaia river - peak instantaneous discharges (1957 - 1982).

(a) Partial duration flood series.



(b) Annual flood series.

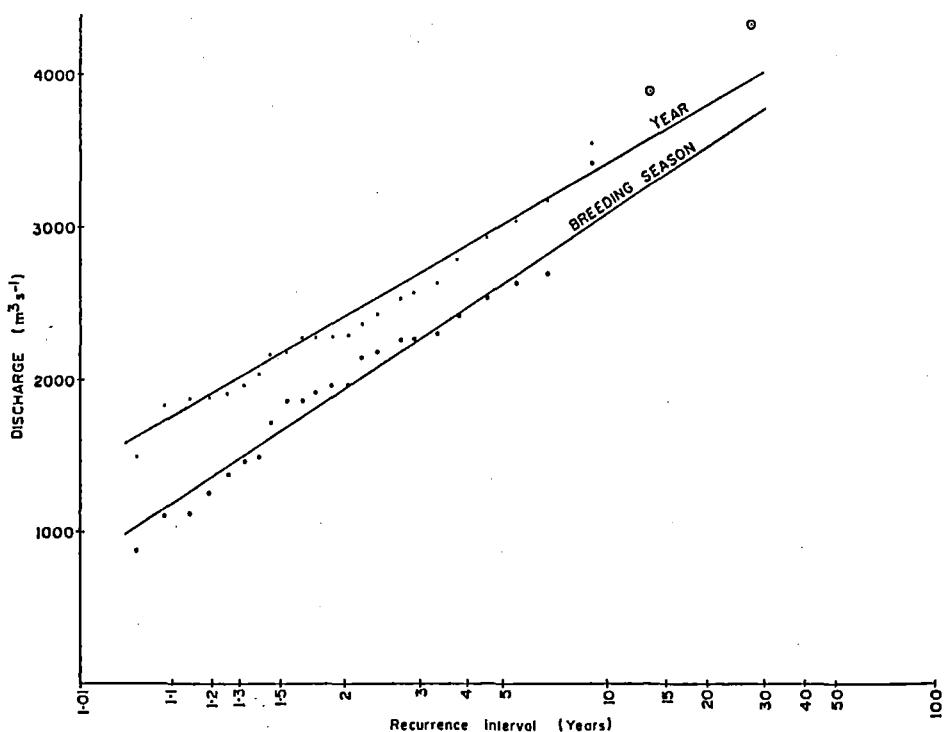
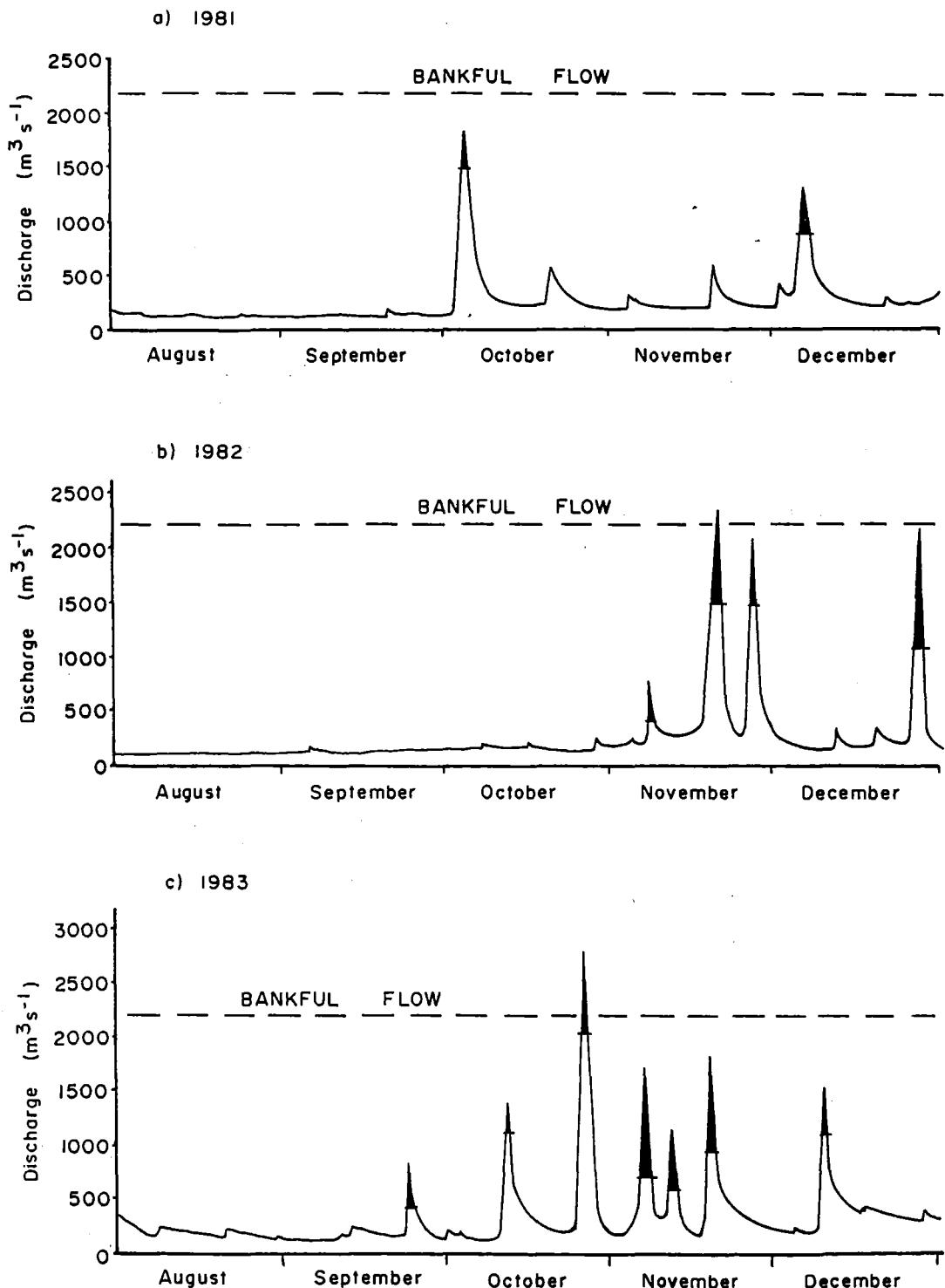


FIGURE 3-8 : Daily flow pattern of the Rakaia river during three breeding seasons : 1981-83 inclusive.¹



¹ Shaded areas represent peak instantaneous discharges.

FIGURE 3-9 : Daily mean flow pattern of the Ashley river during the 1982 and 1983 breeding seasons.

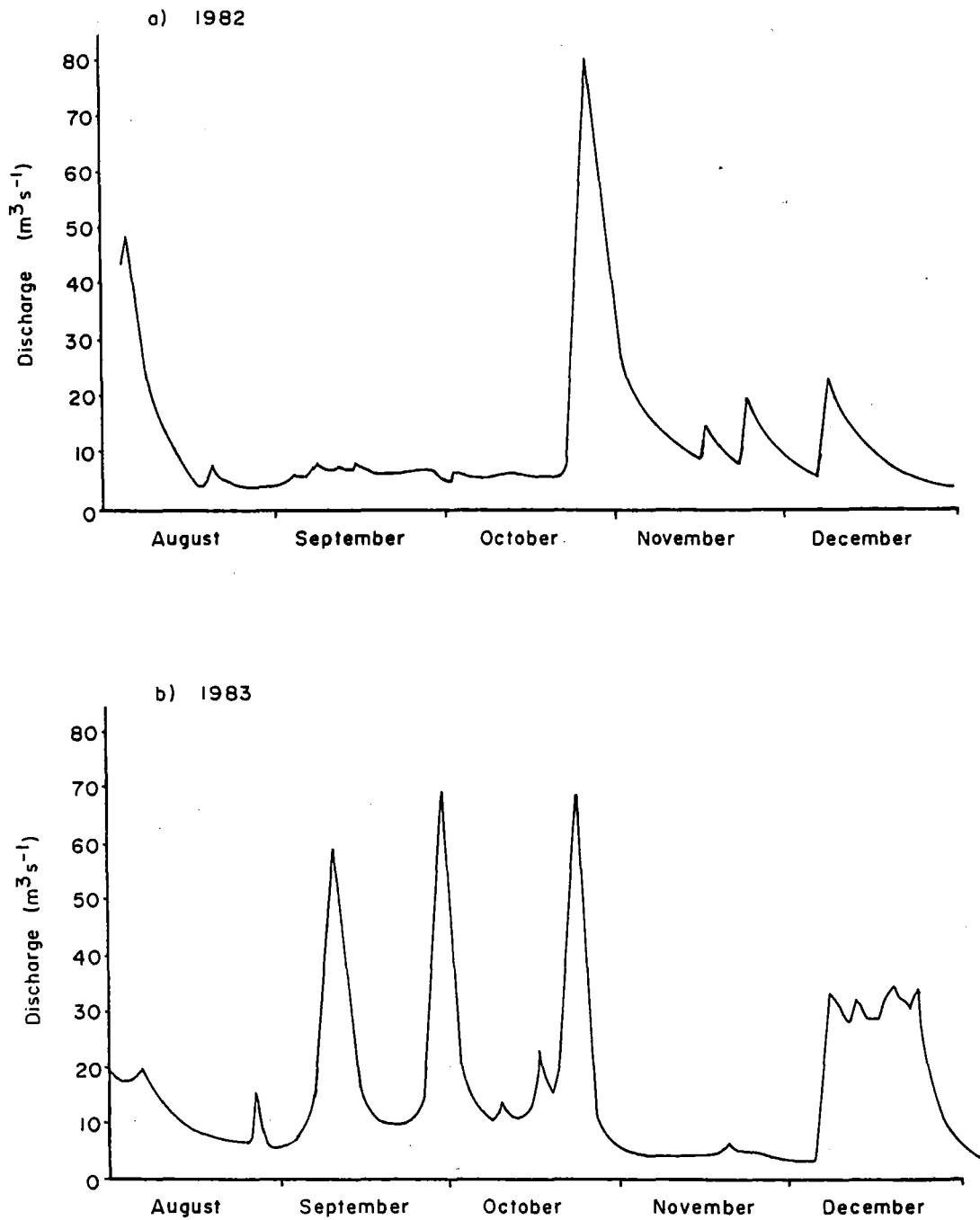
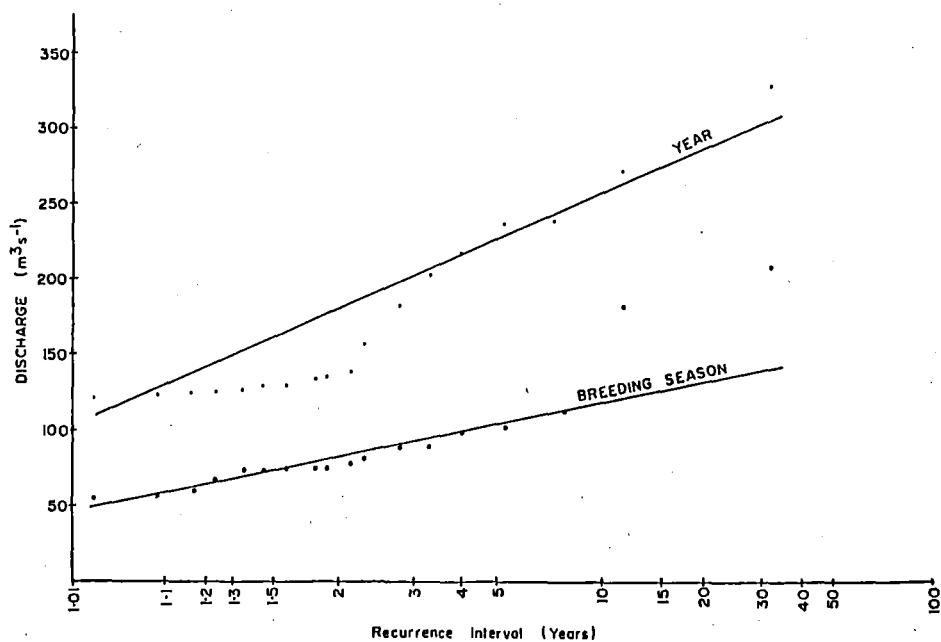
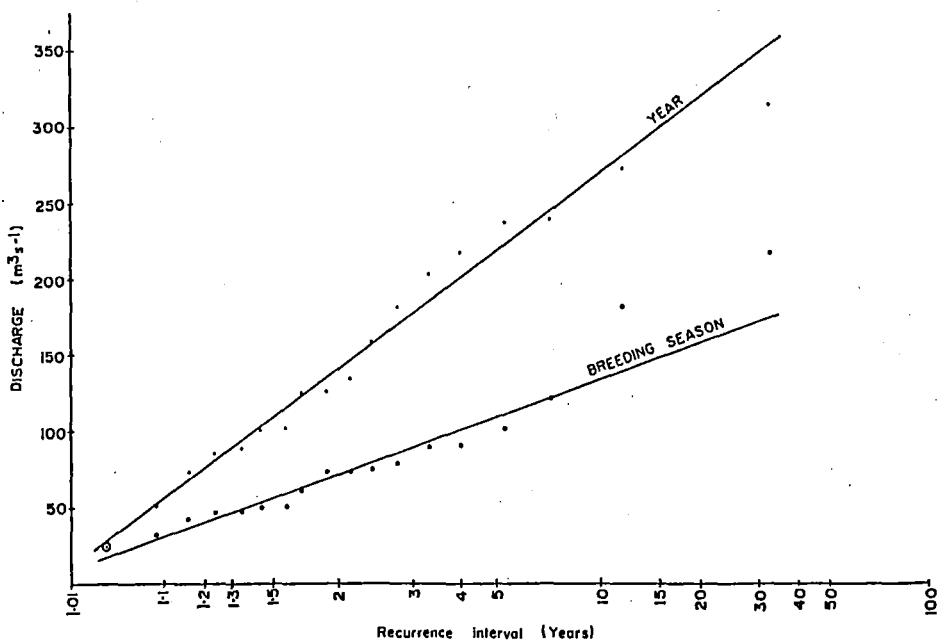


FIGURE 3-10 : Partial duration and annual flood series for the Ashley river - mean daily flows (1966 - 1983).

(a) Partial duration flood series.



(b) Annual flood series.



3.4.4. Nest site characterisation

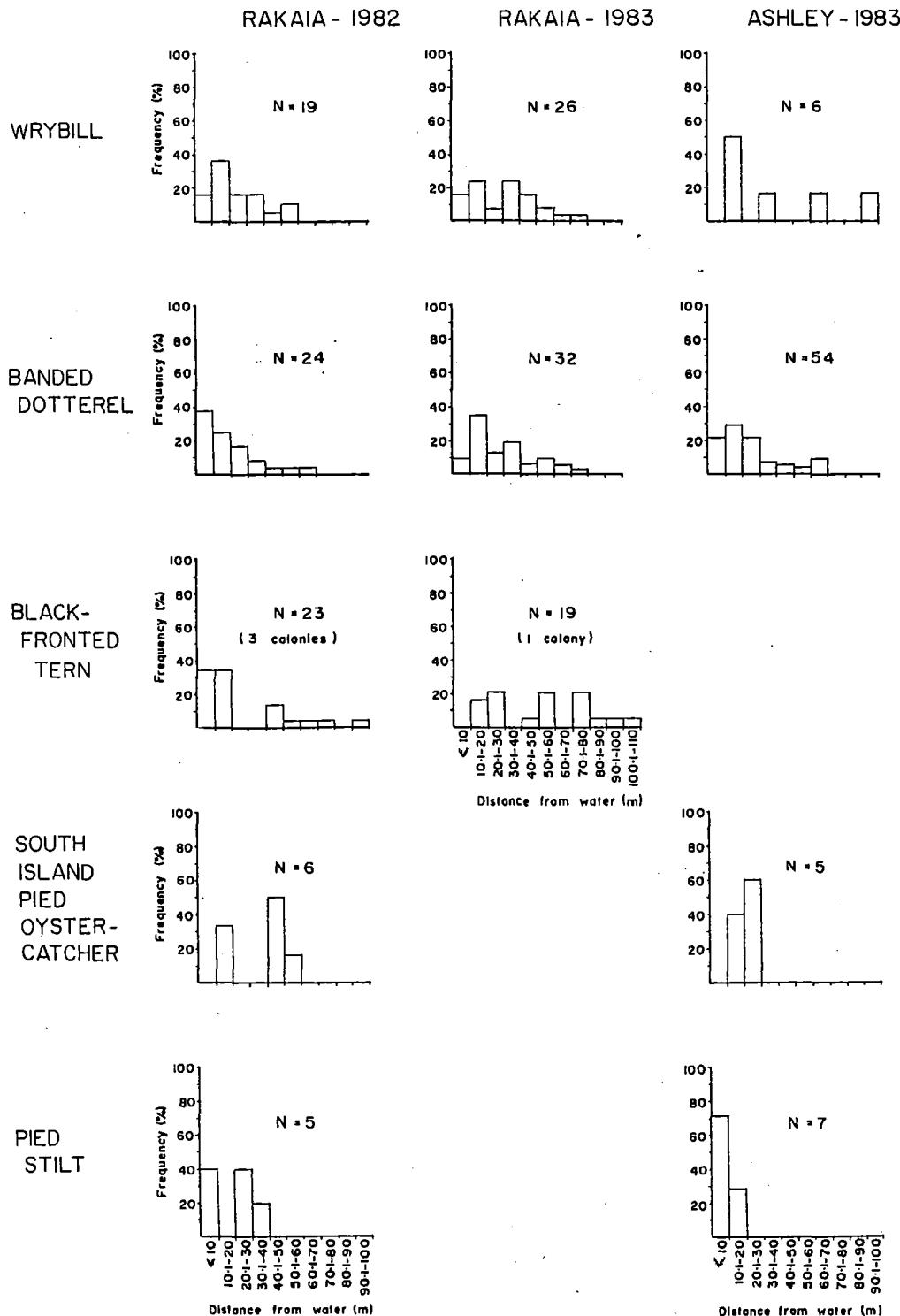
3.4.4.1. Proximity of nests to water

The average distance of nests from water (Figure 3-11) was not significantly different between species in 1982 (Mann-Whitney U test; $P>0.05$ for all values). Mean distances were 36.2m for South Island pied oystercatchers (Range=14-59m; SD=17.6m), 26.0m for wrybills (Range=6-67m; SD=18.0m), 25.9m for black-fronted terns (Range=5-94m; SD=25.4m), 20.9m for banded dotterels (Range=3-61m; SD=16.4m), and 20.6m for pied stilts (Range=5-32m; SD=12.6m). Although no significant difference existed between wrybill and banded dotterel nests on the Rakaia in 1983, both species nested closer to water than the average for nests in the one black-fronted tern colony ($P<0.05$ and $P<0.01$ respectively). The mean distance of black-fronted tern nests from water was 52.9m (Range=11-105m; SD=29.8m), for wrybill was 31.2m (Range=6-75m; SD=19.0m), and for banded dotterel was 30.2m (Range=3-77m; SD=19.5m). Because only two South Island pied oystercatcher (and no pied stilt) nests were found on the Rakaia in 1983, they were not included within the analysis.

All five study species were well represented on the Ashley in 1983, but the black-fronted tern colony was destroyed before nest site measurements were made. There were no significant differences among wrybill, South Island pied oystercatcher, or banded dotterel nests, but all were significantly further from water than pied stilt nests ($P<0.01$ for wrybill and banded dotterel, and $P<0.05$ for South Island pied oystercatcher nests). Wrybill nests averaged 36.1m (Range=11-97m; SD=32.6m), banded dotterel 24.5m (Range=1-69m; SD=18.0m), South Island pied oystercatcher 20.2m (Range=12-27m; SD=5.9m), and pied stilt nests averaged 8.1m (Range=3-18m; SD=5.2m) from water.

Intra-specific comparisons between years on the same river, and in the same season but between rivers, were also made. No significant differences were found for wrybills, or for the 1983 comparison between Ashley and Rakaia banded dotterel nests. However, banded dotterels nested further from water in 1983 than in 1982 (30.2m and 20.9m; $P<0.05$) on the Rakaia, as did black-fronted terns (52.9m and 25.9m; $P<0.001$).

FIGURE 3-11 : The distance of nests from water for five riverbed bird species nesting on the Rakaia and Ashley rivers.



3.4.4.2. Nest location in relation to channel form

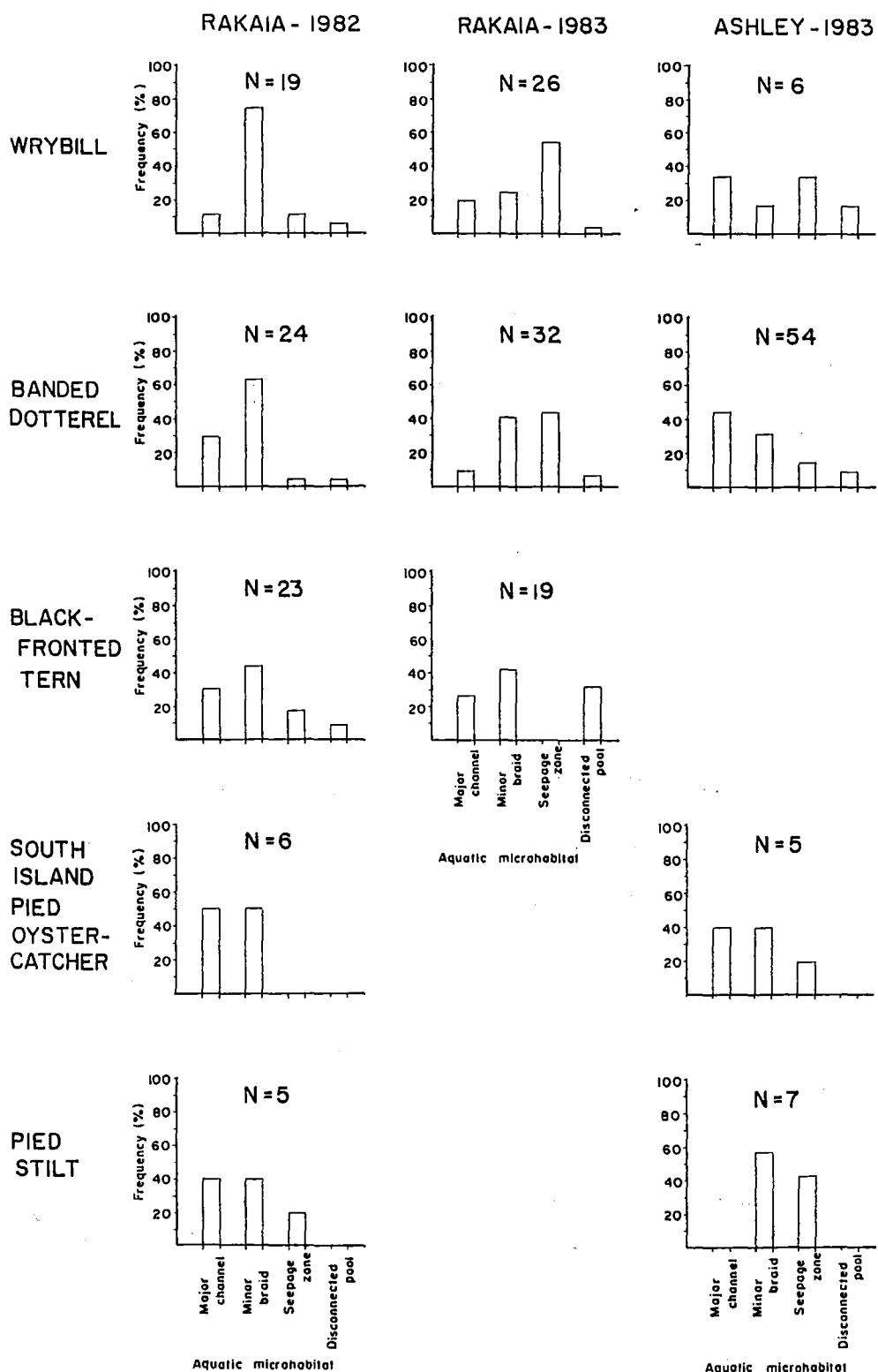
The aquatic microhabitat closest to the nests for all species is shown in Figure 3-12. When examined in terms of a major channel, minor channel, and disconnected pool association, there was no significant difference in inter-seasonal or inter-river location for wrybills on the Ashley and Rakaia rivers ($P>0.05$). Similarly, there was no significant difference between the location of banded dotterel nests in relation to channel form on the Rakaia river between 1982 and 1983. However, more nests in the Ashley were located near major channels than for the Rakaia in 1983 ($P<0.001$). Banded dotterels displayed a preference for nesting near major channels ($P<0.05$) on the Ashley, in contrast to pied stilt nests which were closely associated with the presence of minor channels ($P<0.05$). For all other species and years there were no significant differences between the location of nests and preference for, or selection against, the main aquatic microhabitats ($P>0.05$).

Within the minor channel classification, wrybills and banded dotterels displayed marked inter-seasonal variations in nest site location ($P<0.001$). Minor channels may be further subdivided into seepage zone braids, which are not linked at their source by surface flow to the river proper but are fed by gravel throughflow, and minor braids. In general, seepage zones are the most stable of all channel types in a braided river (pers. obs.) and are therefore the most productive aquatic microhabitats. In 1982 most wrybill and banded dotterel nests (which were nearest to minor channels) were associated closely with minor braids (87.5% and 93.8% respectively). However, in 1983 the nests of both species were associated closely with seepage zones (70% of wrybill and 51.9% of banded dotterel nests). There was no significant inter-seasonal difference for black-fronted terns. Insufficient data were obtained for pied stilts and South Island pied oystercatchers.

3.4.4.3. Distance of nests from dense and mature stands of exotic vegetation

Wrybill nests on the Rakaia were further from dense, mature stands of exotic vegetation in 1982 than 1983 ($P<0.05$; Mann-Whitney U test), and further on the Rakaia than on the Ashley ($P<0.05$). For all other wrybill-banded dotterel and intra-specific banded dotterel comparisons there were no significant differences ($P>0.05$). Wrybill nests were

FIGURE 3-12 : The aquatic microhabitats closest to the nests of five riverbed nesting bird species on the Rakaia and Ashley rivers.



90.1m (N=19; Range=36-140m; SD=35.9m) from vegetation on the Rakaia in 1982, 66.3m (N=26; Range=10-150m; SD=37.3m) in 1983, and 38m (N=6; Range=15-70m; SD=26.2m) on the Ashley. Banded dotterel nests averaged 66.7m from vegetation (N=31; Range=5-140m; SD=66.7m) on the Rakaia in 1983, and for the same year on the Ashley were 51.7m from vegetation (N=54; Range=3-120m; SD=37m).

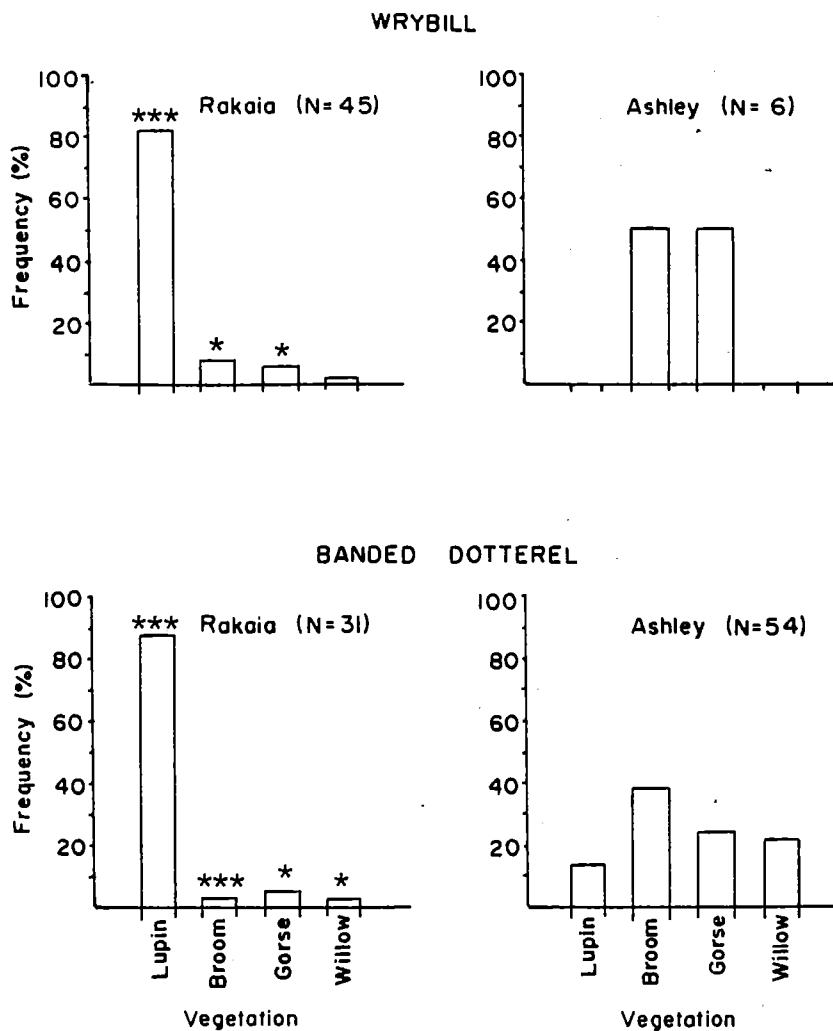
Combining years for the Rakaia and comparing this total with the Ashley according to the dominant plant species of the nearest dense and mature vegetation provides an insight into the hydrology-vegetation relationship for each river (Figure 3-13). Most wrybill nests on the Rakaia were nearest to dense stands of lupin, whereas on the Ashley half of the nests were closest to broom and the other half closest to gorse. The difference between the closest vegetation to nests on an inter-basin comparison was highly significant for lupins ($P<0.001$) and also significant for broom and gorse ($P<0.05$). The same pattern also emerged for banded dotterel nests.

3.4.4.4. Nest site vegetation tolerance

Studies of nest site vegetation characteristics began in 1981 with the establishment of 10x10m plots around 10 wrybill nests on the Rakaia. Floods destroyed all plots. In subsequent seasons the approach was simplified with measurements confined to the immediate nest surroundings and a limited sampling of alternative sites was carried out during cross-section surveys. Percent ground cover and plant density were the two parameters examined in this study.

Lupin was the dominant plant species around all nests on the Rakaia. There was no significant difference between density or percentage ground cover within 1 metre of nests from 1982 to 1983. Over 50% of wrybill nests had low plant densities (0-2 lupins) and percent ground cover (<1%). However, in 1983 for both measures, there were significantly ($P<0.05$) more nests in totally non-vegetated areas. Subsequent surveys of wrybill nests at approximately three-weekly intervals in 1982 (Figure 3-14) were used to watch the change in nest site vegetation over time. The decline in sample size with later surveys was because some nest sites were flooded. Although a trend toward increasing ground cover with time existed, the differences between surveys 1, 2, and 3, were not significant ($P>0.05$).

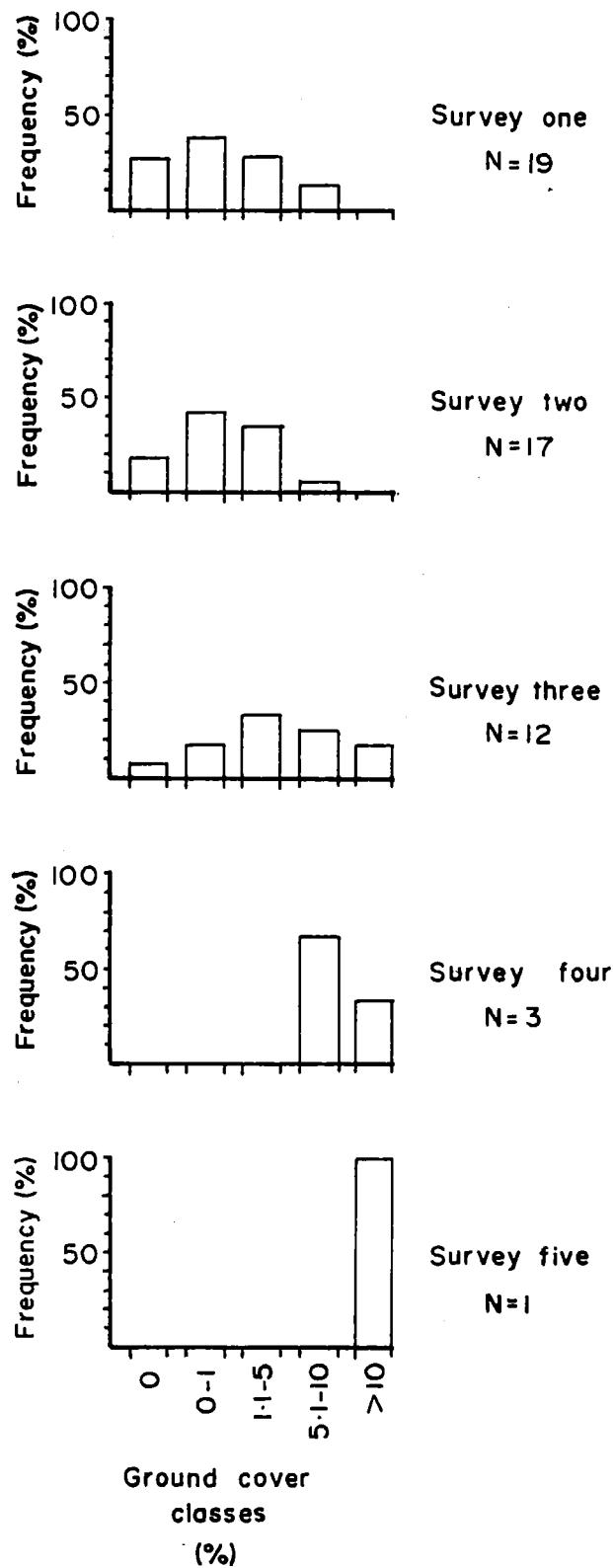
FIGURE 3-13 : The location of wrybill and banded dotterel nests in relation to the dominant plant species of the nearest dense and mature stand of exotic vegetation on the Ashley and Rakaia rivers.



KEY: Asterisks above columns indicate significant differences between corresponding columns on the Ashley river graphs.

* = $P < 0.05$
*** = $P < 0.001$

FIGURE 3-14 : Changes in percentage of vegetative ground cover within one metre of wrybill nests on the Rakaia river in 1982.^a



^a Surveys taken at time of nest location and subsequently at approximately 3-weekly intervals.

Nest sites of banded dotterels and black-fronted terns also had low plant densities and low values of percent ground cover within one metre of nests. For both species, inter-seasonal differences on the Rakaia were significant ($P<0.01$), with more nests in 1983 being found on non-vegetated sites than in 1982. There were no significant differences between wrybills and banded dotterels on an inter-seasonal basis, or when the two years were combined for plant density around the nest site. However, for percent ground cover there were significant inter-specific differences for 1983, and when both years were combined ($P<0.05$). Similar results occurred for inter-specific comparisons with black-fronted terns.

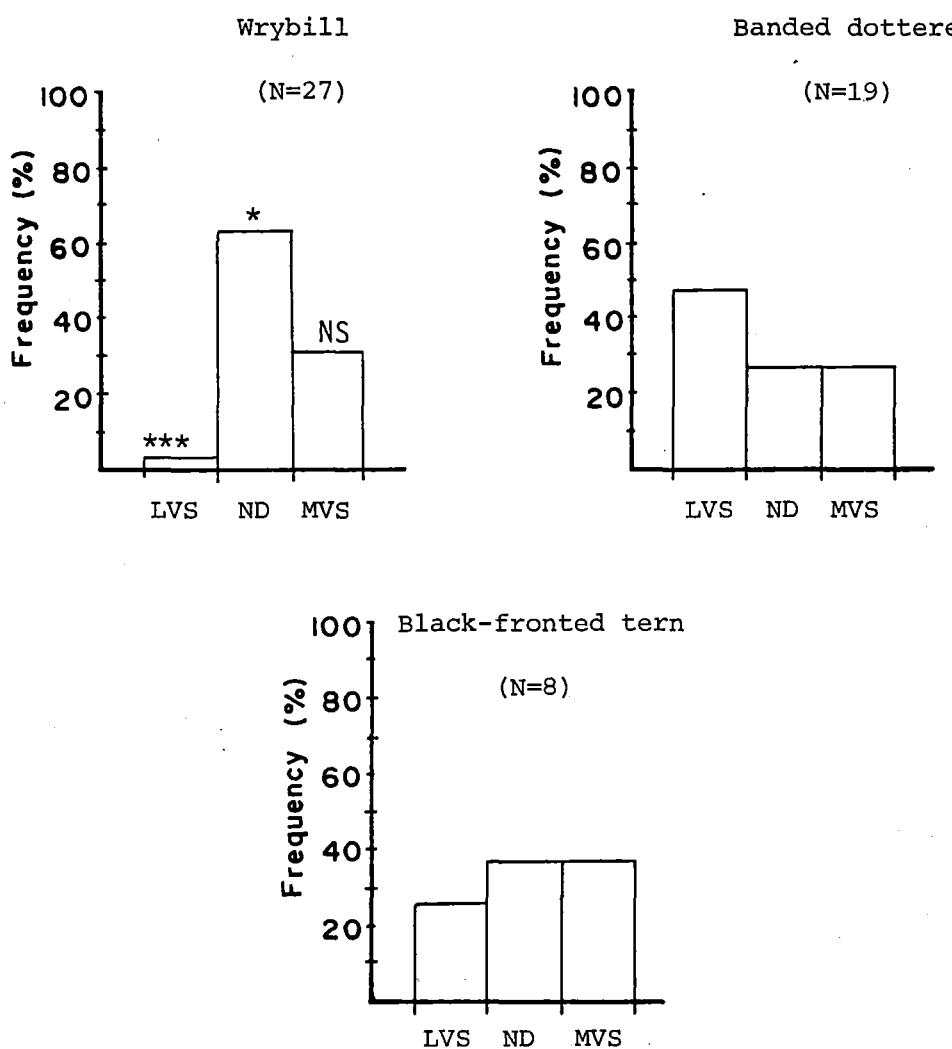
The availability of alternative nest sites with greater plant density and ground cover, or lower density and ground cover, was determined for a sample of wrybill, banded dotterel and black-fronted tern nests on the Rakaia (Figure 3-15). Only sites at the same or higher levels on the cross-section were assessed. One of 27 surveyed wrybill nests was located on a site of equivalent or lower level to a less vegetated alternative. In contrast, 47.4% of banded dotterel ($P<0.001$ compared with wrybill), and 25% of surveyed black-fronted tern nests were found at these locations. Most wrybill nests were located on sites of the same vegetation character to those available at equal or higher levels, although 33.3% were sited at the highest level possible without having to nest on a more densely vegetated site. There were no significant differences between selection preferences of wrybills and black-fronted terns, or banded dotterels and black-fronted terns.

In the 1982 breeding season approximately 33% of the Rakaia study area was covered with dense and mature vegetation. By December 1983, this area had declined to 25% of the riverbed.

3.4.4.5. Nest site substrate character

The substrate characteristics at nest sites of wrybills, banded dotterels and black-fronted terns were determined on the Rakaia in 1982 and 1983, and on the Ashley in 1983. Because substrate distributions vary little over a range of flows and between floods (Mosley, 1983a), data from 1982 and 1983 on the Rakaia were combined (Figure 3-16). Most wrybill nests were on substrates dominated by the shingle size fraction (2-32mm), with secondary classes being stones (32-64mm) and sand (<2mm). Banded dotterel and black-fronted tern nests occurred on a wider range

FIGURE 3-15 : The potential availability of nest sites with lower plant densities and percent ground cover at the same or higher levels along the surveyed cross-sections of wrybill, banded dotterel, and black-fronted tern nests on the Rakaia river.



KEY: LVS = Less vegetated sites available.
ND = No difference between sites.
MVS = More heavily vegetated sites.

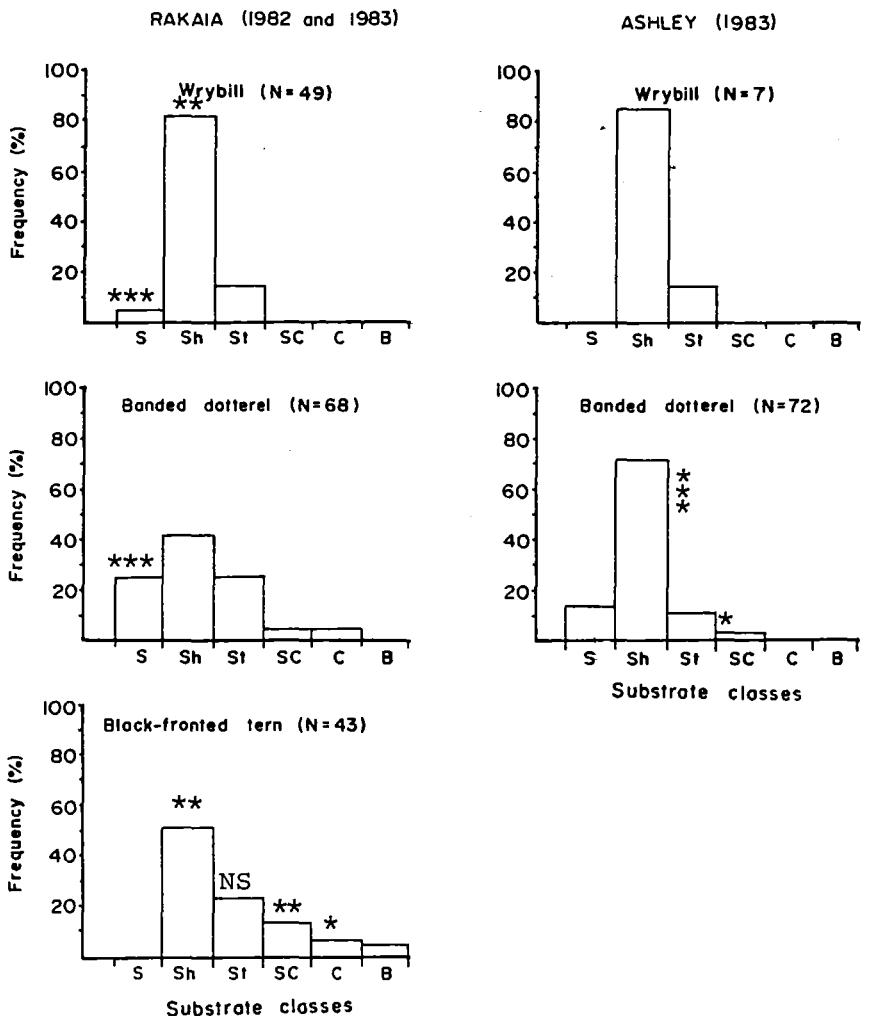
Asterisks above wrybill columns refer to significant differences between adjacent banded dotterel values.

* = $P < 0.05$

*** = $P < 0.001$

NS = Not significant

FIGURE 3-16 : Dominant substrate size classes within one metre of wrybill, banded dotterel, and black-fronted tern nests on the Rakaia and Ashley rivers.



KEY: Asterisks above the columns in each Rakaia graph relate to the following inter-specific comparisons:
 (i) wrybill with banded dotterel;
 (ii) banded dotterel with black-fronted tern;
 (iii) black-fronted tern with wrybill.

Those beside columns on Ashley graphs relate to intraspecific differences with adjacent Rakaia columns.

* = $P < 0.05$
 ** = $P < 0.01$
 *** = $P < 0.001$

KEY: Substrate classes

S - sand = < 2 mm
 Sh - shingle = 2-32 mm
 St - stones = 32-64 mm
 SC - small cobbles = 64-128 mm
 C - cobbles = 128-256 mm
 B - boulders = > 256 mm

of substrates, although shingle was still the major fraction. Significantly more wrybill nests were located on shingle than either banded dotterel or black-fronted tern nests ($P<0.01$). In contrast, significantly more banded dotterel nests were found on sand than were wrybill or black-fronted tern nests ($P<0.01$). Black-fronted tern nests were on larger substrate classes than were wrybill. Shingle was also the dominant substrate around wrybill and banded dotterel nests on the Ashley. There were no significant differences in substrate use between wrybills nesting on the Ashley or Rakaia rivers. However, banded dotterel nests were significantly more common on shingle ($P<0.001$) and less frequent on stones ($P<0.05$) on the Ashley.

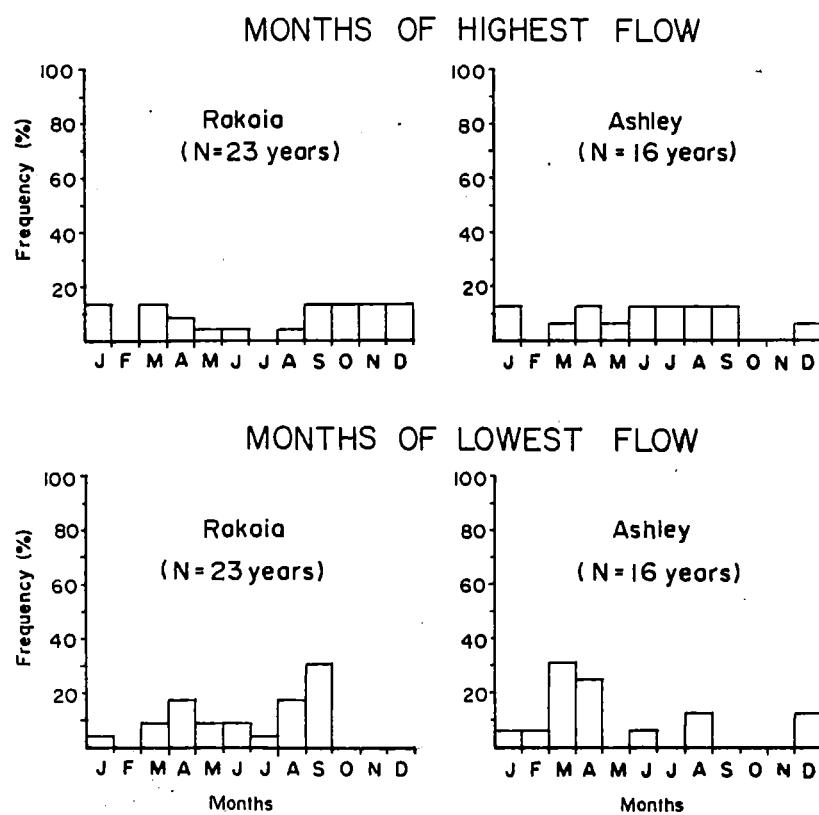
On the Rakaia, substrate overlap was 0.60 between wrybills and banded dotterels, 0.66 between wrybills and black-fronted terns and 0.73 between banded dotterels and black-fronted terns. Wrybill-banded dotterel substrate overlap on the Ashley was 0.83. Intra-specific overlaps between the Ashley and Rakaia rivers were 0.96 for wrybills and 0.69 for banded dotterels.

3.5. Discussion

3.5.1. Breeding

The only previous study of wrybill breeding, Hay (1984), used the Mayfield estimator to determine survival probabilities. A major limitation of this method occurs with species where there are varying probabilities of egg or chick survival. This study has shown that egg losses vary greatly over a range of flood flows, and that losses are characterised by a species-specific response to nest site selection. Specialists like the wrybill choose sites at higher levels than those of the generalists such as banded dotterels and black-fronted terns. [This has the effect of altering survival probabilities for each species] thus introducing a bias into the method. There is also a time span difference in survival probabilities depending on which stage of the breeding season a species chooses to begin nesting. On a monthly basis (see Figures 2-2 and 3-17), September has the most variable flows on the Rakaia, and it is one of six months having the number of the annual highest monthly flow, but it stands alone as the only month with more than 30% of annual low flow records. A similar problem exists on the Ashley, but because the seasonal flow pattern is different from the Rakaia, survival estimates determined for each river would not be

FIGURE 3-17 : Monthly high and low flows for the Rakaia and Ashley rivers.



directly comparable. The use of traditional methods, even with their inherent limitations, was readily justified in these circumstances, and although not used by Hay (1984) can be compared directly with Hay (1979) and other New Zealand studies.

Rates of nesting and hatching success are a direct function of discharge for all riverbed birds. Large within and between seasonal variations in flow are, therefore, directly linked to nesting and hatching success for each species. Hay (1984) described how one flood on 5 December, 1976, (with a peak instantaneous discharge of 2271 cumecs) destroyed all wrybill nests in his study area. Several floods with similar and even higher flows occurred during this study, with varying impacts on wrybill breeding success. Although nesting success was not measured in 1981, a flood with a peak instantaneous discharge of 1851 cumecs on 5 October, and one of 1311 cumecs on 8 December, each destroyed many nests. In 1982 there were no significant floods during the breeding season until early November. This allowed a high hatching success and nesting success of first clutches, which probably offset the impact of several, large, later floods which destroyed all second or repeat clutches. Conversely, in 1983, larger floods were scattered throughout the breeding season, resulting in the lowest level of wrybill breeding success recorded. However, on the Ashley, which is less affected by the impacts of breeding season floods, breeding success was the highest on record. It may be inferred from this that fledging success was reduced on the Rakaia because of the direct impact of flooding on eggs and young chicks, and from the indirect impact which flooding had on the food supply of adults and chicks (see Section 6.5.4). While direct measurements of this probable impact on chicks were not made, the inference seems logical given the existing conditions.

As a result of these probable impacts it has been suggested (Hughey, 1985; see Appendix 2 for the full text) that there may be ways of establishing a long term relationship between flood flows on Canterbury rivers and the wrybill population. By using the numbers of birds spending the summer on northern harbours (assuming that most are first year non-breeders) as an indicator of breeding success from the previous year, it was shown that a long term correlation existed with peak Rakaia flows during the breeding season. Hughey (1985) showed that a year of poor breeding success would probably be reflected in very low

numbers of wrybills spending the summer on northern harbours. Such a problem could be a warning to wildlife managers, who should consider conserving some of the presently less highly regarded wrybill habitats, e.g., the Ashburton and Ashley rivers.

It was notable that during 1983, six wrybill pairs on the Ashley had a population recruitment of about three times that of the estimated 30 pairs on the Rakaia study area. This high recruitment level may be characteristic of these smaller rivers. If so, then there are two possible explanations for this apparent anomaly:

- (a) Rivers such as the Ashburton and Ashley have only recently been colonised by wrybills. Hay's (1984) river surveys support this argument, and the increased numbers on the upper Ashburton (Moore, pers. comm.) and movement into the central reaches of the river (pers. obs.) also support this explanation;
- (b) Extra recruits from the Ashley are surplus to the carrying capacity of that river and therefore breed elsewhere, such as on the Rakaia. This explanation seems unlikely because there are large empty areas of suitable wrybill habitat on the Ashley.

It therefore seems that colonisation of the Ashburton and Ashley rivers has occurred recently, and that probably only in the past few years has the Ashley population established a stabilised age structure. If breeding conditions remain suitable the population on the Ashley could grow substantially.

Banded dotterel fledging success was more difficult to determine than for wrybills. There were two main reasons for this:

- (1) Fully fledged, juvenile banded dotterels tended to leave the study area immediately they could fly. Because these areas were a long way from estuaries or lagoons it was extremely difficult to find birds thought to have left the study area;
- (2) By operating study areas on different rivers, full-time observation could not be sustained on either study area. Hence, fledging and, migration or local movements of individuals could easily have occurred while the observer was working on another area.

Estimates of banded dotterel fledging success are, therefore, probably considerably lower than actually occurred. The problem was likely to

have been greatest on the Ashley where numbers were highest but observer presence lowest. Hence, fledging success on the Ashley was probably significantly higher than recorded, and certainly much higher than on the Rakaia, which is not apparent from the results.

Rates of hatching and nesting success for banded dotterels on the Rakaia in 1982 and Ashley in 1983, were higher than those recorded by Bomford (1978) on stabilised berm land on the Cass river delta. Hatching success in both cases, and fledging success on the Ashley in 1983, were considerably lower than for wrybills. In contrast, hatching success on the flood-dominated Rakaia in 1983 was lower than that recorded by Bomford (1978), but higher than for wrybills in the same season. This is surprising in terms of the generalist-specialist behaviour of the two species. Although wrybills nested at higher and less flood-prone levels than banded dotterels, this advantage was lessened by several behavioural and physical limitations:

- (a) The 30-day incubation period of wrybills (Hay, 1984) is longer than the 28-day period recorded for banded dotterels (Oliver, 1955; Bomford, 1978). To some extent, the greater frequency of small floods likely to affect a species nesting lower on the island cross-sectional profile is balanced by a shorter incubation time, but certainly not sufficiently to explain the large difference in hatching and nesting success rates;
- (b) Floods in 1983 were on average much larger than those of most other years, although the return period of all floods was little different from average. The advantage of higher nest site location for wrybills was negated by these larger floods which destroyed most nests each time;
- (c) In 1983 most banded dotterels laid first clutches earlier than did wrybills, thus avoiding the most serious impacts of flooding. Others did not lay repeat clutches until late November-early December, after the most serious flooding.

A higher proportion of banded dotterel pairs which had lost first clutches laid repeat clutches in 1982 and 1983 than did wrybills. This suggests that conditions in both seasons favoured banded dotterels, at least as far as the ability to prepare and lay a repeat clutch is concerned. Banded dotterels, which forage more on terrestrial habitats

(see Figure 6-1) are probably less affected (apart from higher nest losses) by flooding than wrybills (see Section 3.4.3). On the lower Rakaia the two species occupied similar microhabitats, although there were considerable differences in the patterns of microhabitat use. Furthermore, densities of banded dotterels were slightly greater than for wrybills, also suggesting that, for this area, banded dotterels are better adapted to active-riverbed life than are wrybills. The almost complete habitat separation of the species on the upper Rakaia is based on:

- (1) wrybills occupying the active, vegetation-free riverbed; and
- (2) banded dotterels nesting on the higher, low profile vegetated, more stable riverbed (Hay, 1984).

On the lower Rakaia, the encroachment of exotic vegetation has displaced the natural successional processes on unmodified habitats. Hence there is only a short term (one nesting season if floods do not affect the area) intermediate stage between bare shingle and dense, high profile vegetation cover. Both plover species nest on bare shingle, and on shingle in the early stages of vegetation encroachment. The short term advance toward vegetation maturity means, however, that typical behavioural patterns related to natural vegetative cover are not given time to develop, resulting in changes in site-tenacity and overall habitat overlap.

Rates of nesting and hatching success of black-fronted terns and pied stilts were closely related to variations in the flow regime. In 1982, the low success rates on the Rakaia were much less than for all other species. Both species nested later in the season and were, therefore, more susceptible to flood losses, and both selected nest sites at lower levels than wrybills, banded dotterels, or South Island pied oystercatchers. Black-fronted terns were later at initiating nests on the Rakaia in 1983. However, although rates of hatching and nesting success were high, it appeared that fledging success may have been very low. This was apparent as a result of colour banding for the Ornithological Society of New Zealand. Of 20 chicks banded on 13 January, 1984, only one was subsequently found on 21 January, when a further chick was banded. On a later visit to the colony site in February all the birds had departed. The impact of human-induced disturbance on breeding black-fronted terns is most noticeable and was a

major cause of nest failure on the Rakaia in 1982 and on the Ashley in 1983. Burger (1984) attributed the failure of 45% of least tern (Sterna hirunda L.) colonies to human disturbance, due principally to off-road vehicles and people walking through the colonies. Management of black-fronted terns should include attempts to reduce human-induced disturbance.

The low rates of hatching success and nesting success for pied stilts were almost totally caused by flooding of the low level nest sites. On the Ashley, one pair which nested on a small island less than 200mm above water was washed out by a small fresh. They re-nested on the same site but were again washed out by a similar sized flow. Pierce (1982a) also reported low success rates for pied stilts on the Cass river. For all habitats, he recorded a 60.8% nesting success rate, but this dropped to only 29.2% on the active riverbed. In contrast, South Island pied oystercatchers tended to select nest sites at high cross-sectional levels (pers. obs.) on both rivers. As a consequence, nesting success and hatching success were comparatively high. When compared with results obtained by Harris (1967) on a permanent land mass, hatching success on the Ashley and Rakaia rivers was very similar, but fledging success was lower. For wrybills, banded dotterels and South Island pied oystercatchers, rates of hatching success and fledging success were quite similar to those reported for many European waders (e.g., Soikkeli, 1967; Nethersole-Thompson and Nethersole-Thompson, 1979; Jackson and Jackson, 1980), which unlike this study, do not have flooding as the principal cause of nest loss. Instead, breeding success among European waders is often limited by the effects of mammalian predators.

Despite predation by mustelids, breeding success of birds on active riverbeds is still quite high. Bomford (1978) found predation was the principal cause of low banded dotterel nesting and hatching success rates on stable berm land adjacent to the Cass river delta. Predation caused 35.6% of banded dotterel nest failures in this study, but was responsible for 48.3% of losses on the Ashley alone. It would appear that the braiding pattern provides some protection against predation by mustelids. The Rakaia which is much more braided than the Ashley and subject to large and comparatively frequent floods, seems less suitable as a habitat for predators than the Ashley. This is supported by Hay (1984) who reported that wrybill breeding failure due to predators was

low and insignificant on the upper Rakaia.

3.5.2. Inter-specific aspects of nest site selection

Data on the characteristics of nest site selection can be broadly interpreted in three ways to:

- (1) determine the extent of inter-specific overlap in nest site character;
- (2) examine the extent to which the availability of nest sites is a function of hydrological processes; and
- (3) help determine the differences between generalist and specialist riverbed breeders and the implications of these groupings for wildlife management.

In general, intra-specific overlap values which are calculated on an inter-seasonal or inter-basin basis will be higher for specialist species which have a narrow range of microhabitat preferences and tolerances, than for generalists. Of course there are situations where generalists may be at the edge of their tolerance range when such a classification is applied, and this could be established by an examination of comparative rates of breeding success over a range of habitats, as attempted for banded dotterels in this study.

Overlap in nest site substrates was very high for wrybills nesting on the Ashley and Rakaia rivers, and while still high for banded dotterels, was nevertheless substantially lower than for wrybills. The significance of these intra-specific overlap differences becomes apparent when the proportions of nest sites dominated by different substrate classes are subjected to a heterogeneity test. No significant differences occurred between wrybills nesting in the two study areas, but banded dotterels on the Rakaia used sandy and cobble substrates significantly more than those on the Ashley. There are three possible explanations related to specialist-generalist behaviour:

- (a) Wrybills select for a restricted range of substrate sizes, wherever they nest, thereby displaying specialist behaviour;
- (b) Banded dotterels choose nest sites in proportion to substrate occurrence on each river which would indicate a habitat generalist pattern of selection;

(c) Competitive exclusion is operating on the Rakaia and banded dotterels are being forced to nest on substrates outside their preference range.

On the basis of other observations, the first two explanations appear the most likely. High banded dotterel densities on the Tukituki river in Hawkes Bay, where substrate is generally much smaller (Phillips, 1980) than on the Ashley or Rakaia (pers. obs.), support this argument. Competitive exclusion is a possible explanation regarding the use of different microhabitats for foraging (see Section 6.5.2), but the nature and large extent of terrestrial substrate makes it unlikely that it would occur under these circumstances. Indeed, no evidence was found that any of the study species competed with regard to any aspect of nest site selection. However, other physical parameters examined did provide additional information about the specialist-generalist species status.

Hay (1984) identified proximity-to-water as being a characteristic of wrybill nest site selection. However, in relation to most other nesting species of riverbed birds examined here, there were few inter-specific differences. This is probably due to all species relying on aquatic feeding which is then reflected in the choice of nests relatively close to water. The large variability with black-fronted terns relates to the dispersed nature of colonies, and to this tern species being an aerial feeder with only loose and periodic territorial bonds. Pied stilts nested close to water on both rivers, and this was also observed on other rivers periodically visited during the study. Data supplied by Pierce (pers. comm.) showed mean distances to be much further from water for pied and black stilts nesting on the active Cass riverbed. However, variability was large with some nests less than two metres from water. This could be due to the low site-specificity of feeding in stilts, and helps confirm the generalist behaviour of both species with respect to nest selection.

There was a substantial inter-seasonal difference on the Rakaia in the relationship between nest site selection and the nature of the closest aquatic microhabitats. Whereas in 1982 most wrybill nests were located near minor braids, in 1983 most were found near seepage zones. A similar, if less marked, difference was also recorded for banded dotterels, but not for black-fronted terns. For wrybills, and to a

lesser extent banded dotterels, this shift was probably related to food supply. Stable winter and early spring flows in 1982 allowed invertebrate densities to reach high levels in all aquatic microhabitats. In contrast, in 1983, the flood-dominated flow regime led to comparatively low densities of aquatic invertebrates (see Figure 6-11). As a result, wrybills and banded dotterels selected nests close to seepage zones where the effects of small to medium freshes on invertebrate density were minimised. The shift was probably smallest for banded dotterels, because they rely less on aquatic microhabitats for feeding than do wrybills, while the lack of change by black-fronted terns reflects their position as a dispersed colonial breeder feeding far from the nesting areas.

Species nesting at higher cross-sectional levels on braided rivers appear more specialised than those nesting at low, or over a wide range of levels. However, it must also be noted that the adaptive significance of this behaviour is most apparent on rivers with similar flow regimes to the Rakaia, rather than on those like the Ashley which are not subject to the same degree of breeding season flooding. The value of specialisation is therefore maximised on the Rakaia and minimised on the Ashley. Based on the wrybill, banded dotterel and black-fronted tern surveys on the Rakaia, the following order of specialist to generalist site selection can be established:

Wrybill > Banded > Black-fronted
dotterel tern.

The variability about these nest height averages also increased with movement from specialist to generalist behaviour, indicating a further non-specialist approach to site selection. As presented, the results conflict with some widely held views concerning the adaptive behaviour of the riverbed birds for nesting. O'Donnell and Moore (1983) considered each of the species to be adapted to riverbed life in a number of ways, particularly breeding. Of the study species only wrybills lay eggs which match the substrate colour on the Rakaia, although on the Ashley there is a heterogeneous mix of substrate colours, ranging from grey to brown, which help conceal both wrybill and banded dotterel eggs, and to a lesser extent also those of black-fronted terns, South Island pied oystercatchers, and pied stilts. To some extent, therefore, the adaptive advantage of various aspects of the

nesting behaviour of riverbed birds is dependent on the hydrology and geology of the river and catchment area in which the birds are being studied.

The limited data collected on the effect of different sized floods on nest viability support these relationships, and also indicate that in most years flooding will have a greater impact on the generalists than the specialists. Results were not quite so conclusive in 1983 because of the extraordinary frequency and size of floods in that season. The findings also contrast with those of Hay (1984), who reported that a fresh with a mean daily discharge of only 203 cumecs, which occurred in early October 1976, led to the loss of wrybill nests on the upper Rakaia river. Hay (1984) attributed this to a low late-winter base flow which apparently led to nests being built on relatively low-lying islands. A study of the daily flow records for 1976 and 1977 showed that flows averaged approximately 20 cumecs less in the 1977 season when a fresh of 356 cumecs in late October apparently caused no nest destruction. It is therefore difficult to understand how Hay (1984) could have drawn such a conclusion. Furthermore, there is no way of determining from Hay's work how many, or what proportion, of nests were affected by this comparatively small fresh.

The timing of laying for each species has a considerable impact on nesting success and depends also on river hydrology and the relative height of nest sites. On rivers like the Rakaia which often flood during the breeding season (particularly from October onwards) strategies which include high level and/or early season nesting would minimise the potential impact of flooding. Wrybills and banded dotterels tend to lay first clutches in late August or September, but the latter two species nest much higher on island cross-sections, thereby minimising the likely impact of any early season floods. Wrybill nesting appears to be related to the food supply (see Section 5.3). Nesting in 1982 was earlier in the season than in 1983, with stable winter flows in 1982 contrasting with periodic flooding and a subsequent drop in the supply of aquatically derived food items in 1983. Banded dotterel nesting did not show any inter-seasonal variation, probably because the greater proportion of the diet is of terrestrial origin (see Figure 5-7). Pied stilts were late nesters on both study areas, as they were on the Cass river valley (Pierce, 1982a). In association with low level nest sites, this puts nesting at great risk

on the Rakaia, but on the Ashley and other rivers such as the Ashburton, which have declining flows at this time, the effects of floods would be reduced. Declining flows in these rivers would also be associated with greater aquatic invertebrate densities on which pied stilts are highly dependent for feeding (see Section 6.5.4).

Black-fronted tern nesting also relies on the nature of the flow regime. Breeding in 1982 on the Rakaia occurred much earlier than in 1983, probably as a result of the almost continuously low level of aquatic invertebrate food supply. However, even in 1982, breeding was only started in late October with the result that flooding led to many nest losses. Delayed breeding in 1983, although resulting in high levels of nesting success, was probably too late for young birds to survive because of reduced food availability. Later nesting on rivers like the Ashley tends to avoid severe flooding and at the same time corresponds with high levels of food supply. It appeared that only on these rivers do low level nest sites, in association with delayed nest initiation, lead to sufficiently high nesting success to sustain high population levels.

3.5.3. Vegetation tolerances and the flow regime

All of the species examined in this study show a certain tolerance to varying densities of vegetation and a low amount of plant cover around nest sites. On the Rakaia, this equates with low profile and immature lupin, the dominant plant species on this river. Only in 1982 was it possible to assess the changes in vegetation status with time, at individual nest sites. However, the small sample sizes, often restricted by the impact of flooding, made it very difficult to develop firm conclusions. Even this problem has indirectly assisted in identifying the relationship between flooding and the provision of nest sites. It was also noticeable that in 1983 there were significantly more nests than in 1982 located on sites with no vegetative cover within one metre of the nest. That this occurred for wrybills, banded dotterels and black-fronted terns indicates the opportunist approach to site selection when choices are made from the range 0-5% ground cover, where most nests are located. Furthermore, it also shows the impact which varying seasonal flows can have on nest site provision:

- (1) In the period 5 June to 11 November, 1982, there were no major floods in the Rakaia. This long interval allowed medium to dense areas

of low profile, immature lupin to establish over much of the riverbed. In general, ground cover in these areas was less than 5% (visual estimate) and the plants were seldom more than 200mm high;

(2) During the 1983 breeding season there were several large floods which cleared most of the low profile, immature vegetation from the riverbed. Much of the dense and mature lupin was not greatly changed despite having been flooded. As a result, most nests were located on bare shingle.

Lupins grow rapidly, as shown by the increasing percentage ground cover around the nests which could be measured over a two or three month period in 1982. Declining sample sizes caused by flooding meant the changes were insignificant. However, there was a trend for sites to change quickly from usable (<5% cover) to marginal (5-10%) to unusable (>10%). Although highly unlikely, given the existing nature of the flow regime, a breeding season to breeding season interval without a medium to large flood could lead to much of the prime nesting habitat of wrybills on the lower Rakaia being marginal or totally unsuitable. In this case, wrybills would most likely forsake high levels on the cross-section for lower sites clear of vegetation. There is some evidence to support this from the examination of alternative nest site availability for wrybills, banded dotterels and black-fronted terns nesting on the Rakaia (see Figure 3-15). Wrybills seldom selected nest sites at lower levels than other levels where there were lower plant densities or percentage ground cover. In contrast, banded dotterels and black-fronted terns often chose sites at levels where others with lower densities of ground cover were present at higher cross-sectional levels. Consequently, reduced flooding, whether caused by natural or artificial reasons, will probably result in wrybills and the other study species choosing lower level nest sites.

The relationship between lower level nest site selection and nesting success will vary according to the length of each species' incubation period, and the degree of any changes caused in the peak flow regime. Wrybills and banded dotterels, which have the longest incubation periods, would be most affected. Reducing flood peaks, but not periodicity, by damming a major tributary catchment, would have an impact different from that of reducing peaks and frequency. Dams have the greatest potential to modify flood flows in large rivers. By

storing peak flows they depress the variability or extremes of the flow regime, and often change the return period of different-sized floods. For instance, frequent releases of water which approximate medium sized floods may have a greater impact on nesting success and food supply than that of occasional large floods. Such releases have not been designed to meet the probability of nest loss to which wrybills and other species appear adapted.

Reduced peak discharges will increase channel stability and, with less erosion and deposition, diminish the scouring process which removes dense and mature vegetation. With time, this will lead to a much greater area being covered by vegetation, at the expense of breeding habitat for riverbed birds, and although flood peaks may be lower, bird habitat and viability will be threatened in two main ways by:

- (a) a reduction in the amount of bare shingle used for feeding over by wrybills, South Island pied oystercatchers, and banded dotterels; and
- (b) a likely increase in predator numbers associated with increased river stability and a greater expanse of vegetative cover.

Greater stability also encourages land reclamation and, as with the Waitaki river, leads to a contraction of active riverbed width at the expense of the increased need for compensatory habitat (pers. obs.).

Stead (1932) described how the introduction of lupins led quickly to a reduction in wrybill numbers on the lower Rakaia river. At present the maintenance of a long term equilibrium between lupin encroachment and the provision of suitable breeding habitat for wrybills is dependent on the peak flow regime remaining substantially unaltered. However, even this appears to be sustaining a population at a much lower level than the river could have naturally sustained (see Section 4.3.1).

Perhaps of greater note is the variation in the nature and extent of vegetation cover between the Ashley and Rakaia rivers. On the Ashley, medium to dense stands of relatively low profile (generally <1m high) gorse and broom dominate over lupins. Both appear to have slower growth rates than lupin, but why they should be so dominant on this river is not known. Of more concern is the extent of willow growth on the Ashley, which appears to be increasing rapidly and resulting in greater channel stability (Mosley, 1983a). Willows are phreatophytes, i.e., they have long root systems which tap the river underflow, and

which prove difficult to move, even during very large floods. Therefore, the establishment of additional trees is usually not counterbalanced by the loss of others. Without some form of control, the next few decades could witness the almost total destruction of the Ashley as a riverbed bird habitat. A similar occurrence in Central Otago reduced breeding habitat for pied stilts, leading to a reduction in their numbers (Child, 1983).

3.5.4. Management considerations

The highly variable rates of nesting and hatching success found are caused by generalist-specialist patterns of behaviour. These patterns are influenced strongly by the flow regimes typical of Rakaia and Ashley type rivers. From a management viewpoint it is important to recognise that the riverbed environment contains three broad groups of species which can be categorised according to habitat use:

- (1) Specialists, those birds adapted to the hydrological character of braided rivers. Only the wrybill should be regarded as a true specialist, although some other species display aspects of specialist behaviour concerning different aspects of habitat use. The degree of wrybill specialisation means that the species is restricted to braided rivers;
- (2) Generalists, which can breed successfully on a range of habitats. Pied stilts, South Island pied oystercatchers and banded dotterels fit this classification;
- (3) Restricted generalists which formerly bred on a range of habitats but which for a variety of reasons are now restricted to riverbeds. In general, their behavioural patterns are more generalist than specialist, i.e., black-fronted terns.

The loose colony formation of black-fronted terns compared with the tighter black-billed gull colonies is of doubtful adaptive advantage. The gulls nest very close together on the high points of islands, which minimises potential flood loss. Black-fronted terns have colonies often encompassing several islands and covering a range of potential nest heights. O'Donnell and Moore (1983) claimed this was a behavioural adaptation intended to minimise nest losses. In all but a few circumstances, flooding which leads to the erosion of islands sufficient

to affect some nests, will destroy all nests. Selection for a densely nesting species on a high cross-sectional level appears much more advantageous if the birds are colonial breeders. There is further evidence of the generalist form of black-fronted tern nest selection. Potts (1882) recorded terns breeding on the Canterbury Plains before agricultural development. Thus, although the species is now restricted to riverbeds, this does not necessarily imply riverbed preference or specialist breeding behaviour.

In some ways, restricted generalists like black-fronted terns are the most difficult species for which to plan a conservation strategy. It must not be assumed that any natural flow regime will provide an ideal set of microhabitat requirements, because it is unknown whether its present habitat was formerly its preferred habitat or, instead, a habitat at the edge of its generalist range. To maximise the likelihood of continued existence, an understanding of basic habitat needs and use patterns, plus a knowledge of positive, neutral, and negative impacts which different flow regime parameters have on the species should be determined. For black-fronted terns, several nesting characteristics place it at considerable risk on braided rivers, particularly of the Rakaia type, because:

- (a) they nest in loose colonies with great variability in cross-sectional nesting heights. Even comparatively small floods can destroy many of the low-lying nests;
- (b) by nesting in loose, rather than tight colonies on high points of islands the area over which erosion due to medium floods can extend is increased, thus raising the likelihood of nest loss; and
- (c) the late initiation of nesting (October to November) corresponds with the peak probability of nest loss due to flooding.

For each of these considerations the probability of nest loss is greatly reduced on Ashley type rivers. However, the susceptibility of black-fronted terns to man-induced nest desertion is also most likely on the latter river type. These foothill catchment rivers are much smaller than Rakaia type rivers and, with declining discharges throughout the spring-summer period, are heavily used by recreationists including anglers, swimmers, trailbikers, and occupants of four wheel drive vehicles. All of these activities, unless carefully controlled, can

lower black-fronted tern breeding success on these rivers. In spite of these difficulties, the flow regime of these systems is more suited to tern breeding than that of the Rakaia type rivers in the low country. Consequently, conservation measures for black-fronted terns should be concentrated on these rivers.

Pied stilts are habitat generalists during the breeding season. Conservation measures which concentrate on sustaining species diversity in individual habitats mean it is important to have regard for the habitat requirements of this species. In general, pied stilts suffer from the same behavioural limitations which restrict black-fronted terns breeding on large, unstable braided rivers like the Rakaia. They are therefore better suited for nesting on rivers such as the Ashley and Ashburton.

Although they were successful breeders on both river systems, South Island pied oystercatchers should also be regarded as habitat generalists because they breed in a wide range of habitats, including farmland. Selection of cross-sectional high points is probably more of an anti-predator response than a behavioural adaptation designed to minimise flood-induced losses. South Island pied oystercatchers normally leave their nests and quickly move off when intruders are several hundred metres away, in contrast to wrybills which remain on the nest. Consequently, South Island pied oystercatchers require high points to enable easy intruder awareness, and as a result have similar nest site needs to wrybills and banded dotterels, and are therefore likely to be safeguarded by similar conservation measures.

Flood prone rivers like the Rakaia are presently the dominant breeding area for wrybills. Wrybills appear well adapted to life in this type of river over a wide range of environmental conditions. However, this study and Hughey (1985) show that extreme high flow conditions on these rivers could quickly put the population at risk. Indeed, there is now limited evidence, including this work and North Island winter censuses, which indicate there may presently be a decline in wrybill numbers. Should these conditions persist then the small, but productive, populations on the Ashley and Ashburton rivers may become critical to the conservation of this species. Therefore, while it is important to safeguard the Rakaia, it is equally important to conserve the essential habitat of the Ashley and Ashburton rivers as a safeguard

against possible future population declines on the main rivers.

For physical aspects of nest site selection, particularly those parameters associated with vegetation tolerance, it is important that the peak flow regime of rivers remains substantially unmodified. In some circumstances even this may not be sufficient. In these cases, which include parts of the Ashley river, willow encroachment should be curtailed.

Although there was no evidence to confirm Hay's (1984) assertion that low river levels during one winter had led to the selection of low-lying nest sites by wrybill, it appears that this may occur under appropriate conditions. However, it would appear that these circumstances would occur only if river flows were greatly below natural low flow levels, and this event was then associated with the drying up, or large reduction in width, of many channels. On the Rakaia, such management impacts seem unlikely, especially as the draft National Water Conservation Order for the river (NWASCA, 1984) recommends a minimum breeding season discharge of 90 cumecs, compared to a natural low of approximately 79 cumecs.

3.6. Summary and conclusions

This study examined breeding success in two closely related plovers nesting on rivers which have significantly different seasonal flow patterns. On the Ashley river, wrybills, banded dotterels, South Island pied oystercatchers and pied stilts had higher success rates than for the same species nesting on the Rakaia. Flows in the Ashley were generally in decline for much of the breeding season, while on the Rakaia, floods occurred in all months. Flooding was not unexpectedly the main cause of breeding failure on both rivers, although on the Ashley, predation was also very important. The relationships between flooding, cross-sectional nest-height selection, and nesting success were used to define specialist, generalist, and restricted generalist species. In general, wrybills, which are the most specialised riverbed nesters, are also least affected by flooding, and are therefore best adapted to life on rivers like the Rakaia. The other species, including banded dotterels but excluding South Island pied oystercatchers, appeared best suited to breeding on rivers like the Ashley, with their declining breeding season flows.

Each species showed some degree of tolerance to vegetation encroachment around nest sites, but when this exceeded approximately 5% ground cover, wrybills chose alternative nest sites. Although not quantified, evidence relating to generalist habitat use patterns of the other species indicates they are more tolerant of greater plant cover, i.e., South Island pied oystercatchers, banded dotterels and pied stilts all breed on pasture as well. However, in all of these circumstances, low profile ground cover is tolerated much more than upright growth, i.e., mat plants are preferable to lupin. Maintenance of the natural flood regime is imperative to maintain an equilibrium between nest site needs and the extent of vegetation encroachment. In some circumstances, such as where willow encroachment has reached an advanced stage, even continuation of the natural flood regime may be an inadequate control measure.

The study provides a basis for establishing conservation priorities based on species preference for river form. To some extent, the indicator species approach adopted in this study, and which showed wrybills to be the most specialised riverbed species, is weakened because the flows necessary to conserve wrybill habitat often occur at the expense of successful nesting of the other species. Therefore, in order to conserve the range of species, it is important to conserve a representative range of river systems. For wrybills, the Rakaia, and for the other species, the Ashburton and Ashley, appear the most appropriate of the rivers flowing over the Plains.

4. BIRD DENSITY IN RELATION TO BRAIDED RIVER HYDROLOGY

4.1. Introduction

Estimating home range size and shape is common in studies of animal spacing patterns, e.g., Jorgensen and Tanner (1963), Van Winkle *et al.* (1973), Davies (1976), Ford (1979), Anderson (1982), Davis (1982). Odum (1971) defined the home range as that area to which individuals, pairs, or family groups of vertebrates and the higher invertebrates commonly restrict their activities. If part or all of this area is actively defended then it is referred to as a territory. The adaptive significance of home range and territoriality has been widely discussed, e.g., Brown (1969), Harris (1970), Davies (1976, 1981), Verner (1977), Krebs (1981). These studies have assessed the role of territoriality in terms of nest site selection and spacing, feeding, population dynamics, resource partitioning, competition and defence. In all studies of space use patterns a recognisable individual must be located at successive points in time and its position recorded (Ford, 1979). The results of this work have been used in evaluating optimal foraging theory (e.g., Davies, 1981) and territory size as a function of habitat quality (e.g., Davis, 1982).

Hay (1984) found that wrybills are highly territorial while on riverbeds. However, he did not study the significance of territory or home range size and spacing in relation to river hydrology. Black-fronted terns maintain loose colonial nesting territories but feeding territories are formed only at times of low flow and even then are poorly defined (Lalas, 1977). Banded dotterels are similar to wrybills in that they are highly territorial while breeding (pers. obs.). On the other hand, pied stilts behave in a similar fashion to black-fronted terns (Pierce, 1982a). In this chapter, home range size, breeding bird densities and site tenacity are studied to find their relationships to the hydrology of braided rivers. Odum's (1971) definition of home range is modified here to mean the area to which all observations of adult birds are confined during breeding.

4.2. Developing a model to measure home range size on riverbeds

One of the problems associated with accurately measuring home range size is choosing from the wide range of available methods (Jennrich and Turner, 1969). Despite this, the determination of the home range of an individual is valuable when analysing the effects of competition and density, and in the assessment of resources (Brown and Orians, 1970). The simplest and perhaps most widely used method of estimating home range is the A1 index (Jennrich and Turner, 1969). The smallest convex polygon containing all of the capture points (p_1, p_2, \dots, p_n) for an animal is drawn, and:

$$A1 = \text{area of convex polygon}$$

provides an index of the animal's home range (Southwood, 1978). A number of factors limit the value of this method:

1. In this and other methods there is an assumption of statistical independence between successive observations of the animal. Small sample sizes of highly correlated observations may therefore produce sizeable errors (Anderson, 1982).
2. Estimations of home range size normally increase with the number of observed positions (Jennrich and Turner, 1969).
3. There is the assumption that home range shape is a convex polygon. Anderson (1982) concluded that this is probably unreasonable, especially when the habitat is heterogeneous. This weakness may be particularly apparent for a braided river where habitat is seldom, if ever, homogeneous.
4. The convex polygon method fails to identify the intensity with which various parts of a range are used. This unequal use can be defined in terms of a density probability function (Jorgensen and Tanner, 1963). A number of probabilistic models have been developed, e.g., Van Winkle *et al.* (1973), Ford (1979) and Anderson (1982), but none of these methods of estimating home range is free from problems (Anderson, 1982).

Braided river heterogeneity and unpredictability are the main limitations to using the A1 index and other methods of measuring home range size. Considering Anderson's (1982) conclusion that estimating

home range size should be avoided if the question of interest can be answered by statistically analysing all of the independent observations, then perhaps an alternative approach may be considered. Hilden (1965) suggested that habitat selection relies on the animal's assessment of certain environmental factors directly associated with food. Davis (1982) studied belted kingfishers (Megaceryle alcyon L.) along stream habitats. He showed that territory size is consistently related to the proximity of productive food patches near the nest. Davis (1982) concluded that defence of a small territory may lead to savings in time and energy. Other studies by Newton et al. (1977) for sparrowhawks (Accipiter nisus L.) and by Seastedt and Maclean (1979) for Lapland longspurs (Calcarius lapponicus Walker) indicated that species responded to other habitat parameters, rather than directly to food. Nesting and roosting sites may also be important.

The A1 index modified to allow for habitat heterogeneity, was used as a simple measure of home range size. By determining the proportion of preferred habitat as a function of size it may be possible to demonstrate a relationship between habitat quality and home range size. It is further hypothesised that home range size is some function of river hydrology. This suggestion, which is supported by the observation that certain species inhabit larger areas if their preferred habitats are sparsely distributed, and that others expand their territories in habitats seemingly less rich in preferred food (Schoener, 1968), could be critical in the assessment of potential water development impact.

4.3. Methods

Home range size determinations were based on the A1 index. Time limitations meant it was not possible to examine territory size. All location points were recorded during time-budget and habitat use studies, and were only undertaken for pairs where either one or both adults were colour banded. Observations were made at high, medium and low flows. Unfortunately, during large floods, it was impossible to obtain any records because it was too dangerous to cross channels. However, this was normally only for one to three days at a time, and it is behaviour at low flow that was considered to be critical to this study. Twenty records per pair were considered a minimum acceptable sample size for further analysis. For smaller numbers of observations an approximate home range size was mapped. Home range size was

determined for wrybills on the Rakaia in 1982 and 1983, and on the Ashley in 1983. For banded dotterels, it was measured on both rivers in 1983. Observation points were mapped on aerial photo overlays of each river, and then cut out for measurement. All area measurements were made using the leaf area index machine, courtesy of the Ministry of Agriculture and Fisheries, Lincoln College. Size variations were then compared with differences in habitat quality measured by the occurrence of preferred aquatic microhabitats. The Mann-Whitney U test was used to compare the samples statistically because the data did not conform to the assumptions necessary to use Student's t-test.

Wrybills (Hay, 1984) and banded dotterels (Pierce, pers. comm.) are considered to display high degrees of site tenacity on an intra- and inter-seasonal basis, at least on the relatively unmodified habitats of the upper Rakaia and Cass rivers respectively. In this study intra- and inter-seasonal shifts in wrybill home ranges were monitored on the Rakaia, with intra-seasonal shifts for banded dotterels being examined on both rivers in 1983. Home range shifts were mapped to determine the nature and extent of movement.

4.4. Results

4.4.1. Density considerations

The location and number of wrybill, banded dotterel, South Island pied oystercatcher, and pied stilt breeding pairs were recorded on each river, and both the numbers per unit area of riverbed, and numbers per unit area with patches of dense and mature vegetation excluded, were compared (Table 4-1). Density was greater on the Ashley for all species. All breeding pairs of all species nested near water. Therefore large areas existed on both riverbeds where none of these species bred. Nest locations are mapped in Figures 4-1,2,3 for the Rakaia in 1982 and 1983, and the Ashley in 1983 respectively. The locations of colonial nesting black-fronted terns, black-backed and black-billed gulls are also given. Riverbed width also affected densities, so that up to three wrybill pairs were located on a single cross-section of the Rakaia, whereas only one was located on any given cross-section of the Ashley.

TABLE 4-1 : Densities of solitary breeding bird species on the Ashley and Rakaia river study areas in 1983.

Species	ASHLEY RIVER		RAKAIA RIVER	
	Breeding pairs per ha of total riverbed area	Breeding pairs per ha of vegetation free riverbed	Breeding pairs per ha of total riverbed area	Breeding pairs per ha of vegetation free riverbed
Wrybill	0.04	0.05	0.02	0.03
Banded dotterel	0.30	0.42	0.02	0.03
Pied stilt	0.05	0.07	-	-
South Island pied oystercatcher	0.04	0.05	-	-
Total density	0.43	0.59	0.04	0.06

FIGURE 4-1 : Nest site locations and home ranges of riverbed bird species on the Rakaia River in 1982.

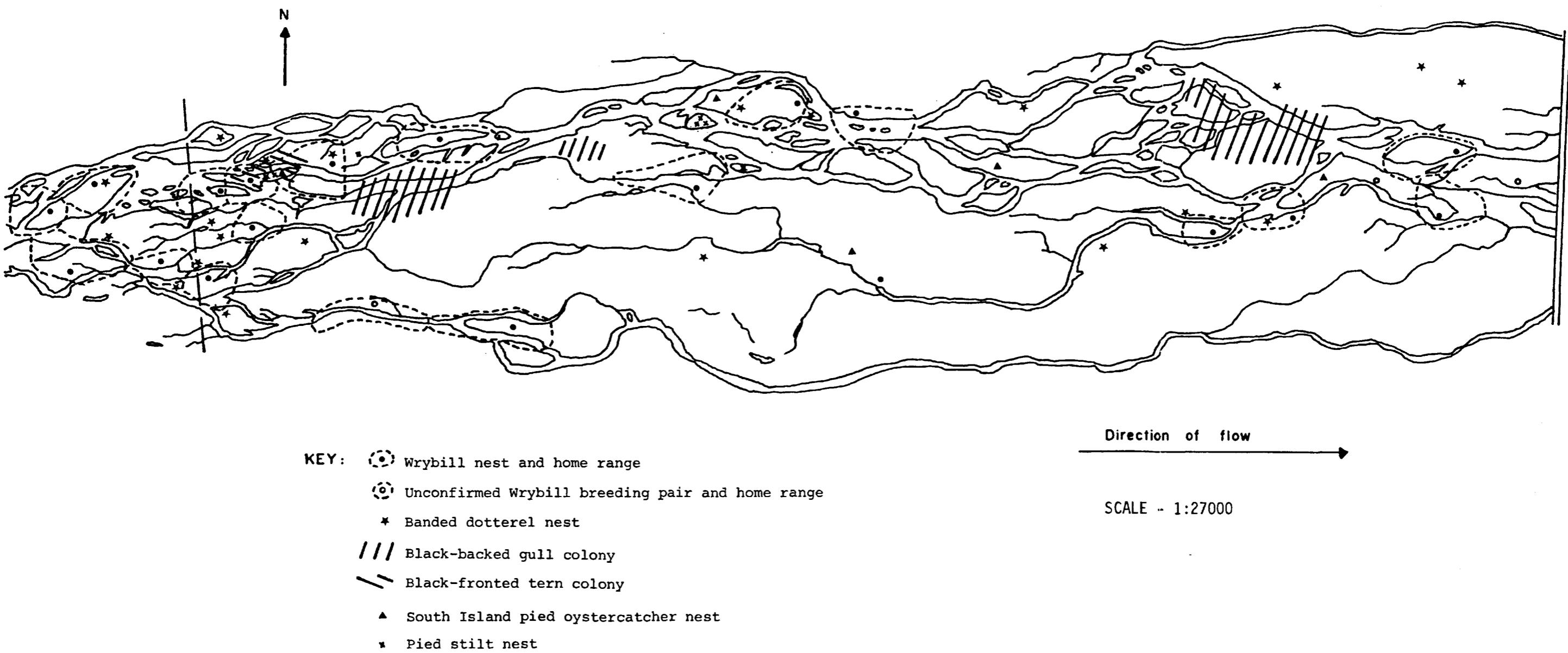


FIGURE 4-2 : Nest site locations and home ranges of riverbed bird species on the Rakaia River in 1983.

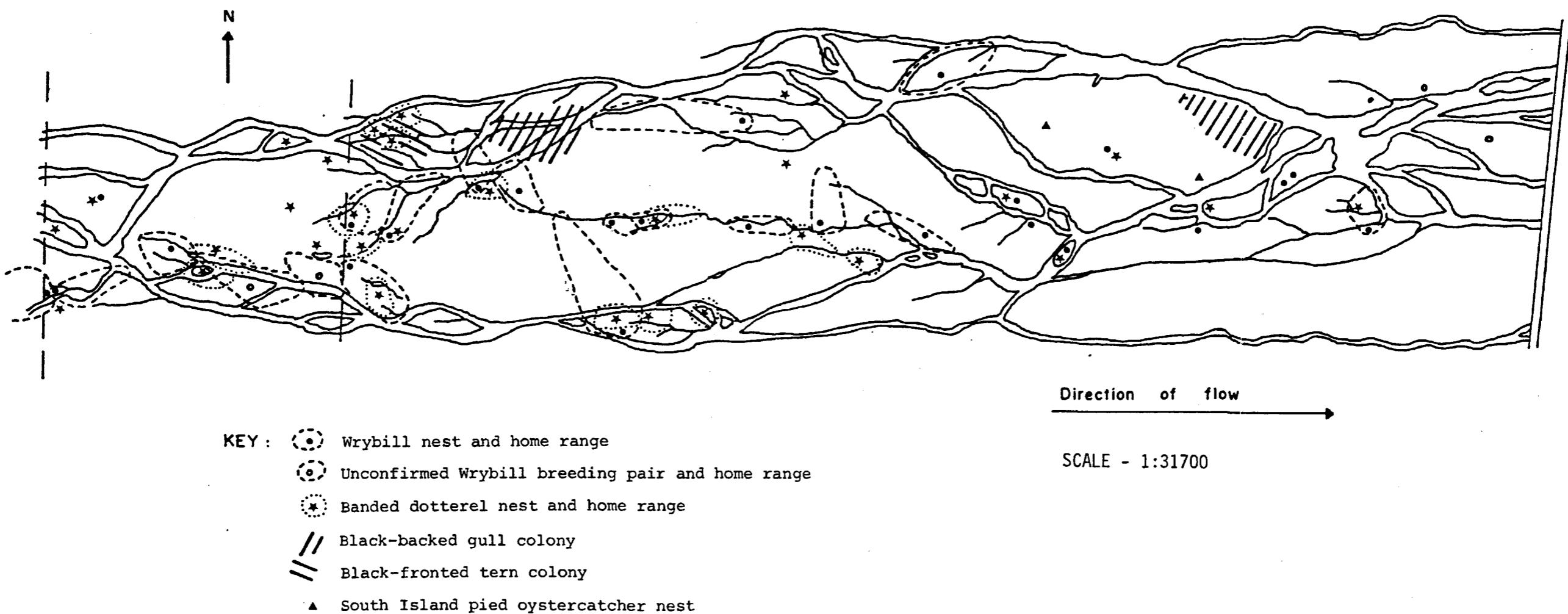
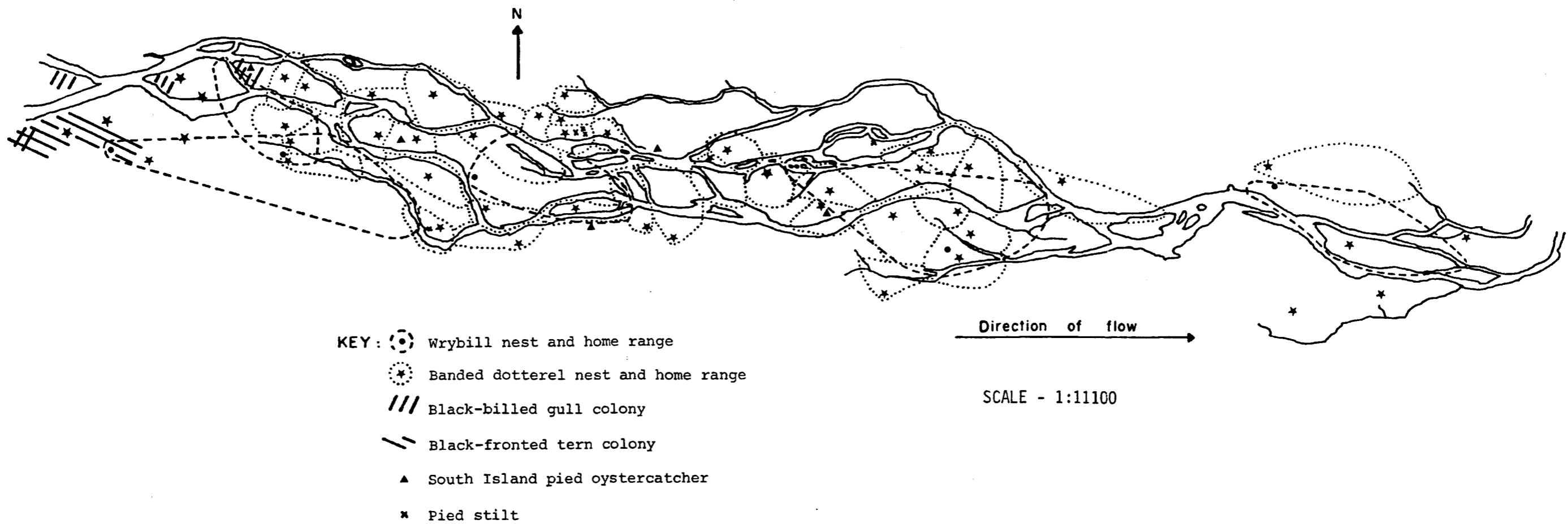


FIGURE 4-3 : Nest site locations and home ranges of riverbed bird species on the Ashley River in 1983.



4.4.2. Home range sizes

Wrybill and banded dotterel home ranges are shown on Figures 4-1,2 and 4-3. Wrybill home ranges averaged 6.1ha (N=5; Range=3.1-9.4ha; SD=2.4ha) on the Ashley in 1983, 5.2ha (N=19; Range=3.1-8.2ha; SD=1.5ha) on the Rakaia in 1982, and 4.5ha (N=18; Range=1.0-11.3ha; SD=2.5ha) in 1983 on the Rakaia. On the Ashley, banded dotterel home ranges were an average of 1.0ha (N=28; Range=0.3-3.4ha; SD=0.6ha) while on the Rakaia they averaged 1.5ha (N=15; Range=0.7-2.5ha; SD=0.5ha). Wrybill home ranges were significantly larger than those of banded dotterels on both the Ashley and the Rakaia rivers in 1983 (Mann-Whitney U-test; $P<0.001$ for both rivers). There were no significant differences between the sizes of wrybill home ranges on the Ashley or Rakaia ($P>0.05$) in 1983. In contrast, banded dotterel home ranges were significantly larger on the Rakaia than on the Ashley ($P<0.01$).

On the Rakaia, a simple assessment of the relationship between wrybill home range size and microhabitat character was undertaken. Home ranges dominated by minor channels and, more specifically, seepage zones, were compared with others dominated by major channels (Table 4-2). In 1982 and 1983, home ranges were significantly smaller when associated with minor channels and seepage zones ($P<0.01$). There were no significant differences between seasons. On the Rakaia the extent of home range packing was greatest in the area approximately 8km west of the State Highway One bridge, which was also the part of the study area where the degree of braiding was highest. The main reason for the non-contiguity of home ranges was the disruptive presence of dense and mature areas of exotic vegetation.

TABLE 4-2: Variability in wrybill home range sizes on the Rakaia river according to microhabitat character.

	Home range dominated by major channels.		Home range dominated by minor channels.	
	1982	1983	1982	1983
Number	13	8	6	10
Mean area (ha)	6.0	6.4	3.6	2.9
Range (ha)	3.9-8.2	3.9-11.3	2.4-5.1	1.0-4.1
SD (ha)	1.2	2.6	0.7	1.0

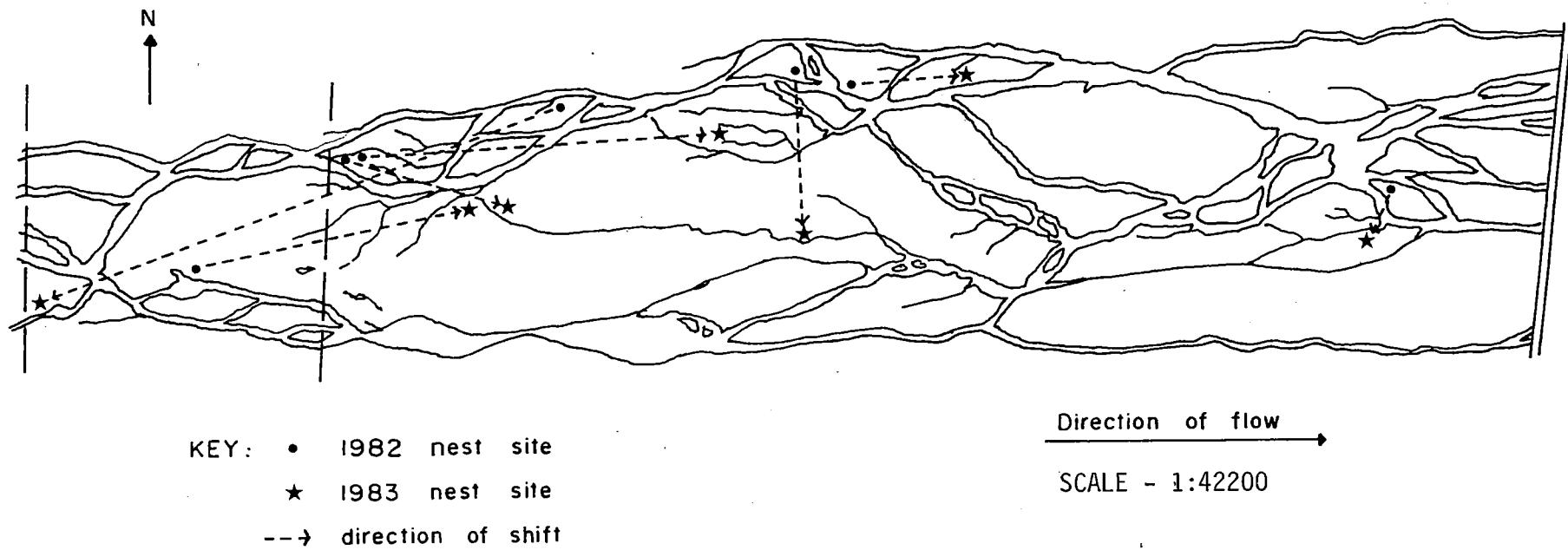
4.4.3. Home range site fidelity

Intra-seasonal shifts in home range location were recorded for banded dotterels and wrybills on the Rakaia. The absence of a colour banding permit for banded dotterels restricted the inter-seasonal evaluation to wrybills. No intra-seasonal home range shifts were observed for wrybills on the Ashley or Rakaia rivers, or for banded dotterels on the Ashley. Furthermore, only one banded dotterel pair on the Rakaia was observed to shift home range in 1983, moving approximately 2km upstream. Between 1982 and 1983 there was a major change in the location of several wrybill home ranges on the Rakaia (Figure 4-4). Several pairs had moved up to 1km, while another two had each shifted approximately 2km. However, most pairs returned to, or close to, their 1982 site. Following breeding, home range boundaries quickly broke down for both wrybills and banded dotterels.

4.4.4. Space use in relation to inter-specific considerations

While wrybill home ranges overlapped with those of banded dotterels, there were striking differences in the patterns of microhabitat use. In general, these differences were determined by the behavioural dominance of wrybills which led to the exclusion of banded dotterels from preferred wrybill foraging zones. Two wrybill home ranges that were studied intensively on the Ashley in 1983 helped

FIGURE 4-4 : Home range movements of wrybill pairs on the Rakaia study area from 1982 to 1983.



identify these patterns. In home range one (Figure 4-5a) the nest was located a long way from the centre of foraging activity. Indeed, the home range overlapped those of both another wrybill and several banded dotterels. The points (nodes) of greatest foraging intensity were generally outside or at the edge of banded dotterel home ranges, and were not within the overlapping wrybill home range. A similar pattern emerged in home range two (Figure 4-5b), although foraging was generally less than 100m from the nest, and the home range overlapped with those of more banded dotterels. As expected, wrybills mainly frequented aquatic microhabitats.

No wrybill or banded dotterel nests were found within close range of black-backed gull colonies on the Rakaia (see Figures 4-1 and 4-2). Both species were found close to black-billed gull colonies, and nests were found within the confines of black-fronted tern colonies on both rivers, without any noticeable impact on breeding success. Numbers of pied stilts and South Island pied oystercatchers were too low to draw any valid conclusions.

4.5. Discussion

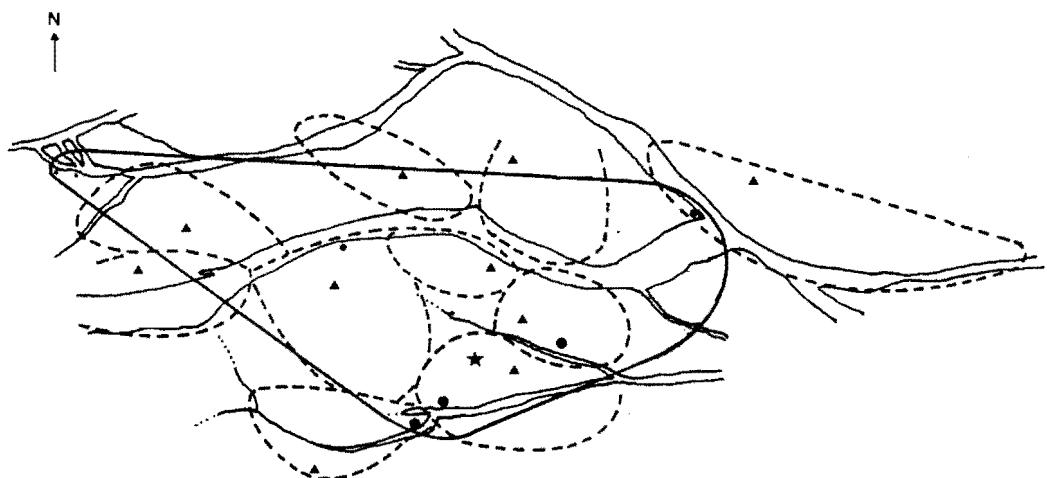
Previous work has generally ignored inter-specific aspects of riverbed bird breeding densities. It is therefore interesting to observe the much higher banded dotterel and wrybill densities recorded on the Ashley study area than on the Rakaia. This difference appears almost wholly attributable to the greater flow stability and food availability of the Ashley. In spite of this, and due primarily to its much greater width, the Rakaia still has many more breeding wrybills and banded dotterels (O'Donnell and Moore, 1983).

Breeding of most species is closely associated with water because it is there that most food is found. The locations of nests and home ranges of wrybills and banded dotterels reflect this link. None breed in large areas with no water. It follows that a loss of water, especially in minor braids, could result in a decline in breeding density. Evidence for this suggestion comes principally from three sources:

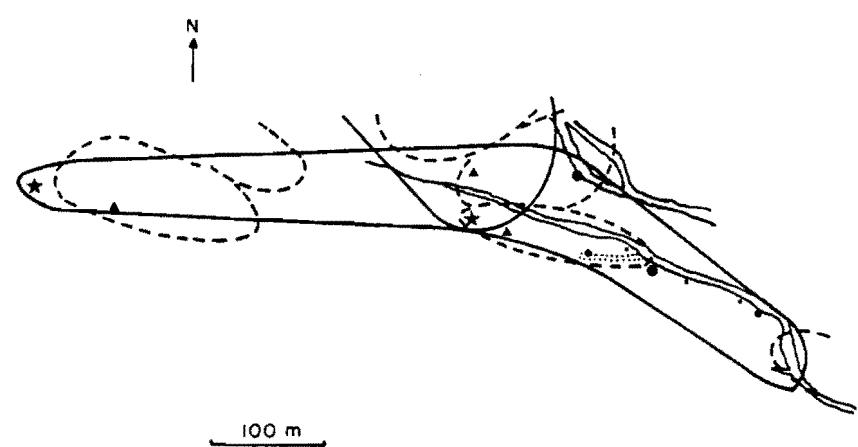
- (1) Home range size on riverbeds is related to water flow and habitat. The more stable the flow and the greater the occurrence of preferred feeding areas, then the smaller the home range size is likely to be;

FIGURE 4-5 : Pattern of space use for breeding pairs of wrybills and banded dotterels on the Ashley River in 1983.

(a)



(b)



- KEY:
- >20% of observations
 - 10-20% of observations
 - <10% of observations
- ★ Wrybill nest and home range
△ Banded dotterel nest and home range

(2) Home range spacing is a function of channel size and the braiding pattern. For instance, the most highly braided section of the Rakaia study area contained the greatest density of both wrybills and banded dotterels. This area was also characterised by greater levels of weighted usable area (see Section 7.4) than occurred on the less braided middle section;

(3) Home range spacing is a function of river width. The wider the riverbed, depending of course on whether it contains a suitable number of braids, the more likely there will be more than one pair per cross-sectional reach (see Figure 4-4).

The Ashley had greater densities on a per unit area basis, but assessed solely on the length there were higher numbers per kilometre on the Rakaia. The much higher number of minor braids on the Rakaia, and the greater overall width of the active riverbed, are largely responsible for this pattern. In contrast, high densities on the Ashley are probably attributable to the comparatively stable flows during the breeding season which lead to high nesting and hatching success, and food productivity.

Evidence regarding the relationship between the number of braids and discharge is conflicting. Mosley (1982a) found no relationship over a wide range of flows in the Ohau river. Bowden et al. (1982) found for the Ashley that down through the range 24.7 to 1.3 cumecs, the number of channels declined from 7 to 2 in a reach which was also used in this study. Unfortunately, during their 18 month study there were several large floods that could have had a significant impact on channel morphology. Consequently, their findings should be viewed with caution. In contrast, this study (see Section 7.4.4) has demonstrated a clear relationship on the Ashley between falling discharge and the number of channels in highly braided cross-sections. However, the nature of the Ashley discharge regime means that without major flow modification, this characteristic is unlikely to cause difficulties before December, at least in most breeding seasons. The number of channels in a cross-section of the Rakaia does not appear to decline in the same obvious way as on the Ashley. For instance, Glova and Duncan (1985) found that over a range of medium to extremely low flows only one or two minor braids dried up out of up to 18 in a cross-section.

Home ranges on the Ashley were larger than on the lower Rakaia, but the difference was not significant. It might be expected that home range size would be significantly smaller on the lower, than on the upper, Rakaia. However, Hay (1984) reduced home range size to territory size so that a direct comparison cannot yet be made between upper and lower rivers.

On the upper Rakaia, Hay (1984) found wrybill territories were maintained constantly during breeding, and he concluded that breeding territories must be large enough to ensure sufficient food supply during periods of high river flow. Although this study examined home ranges, the results still support that view. Wrybills therefore select home ranges where an adequate food supply can be obtained even during floods when food supply may be reduced. This supports the super-territory concept of Verner (1977).

Mapping important foraging nodes gives some indication of the variable space use patterns of wrybills and banded dotterels, but does not show how these change in response to variations in the flow regime. As flows declined on the Ashley there were fewer minor braids, often leading to wrybills foraging in different locations, or being further concentrated on other nodes as these became more productive in association with long term flow stabilisation. This led to a contraction in home range size, but only when such losses were at the outer margins of the home range. Such a decline is entirely predictable when assessed in terms of optimal foraging theory, i.e., it would be uneconomic for birds to venture to points where it was no longer worthwhile feeding.

The assessment of the relationship between wrybill home range size and habitat quality supports Davis (1982), who found territory size for belted kingfishers in North America to be related to the number and productivity of riffles along a single channel stream. Hay (1984) did not make a similar assessment because of the difficulty of taking such measurements on unstable rivers. The comparison between home ranges in this study was based on an examination of aerial photos and ground level observations of minor and major braids in each home range. This suggested that:

- (a) minor braids are more productive than major channels; and

(b) minor braids provide more preferred foraging microhabitat than major channels.

From this it follows that home ranges dominated by minor braids would be significantly smaller than those dominated by major channels. The first of these observations is from the work of Sagar (1983a), while the second is based on the assessment of weighted usable area reported later (see Section 7.4.3). Since home range size appears to be a function of habitat quality so that the smallest home ranges are located near the most stable and productive microhabitats, it is important in areas where home ranges abut each other that this microhabitat quality is maintained. If the flow regime is made more variable, food resources may be reduced and home range size would have to increase and the carrying capacity for these birds would decrease. To minimise this, management should concentrate on maintaining the stability of the minor braid network, while controlling the encroachment of vegetation by leaving the flood regime essentially unaltered.

Banded dotterel home ranges were significantly smaller than those of wrybills on both rivers. The much greater proportion of foraging time spent on terrestrial microhabitats by banded dotterels (see Figure 6-1) helps explain this. Because they did not have to venture as far to feed, and by foraging on a range of microhabitats (often close to the nest), banded dotterel home ranges tended to be comparatively small. Furthermore, banded dotterel home range sizes on the Rakaia were significantly greater than on the Ashley. This provides further indirect evidence to show the greater productivity of the Ashley.

Flow instability clearly affects the densities of banded dotterels on the Ashley and Rakaia rivers. Further increases in flow variability as a result of water resources development may further reduce their density on the Rakaia, either as a result of reduced breeding success or by an increase in the home range size needed to satisfy basic needs. The former appears more likely in view of the excess space which apparently exists on the riverbed at present. This apparently wasted space may remain under-utilised for a number of reasons:

(1) At present there is a dynamic but variable relationship between the encroachment of exotic vegetation and the flow regime. Several seasons of low to moderate flows would almost certainly lead to a substantial increase in the area of unsuitable habitat. Banded dotterel and

wrybill populations may be adjusted to some average annual level of usable riverbed. From 1982 until the end of the 1983 breeding season, the periodic but large floods increased the area of usable habitat on the riverbed;

(2) The presence of large vegetated areas may be reducing breeding success and thus population size. Vegetation could harbour predators and their prey thus increasing the threat to riverbed birds. Since vegetation encroachment is most extensive on high points which are also favoured nesting sites, birds are forced to nest at lower levels, and so are vulnerable to smaller floods which would otherwise have been avoided;

(3) Excess space may be advantageous in allowing some flexibility in nest and home range site selection. The few, large distance, inter-seasonal shifts in home range location recorded for wrybills on the lower Rakaia contrasts with the high degree of site fidelity displayed on the upper Rakaia (Hay, 1984). The increase in habitat instability caused by vegetation encroachment probably encourages such behaviour.

Perhaps a combination of the above factors may have resulted in the excess space for wrybills and banded dotterels on the lower Rakaia.

Wrybills and banded dotterels are averse to nesting close to black-backed gull colonies. These colonies take up a considerable space, both for nesting and roosting sites. On the Rakaia, two large colonies were present in the study area and maintained the same general nesting zones from 1981 to 1983. The black-backed gull population appears to have increased greatly in recent decades. The huge increases recorded on the lower Waitaki river are attributed to intensified farming, which in itself is closely associated with large scale irrigation schemes (O'Donnell and Moore, 1983). Similar schemes planned for the Central Canterbury Plains would probably result in a corresponding increase in gulls with more riverbed space used by a species which does not face any obvious population threat. This would almost certainly lead to a reduction in wrybill numbers as the available breeding area progressively declined.

4.6. Summary and conclusions

Space use by breeding riverbed birds was studied with particular emphasis on aspects of home range use by wrybills and banded dotterels. Wrybill home ranges were significantly larger than those of banded dotterels on both rivers, but there was no significant difference between wrybill home range sizes on an inter-basin comparison. However, banded dotterel home ranges on the Rakaia were significantly larger than those on the Ashley, where density was higher for both species. This size difference may be density dependent, but it appears more likely that the greater instability and lower food availability on the Rakaia has resulted in expanded home range sizes on that river.

These results provide the data for a number of management suggestions. On rivers with an unstable flow regime like the Rakaia, the maintenance of riverbed width is necessary to maintain a high bird population. It is also necessary to maintain the dynamic nature of the braiding pattern. Furthermore, because home range size appears to be related to the presence of minor braids, it is important to sustain minimum flows at levels which will not significantly reduce the number of braids in the river cross-section. Neither banded dotterels nor wrybills nest near black-backed gull colonies. As the gull population will probably increase with the intensification of land use for agriculture, it may become necessary to institute a population control programme on the Rakaia and Ashley rivers.

5. WRYBILL TIME-BUDGETS

5.1. Introduction

The most important activity of an animal is feeding to accumulate sufficient energy to meet metabolic needs (Powlesland, 1981a). Until these basic needs are met other activities which require extra energy and time (such as reproduction) cannot be undertaken. The allocation and use of time to meet these needs is therefore vital to animal survival. Analysis of time-budget records is the method commonly used to examine this relationship between time and its allocation to meet metabolic and behavioural needs.

Orians (1961) argued that even very subtle differences in time-budgeting can affect an individual's reproductive success. These differences may be manifested in an unpredictable environment (such as a braided river) which can be easily modified by man. Verner (1965) proposed that selection should favour an adaptable time-budget which is strongly influenced by environmental factors. The impact of the unstable braided river environment on resource provision has been well documented (Pierce, 1982a; Sagar, 1983a, 1983b). In general, resource provision is a direct function of the flow regime so that a long period of stable flow results in high aquatic invertebrate biomass, while floods lead to massive biomass decline.

A braided river is a complex mosaic of patchy resources. It appears likely that resource use would match this patchiness. Since habitat quality in a braided river is a direct function of hydrological conditions, it may be hypothesised that variable discharge will lead to changes in resource use and behaviour by waders, which will reflect in variations in their time-budgets. These differences may be marked for a species which inhabits two rivers with different flow regime patterns.

5.2. Methods

Time-budgets of wrybills were studied during the 1982 and 1983 breeding seasons on the Rakaia river, and for the 1983 season on the Ashley river. Observations of wrybill behaviour were made at dirty (fresh or flood), milky (high or average) and clear (average or low) flows, to reflect variations which may occur in association with typical flow changes. All turbidity conditions were assessed visually.

Migratory behaviour restricted the principal recording period to late August to early January inclusive. Outside this period territory bonds are weak (Hay, 1984) and the increased freedom provides an opportunity to reduce the effects of local food shortages. Also, immediately after breeding, there is a reduction in wrybill numbers which is almost as quick as the pre-breeding increase in late August. The value of observations outside the breeding period would therefore be questionable.

Because of the small population size on the Ashley river some individuals were studied more than others. This problem occurred for the Rakaia sample only when riverbed access was restricted by floodwater. When possible, equal numbers of males and females were observed. Chicks and fledglings were not studied because the data would have biased the results and, for this study, it was adult time-budgets which were considered most important.

Behaviour was timed by stopwatch and the elapsed time for each activity recorded. Where possible a 60 minute observation period was used for each bird, with 10 minutes considered a minimum for an observation to be deemed successful. This minimum was based on a large number of observations which indicated that rapid changes between patches were the norm, so that in a 10 minute interval several microhabitats would be used. To take account of the variable occurrence of microhabitat types on the Rakaia river in particular, observations were made so that they included a representative incidence of wrybills occupying home ranges within the various microhabitats. Therefore, with approximately 30% of wrybill home ranges on the Rakaia including a segment of the main channel, this 30 percent was proportionally represented within time-budget observations.

Wrybill behaviour was categorised into seven distinct activities:

(1) Foraging - the process of searching for and eating prey. Foraging methods were divided into pecks, defined as very rapid movements in which the bird picked at, or seized an organism on the ground, on the water surface, in the water column, or on the stream bed. As pecking is regarded as a visual foraging method (Baker and Baker, 1973), within water-column and streambed feeding involving rapid bill movements can be safely regarded as pecking. Probing represents tactile foraging (Baker and Baker, 1973) and is defined as a prolonged insertion

of the bill into the stream bed or under stones. All observations were made using 7x40mm binoculars. Results relating to feeding behaviour are presented separately in Section 6.4.4, while the physical characteristics of the habitats used are reported in Section 6.4.1.1.

(2) Body maintenance - principally the processes of head-scratching, beak-wiping, toe-nibbling, bathing, and stretching. Many of these events are of only short duration, so recordings were often estimated to the nearest five seconds.

(3) Territory activities - including posturing, displaying, flying, running, and singing associated with territorial defence or attack.

(4) Breeding - interactive pre-breeding and mating displays, song, care of young and incubation. For all activities other than incubation, the activity was observed from beginning to end. It was hoped to be able to incorporate an allowance for incubation time within this analysis, based on the findings from Hay's (1984) study of wrybill breeding ecology.

(5) Flying and (6) Walking - times were recorded for these activities when they were involved with inter-patch movements, returning to nests, or securing sites to undertake body-maintenance, breeding, or loafing activities. Recordings were again to the nearest five seconds.

(7) Loafing - when birds rested.

Time-budget records were subdivided in the following ways for analysis:

- By flow according to the categories: dirty, being in fresh or flood; milky, as declining after a flood or fresh; and clear, during average to low flows;
- By river, with all observations for each river being combined;
- By month pairs: August to September (period 1); October to November (period 2); and December to January (period 3).

This subdivision was based on the characteristic flow pattern of each river (see Figure 2-2). Period 1 typically represents a time of high average flow on the Ashley and low mean flow on the Rakaia. Conversely, period 2 is one of high and unstable flows on the Rakaia, but declining flows on the Ashley. Period 3 is also a period of high average flow on

the Rakaia, but is a time of low flow on the Ashley river. The 'G test' for testing the equality of two percentages (Sokal and Rohlf, 1981) was used to evaluate the significance of the differences between the proportions of time spent on each activity.

5.3. Results

5.3.1. Breeding season time-budgets classified by flow

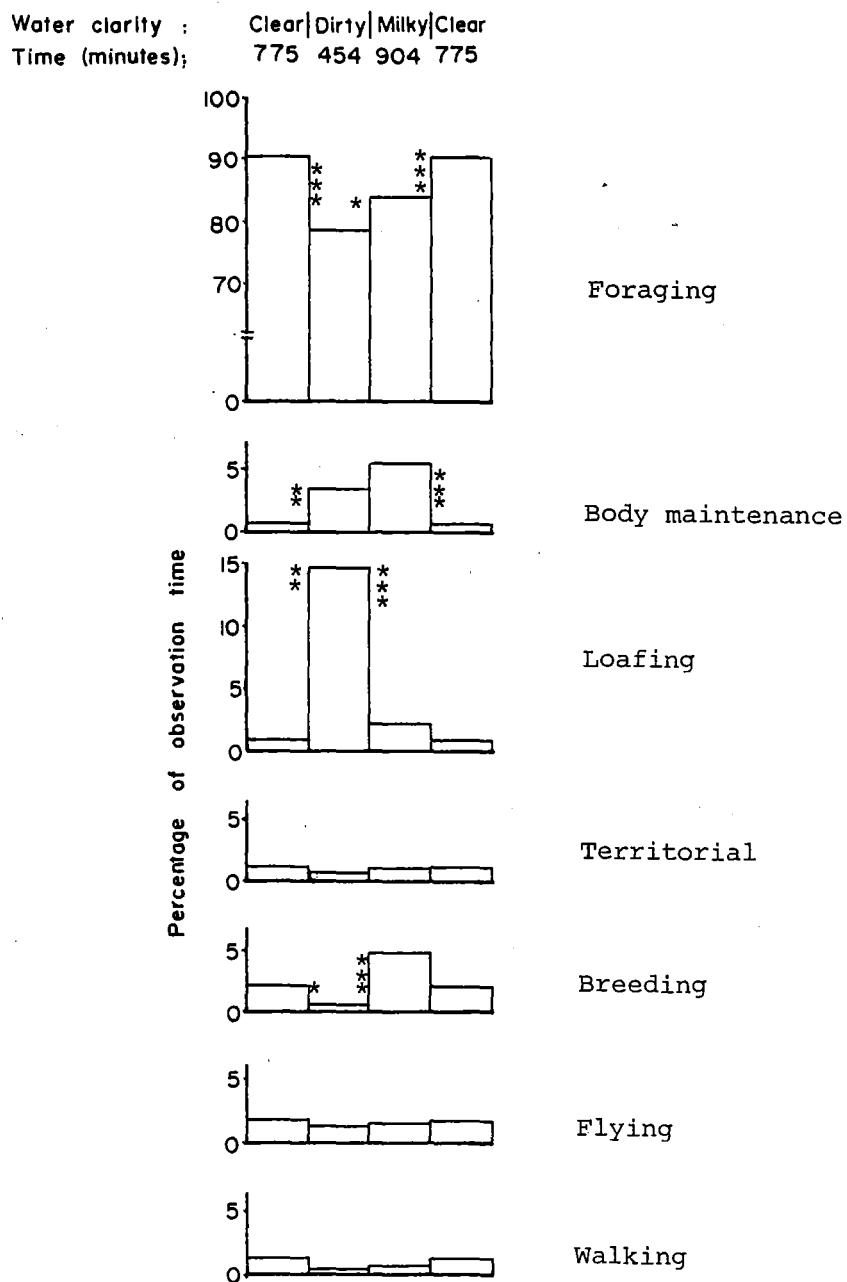
Time-budgets from 1982 and 1983 on the Rakaia were combined to provide sufficient data, and then subdivided according to river condition (Figure 5-1). Over the period of study the river was clear for 51.4% of field days, milky for 35.4% and dirty for 13.2% (N=144 days).

Overall differences between time-budgets classified by flow were highly significant ($P<0.001$). Time spent foraging was significantly greater during clear river conditions than during dirty and milky flows. The difference between dirty and milky flows was also significant, with less time spent foraging in the former. Body maintenance activities increased significantly after the change from clear to dirty river conditions, but a further rise with the transition to milky flows was not significant. The difference between milky and clear conditions was significant. The proportion of time spent loafing increased from 2.0% at clear flows to 14.7% at dirty, and then declined to 2.3% while the river was milky. The differences between clear and dirty and between milky and clear flows were significant but that between clear and milky was not. Patterns of territorial behaviour did not change significantly between flows, although there was a slight trend toward increasing territorial activity as the river changed from dirty to clear. Breeding behaviour was significantly higher at milky flows than at either dirty or clear flows. Breeding activity was also higher at clear than during dirty flows. No significant differences existed between flows for flying or walking, although a slight trend toward increases in these activities occurred as water clarity changed from dirty to clear.

5.3.2. Bi-monthly breeding season time-budgets

Figure 5-2 shows the time-budgets divided into three bi-monthly periods. Considerable differences existed between time-budgets of adjacent periods on the same river, and between rivers for corresponding periods. Results in this section should be interpreted in relation to

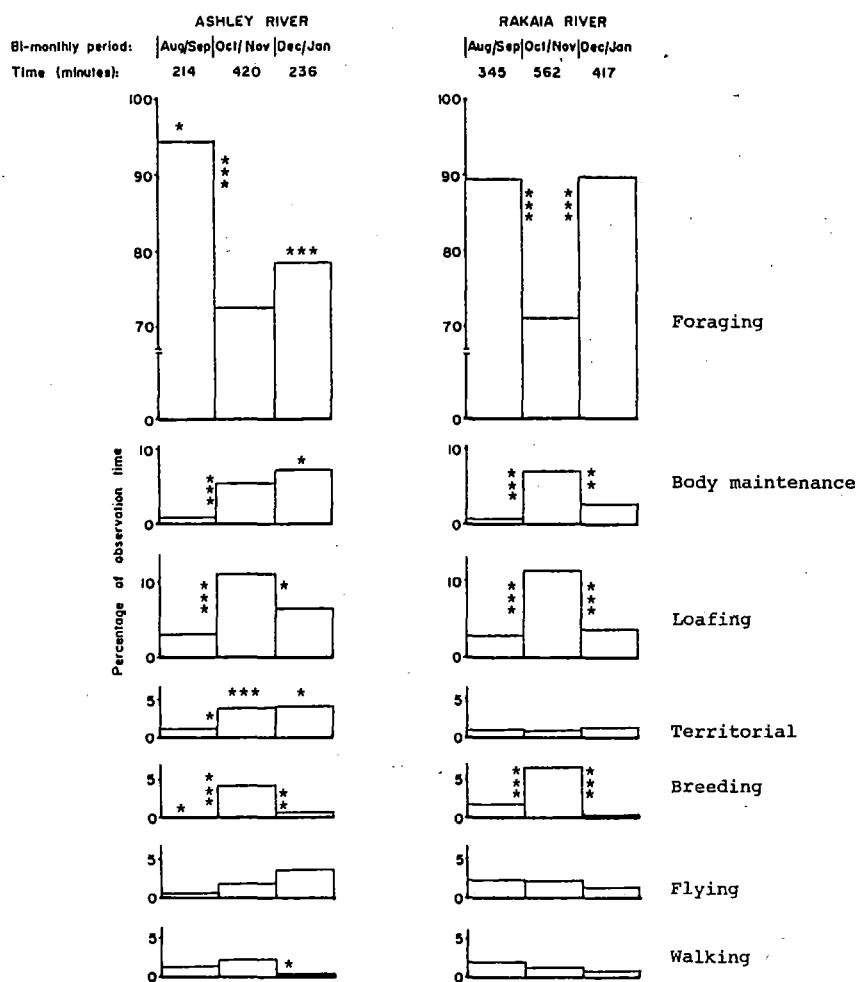
FIGURE 5-1 : Time-budgets by river condition for adult wrybills on the Rakaia river in 1982 and 1983 breeding seasons.



KEY: Asterisks beside columns indicate significant differences between adjacent columns.

* = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$

FIGURE 5-2 : Bi-monthly time-budgets for adult wrybills on the Ashley and Rakaia rivers for the 1983 breeding season.



KEY : Asterisks above columns indicate significant differences on an inter-river basis for the same bi-monthly period, while those on the sides of columns indicate significant differences between adjacent bi-monthly periods for Wrybills on the same river.

* = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$

the respective hydrographs for both rivers during the 1983 breeding season (Figures 3-8 and 3-9).

For the Ashley, significantly more time was devoted to foraging during period one (August to September) than in period two (October to November). In period two more time was spent on body maintenance, loafing, territorial interactions and breeding behaviour, than during period one. For period three (December to January), significantly less time was devoted to loafing, breeding behaviour, and walking than occurred in period two. On the Rakaia river, significantly more time was spent foraging during period one and period three than during period two. During period two, the time spent on body maintenance was greater than for periods one and three, as was the time devoted to loafing and breeding behaviour.

In an inter-river comparison, significantly more time was spent foraging on the Ashley in period one, with significantly less breeding behaviour at the same time. The proportion of time involved with territorial disputes was much greater on the Ashley during period two than for the same period on the Rakaia. Significantly more time was spent foraging on the Rakaia than on the Ashley for period three. In the same period more time was involved with body maintenance and territorial interactions on the Ashley river. No significant inter-basin differences could be determined for loafing, flying or walking, for any of the periods.

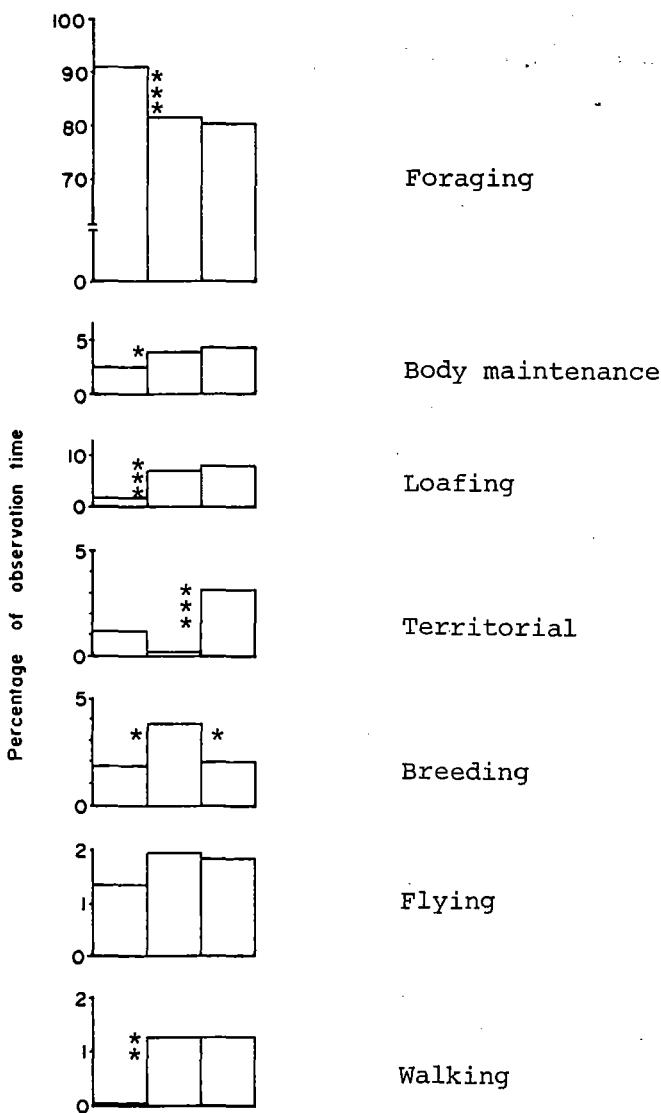
5.3.3. Breeding season time-budgets

Foraging was the dominant activity for all time-budgets, accounting for more than 80% of observation time (Figure 5-3). Foraging time on the Rakaia was greater than on the Ashley in both seasons, but the difference was significant only for 1982. This inter-basin, inter-season comparison was considered justifiable in light of the proposal that river flows are the dominant control on time-budgets and other biological factors. On the Rakaia in 1983, coupled with reduced foraging was a significant increase in body maintenance, loafing, breeding and walking activities.

Although there was a significant difference between the 1983 breeding season time-budgets on the Ashley and Rakaia rivers ($P<0.01$), most of the difference can be explained by changes in time devoted to

FIGURE 5-3 : Breeding season time-budgets for adult wrybills on the Rakaia river, 1982 and 1983, and Ashley river, 1983.

River	:	R	R	A
Year	:	82	83	83
Time (minutes)	:	804	1331	901



KEY: Asterisks beside columns indicate significant differences between adjacent columns.

* = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$

territorial and breeding activities. The time devoted to territorial interactions on the Ashley was significantly greater than that recorded on the Rakaia. In contrast, more time was spent on breeding behaviour on the Rakaia than on the Ashley. No significant differences between the other wrybill activities existed.

5.4. Discussion

Significant behavioural plasticity was found in a comparative study of the time-budgets of two populations of adult male South Island robins Petroica australis australis Sparrman (Powlesland, 1981a). Powlesland (1981a) concluded that the formulation of theories and models of bird behaviour should not be attempted on the basis of the study of just one population. This study of wrybill time-budgets on two geographically discrete and hydrologically different braided rivers reinforces this conclusion. Large and significant differences were found in:

- (1) time-budgets of wrybills at different flows;
- (2) bi-monthly time-budgets between adjacent periods on the same river, and between corresponding periods on different rivers; and
- (3) breeding season time-budgets in different years on the Rakaia, and between the Rakaia and Ashley in the same year.

The implications of these findings should be assessed in terms of food availability (see Figure 6-11) and breeding success data (see Section 3.4.1.1).

Foraging was the dominant activity in all wrybill time-budgets, involving more than 70% of observation time. These figures should be interpreted with caution because no allowance for incubation time was included in this study. It was initially proposed to use Hay's (1984) results to adjust each time-budget where incubation was known or thought to be occurring. However, his determination of sexual differentiation in incubation (70:30 ratio of female to male) was based on spot recordings made during each visit to a nest, rather than by a more rigorous time-budget approach. Furthermore, he did not provide any data or comment on the amount of time spent with both parents off the nest feeding (in 1982 in the present study, two known nests were left for periods of up to 30 minutes, several times a day, in overcast, cool weather conditions; both nests successfully hatched young). Including a

correction factor based on Hays' research could have produced misleading results. Therefore, it was decided to exclude incubation time, and instead to note peak laying and incubation periods determined in the study of breeding success (see Figure 3-1). While this may weaken the study's value, such research should, even under the most stringent conditions, be seen as only indicative of behavioural patterns.

Proportionately more time is spent foraging during clear flows than during milky or dirty flows. Pierce (1979) found an inverse relationship between peck rates and discharge with highest rates occurring at the lowest flows. The high percentage of time devoted to loafing during flood flows may be viewed in relation to the economics of foraging. Thus, if food intake provides a lower energy return than that needed to obtain it, then an optimal forager would have two main options:

- (1) Reduce energy loss to a minimum by loafing. To be effective, this strategy implies that resource depletion is temporary and that food availability will quickly rise again to a level where it becomes profitable to resume foraging. Flood peaks on the Rakaia are generally short-lived (considerably less than one day), and flows quickly decline with an associated change to milky water within 2-4 days of the peak passing;
- (2) Shift to a different microhabitat (or patch) where it becomes economic to feed. The peaks of large floods may cover all riverbed habitats, reducing their energy value as feeding sites. At floods less than the bankful discharge it may be profitable to forage terrestrially. This shift is noticeable in the feeding time-budgets classified by discharge. On the lower Rakaia, where the active riverbed is bordered by heavily vegetated riparian margins, a movement to adjacent terrestrial habitat during large floods is impossible. High wrybill numbers on Lake Ellesmere during the 1982 and 1983 breeding seasons (O'Donnell, pers. comm.; pers. obs.) may have been a result of widespread resource depletion leading to a long distance shift in habitats.

It appears likely that wrybills exploit to the fullest possible extent a combination of both options, depending on the duration and severity of floods in any one breeding season. During small to medium floods a shift to riparian foraging would be profitable, but for larger floods

loafing would appear to limit potential energy losses. Repeated large floods would result in complete movement off the river.

Apart from the highly significant increase in time spent loafing during floods, all other activities, except body maintenance, occurred at lower levels than during clear (low to medium flow) river conditions. Although these differences were significant only for breeding, the overall trend still deserves comment. Territory, breeding, flying and walking activities require the expenditure of large amounts of energy. For instance, flying increases the metabolic rate in birds by five to twenty times (Tucker, 1969), while West (1968) reported a 21% rise in energy use during egg production by willow ptarmigans (Lagopus lagopus L.). Thus, for the conservation of energy through a rise in loafing time to be effective, other energy-costly activities must also be reduced, even if only by small amounts. Body maintenance is often associated with loafing (pers. obs.) and, although requiring body movement, is generally undertaken when the bird is standing, thereby minimising energy expenditure. This combination of adjustments supports the contention that food availability is a limiting factor on riverbeds during floods. Furthermore, if artificial modifications to the flow regime disrupted food provision at low (clear) or moderate (milky) flows, then wrybills may not be able to sustain the energy levels required for successful breeding.

With declining discharge from floods (dirty) to moderate flows (milky) there are increases in all activities, except for loafing which declines greatly. Breeding behaviour rises substantially as does the time involved in foraging. The two activities are closely related so that successful mating and egg production will not be accomplished until energy levels are sufficiently high to sustain breeding activities. Floods lead to the movement of bed sediment and thus initiate catastrophic drift of aquatic invertebrates. At and around peak flood flows, the water volume to invertebrate ratio is at a maximum. With the rapid decline of flows after this peak the ratio falls quickly. Many invertebrates become stranded on the water's edge, particularly in disconnected pools and small side eddies of runs which then become preferred and rich feeding patches (see Figure 6-2). This shift in microhabitat preference supports the contention that wrybills are opportunist feeders (Pierce, 1979; Robertson et al., 1983).

Concentrating mating behaviour during milky river conditions may also have an adaptive advantage for wrybills on rivers with flow regimes like the Rakaia. Assuming an equal probability of occurrence throughout the majority of the breeding season the likelihood of another flood must obviously increase as flows become clearer and lower (i.e., as the time from the previous flood lengthens). Wrybills have an incubation period of approximately 30 days. Therefore, to limit the likelihood of nest loss due to flooding (the major cause of nest failure) breeding should commence as soon as metabolically possible after the last flood peak. Breeding is probably still initiated by photoperiod changes (e.g., gonad development) but the consummation of activities resulting in egglaying could, on occasion, be entrained by flood peaks. The time-budget study supports this suggestion. As the time interval between floods lengthens, an increase in the level of aquatic and terrestrial invertebrate recolonisation will have occurred, which is advantageous to newly-hatched, inexperienced chicks. Thus, the adaptive advantages of increased levels of mating behaviour after floods and during milky flows are twofold:

- (1) The probability of incubation being successfully completed is maximised;
- (2) Newly hatched chicks have the greatest chance of obtaining sufficient aquatic and terrestrial food supplies.

The significant decrease in time spent foraging between August to September and October to November on both rivers was matched by increases in time spent on body maintenance, loafing, breeding and, on the Ashley, territorial behaviour. This indicates that wrybills reached a body weight sufficient to undertake these other activities and, because there were no significant differences between rivers (except for the level of territorial behaviour being higher on the Ashley; $P<0.001$) the basis existed for a successful breeding season. That this did not eventuate on the Rakaia is almost totally attributable to the direct and indirect impacts of flooding. Early season flow instability delayed breeding until late September to October at which time floods destroyed almost all first clutch nests. Subsequent floods and freshes did not allow wrybills to obtain sufficient energy to successfully renest. The higher percentage of time devoted to foraging during December to January, which was significantly greater than on the Ashley at the same

time, seemed inadequate to meet these needs. Even where repeat clutches were attempted the mean clutch size was smaller than expected, again suggesting a food deficiency. In contrast, and despite the occurrence of several freshes and significantly more time involved with territorial behaviour, breeding success on the Ashley was very high. The increased amount of time spent on territorial disputes had no noticeable effect on breeding success. As most disputes involved interactions with the more common banded dotterels, it would appear that while food supply remains adequate, inter-specific competition with banded dotterels does not affect wrybills. Water management which may improve banded dotterel habitat without affecting wrybill habitat would be unlikely to reduce wrybill numbers.

More time was spent foraging, and less on body maintenance, loafing and walking activities, on the Rakaia in 1982 than on either the Rakaia or Ashley during 1983. Breeding success on the Rakaia was substantially higher in 1982 than in 1983 (29.3% c.f. 3.8% fledging success rates) but lower than on the Ashley (42.9% fledging success). However, there was little difference in the time involved with breeding on the Rakaia in 1982 and the Ashley in 1983 when first clutch breeding success was high on both rivers. The poor first clutch breeding success on the Rakaia in 1983 was followed by an equally poor second attempt. As only 20% of wrybill pairs attempt to rear two broods (Hay, 1984), it is not surprising that the time devoted to breeding behaviour was less for wrybills on the Rakaia in 1982 and those on the Ashley in 1983, than for those on the Rakaia in 1983. With almost all pairs forced to attempt renesting on the Rakaia in 1983, doubling the amount of time associated with breeding activities seems quite realistic.

The arrival of wrybills on their breeding ground follows migration from northern wintering sites. Before nesting begins, birds must obtain sufficient energy to copulate and produce eggs (which are in effect, stores of energy) successfully. The time taken to recover depleted energy reserves will depend on the extent and availability of food supplies. Flows in the Rakaia were relatively stable throughout the winter and early spring of 1982. Food availability was therefore high and the time needed to obtain sufficient energy from foraging was probably short. Nest initiation and incubation therefore peaked during mid to late September, with most breeding completed successfully by the end of October or early November. After this, the Rakaia was subjected

to large, frequent floods with associated depressive impacts on food availability. Foraging time would therefore be high in August to September (period one) to obtain sufficient energy for breeding, and remain high after this to satisfy basic metabolic needs and provide for migratory energy requirements.

Examination of 1983 Ashley river time-budgets supports these contentions. The period one time-budget involved a very high amount of foraging, and low levels of body maintenance, loafing, territorial and breeding behaviour. Flows are generally high and unstable at this time on the Ashley, therefore more time was needed to find sufficient food to restore energy levels following the migration than for the corresponding period on the Rakaia. Consequently, breeding behaviour of wrybills on the Ashley was significantly lower than for the adjacent October to November period (period two), and lower than for the same period on the Rakaia. This was also supported by wrybill laying and incubation patterns on the two rivers, where dates for first clutches were considerably later on the Ashley than on the Rakaia. Wrybills require large, sustainable, and accessible food resources during August to September to prepare for breeding. Flooding can reduce invertebrate densities thereby restricting the rate of energy build-up. This may occur even if more time is devoted to foraging at the expense of other activities such as body maintenance and loafing, as may happen with low invertebrate densities associated with lower levels of weighted usable area at high flows (see Section 7.4.3). Such a combination of conditions results in low rates of feeding success, and can lead to delayed breeding, the length of which depends on the extent of resource depletion.

Nesting delays on the Ashley will generally have little effect on breeding success because later months are usually flood free, resulting in high rates of hatching and nesting success. Similar delays on the Rakaia can have disastrous effects on breeding by pushing the principal nesting period into the highly flood-prone months of October to December. This happened in 1983 but not in 1982, when stable flows allowed an early and safe beginning to the breeding season. Any man-induced flow modifications which lead to an increase in flow instability during late July to September on rivers such as the Rakaia should therefore be avoided.

Hockey (1984) found that 39.6% of daylight time was used by non-breeding African black oystercatchers (Haematopus moquini Bonaparte) for foraging. Time-budgets of breeding semipalmated sandpipers (Calidris pusilla L.) were determined by Ashkenazie and Safriel (1979) in Alaska. However, their measurements were made over 24 hour periods and are not directly comparable to this study. Wrybill foraging time is high compared with Gibson's (1978) study which found for the American avocet (Recurvirostra americana Gmelin) that feeding time did not exceed 50% of observation time throughout the range of pre-nesting, incubation, parental care and post-breeding time-budgets. In the pre-nesting period, feeding involved approximately 40% of avocet time-budgets, compared to 95% and 89% for wrybills on the Ashley and Rakaia rivers during the August to September period (pre-breeding for most birds) in 1983. During post-breeding, approximately 47% of avocet observation time was taken up by feeding. December to January, which is the equivalent wrybill period, foraging involved 78% and 89% of time on the Ashley and Rakaia respectively. The bias introduced to this study by the exclusion of incubation time is most apparent during October to November on both rivers, and to a limited extent on the Rakaia during adjacent bi-monthly periods. Certainly on the Ashley, and to a limited extent on the Rakaia, these findings can be directly compared with the avocet study and indicate the lack of flexibility available to wrybills during the breeding season. In unpredictable environments, such as braided rivers, which are subject to existing or planned water resource developments that may increase the duration and extent of this variability, there should be concern regarding the conservation prospects of a species with a finely balanced, inflexible time-budget. In some species with broader habitat requirements this situation would not be as threatening. For instance, Pierce (1982a) reported a shift in pied stilt breeding patterns associated with aquatic resource depletion on the Cass river. On the Rakaia, pied stilts which lost first clutch nests in 1982 due to flooding, left the river completely rather than be subjected to the longer term impact of resource depletion. Consistently variable flows on the Rakaia in 1983 resulted in the almost complete exclusion of the river as a pied stilt habitat. Presumably these birds would have bred on alternative sites such as the Ashburton river, or on irrigated pasture.

5.5. Summary and conclusions

Foraging is the most important activity in wrybill breeding season time-budgets. When sufficient energy could not be obtained, because of unfavourable foraging conditions due to flooding, this delayed and decreased breeding attempts. Therefore the 1983 season on the Rakaia, which was characterised by large-scale flow variability and low invertebrate densities, was a very poor one for wrybill breeding. On the Ashley though, periodic floods did not appear to affect breeding, because the interval between events was longer and their relative size smaller.

Wrybills display an adaptive ability to cope with the short-term impact of periodic flooding, but not with the frequent floods which occurred on the Rakaia in 1983. Unlike the pied stilt with its generalist pattern of habitat use, wrybills cannot simply leave the river and breed elsewhere. This restriction, the limited flexibility of wrybill time-budgets compared to American avocets, and the unpredictable nature of the physical habitat, all combine to put the species at risk from natural and man-induced changes in habitat quality. From the point of view of foraging, which must be energetically successful before other activities can be attempted, wrybills face two principal challenges:

- (1) Natural changes to the weather pattern with associated effects on the pattern of river flows. Depending on the character of such changes, which are as yet unpredictable, the future prospect for wrybills may improve or deteriorate;
- (2) Man-induced changes associated with water resource developments. To date these changes have degraded wrybill habitat but could be beneficial with appropriate management strategies. However, where such changes result in a need for more foraging time, it is unlikely wrybills could cope.

6. FORAGING AND FOOD IN RELATION TO MICROHABITAT USE

6.1. Introduction

As an adequate food intake is needed to perform necessary life support and metabolic functions, the relationships between resource provision, use, and a range of physical factors need to be determined. Although research has been undertaken in this area for black-fronted terns (Lalas, 1977), wrybills (Pierce, 1979), and for pied and black stilts (Pierce, 1982a), there are still major shortfalls in our understanding of these relationships. Research by fisheries scientists (Sagar, 1983a, 1983b; Sagar and Eldon, 1983) has much improved our understanding of the hydrology-resource provision relationship for fish and some of these results can also be applied to birds (Sagar, 1983a). However, the results of invertebrate studies on rivers in general, and on braided systems in particular, are subject to a variety of limitations, some of which have been little acknowledged by field investigators. This chapter reviews the literature and identifies these limitations. Then, bearing these limitations in mind, an approach is developed to best suit the requirements, and the theoretical and practical limitations imposed by the nature of this study.

6.2. Literature review

Central to many studies of bird feeding ecology are the relationships between food, and population size, density and territory. Lack (1954) and Pitelka (1958) proposed that food may be important directly (proximately) or indirectly (but ultimately) in the regulation of population numbers, the timing of breeding seasons, and other annual cycle events. In a study of the niche relationships among six species of shorebird, Baker and Baker (1973) showed that foraging behaviour and habitat selection determine the food resources of a bird. Having considered food to be an important limiting resource, Holmes *et al.* (1979) postulated that communities are structured on the basis of how food is partitioned, with syntopic species differing in behavioural and physical characteristics, resulting in differential food utilisation. For example, Schoener (1965) examined species' niche dimensions by studying bill size and assuming that differences are a significant reflection of the differences in the nature of sympatric congeneric food utilisation (Huxley, 1942; Lack, 1944). Large ratios of character

difference were identified in three general situations:

- (1) Among members of certain families which appear to feed on food of relatively low abundance;
- (2) In sympatric congeneric species associations on islands, especially small islands;
- (3) Among birds whose body sizes are relatively large in proportion to the total abundance of their food.

A common but not universal consequence of the foraging activities of a predator is a lowering of capture rates of prey in its immediate vicinity, a phenomenon termed "depression" by Charnov et al. (1976) who defined three forms:

- (a) Exploitation depression which refers to the situation where capture rates are lowered because of the harvesting of prey by the predator;
- (b) Behavioural depression which is associated with a change in prey behaviour, e.g., heightened alertness and reduction in activity;
- (c) Microhabitat depression which occurs when prey change locations to a position where the predator finds it harder to encounter or capture the prey than in the original position.

Recovering from resource depression is typically a function of the form of depression. Thus, the rate of recovery from behavioural or microhabitat depression can be very rapid, depending of course, on the location of the potential predator. However, recovery from the effects of exploitation depression, which depends on birth and growth rates of individuals already on the site and immigration of individuals, is highly variable. For instance, the supply of emerging aquatic insects exploited by several blackbird species in western North America recovers quickly because the rate of emergence of new insects from the adjacent water is so rapid that the encounter rates with prey are not determined by the predation rate but mainly by the rate at which new prey emerge from the water (Orians, 1966; Orians and Horn, 1969). The prey is highly mobile in his example and are drawn from a large pool which cannot be directly exploited by the predators causing the instantaneous depression (Charnov et al., 1976). Where external pools do not exist, recovery comprises birth, growth, and a much lower immigration rate,

together with microhabitat shifts of prey already within the foraging area. In this situation, recovery rates are generally much longer (Charnov et al., 1976).

There is some evidence that enhancement of encounter rates with prey results from the activities of other predators (Charnov et al., 1976). By using mayflies (Baetis spp.) as prey, and kokanee salmon (Oncorhynchus nerka Walbaum) as a predator, the prey displayed a microhabitat response by making itself less available to the predator (Charnov et al., 1976). Mayflies (Deleatidium sp.) are the most abundant food in the Rakaia benthos. They also comprise a substantial proportion of the diet of seven fish species, including quinnat salmon, in the river (Sagar and Eldon, 1983). Most of these fish species have microhabitat preferences which include greater depth and faster velocity requirements (Glova, 1982) than those determined for the feeding needs of riverbed birds. It is therefore possible that a microhabitat response involving a movement from water of greater depth and velocity, into shallower and slower areas, may enhance encounter rates for wading birds. It would follow that the deeper and faster the water a wader is feeding in, the greater the chance it can then take advantage of such prey enhancement so long as it is in water shallower and slower than where the fish occur. Testing this hypothesis for riverbed waders would require intensive laboratory experimentation with fish and invertebrates. This is an example of the variables which tend to cloud the potential for quantifying the flow-food resource relationship.

Goss-Custard et al. (1977) demonstrated a direct correlation between bird numbers and food supplies for waders. For the golden-winged sunbird (Nectarinia reichenowi Fischer), the size of territories varied more than ten-fold, but at any one time each territory contained enough food to supply the owner's needs, and over a period of time territories were expanded as their food-content declined (Gill and Wolf, 1975). Where each bird, or pair of birds, is holding a territory of a size dependent on food, the density of birds over a wider area can become related to food over a wide area (Newton, 1981). Sagar (1983a) showed that the density of invertebrates in Rakaia aquatic habitats is dependent in part on braiding hydrology, with minor braids having the highest densities. While the evidence is conflicting (Mosley, 1983a), some research indicates a relationship between falling discharge and a drop in the number of minor braids in a channel

cross-section (Bowden *et al.*, 1982; Glova and Duncan, 1985). This occurrence could lead to a drop in the available food resources of a territory and may lead to an upward adjustment in territory size which would also reduce the carrying capacity of the breeding habitat. An absence of pied stilts on the upper Rakaia was attributed to the discontinuous supply of aquatic invertebrates as food (Pierce, 1979) and was the reason cited for a similar, one year in three, study event on the Cass river (Pierce, 1982a).

Pierce (1979) used direct observation and the experimental provision of different invertebrates to determine the food of wrybills on the upper Rakaia. Both methods are of limited value when attempting to determine quantitatively the diet of riverbed birds, and should be seen only as indicators of general food preferences. Thus, Pierce (1979) concluded that mayfly larvae appeared to be the staple diet of wrybills at each high country study area, despite the presence of a diverse aquatic fauna. He also considered wrybills to be opportunist feeders (Pierce, 1979). Therefore the experimental provision of food items is likely to result in actions resembling the feeding frenzy which can occur during brief periods of catastrophic drift, so that in most cases the bird would eat the prey provided, even if it is of only marginal importance to its total diet. Direct observation is also of limited value, especially when dealing with a small bird which is feeding on very small food items, some of which cannot be seen during mandibulation, as reported by Pierce (1979). Gut analysis of wrybills cannot be contemplated for ethical reasons, while emetic techniques are known to result in high bird mortality, e.g., Davies (1977). This leaves faecal analysis as the only practical method of dietary analysis.

Black-fronted terns are aerial feeders which forage in swallow-like fashion over a variety of aquatic habitats (Lalas, 1977). The main prey (determined by direct observation) for birds of the MacKenzie Basin is the mayfly, Deleatidium sp., which is caught principally at the stream surface (Lalas, 1977). He also noted that small fish, earthworms and skinks are included in the black-fronted tern diet. Gut analysis was excluded for black-fronted terns for similar reasons to those above. Faecal analysis is also difficult because of the difficulty of collecting verifiable samples.

Limited research and observation have been undertaken to determine the food of banded dotterels. Stead (1932) observed that while on Canterbury riverbeds, food consisted mainly of the fruits Coprosma petrei and Muehlenbeckia axillaris. The stomach contents of a five-week old chick from the Cass river delta supported this conclusion (Bomford, 1978). However, Bomford (1978) also recorded banded dotterels feeding in both aquatic and terrestrial habitats, with mayflies being eaten at the former. Although Bomford took aquatic and terrestrial invertebrate samples, she did not make any direct analysis of diet. Pierce (1976) observed banded dotterels feeding on moths, mayflies and cyclorrhaphan Diptera on the shingle banks of the upper Rakaia and Cass rivers. This led Pierce (1976) to conclude that the normal diet of banded dotterels was very similar to the terrestrial diet of wrybills.

In the only assessment on riverbeds of the effects of prey consumption on resource depression, Pierce (1982a) concluded that the impact was very low. He estimated that during September and October 1977 pied and black stilts consumed approximately 1-2% of mayfly larvae on the Cass river delta. This represented 4-6 million out of an estimated 300-500 million larvae. Pierce (1982a) then suggested that the total avifauna of the river was unlikely to cause more than a 5-10% decline in invertebrate numbers. This deduction led to a further conclusion that physical components of the lotic habitats, particularly during floods, were clearly more important than that of predation by birds in regulating invertebrate numbers (Pierce, 1982a).

Measurements of food stocks, like those of birds themselves, can usually do no more than define periods when food is scarce (Newton, 1981). Further limitations on the use of this data were identified by him as follows:

- (1) In some cases the total stock of food was estimated, but no indication was given of what proportion was available to the birds - a proportion which may have varied with environmental conditions;
- (2) While for some birds all known foods were assessed, in others only favoured or particular foods were assessed. It was always possible that when favoured (or known) foods were finished, the birds could turn to alternatives, perhaps previously unknown to the observer;
- (3) It was not usually known how much food the birds had to remove

before they got into difficulties, and even if they removed nearly all their food, they might still have survived. Alternatively, only a small reduction in food density may have been enough to reduce the birds' foraging efficiency below the level necessary for survival.

The conclusions from Pierce's (1982a) study do not take account of any of the above limitations, yet Newton (1981) concluded that measurements of food supply can normally inform no more than measurements of the bird populations themselves, and indicate likely periods of difficulty. Care is therefore required when drawing conclusions from data collected under such circumstances. Experimental alteration of food-supply and subsequent monitoring of the response against an appropriate control is one means of overcoming these limitations. In a number of studies, e.g., Krebs (1971), the provision of additional food resources resulted in an increase in survival and subsequently in breeding density. A higher banded dotterel density on the Ashley compared with the Rakaia (see Section 4.3.1) may in part result from the greater food availability on the former. On braided rivers the natural variability in food availability and habitat quality appears to be more appropriate for study than the experimental manipulation of the habitat. Experimental manipulation of a braided river would need the assistance of substantial earth moving equipment.

An examination of the value of food availability studies undertaken for riverbed birds exemplifies the limitations identified by Newton (1981). Bomford (1978) and Pierce (1979) sampled the terrestrial substrate by direct capture techniques. When studying the riparian carabid beetles of the Waimakariri river, Herron (1981) discounted the use of either core sampling or direct counting using quadrats because of the nature of the substrate, the swift movement and flight of insects, and the patchy distribution. Herron (1981) finally chose pitfall trapping as the most appropriate means of studying the riverbed terrestrial invertebrate fauna, despite a number of limitations identified by Southwood (1978) and Watt (1980).

Benthic population estimates made in large rivers can be highly variable if invertebrate distributions are highly aggregated or contagious (Elliot, 1977). Because most dispersions are contagious the distribution of density estimates of any particular population will be non-normal and non-random (Downing, 1979). Downing (1979) found that

studies with replicate estimates of the benthic population for rivers and lakes, the most frequent number of samples taken was three. Furthermore, a standard error equal to 20% of the mean density would be found consistently only at densities greater than 1000 animals per m^2 . Since fewer than 20% of densities found in nature lie above this level, 80% of the standard errors found by taking three replicates will be greater than 20% of the mean (Downing, 1979). To increase the level of precision many samples with a small sampler should be taken.

Downing (1979) used the stream benthos data collected by Chutter and Noble (1966) to compare the variabilities for lake and river data from previously published studies. It was suggested that the benthic animals of stream riffles are more variable than those of lakes and rivers, and that sampling programmes for stream benthos should be adjusted accordingly. This supported Resh (1979) who suggested that, for streams, a minimum sample size of 13 was necessary for 95% confidence limits within $\pm 40\%$ of the sample mean. Results from recent invertebrate studies of braided rivers along the eastern South Island (Table 6-1) can be used to assess the reliability of population estimates in light of the limitations identified by Downing (1979) and Resh (1979). The in-river estimates of Pierce (1982a) and Sagar (1983a) for the Cass and Rakaia rivers respectively, fall within the range of a standard error equal to 20% of the mean density, but the estimates of Bomford (1978) and Pierce (1982a) for stable side streams of the Cass river, and of Pierce (1979) for the Rakaia river, are of limited quantitative value.

There are many other factors which can potentially reduce the worth of aquatic invertebrate density estimates, or lead them to being highly variable. For instance, the choice of sampling device can have a great impact on such considerations. Chutter (1972) showed that Surber sampler counts were highly variable. Similarly Kroger (1972), in a quantitative experiment aimed at calculating the extent of underestimation attributable to the Surber sampler, concluded that because they capture only a small percentage of the invertebrates in the areas they sample, they should not be used to estimate standing crops unless the number of each species escaping through the mesh and around the sides of the sampler can be determined. Kroger (1972) showed that the Surber sampler was collecting only about one-quarter of the invertebrates present in the $0.093\ m^2$ sampling areas. Because of this

TABLE 6-1 : A comparison of aquatic invertebrate studies on East Coast South Island braided rivers in view of sample size considerations identified by Downing (1979) and Resh (1979).

Researcher	Site	Sampler	Habitat	Sampler area	Replicate sample nos	\bar{x} invertebrate density	Downing's replicate sample size - rivers	Resh's replicate sample size - streams
Bomford (1978)	Cass river - stable side streams	Surber	Riffles	0.0625 m ²	4	1600 m ⁻²	-	13
Pierce (1979)	Rakaia river	Surber	ALL	0.5 m ²	1	85 m ⁻²	2	-
Pierce (1982a)	Cass - river - side streams	Surber Surber	Riffles Riffles	0.0625 m ² 0.0625 m ²	8 8	ca.1100 m ⁻²) ca.2100 m ⁻²)*	2 -	- 13
Sagar (1983a)	Rakaia river	Hess	Riffles	0.1 m ²	3	800 m ⁻²	2	-

* Averages determined from graphs.

limitation the quantitative estimates of Pierce (1982a) for the Cass river should be treated with caution, as should those using unmodified Surber samplers. In contrast, Sagar (1983a) used a modified Hess sampler which is less likely to cause bottom scouring (Southwood, 1978) or to lose invertebrates around the sides. Only Sagar's (1983a) results can therefore be used to predict confidently, invertebrate densities in riffles in the Rakaia river. However, Pierce's (1982a) results for the Cass river may be useful if an attempt is made to develop a flow hydrograph-relative aquatic invertebrate density index for Canterbury rivers.

Making a substantive effort to quantify the overall instream food resources of the Rakaia and Ashley rivers would involve a major research effort requiring a large allocation of time and labour. Apart from determining the variations in different seasons between a range of flows, and between major channels and minor braids, it would be necessary to measure invertebrate densities of pools, runs, backwaters, and disconnected pools, as well as riffles and terrestrial habitats. To maximise the efficiency of Surber sampling, water velocities typical of those found in riffles are required. The much lower average velocities of pools are likely to induce a further bias into the method. Other samplers may be used, but the range of microhabitats and physical characteristics present make it difficult to find a universally applicable method. The use of two or more samplers in different microhabitats would make interpretation even more difficult.

With riffles being the most productive aquatic microhabitats (Pierce, 1979), an assessment of their standing crop related to flow hydrology may indicate the trends in braided rivers. Pierce (1982a) found that the density of Deleatidium "lillii" in samples was correlated inversely with discharge. A similar relationship may also exist for the density estimates determined by Sagar (1983a) on the Rakaia, although the comparison has yet to be made.

Considering the limitations and complexity of the potential sampling programme, and the labour input necessary, it was decided to use published data as the basis for an assessment of the aquatic food resource-hydrology relationship. Where the data base was too restricted and of limited value, such as for assessments of terrestrial resources and the diets of wrybills and banded dotterels, additional research was

undertaken.

6.3. Methods

6.3.1. Microhabitat use and preference measurements

Studies of the feeding and foraging patterns of riverbed nesting birds must take account of the hydrological factors contributing to variations in behaviour. For this study the aquatic habitat subdivisions were based on those used by Mosley (1982b) but with some minor additions and alterations:

(1) Riffles - which are areas of shallow, usually broken and rapidly moving water on a coarse substrate. They are frequently angled across the channel and form an abrupt step in the bed and water surface profile. The downstream edge of the riffle is usually clearly defined, but the stream bed on the upstream edge often grades steadily from the pool next upstream to the head of the riffle and definition of this boundary is difficult. During low flows much of a riffle may become emergent and form a long boulder bank across the river, with flow concentrated into a number of chute channels over the bank.

(2) Pools - which are areas of slowly moving water with greater than average depth, commonly found at meander bends or downstream from riffles.

(3) Backwaters - which are areas of still water connected to, but not part of, the main low flow channel. They are typically located in the remnant courses of the main channels, or a channel which is active only during flood stages. Backwaters are commonly connected to the main channel at their downstream end, and often water flows into them by gravel seepage, or as backwash from the connecting flow.

(4) Disconnected pools - which are bodies of water in the riverbed not connected to, or accessible from the main channel. Under certain conditions disconnected pools maintain a throughflow from gravel seepage, a situation which commonly occurs on the Rakaia.

(5) Runs - which are defined as any part of the channel which does not fall obviously into one of the other aquatic habitat types; they are not distinctive in any way but are characterised by water moving at slow or moderate speed, with a calm or rippled surface and widths and depths which are close to the average for the channel as a whole. When

compared to the extremes of riffles and pools in terms of depth and velocity, a run can be regarded as 'average'.

In addition the braiding pattern can be subdivided into:

- (a) major channels or braids visually estimated to carry more than five cumecs on the Rakaia, and more than one cumec on the Ashley. This distinction was made to allow for the difference in size of the two rivers; and
- (b) minor channels or braids visually estimated to carry less than five cumecs in the Rakaia and one cumec in the Ashley. Seepage zones, which are a special case of the minor braid classification, also warrant attention because of their particular hydrological character. Effluent water in a seepage zone results from throughflow in the shingle substrate, and the filtering effect of this action results in cooler and clearer water than is found in connected channels. There are two characteristic forms of seepage zone:

- seepage zone braids which normally flow in remnant flood channels or overflow braids. These systems include the morphological features of other braids, but are generally more stable and productive; and
- secondary seepages from banks and sandy areas which flow for short distances (generally less than a few metres) into any of the other channel forms including disconnected pools.

The visual classification of channel size is justifiable on grounds of expediency and experience. Since it is impractical for one person to measure all the relevant channel discharges it is much easier to provide a visual estimate of the relative flows carried by each channel. Several years of working on braided rivers has provided the necessary experience to carry out this assessment.

Observations of microhabitat use for foraging were made for wrybills, banded dotterels, pied stilts, and South Island pied oystercatchers on the Rakaia in 1981, 1982, and 1983, and on the Ashley in 1982 and 1983. Most observations were made during nest searching and therefore constituted a full coverage of the usable riverbed. Transect survey methods were discounted because of access problems. Records of in-water feeding depth and the dominant substrate type (see Section 3.3.2 for substrate classes) were kept in addition to their location, in relation to the previously defined aquatic habitat types. Foraging on

the wetted edge of channels was considered to be aquatic feeding and in such instances depths were recorded as 0-10mm.

Differences between percentage levels of microhabitat use were tested for significance by the G-statistic which was used rather than χ^2 because it is more accurate at lower sample sizes (Sokal and Rohlf, 1981). Microhabitat preferences were examined in relation to their overall occurrence on both rivers. On cross-sections of the Rakaia the minor channel to major channel ratio was about 3:1 while on the Ashley it was about 2:1 (determined from cross-sections established on aerial photos of both study areas). These ratios were further adjusted according to the proportion of each composed of pools, runs, riffles, and backwaters. A further allowance was made for the presence of disconnected pools. Determination of the overall amount of each of these habitat types present was made by measuring the distance along the edge of each unit in both minor and major channels. On three occasions when flows were between 100 and 250 cumecs on the Rakaia, approximately 5km of the braid margins were measured by pacing. Subsequently, the proportion of each microhabitat was determined and used to calculate the microhabitat occurrence ratio. The same procedure was used on the Ashley but with only two replications about, and below, the mean flow.

6.3.2. Diets of wrybills and banded dotterels

Wrybill and banded dotterel faeces were collected from both rivers. All adult banded dotterel and most wrybill samples were collected at the nest site during colour-banding because this often resulted in the dropping of fresh faeces under the trap. In addition, a small number of wrybill faeces ~~was~~ collected during feeding and time-budget observations. For later laboratory analysis all samples were placed in labelled vials with 70% alcohol.

To assist with identification, all faecal remains were subdivided and mounted on microscope slides with a lactaphenol medium. Slides were warmed on a heating tray for several days to allow the clearing agent to work. Each slide was examined under a stereo microscope. Because of the extent of breakdown it was generally possible to identify remains only to ordinal level. However, on some occasions, e.g., for the mouthparts of Deleatidium sp. larvae, it was possible to identify further. Diagnostic features identifiable for most orders were:

- mandibles, elytra and femurs from Coleoptera (beetles);
- head capsules, wings and femurs from Hemiptera (bugs);
- wings from Diptera (flies), Hymenoptera (wasps), Ephemeroptera (mayflies), and Plecoptera (stoneflies);
- mandibles from the larvae of mayflies, stoneflies, beetles, and Lepidoptera (moths and butterflies); and
- legs of Arachnida (spiders), and moths and butterflies.

A reference collection established from pitfall trapping assisted in the identification process. Final identification was confirmed by experts from each taxonomic field.

Faecal remains were assessed by two methods:

- (1) Percent occurrence which is calculated from the number of faecal droppings in which each food type is found;
- (2) Percent abundance calculated from the numerical abundance of each food type, expressed as the total number of prey items in each dropping.

The degree of similarity between wrybill and banded dotterel diets was calculated from the 'probability' method (as proposed by Morisita (1959) and modified by Horn (1966)) used by Pierce (1982a) for pied and black stilt diet overlap in the Cass river valley. The Morisita-Horn method is calculated by:

$$O_{ij} = O_{ji} = 2\sum(O_i \cdot O_j) / \sum O_i^2 + \sum O_j^2$$

where O_i and O_j = proportion of total diet of species
i and j taken from each food category.

This method is also the average of the estimates of alpha in the competition equations used by MacArthur and Levins (1967), and is therefore also used as the overlap measure in physical comparisons of microhabitat use. Overlap between diet and food resource could not be determined because of difficulties in conjunctive sampling of terrestrial and aquatic habitats. Zaret and Rand (1971) considered overlap values in excess of 0.60 to be significant when using the Morisita (1959)-Horn (1966) method, whereas Pierce (1982a) gave only moderate weighting to values up to about 0.70. When interpreting the results from this study, overlap values which exceed 0.70 are considered 'high', and therefore significant. Those in the range 0.50-0.69 are considered 'moderate' while those less than 0.50 are considered to be

'low'.

6.3.3. Food resource availability

In August 1983 a pitfall trapping programme was instituted on the Rakaia and Ashley rivers. Four 350ml pottles containing Gaults solution were placed in each of the representative terrestrial microhabitats on each river and emptied weekly from 27 August 1983 (on both rivers) to 2 December 1983 on the Rakaia and 7 January 1984 on the Ashley:

- (1) Less than one metre from the stream edge in shingle-dominated substrate and on gently sloping banks. Spacing was at five metre intervals;
- (2) On shingle substrate greater than 10m from water, but with substantial areas of low profile vegetation present (less than 300mm high and less than 20% ground cover);
- (3) On shingle substrate greater than 10m from water, and with little or no vegetative cover.

Traps were also placed in sand but the frequent dust storms rendered this impractical. Identification was generally only to the ordinal level, but with expert assistance the ground beetles were subdivided into:

- Actenonyx bembidoides White;
- Bembidion charile Bates;
- other Bembidion spp., all of which were smaller than B. charile;
- Curculionidae (weevils);
- Staphylinidae;
- other adult and larval Coleoptera.

Results from each microhabitat were pooled to determine average numbers for each group trapped. Numbers were then plotted against flows and assessed visually for seasonal and inter-basin differences.

6.4. Results

6.4.1. Microhabitat use

Microhabitat use and preference determination for wrybills, banded dotterels, pied stilts and South Island pied oystercatchers were analysed for observations made on both rivers. Observations were made during each breeding season, and were combined for all years and flows.

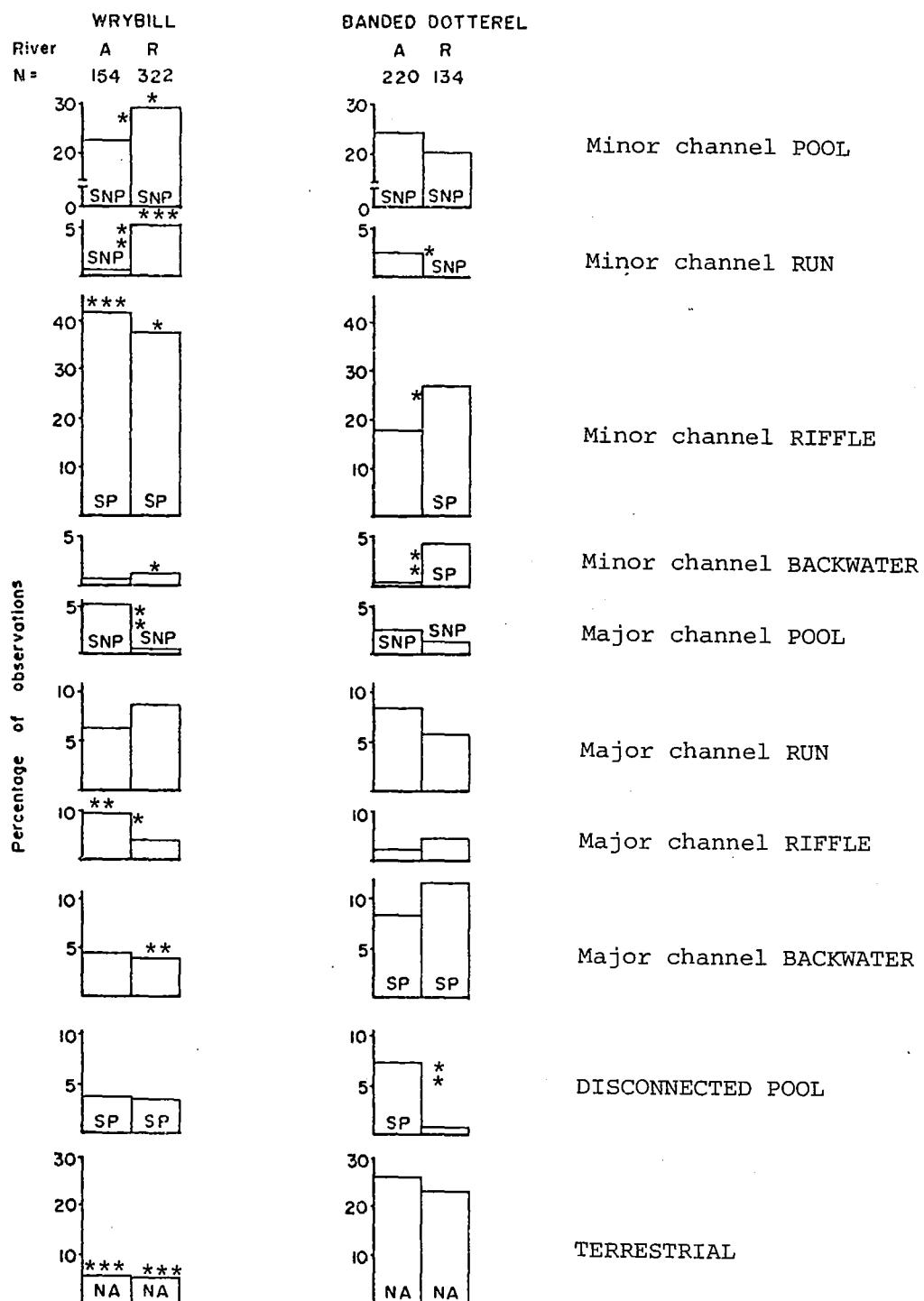
6.4.1.1. Wrybill and banded dotterel microhabitat use

There were few significant differences in the patterns of microhabitat use by wrybills between the Ashley and Rakaia rivers (Figure 6-1). Minor channel pools and runs were used significantly more on the Rakaia, while major channel pools and riffles were used at significantly higher levels on the Ashley. Banded dotterels on the Ashley used minor channel runs and disconnected pools significantly more often than those on the Rakaia, which in turn used minor channel riffles and backwaters significantly more than on the Ashley. The intra-specific/inter-basin overlap value for wrybills was 0.75, and for banded dotterels was 0.85.

Microhabitat preferences were generally consistent on an intra-specific inter-basin basis. Thus, wrybills showed significant selection against the use of minor and major channel pools on the Ashley and Rakaia rivers, and significant preference for minor channel riffles (see Plate 6) and disconnected pools. The only inconsistency occurred with minor channel run use, with wrybills on the Ashley displaying significant selection against use, as opposed to the Rakaia where there was no significant difference between use and occurrence.

Banded dotterels displayed similar patterns of microhabitat preference. As with wrybills, use of minor and major channel pools was significantly less than would occur if habitat use were random. There was a significant preference for major channel backwaters on both rivers, but only on the Rakaia for minor channel backwaters. A significant preference for minor channel riffles occurred only on the Rakaia, while a significant preference for disconnected pools existed only on the Ashley. Use levels for all other aquatic microhabitats were not significantly different from occurrence.

FIGURE 6-1 : Foraging microhabitat use comparisons for wrybills and banded dotterels on the Ashley and Rakaia rivers - spot observations - three seasons.



KEY: (i) Asterisks above columns indicate significant differences on an inter-specific, intra-river basis; while those on the sides of columns indicate intra-specific, inter-basin significant differences in habitat use.

* = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$

(ii) Letters in columns relate to habitat preferences and non-preferences.

SP = significant preference ($P < 0.05$)

SNP = significant non-preference ($P < 0.05$)

NA = not assessed

PLATE 6: An outstanding area of wrybill foraging and breeding habitat on the Rakaia river. (Note the minor braid pool-riffle sequence, and the non-vegetated terrestrial shingle substrate.)



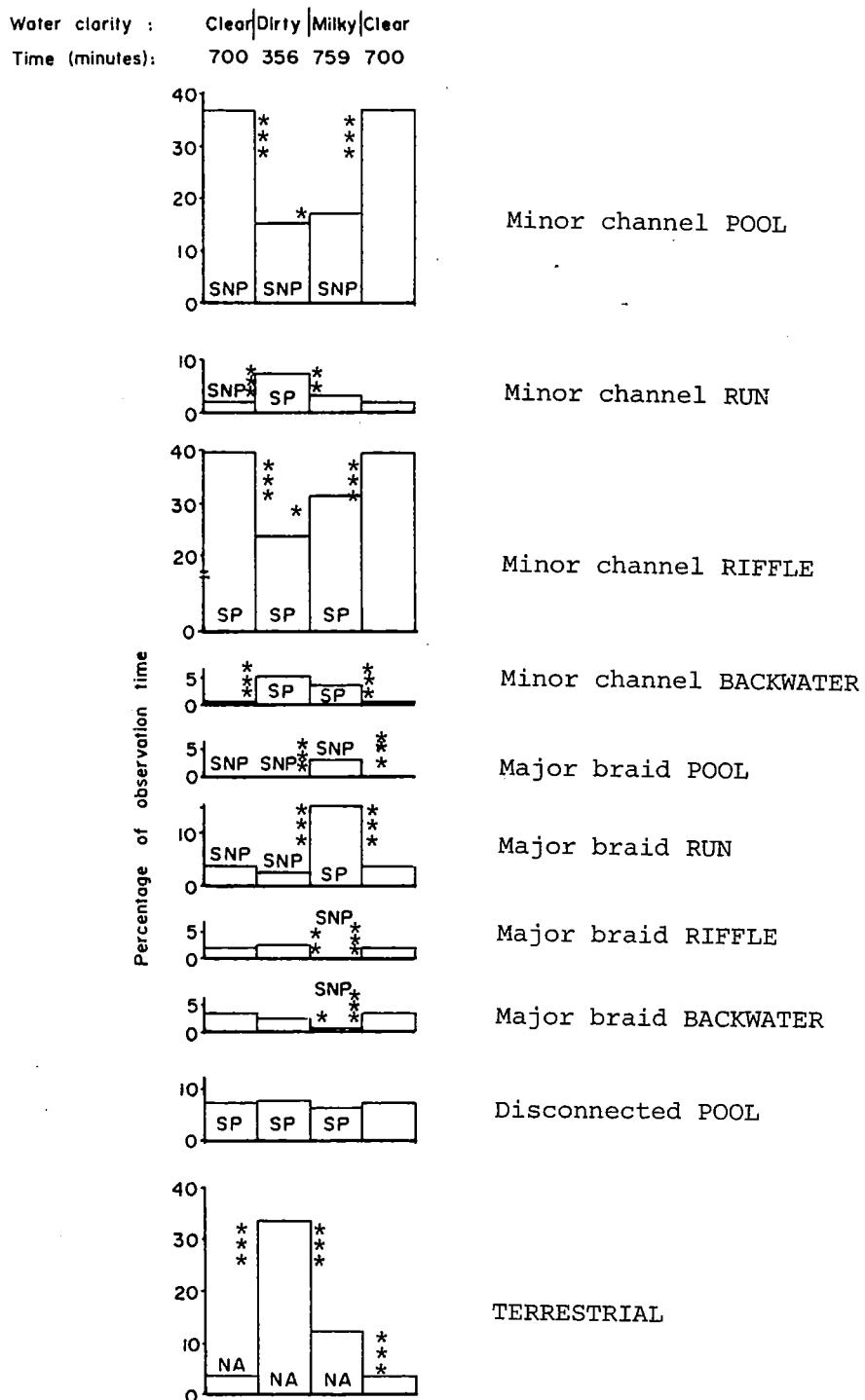
Terrestrial habitat was not assessed for preference because of problems with quantifying various combinations of habitat parameters, e.g., vegetation, substrate, slope, and distance from water. If, however, an attempt is made simply on the basis of quantifying preference by habitat area, it is clear that terrestrial habitat is selected against by all species.

Intra-specific variations in microhabitat use assist in identifying likely areas of highest overlap in relation to preference for, and selection against, the use of particular microhabitats. For the Ashley, wrybill use of minor and major channel riffles was significantly higher than for banded dotterels, while terrestrial habitat use was at a significantly lower level. On the Rakaia, wrybills were recorded significantly more often on minor channel pools, runs and riffles, and significantly less often on minor and major channel backwaters and terrestrial habitats. The wrybill-banded dotterel overlap on the Rakaia was 0.85 and on the Ashley was 0.74.

Wrybill time-budgets classified by flow (see Section 5.3.1) were analysed according to the patterns of microhabitat use. Differences between patterns of use were significant for all discharge classifications ($P<0.001$; Figure 6-2). Time spent foraging in minor channel pools dropped from 37.7% at clear flows to 15.1% when the river was dirty, but rose again to 17.7% as the river changed to milky. Differences between flows were all significant. Use of minor channel runs was significantly greater during dirty flows than at either milky or clear conditions. There was no significant difference between use levels at the latter flows. Foraging time in minor channel riffles was highest at 39.3% during clear flows, then declined to 23.4% when the river was dirty, and increased to 30.1% with the shift to milky conditions. All inter-flow comparisons were significantly different. Time spent in minor channel backwaters increased significantly with the change from clear to dirty river conditions. Subsequent declines in use as flows changed to milky and then to clear were not significant.

Major braid pools were used only during milky flows, with the level of use being significantly greater than at clear or dirty flows. Foraging in major channel runs was significantly greater during milky flows than during clear or dirty flows, but there was no significant difference between use levels during the latter conditions. There were

FIGURE 6-2 : Foraging time-budgets of wrybills classified by river condition on the Rakaia in the 1982 and 1983 breeding seasons.



KEY: (i) Asterisks beside columns indicate significant differences between adjacent columns.

* = $P < 0.05$ ** = $P < 0.01$ *** = $P < 0.001$

(ii) Letters in columns relate to habitat preferences and non-preferences.

SP = significant preference ($P < 0.05$)

SNP = significant non-preference ($P < 0.05$)

NA = not assessed

significant declines in the use of major channel riffles and backwaters as flows changed from dirty to milky, and rises in use with the change to clear flows. Again, no significant differences between the use made of clear and dirty flows in these microhabitats was evident. Foraging time at disconnected pools did not vary significantly over the range of flows examined, but terrestrial habitat use rose significantly from 3.4% at clear flows to 33.4% during dirty conditions, and then declined to 12.1% when the river was milky. Differences between all flows were significant.

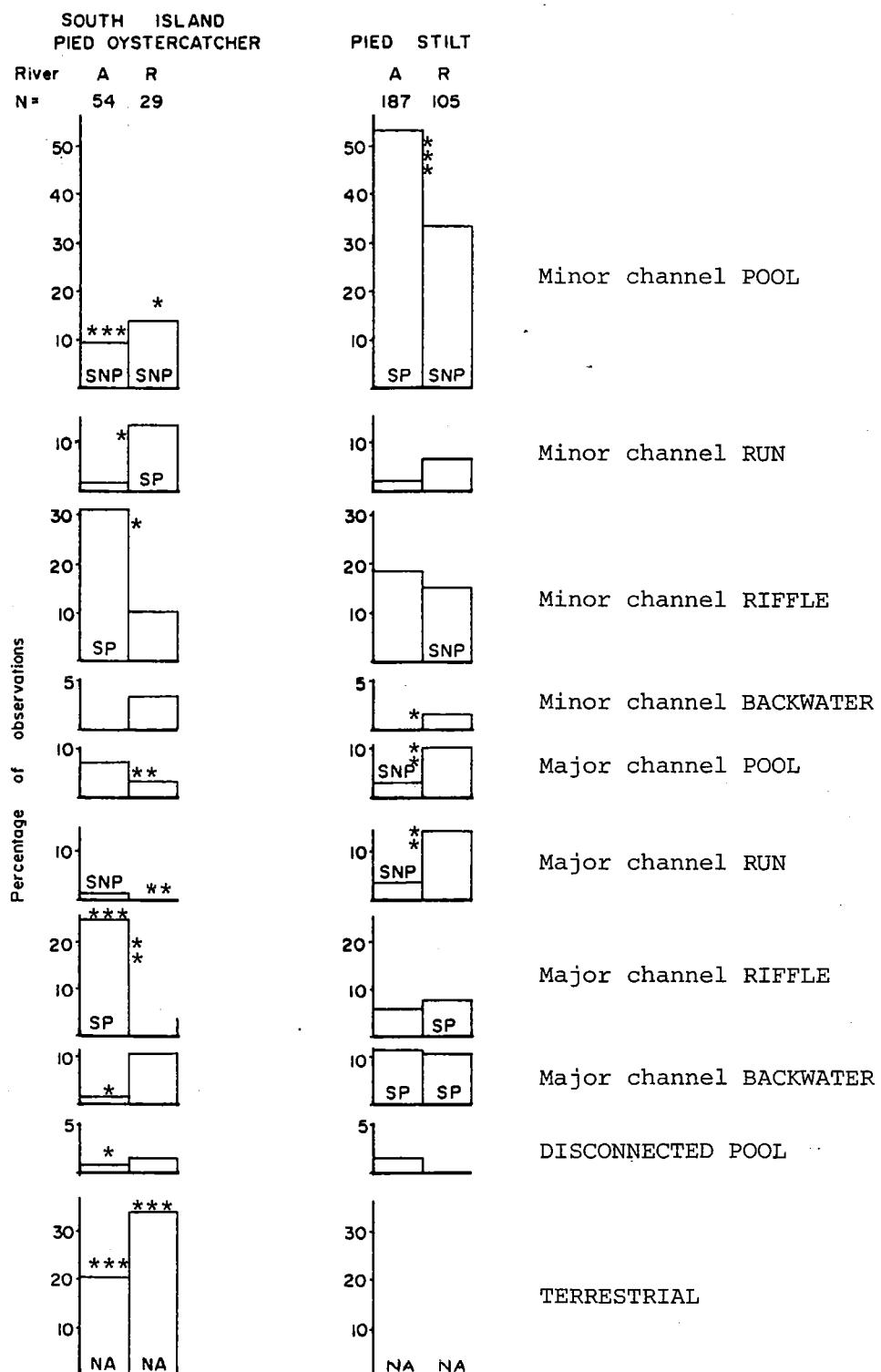
Wrybills displayed a significant preference for minor braid riffles and disconnected pools at all flows. There was significant selection against minor channel runs during clear flows, and a significant preference for them during dirty flows. Significant preferences for minor channel backwaters occurred during dirty and milky flows. A significant preference for minor braid runs existed at milky flows, but a significant selection against them was found during clear and dirty flows. There was also a significant selection against major channel backwaters during milky flows. Microhabitat overlaps by discharge for the Rakaia were 0.66 between clear and dirty flows, 0.80 between dirty and milky, and 0.85 between milky and clear flows.

6.4.1.2. Pied stilt and South Island pied oystercatcher microhabitat use

South Island pied oystercatchers foraged significantly more often in minor channel runs and on terrestrial habitat on the Rakaia than on the Ashley (Figure 6-3). Conversely, South Island pied oystercatchers on the Ashley foraged significantly more often on minor and major channel riffles. Other differences were not significant. Pied stilts on the Rakaia foraged significantly more in minor channel backwaters and major channel pools. On both rivers use was highest in minor channel pools (>30%) and lowest in terrestrial habitat (zero). The intra-specific/inter-basin overlap value for pied stilts was 0.66, and for South Island pied oystercatchers was 0.53.

A significant selection against the use of minor channel pools occurred for South Island pied oystercatchers on both rivers, with significant selection against major channel runs occurring only on the Ashley. South Island pied oystercatchers displayed significant preferences for minor and major channel riffles on the Ashley, but only

FIGURE 6-3 : Foraging microhabitat use comparisons for South Island pied oystercatchers and pied stilts on the Ashley and Rakaia rivers - spot observations - three seasons.



KEY: (i) Asterisks above columns indicate significant differences on an inter-specific, intra-river basis; while those on the sides of columns indicate intra-specific, inter-basin significant differences in habitat use.

* = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$

(ii) Letters in columns relate to habitat preferences and non-preferences.

SP = significant preference ($P < 0.05$)

SNP = significant non-preference ($P < 0.05$)

NA = not assessed

for minor channel runs on the Rakaia. Pied stilts showed a significant selection against minor channel pool and riffle use on the Rakaia, with a preference for major channel pools and backwaters. On the Ashley they had significant preferences for minor braid pools and major channel backwaters, with selection against major channel pools and runs.

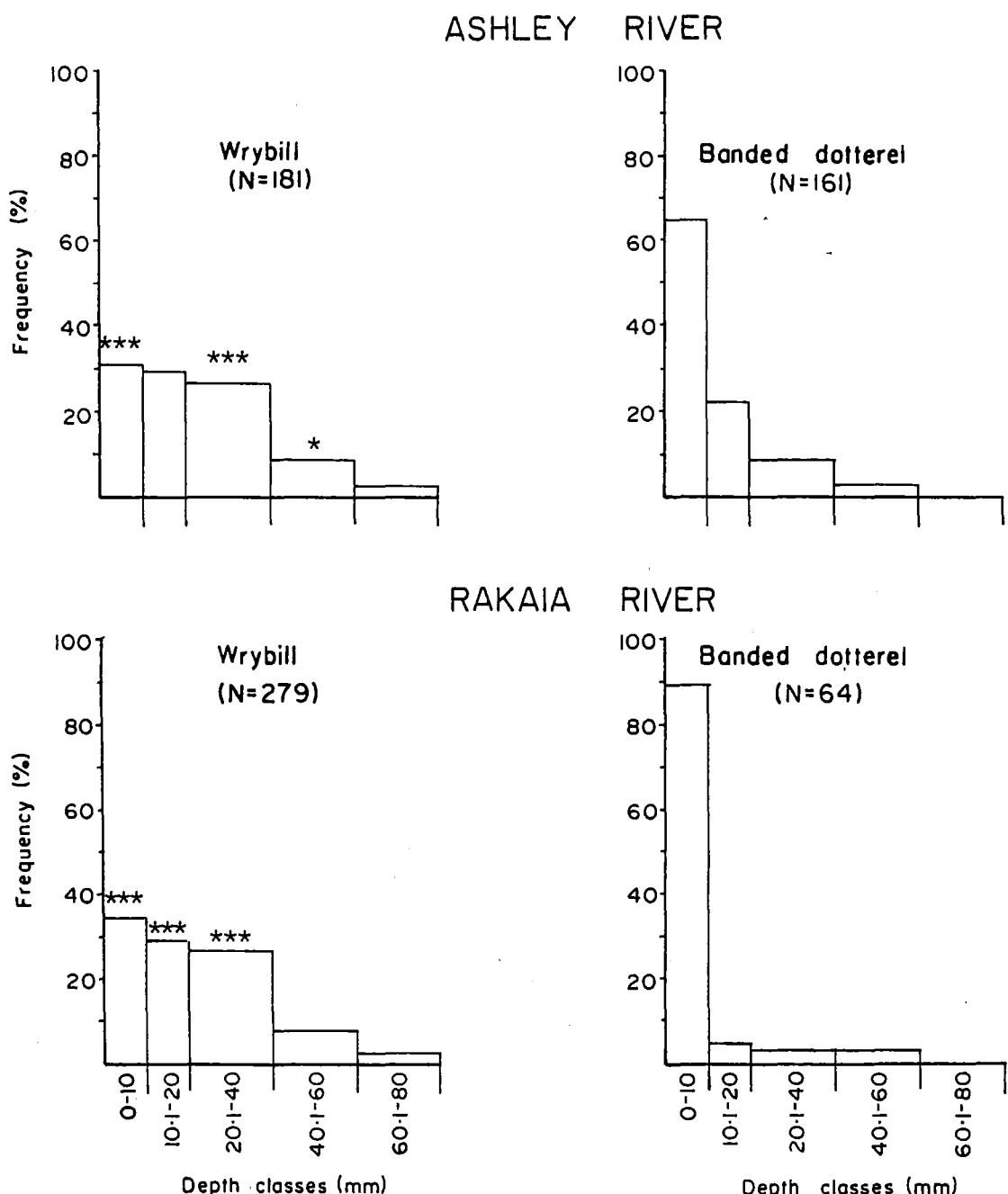
Pied stilts on the Ashley used minor channel pools and major channel backwaters significantly more than South Island pied oystercatchers, whereas the latter were observed more often on major channel riffles and terrestrial habitat. On the Rakaia pied stilts also used minor channel pools significantly more often than South Island pied oystercatchers, and they also used major channel runs significantly more often. In contrast, use of terrestrial habitat on the Rakaia was significantly higher by South Island pied oystercatchers than by pied stilts. Pied stilt-South Island pied oystercatcher overlap on the Ashley was 0.21, and on the Rakaia was 0.24.

6.4.1.3. Depth and substrate requirements

Foraging depths were measured for wrybills and banded dotterels at both study areas (Figure 6-4). Wrybills foraged mostly (>30% of observations) in shallow edge areas (0-10mm) but were also commonly recorded in water of 10-20 and 20-40mm depth on both rivers. There were no significant differences in the proportions of sightings made at each of these depths. Intra-specific wrybill overlap for feeding depths between the Ashley and Rakaia rivers was 0.86. Banded dotterels foraged more frequently in shallow edge microhabitats than wrybills on both rivers ($P<0.001$). However, on the Ashley they were recorded in depths of 10-20mm in similar proportions to wrybills ($P>0.05$). Water of 20-40mm was used significantly less on both rivers ($P<0.001$), but at depths of 40-60 and 60-80mm, where use levels were low (<4% of observations in each case), the difference from wrybills was significant only on the Ashley river ($P<0.05$). Intra-specific overlap for banded dotterels between the Ashley and Rakaia rivers was 0.77, while inter-specific overlap on the Ashley was 0.73, and 0.47 on the Rakaia.

Substrates present when feeding aquatically and terrestrially were recorded for wrybills and banded dotterels (Figure 6-5). On both rivers almost half of the wrybill observations were recorded on shingle substrate, with stones of secondary incidence on the Ashley, and sand on the Rakaia. Banded dotterels on the Ashley were also observed

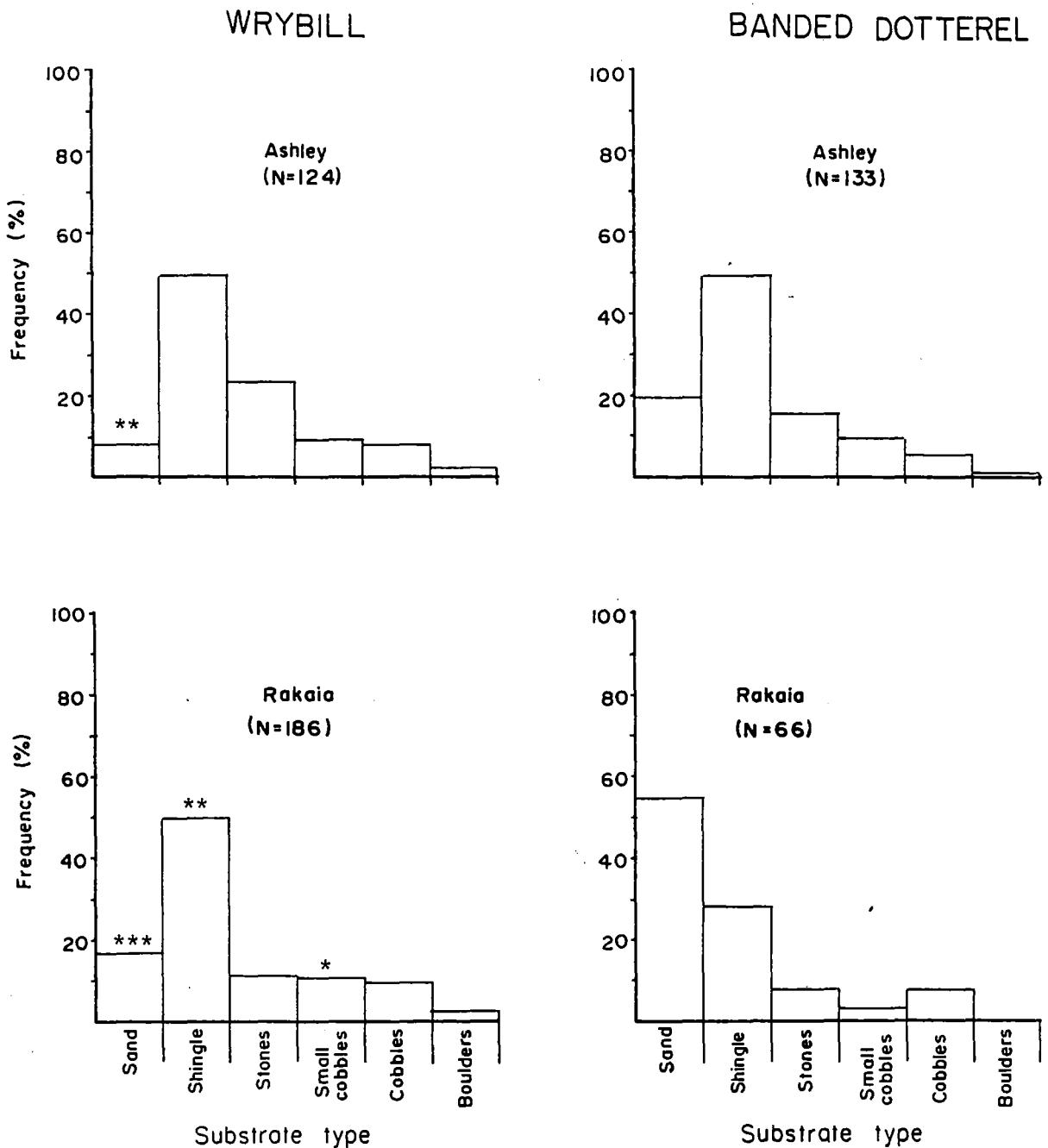
FIGURE 6-4 : Foraging depths of aquatically feeding wrybills and banded dotterels on the Ashley and Rakaia rivers - spot observations.



KEY: Asterisks above wrybill columns indicate significant differences with adjacent banded dotterel columns.

$$\begin{aligned} * &= P < 0.05 \\ ** &= P < 0.01 \\ *** &= P < 0.001 \end{aligned}$$

FIGURE 6-5 : Dominant substrates used by foraging wrybills and banded dotterels on the Ashley and Rakaia rivers - spot observations.



KEY: Asterisks above wrybill columns indicate significant differences with adjacent banded dotterel columns.

* = $P < 0.05$
** = $P < 0.01$
*** = $P < 0.001$

KEY: Substrate classes

S - sand = < 2 mm
Sh - shingle = 2-32 mm
St - stones = 32-64 mm
SC - small cobbles = 64-128 mm
C - cobbles = 128-256 mm
B - boulders = >256 mm

approximately half the time on shingle substrate, whereas on the Rakaia more than half of the observations were recorded on sand. The roles were reversed on both rivers for substrates of secondary importance. For the Ashley river the only significant difference in substrate type was for sand which was foraged over more often by banded dotterels ($P<0.05$). Similarly, on the Rakaia banded dotterels used sand significantly more than wrybills ($P<0.001$). However, wrybills were observed significantly more on shingle ($P<0.01$) and small cobbles ($P<0.05$). Intra-specific substrate overlap values were 0.90 for wrybills and 0.47 for banded dotterels between the two rivers, while inter-specific overlap on the Ashley was 0.79, and on the Rakaia was 0.49.

Substrate-water depth combinations were also examined for both species (Figure 6-6) on the Ashley and Rakaia rivers. Wrybills foraged at greatest depths on shingle substrates in both rivers, but for banded dotterels this occurred only on the Ashley. A pattern of decreasing foraging depth was also associated with the upward progression from substrates larger than shingle. Overlap values were calculated for the depth-substrate relationship. Intra-specific overlap values between rivers were 0.93 for wrybills and 0.66 for banded dotterels, while the inter-specific value for the Ashley was 0.74 and 0.45 for the Rakaia.

6.4.2. Diets of wrybills and banded dotterels

Wrybill and banded dotterel faecal remains were examined, and the results (Appendix 3) analysed by percent occurrence (Figure 6-7) and percent abundance (Figure 6-8). Adult beetles occurred in all banded dotterel and in more than 90% of wrybill faeces. Bugs were present in more than 90% of banded dotterel and more than 70% of wrybill droppings, with flies being found in more than 60% of wrybill and approximately 50% of banded dotterel faeces. Approximately 60% of wrybill faeces from the Rakaia contained mayfly (Deleatidium sp.) larval mouthparts, but only about 20% of banded dotterel remains from both rivers, and one third of wrybill faeces from the Ashley, contained the same remains. However, all wrybill faeces from the Ashley contained caddisfly and stonefly larvae. Other groups present in more than 20% of banded dotterel faeces from the Ashley and Rakaia rivers were beetle larvae, moth or butterfly larvae, wasps, and spiders. Wasps, spiders, and adult mayflies were found in more than 20% of wrybill faeces from both rivers, while almost

FIGURE 6-6 : Combination substrate-water depth used by foraging wrybills and banded dotterels on the Ashley and Rakaia rivers - spot observations.

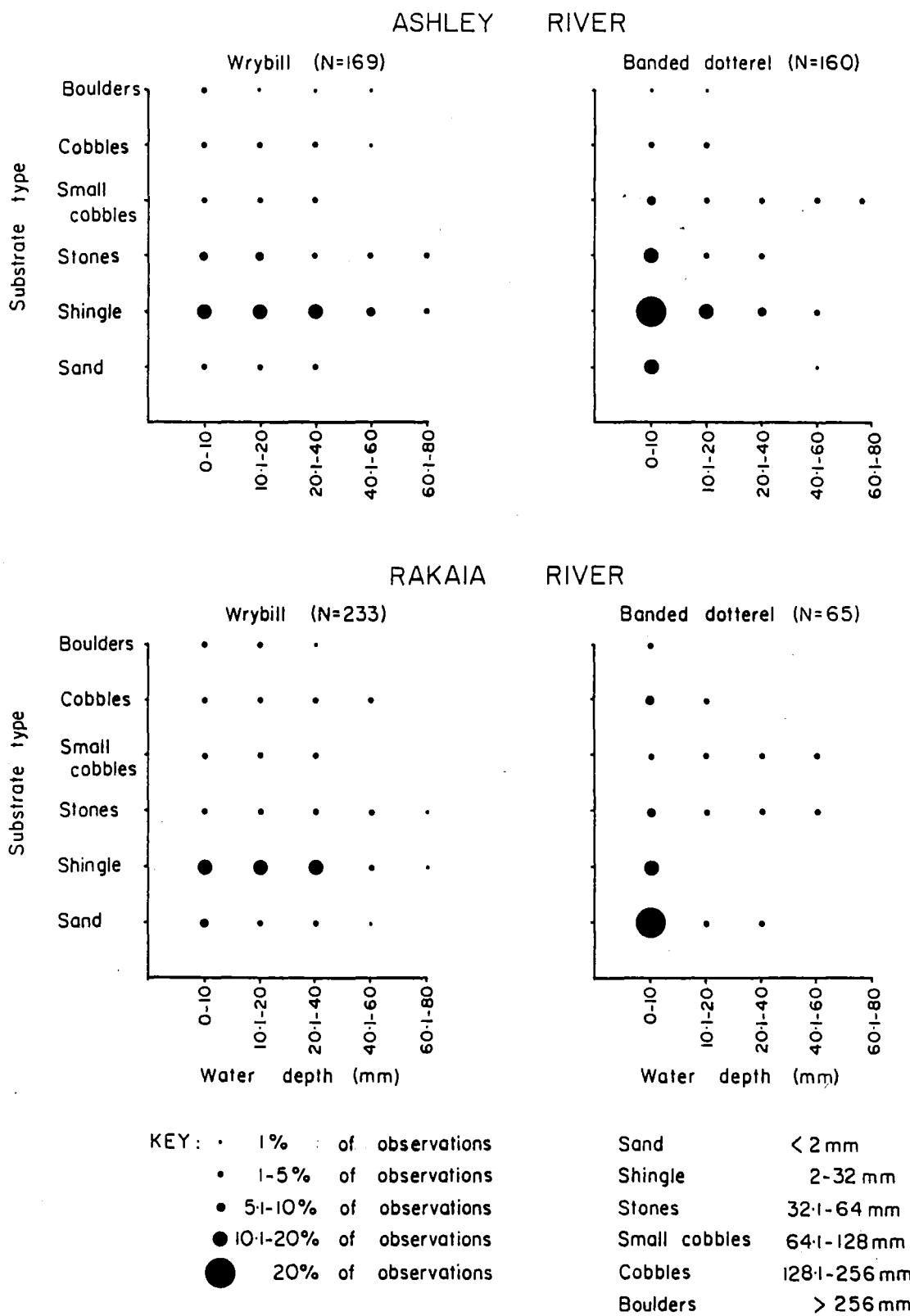


FIGURE 6-7 : Percent occurrence of food items in wrybill and banded dotterel faeces from the Ashley and Rakaia rivers.

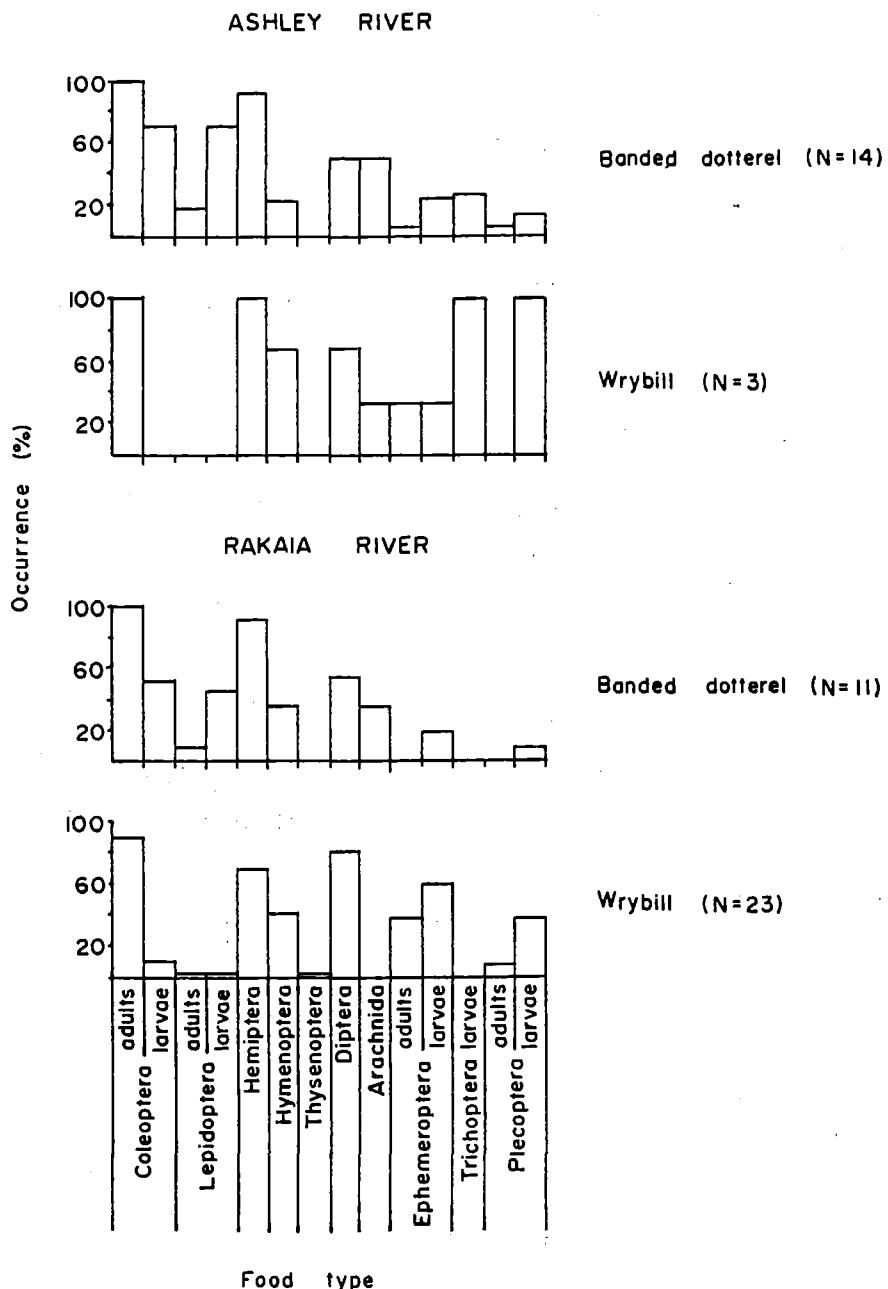
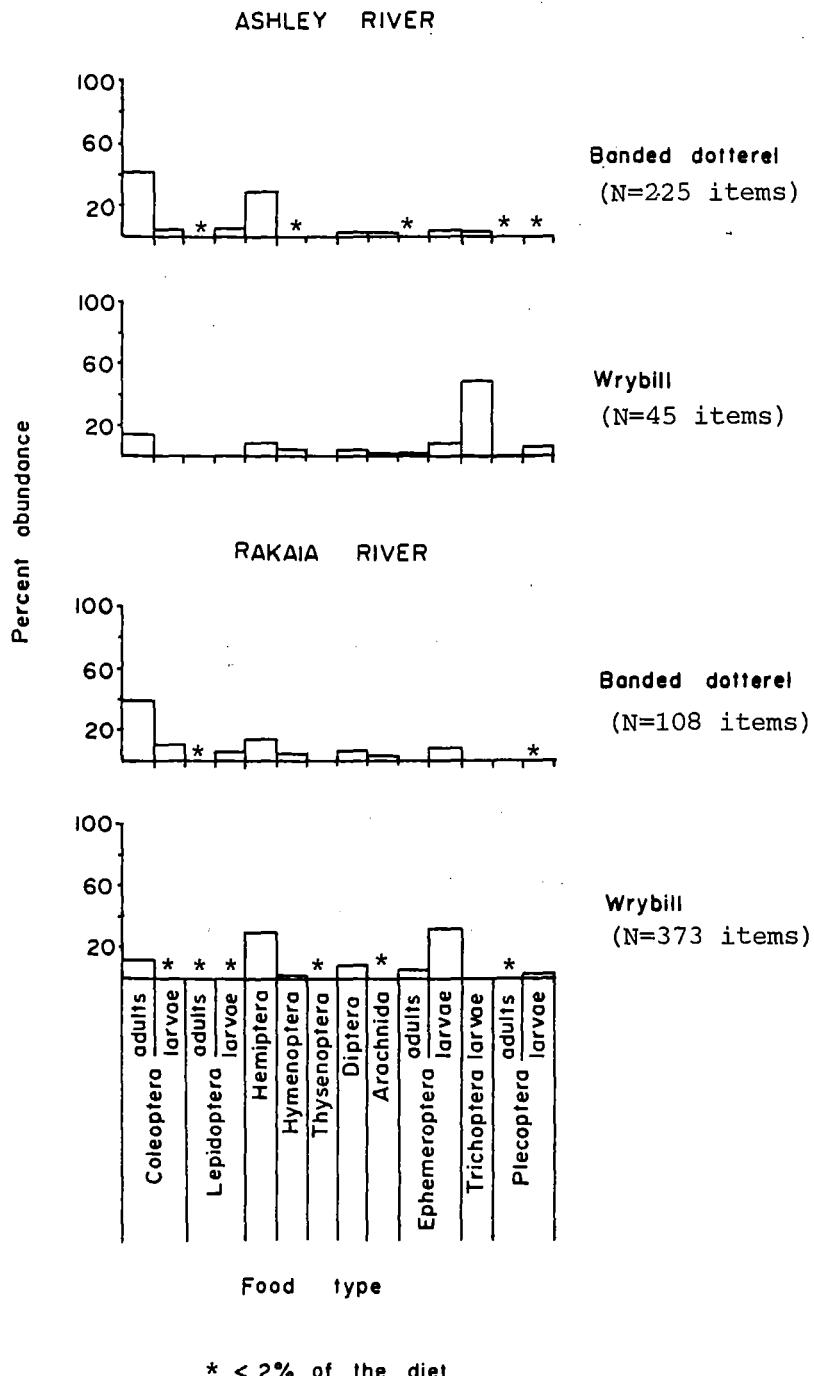


FIGURE 6-8 : Relative abundance of different food items in wrybill and banded dotterel faeces collected from the Ashley and Rakaia rivers.



30% of those collected from the Rakaia also contained stonefly larvae remains.

The relative abundance of different food items in the diet was difficult to determine. Diagnostic features for each order were used as a basis for determining total numbers in each dropping. For instance, beetle mandibles were considered as pairs when determining the number of beetles in each of the faeces. Where possible, mandibles of differing size and structure were separated because each represented a different species, and therefore another individual. A similar technique was used with fly wings, but in many cases fragmentation made it difficult to be as precise as with the beetle mouthparts. Spider remains were particularly difficult to distinguish, and apart from the legs there were no other identifiable diagnostic parts. Similar problems existed with adult Lepidoptera, and with the larval Diptera. In spite of these difficulties it was still considered worthwhile determining the relative abundance of each food type in the faeces.

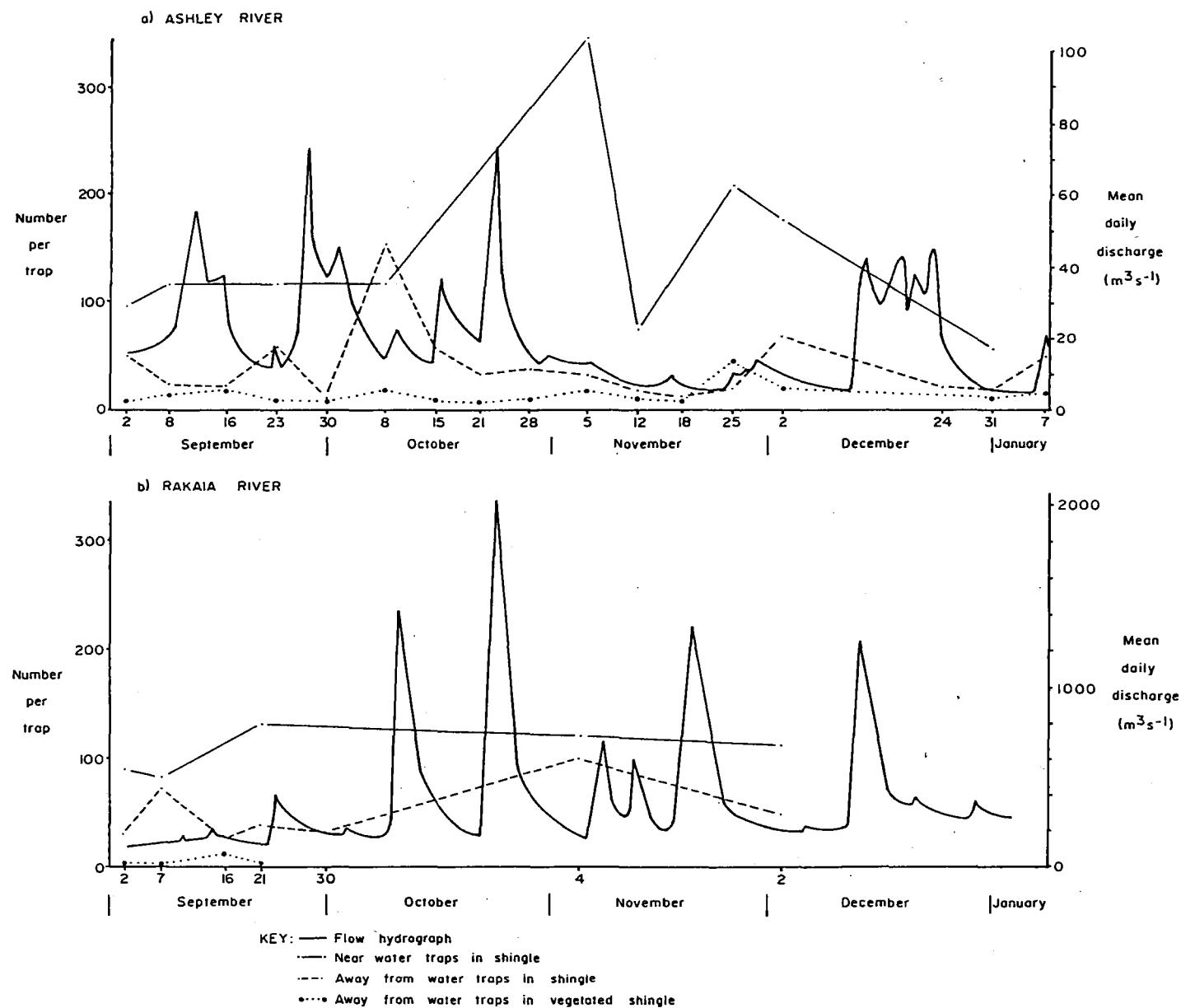
Adult beetles made up approximately 40% of the banded dotterel but less than 15% of the wrybill diet on both rivers. Bugs made up almost 30% of the banded dotterel diet on the Ashley, and of the wrybill diet on the Rakaia, yet fewer than 20% of each species' diet on the other river. Mayfly larvae comprised over 30% of the wrybill diet on the Rakaia river, whereas on the Ashley, caddisfly larvae made up approximately 50% of the diet. Dietary overlaps were:

- 0.09 for the intra-specific overlap calculated for wrybill on the Ashley and Rakaia rivers;
- 0.68 for the banded dotterel intra-specific overlap between the two rivers;
- 0.15 for the wrybill-banded dotterel overlap on the Ashley; and
- 0.33 for the wrybill-banded dotterel overlap on the Rakaia river.

6.4.3. Terrestrial invertebrate productivity

Weekly mean numbers of all insects per pitfall trap were plotted according to sampling site (Figure 6-9) and compared visually with the flow regime of each river. The pitfall trap records are presented in Appendix 4. Small to medium freshes had a severe impact on the 'near water' sampling sites, with only small rises flooding the traps. Larger floods, such as those on the Rakaia during 1983, completely nullified the sampling programme for long periods, and often resulted in major

FIGURE 6-9 : Total invertebrate numbers per pitfall trap in three sampling locations on the Ashley and Rakaia rivers in 1983.



morphological changes to sites. This necessitated the selection of new 'near water' sites on the Ashley (twice), and of all sites on the Rakaia (five times). Moreover, several floods on the Rakaia were so severe that they almost completely removed low profile, sparse vegetative cover. This is reflected in the lack of sampling from this habitat type after 21 September. Trampling by cattle on both rivers, and the attention of vandals and wave action from jetboats on the Ashley, also affected several 'near water' sampling sites.

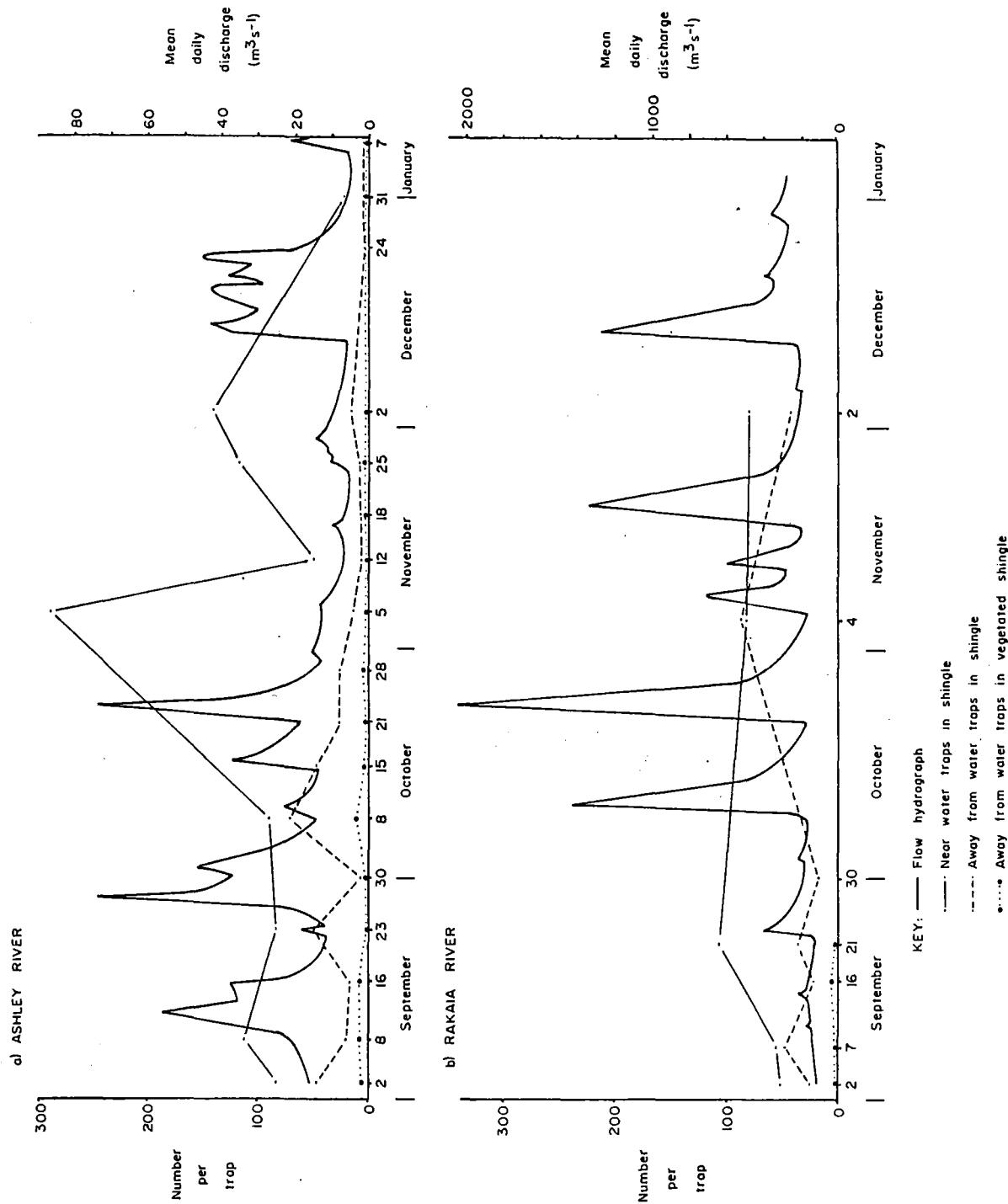
On both rivers, insect numbers varied according to sampling site. Numbers caught in 'near water' traps on the Ashley were, with only one exception, always greater than on shingle substrate away from water. The latter, also with one exception, contained more than traps located in partly-vegetated areas. Without exception, traps on the Rakaia located near water contained more invertebrates than those on shingle away from water, which in turn contained more than those in areas of low profile immature vegetation. In general, there was little difference between the Rakaia and Ashley during September, when the greatest successful sampling overlap occurred. Numbers caught in 'near water' traps on the Ashley fluctuated sharply in association with changes in site location after freshes; the highest counts, on 5 November and 25 November, followed freshes. In spite of similar site changes on the Rakaia, these dramatic fluctuations in numbers were not evident, suggesting lower densities on this river.

Beetles, principally Actenonyx bembidoides and Bembidion spp., were the dominant animals collected (Figure 6-10). On the Ashley more were caught in 'near water' traps than in bare shingle away from water, and in turn more were caught there than in vegetated sites. The proportion of beetles in the catch declined with distance away from water, and with increasing vegetation density.

6.4.4. Wrybill feeding behaviour

Pierce (1976) examined the foraging behaviour of wrybills on the upper Rakaia and Cass rivers. In this study the feeding actions of wrybills in the lower Rakaia and Ashley rivers were checked against those in the upper reaches (Table 6-2). To obtain a direct comparison, all of Pierce's three direct peck classifications were included as pecks, and his five classes associated with clockwise, probe and miscellaneous movements were combined and jointly defined as probing.

FIGURE 6-10 : Numbers of Actenonyx bembidoides and Bembidion spp. (Order Coleoptera) per pitfall trap in three different microhabitats on the Ashley and Rakaia rivers in 1983.



There was a highly significant difference between proportions occurring in the upper and lower reaches ($P<0.001$).

TABLE 6-2: Wrybill feeding methods on the lower Ashley and Rakaia rivers combined, compared with those determined on the upper Rakaia by Pierce (1976).

	Dirty Pecks probes		Milky pecks probes		Clear pecks probes		Total pecks probes	
	%	%	%	%	%	%	%	%
Pierce (1976)	-	-	-	-	-	-	59.5	40.5
This study	99.1	0.9	98.7	1.3	96.4	3.6	98.1	1.9

6.5. Discussion

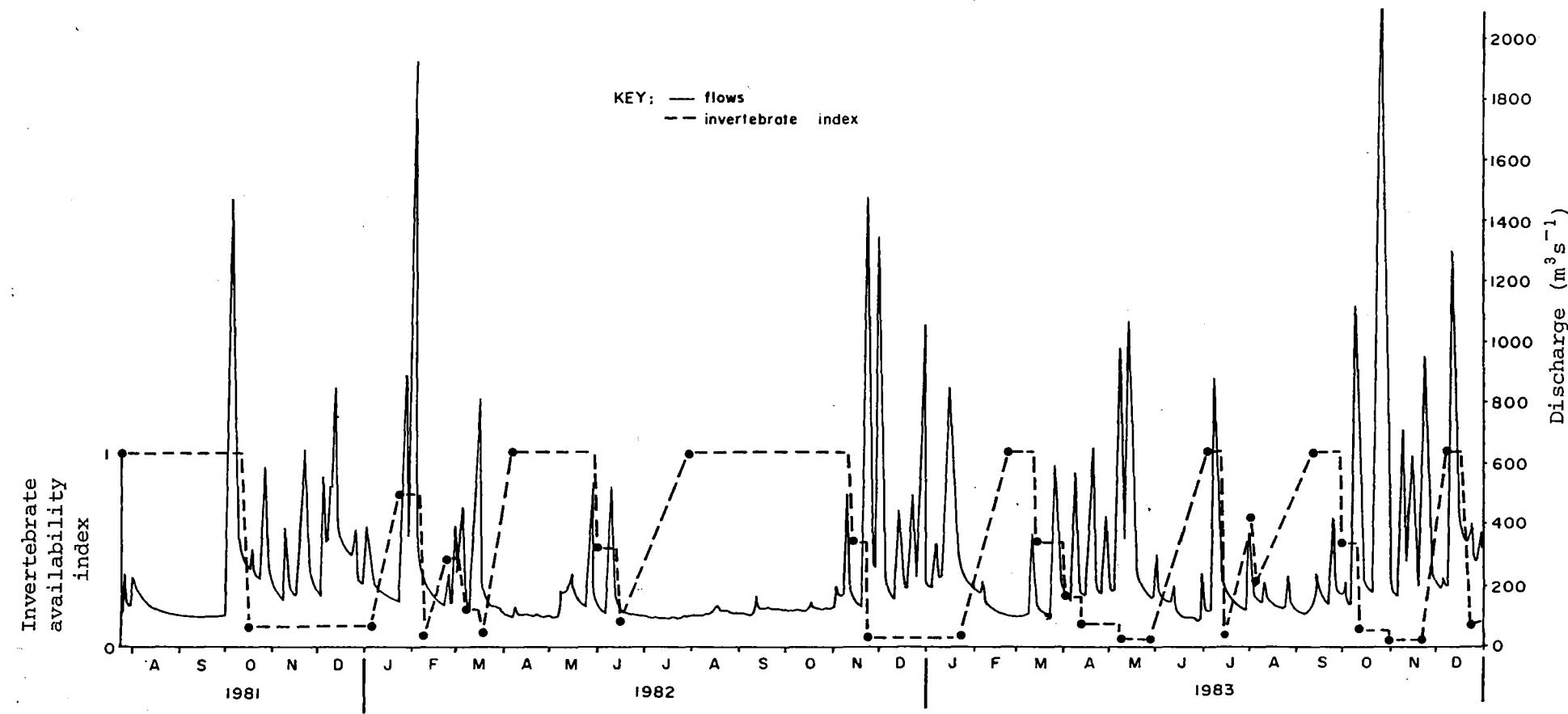
6.5.1. Microhabitat use and preferences

Microhabitats associated with minor channels were preferred by all the wader species studied. However, use patterns varied markedly according to the morphological and behavioural characteristics of each species. The long thin legs and bill of pied stilts were suited to slow flowing microhabitats with sandy substrates such as pools and backwaters, whereas the shorter but stouter legs and bill of the South Island pied oystercatcher enabled stony substrate in riffles to be used, and at greater depths than frequented by either banded dotterels or wrybills. Although wrybills fed at shallower depths than either pied stilts or South Island pied oystercatchers, they were often in significantly deeper water than banded dotterels. These greater depths could be expected to be associated with riffle-foraging on a shingle substrate. Larger substrate sizes would tend to make foraging more difficult and probably less rewarding, while sand, which was the dominant feeding substrate for banded dotterels on the Rakaia, is generally not found in riffles, but rather in pools and backwaters which were used extensively by this species.

Robertson et al. (1983) classified water depths as <80mm, 80-160mm, and >160mm, and substrate as sand (<10mm), fine shingle (10-60mm), cobbles (60-200mm), and boulders (>200mm in diameter). Wrybills and banded dotterels observed during the Ahuriri study were generally found in water less than 80mm deep (Robertson et al., 1983). The use of such coarse subdivisions is justifiable in a study which examines the great range of species inhabiting a wetland like the Ahuriri river catchment. However, when these subdivisions are then used to determine precise habitat overlap (Robertson et al., 1983), calculated values may greatly overestimate the true extent of overlap. To avoid this problem, water depths and substrate were examined in more detail in this study. Consequently, it has been shown that wrybills tend to forage in deeper water than banded dotterels, and on both rivers these differences were significant between the two species, as were differences in substrate type used. The substrate classification used here had the added advantage that it could be compared directly with that used by Mosley (1983a) and Glova and Duncan (1985) when modelling changes in available habitat as a function of discharge (see Chapter 7).

Wrybills, banded dotterels and South Island pied oystercatchers used a broad range of aquatic microhabitats and also foraged extensively over terrestrial substrates. In contrast, pied stilts foraged only in aquatic microhabitats on both rivers. Furthermore, pied stilts were the only birds that preferred to feed in pools and this, in association with their totally aquatic feeding, separated them from the other species. This lack of flexibility helps explain the patterns of microhabitat use made by pied stilts on the Ashley and Rakaia rivers. Whereas the Ashley is characterised by declining monthly mean flows during the breeding season, the Rakaia is characterised by instability and rising monthly mean discharges. Ashley flows favour high aquatic invertebrate productivity and therefore encourage use by pied stilts, while on the Rakaia aquatic invertebrate availability roughly matches the fluctuating flow regime (see Figure 6-11). Hence the lack of pied stilts breeding on the Rakaia in 1981 and 1983, and after the November floods of 1982, is because they could not get enough food. Large numbers of pied stilts on foothills sourced rivers such as the Ashley and Ashburton reflect breeding season flow stability and high invertebrate densities. Pierce (1982a) attributed a lack of pied stilts breeding on the active riverbed of the Cass river to the same flow instability. Other species,

FIGURE 6-11 : Proposed invertebrate availability index for the Rakaia River over the period, August 1981 to January 1984.



including wrybills, banded dotterels and South Island pied oystercatchers, have the ability to make use of terrestrial invertebrates at such times. It follows, albeit indirectly, that wrybills and banded dotterels require an adequate supply of both aquatic and terrestrial food resources for successful breeding.

6.5.2. Overlap in microhabitat use

In this study of the foraging-hydrology relationship, overlap values were determined for five parameters, and for intra-specific and inter-specific relationships. Four of these parameters related principally to physical aspects of microhabitat use, and the fifth to diet. Intra-specific overlap values between rivers for wrybills were high for all the physical parameters measured. This shows that in spite of major seasonal variations in river flow regimes, the overall pattern of microhabitat use between the Ashley and Rakaia rivers is very similar. When the same intra-specific values are compared with those for banded dotterels, microhabitat and depth overlap values were high, substrate overlap was moderate, and depth-substrate overlap was low. In effect, the depth, substrate, and depth-substrate parameters are more detailed classifications of the initial microhabitat separation. The higher values for wrybills seem to indicate strong underlying behavioural patterns that occur despite the major hydrological differences between the two rivers.

Inter-specific microhabitat overlap values were high on both the Ashley and Rakaia rivers. On both rivers banded dotterels were significantly greater users of terrestrial habitat than wrybills, and in addition they showed a consistent preference for major channel backwaters. It is apparent from these high values for overlaps in microhabitat classification that even at this relatively refined level of separation (compared to Robertson *et al.*, 1983) critical dividing parameters could not be identified.

6.5.3. Diet composition and overlap

The final, and perhaps most critical, overlap measure is diet. Previous workers have based conclusions on assessments which have not included diet studies, e.g., Pierce (1979), Robertson *et al.* (1983) and Hay (1984). Faecal analyses show that both species have broad diets, befitting their description as opportunist feeders (see Figure 6-7).

Although the sample number of wrybill faeces from the Ashley is very small, it was nevertheless considered worthwhile to include the sample within the analysis. With a few minor exceptions the same range of food items was included within the overall diet of both species. Not surprisingly, however, only Ashley river samples contained the identifiable remains of caddisfly larvae. This was the most noticeable difference between species on the two rivers, and it occurs because only on the Ashley is the flow regime stable enough for stony-cased caddis to survive. Note also that although the diet was broad at the ordinal levels studied, it is highly likely that resolution to finer taxonomic levels would highlight feeding diversity. Furthermore, conclusions about opportunist feeders which are based only on percent occurrence in the diet are unlikely to yield adequate information on overall food overlap.

Evaluation of the relative abundance of different food types in the total diet can be used to discount the assumption that Pierce's (1979) results on the upper Rakaia are universally applicable to all other wrybill habitats. Pierce (1979) concluded that mayfly larvae appeared to be the staple diet of wrybills on the Rakaia river. Others, including O'Donnell and Moore (1983) and Sagar (1983a), have applied this conclusion to other rivers and sections of rivers. Although mayfly larvae were the dominant single food, the relative contribution to total diet was only about 30% on the Rakaia, and 10% on the Ashley. This result supports the suggestion that dietary studies which draw conclusions from the experimental provision of food and direct observation of an opportunist feeder, may well provide misleading results. Caution is also required in making quantitative conclusions from the faecal analysis carried out in this study. While the mandibles of beetles and mayfly and stonefly larvae persist in the faecal remains, other soft bodied insects with sucking mouthparts or easily broken wings, such as flies, are more difficult to identify in the diet. As a result the relative importance of flies and spiders may have been substantially underestimated, especially because both were particularly common in the pitfall traps. Moreover, some sample sizes were not large.

Diet overlap between wrybills and banded dotterels was low on both rivers, which was surprising in view of the high levels of microhabitat overlap. This difference in diet overlap should again be treated with caution since more intensive taxonomic resolution would again almost certainly prove it to be lower than is shown here. Allowing for this, the diet study and overlap indices have shown that any competition between the species may be reduced significantly by concentrating on different food items. No inferences concerning competitive exclusion between the two species can be drawn because of conflicting results from the different parameters. It would be dangerous therefore, to suggest that competitive exclusion is occurring on one or other of the study areas without further detailed research.

6.5.4. Food resource provision and availability

Water edge feeding (0-10mm) is important for both wrybills and banded dotterels. Invertebrate numbers in pitfall traps located less than one metre from water were almost invariably greater than in the other microhabitats sampled. Hay (1984) carried out a short term pitfall trapping programme on the upper Rakaia, but unfortunately he lumped the results from all surveyed microhabitats so the results contribute very little to an understanding of terrestrial food resources. Pierce (1979) sampled the terrestrial substrate by direct counting, a method criticised by Herron (1981) because of the potential for underestimating beetle numbers. Although there is no delineation between the sampled microhabitats, and remembering the sampling difficulties, Pierce's results suggest that terrestrial invertebrate numbers increased as the breeding season progressed. Warmer temperatures on the lower compared with the upper Rakaia river, which Pierce studied, probably resulted in the presence of a more diverse terrestrial fauna earlier in the season and, although not directly comparable, would indicate a greater density of terrestrial invertebrates available for feeding.

Sagar (pers. comm.) found that terrestrial beetles are an important component of surface and sub-surface drift in the Rakaia. Thus, although floods often interrupted the 'near water' sampling programme, drift of terrestrial invertebrates probably provided an important food source for banded dotterels and wrybills. This supports Herron (1981) who observed that during the rising stage of a flood there

is not a 'mad scramble' by beetles hurrying to keep out of the water's reach. However, it conflicts with her assumption that during floods some Bembidion species remain in situ. The latter is plausible only if the substrate is not moving, or if the insects burrow into the substrate. For instance, sometimes on the Rakaia and Ashley rivers small freshes flooded pitfall traps although not disturbing their positions, but larger floods led to their displacement and loss. During these larger floods it seems certain that beetles would be washed into the drift and moved downstream into backwaters or small eddies where they would fall easy prey to birds.

An attempt to portray the availability and provision of aquatic food has been made, based on the work of Sagar (1983a, 1983b). Invertebrate density in samples from riffles was determined for major and minor channels (Sagar, 1983a), and recolonisation rates of previously dry channels (Sagar, 1983b). Together the two studies can be combined to provide the basis for an index of invertebrate availability which is a direct function of discharge. Sagar (1983b) showed that invertebrate recolonisation of a previously dry channel of the Rakaia was complete after 33 days in winter, and 15 days in summer. Invertebrate numbers were also found to be higher in minor channels than in major braids, although the difference was significant in only one of 14 sampling days spread over a survey year. Although floods depressed invertebrate numbers, they did not destroy them over a mean daily flow range of 112-850 cumecs (Sagar, 1983b). This highest mean daily flow equated with a peak instantaneous discharge of 1371 cumecs. From an examination of Sagar's results it appears that floods of up to about 1500 cumecs depress invertebrate densities by about half the pre-flood levels, but at the same time also play a role in recolonising other areas. Larger floods which approach or exceed the bankful discharge, appear likely to reduce densities to extremely low levels.

An index of one is given to aquatic invertebrate availability after a long period of stable flow. Although it takes no account of seasonal changes this index appears to be the sustainable level under average to low flow conditions. Freshes and small to medium floods lead to a decline to half the pre-flood level, or an index value of about 0.5. Larger floods probably reduce the index to at least 0.1 of pre-flood invertebrate availability.

For freshes and floods resulting in a 50% decline in the invertebrate availability index, periods of 17 and 8 days respectively should be allowed for full winter and summer recolonisation. For larger floods, which may result in substantial changes to bed morphology and therefore the braiding pattern, the full recolonisation periods should be allowed for in calculating the index values. Sagar's winter experiment was extended slightly past the end of the winter solstice (September 22). In this study, and in order to fit in with the bi-monthly time-budget periods, the winter-summer split has been made on 30 September, of each study season. The index established here is an extension of the results of Sagar's one year study which was completed in July 1981 (Figure 6-11). Thus, the index covers the three breeding seasons of this project.

Aquatic invertebrate densities in samples on the Rakaia are typically much higher in winter (stable flows) than during late spring and summer (see Sagar, 1983a). Steeper recovery slopes during summer indicate faster recolonisation rates than occur during winter. Apart from September and early October, 1981, when index values were near unity, index values during the breeding season were consistently low. Following the large flood in October the river was very unstable throughout the rest of the breeding season (until the end of December), with an average period of 8.8 days between floods of a mean daily flow in excess of 300 cumecs, and 14.7 days between those exceeding 500 cumecs. In 1982, the river remained stable for much of the winter and the subsequent breeding season until early November. Index values were high until 11 November when they began to decline. Several large floods occurred after this date with the mean flood interval being 8.8 days for those exceeding 300 cumecs, and 10.2 days for those in excess of 500 cumecs. Index values were low for most of the 1983 breeding season; the maximum value of one was most likely reached for a limited period in September and then again in early December and January. The wildly fluctuating flow regime at other times would be reflected by low invertebrate availabilities. The average interval between mean daily flows exceeding 300 cumecs was 10.1 days, and for those in excess of 500 cumecs was 16.8 days.

Because of the variable invertebrate availability, the index established here may prove as reliable as the results from a long term aquatic invertebrate study. As expected, floods on the Rakaia led to dramatic declines in invertebrate availability, but seldom to the extremely low levels reported by Pierce (1979). The reasons for this are unclear but may reflect substrate differences, or even sampling method.

Birds which feed both terrestrially and aquatically appear more able to cope with the impacts of aquatic resource depletion than are those which feed only aquatically. The reduction in the aquatic invertebrate index due to flooding in all three breeding seasons probably led to the almost complete abandonment of the river as a pied stilt breeding habitat. Furthermore, the low proportion of wrybill and banded dotterel breeding pairs which attempted to renest after the loss of first clutches in 1982 and 1983 is probably attributable to this resource depression. The higher proportion of banded dotterels renesting on the Rakaia in 1983 was probably a result of the greater proportion of time spent feeding in terrestrial habitats, for which the supply of invertebrates was restricted, but not to the same extent as in the aquatic habitats. At the same time the more stable flows in the Ashley would have maintained invertebrate availability at high levels in aquatic and terrestrial habitats.

6.5.5. The impact of fluctuating flows on patterns of resource use

Flooding has a greater and more sustained impact on resource depletion in aquatic habitats than on terrestrial ones. Even after flooding of terrestrial areas pitfall traps tended to capture similar numbers and species of invertebrates. The ability of many terrestrial insects to fly and the probable rapid recolonisation from riparian areas, may well contribute to this. By contrast, floods of medium size and larger, result in long periods of medium to low aquatic invertebrate densities in samples (Sagar, 1983a), which in some seasons may have contributed to the ultimate abandonment of breeding by wrybills. This appears to be more common on high country rivers where resource depression is probably greater, due to the relatively heavier impact of flooding, and slower recolonisation rates because of lower upstream water temperatures. Thus, in 1983 wrybills on the Cass river abandoned

breeding early in the season (Pierce, pers. comm.), but on the Rakaia study area some pairs attempted to renest and one was successful. The greater terrestrial invertebrate diversity and density on the lower Rakaia and Ashley rivers, and the higher numbers of aquatic invertebrates present despite the impact of flooding, mean that wrybills in these areas have an advantage over their high country counterparts. For feeding at least, birds on the lower sections of rivers appear to be more likely to obtain the resources necessary for breeding in marginal seasons than those breeding in other areas.

Predictions concerning the impact of lowered flows are much more difficult to make. Long periods of stable flows typically imply a declining discharge, which in turn has been assumed to result in a fall in the number of minor braids as they dry up (Davis, 1979; Bowden *et al.*, 1982). Mosley (1982a) found no relation between number of channels and discharge over a flow range of 25-500 cumecs in the Ohau river, but he did find on the Rakaia that as flows dropped below the mean discharge the number of braids in a cross-section declined (Mosley, 1984). Glova and Duncan (1985) observed the loss of some minor braids in two study sections of the Rakaia river as flows declined, and Duncan (pers. comm.) considered others may have dried up had the experimental reduction of flows been continued for longer periods. Furthermore, the flows studied in the Glova and Duncan experiment were generally within the range of natural low flows, so that the major difference was in the speed of channel loss rather than an increase in number.

Whether or not the short term loss of one or two minor braids in a channel cross-section will have a major impact on the patterns of resource use and provision, and ultimately on breeding success, is problematical. Gravel throughflow is an important component of river flow at all times, and it may be that even if surface flow dries up, a continued underflow will remain. Research overseas has shown aquatic invertebrates capable of surviving deep in the substrate. Williams and Hynes (1974) found ephemeropteran larvae to a depth of 700mm in the substrate with a usual maximum depth of about 400mm. Furthermore, the number of animals occurring on the substrate surface of this North American river were much lower than numbers beneath it. Samplers which measure only the top 50-100mm of the substrate could grossly underestimate invertebrate densities. During temporary periods of no surface flow the fauna may well move deeper into the substrate, where

water could still be flowing. The large amount of interstitial space in the uncompacted gravels of the Rakaia could act as a bank for subsequent recolonisation when surface flow resumes. A similar response may also occur during floods.

During Sagar's (1983a) summer recolonisation experiment, samples from a riffle in a permanent side braid were taken at the beginning and end of the study. Despite a substantial flood shortly before the second sample was collected, invertebrate densities remained almost unchanged, yet those taken from the recolonisation channel were considerably lower. Unfortunately, Sagar used different sampling devices in each site. Without an examination of the respective sampling efficiencies of the two techniques it is difficult to make an accurate assessment of this result. Despite this limitation, the results still warrant comment. If the findings of Williams and Hynes (1974), and those of Clifford (1966) who found that the surface fauna may move deeper into the substrate during spates, can also be applied to a river like the Rakaia, then the apparent anomaly in Sagar's findings may be explained as follows:

- (1) The flood caused bed load movement which resulted in a rise in the level of invertebrate drift, and at the same time a movement of others deeper into the substrate. This would lead to a temporary decline in invertebrate numbers recorded in samples, but in the permanent flow channel these would quickly recover as flows stabilised and there was a reverse movement of invertebrates back to the substrate surface;
- (2). In the experimental channel, which had previously been dry for a long period of time (Sagar, pers. comm.), the initial process of recolonisation would mainly have occurred from downstream drift. This would mean the first area to be colonised was the substrate surface. Presumably, colonisation to greater depths would not occur until the carrying capacity of the surface layer was approaching its sustainable level. Floods at this time would disturb the surface layer leading to drift and movement deeper into the substrate. Following the flood, density recovery rates would be slower than in the permanently flowing side braid because invertebrate densities deeper in the substrate would not be in excess of the physical carrying capacity, and hence there would be less need to return to the surface.

It now seems that only large, extended floods result in a severe medium term decline of aquatic invertebrate densities in samples in the lower Rakaia. Flash floods, so long as they do not cause substantial alteration to bed morphology, probably cause only temporary declines. In contrast, even relatively small, but extended, floods may lead to substantial bed sediment movement and result in a large decline in densities. On the other hand, short periods of low flow may also have a relatively minor impact on food availability, so long as there is a sufficient discharge to maintain gravel throughflow under remnant channels. Flow resumption in these circumstances should be accompanied by rapid recolonisation of the surface layer of gravel:

The impact of flow reductions which lead to the desiccation of minor braids may have a more severe impact on the occurrence of terrestrial invertebrates, particularly the beetle fauna. Results from this study and those of Herron (1981) on the Waimakariri river show that numbers of Actenonyx bembidoides and Bembidion spp. declined significantly with distance away from water. However, in contrast to Herron (1981), increasing distance from water did not result in the absence of Bembidion spp., but rather in lower numbers. Although temperature evidently did not affect the distribution, humidity appeared to be a major limiting factor (Herron, 1981). Thus, Bembidion spp. are susceptible to desiccation which may occur with the drying up of minor braids. Whether beetles die or move to other areas when the braids dry up is unknown. It is also not known what the recolonisation rate of terrestrial habitats is for beetles. The answers to both of these questions could have considerable bearing on the reproductive potential of banded dotterels and wrybills which feed extensively on the beetle fauna.

6.6. Summary and conclusions

Most of the foraging of banded dotterels, wrybills, South Island pied oystercatchers and pied stilts occurred in, or on the edge of, aquatic microhabitats of the Ashley and Rakaia rivers. Although microhabitat overlap was apparently high between all species, when assessed at a higher level of resolution the variations in morphological character between the smaller banded dotterels and wrybills, and the much bigger South Island pied oystercatchers and pied stilts, led to separation by their use of various depth and substrate combinations and

different channel types. A progression of average feeding depths could be established as:

Pied > South Island pied > wrybill > banded
stilt oystercatcher dotterel

Sandy substrates were generally more heavily used by banded dotterels and pied stilts than by South Island pied oystercatchers and wrybills, which were most frequently observed on shingle or stone substrates. The overall pattern of microhabitat use was fairly consistent between rivers for all species. However, basing management recommendations for feeding habitat needs on the preferences of wrybills as an indicator species would probably not provide for the requirements of South Island pied oystercatchers or pied stilts, particularly with regard to their need for greater water depths for feeding.

Overlap in diet between wrybill and banded dotterel appeared low on the Ashley and Rakaia. Small sample sizes, particularly on the Ashley, meant it was dangerous to draw too many conclusions from the results. However, both species appear to have broad diets, including invertebrates of aquatic and terrestrial origin, indicating opportunist foraging. This flexibility is most surprising for wrybills because previous research on the upper Rakaia had concluded that Deleatidium larvae were probably the staple diet. Pitfall trapping on the lower Rakaia and Ashley rivers revealed a more diverse terrestrial invertebrate fauna which, due to a warmer climate, is probably also more abundant than in high country areas. The more broadly based diet of wrybills therefore reflects the wider variety of food resources available to these birds on lowland river systems and leads to the conclusion that they are primarily opportunist feeders. This may also mean that the impact of water development would be less in these areas. It was also noteworthy that a lack of flooding on the Ashley means a long term sustainable food resource is present on which birds can feed. This may explain the higher density of birds on this river, and indicates that residual flows based on feeding requirements should be designed to minimise fluctuations during the September-December breeding season.

7. THE INCREMENTAL APPROACH TO IMPACT ASSESSMENT

7.1. Introduction

Previous studies of bird feeding ecology have provided data which indicate possible trends and impacts which may result from various types of water resource development. However, when determining the relationship between feeding and river hydrology it would be helpful to have a quantitative method for predicting changes in the amount of preferred habitat provided over a range of discharges. Predictions from such methods are easier to incorporate within multiple use water management plans. Although no such mechanism has been formulated to define these relationships for birds, the Inland Flow Group in the United States has developed a method referred to as 'incremental analysis' which has been widely used to determine minimum flows for fish (Bovee, 1978). The method has now been applied with varying success to freshwater fisheries impact assessment in New Zealand (Glova and Duncan, 1985; Jowett, 1980; Jowett and Wing, 1980; Mosley, 1983a). This chapter details the first application of the method to determine the minimum flow needs of feeding birds for the Rakaia river.

7.2. Literature review

An advantage of the incremental method is that it is objective and as such is more defensible in water right hearings than subjective opinion (Jowett, 1982). However, in New Zealand, and particularly for the braided rivers on the eastern South Island, the technique has received considerable criticism. Before these criticisms are evaluated it is important to assess the potential use of this method for riverbed birds.

In brief, incremental analysis permits quantitative determination of changes in potential habitat with alteration in stream flow. The approach assumes that the suitability of habitat for a particular species can be described by measuring selected instream variables such as water depth, velocity, and substrate composition. By quantifying the changes in these variables with incremental changes in stream flow, the changes in potential habitat can be predicted at unmeasured flows (Glova, 1982). In fisheries evaluations all life stage measurements typically occur within the water body under investigation. This situation obviously does not apply to nesting riverbed birds, all of

which nest on terrestrial substrates and most of which feed to varying degrees aquatically and terrestrially. Furthermore, some species, including the black-fronted tern, and black-billed gull, feed over adjacent riparian areas. While it is theoretically feasible to include further variables, this would add considerably to the already acute sampling problems associated with the collection of hydrological data.

Pierce (1979) showed that wrybills feed predominantly in aquatic margins, except during floods when there is a shift to terrestrial foraging. Similar behaviour was recorded on the lower reaches of Canterbury rivers (see Section 6.3.3.1). The physical character of the terrestrial habitat undergoes a greater change during periods of bedload movement associated with bank erosion and deposition during floods than during average to low flows when little change occurs (Mosley, 1983a). Consequently, it is unnecessary to include the terrestrial habitat component in a predictive model dealing with a species which is primarily an aquatic feeder. The incremental method is therefore potentially applicable as a predictive tool for the assessment of the impact of flow modification on preferred wrybill feeding habitat. Different techniques are necessary to determine other aspects of overall habitat requirements.

Jowett (1982) listed three limitations associated with use of the model for fisheries investigations in New Zealand rivers:

- (1) Under certain conditions, such as shallow braids or very turbulent waters, hydraulic predictions cannot be made and the predictive component of the method should not be used. In this case river surveys at two or three different flows can be used for a limited amount of prediction. Glova and Duncan (1985) have recently used the approach for the Rakaia river.
- (2) Ideally habitat preference curves should be developed for salmonids in New Zealand conditions, in case those developed in North America are not appropriate for such use. Since the method has never been applied to birds this is clearly a necessity. Thus, precise habitat use measurements of substrate, velocity, and water depth were necessary.
- (3) The method cannot be used to predict the effect on fishery production. Weighted usable area, which is the end product of the incremental approach should, therefore, be regarded as an indicator of

the variation of habitat provision with changing flow.

The first and last of these limitations place restrictions on the use and applicability of the incremental approach. Cowie (1983) emphasised the biological limitations of the method in an evaluation of the analysis applied to the Rakaia river. During declining flows in a braided river, changes in weighted usable area may underestimate the impact on available fish habitat. This is partly attributable to the fact that minor braids provide weighted usable area out of all proportion to relative discharge when compared to major channels (Mosley, 1983a). As flows decline and some minor braids dry up, other formerly larger streams, through transition, become minor braids and hence weighted usable area is transferred to these new habitats. No account is taken of channel loss in the incremental analysis. In these shifts of preferred habitat, which may be masked in weighted usable area calculations, substantial losses in food production could occur which may have a range of impacts on the feeding ecology of riverbed birds. Intuitively though, it would appear that birds are better equipped to deal with such occurrences than are fish.

In spite of these limitations, the incremental approach remains useful as the only model currently available for making some quantitative predictive comment on the likely changes of habitat occurring with reductions in discharge. The important point to remember is that although the incremental approach is a model generated by the relationship between habitat use characteristics and river hydrology, it does not measure changes in aquatic productivity. If this limitation is borne in mind, then the incremental approach can be used in association with other study results to determine the potential impacts of flow changes on riverbed birds.

7.3. Methods

There are four components of the incremental method (Bovee, 1978):

- (1) Simulation of the stream;
- (2) Determination of depths, velocities, substrates, and cover objects, by area;
- (3) Determination of a composite probability of use for each combination of depth, velocity, substrate, and cover (where applicable) found within

the stream reach for each species and life history phase under investigation;

(4) The calculation of a weighted usable area (roughly a habitat's carrying capacity based on physical conditions alone) for each discharge, species, and life history phase under investigation.

These same procedures were broadly applied to the determination of wrybill feeding habitat requirements on the Rakaia river.

7.3.1. Stream simulation

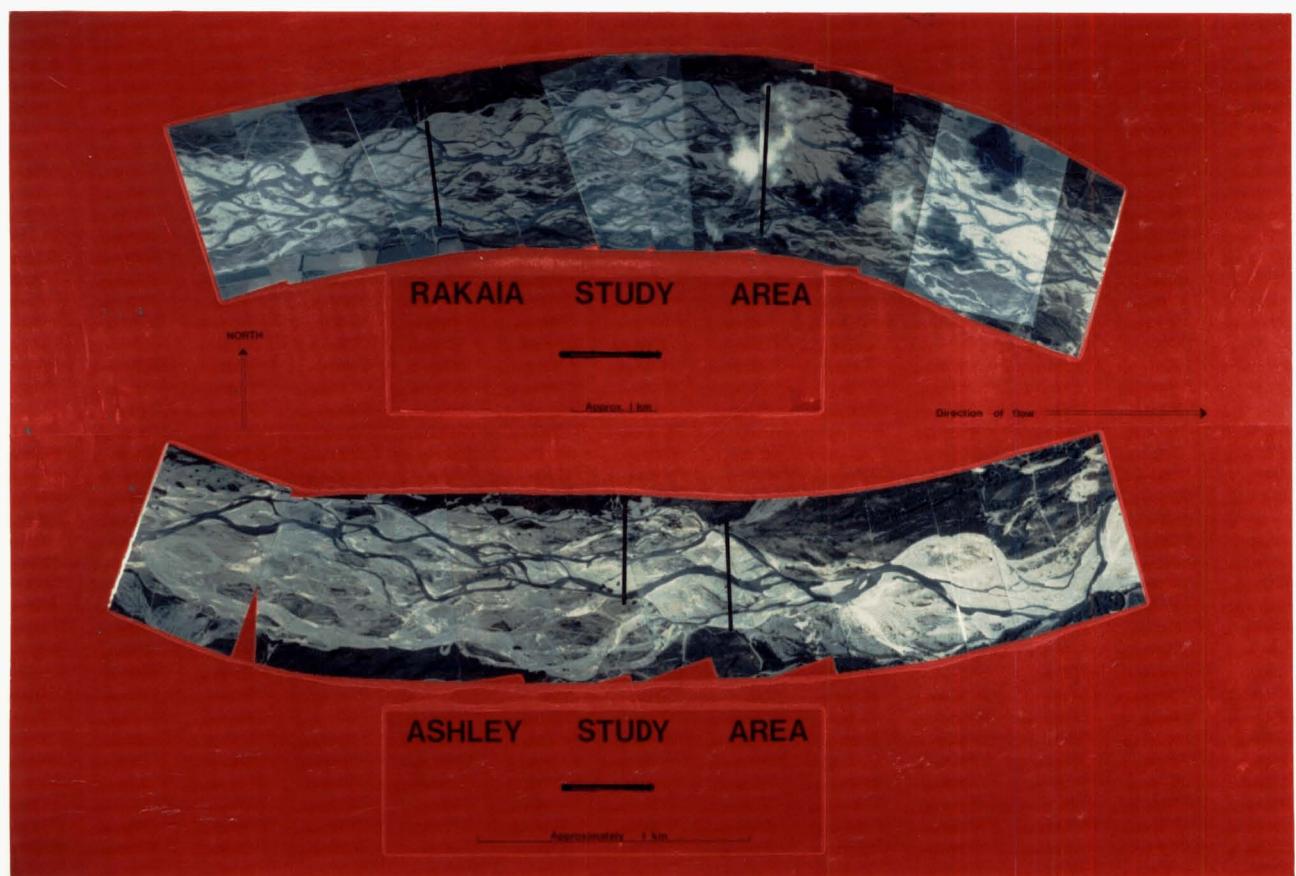
In 1981, two attempts were made at different flows to obtain the hydrological data necessary to complete a modified simulation of the river flow character within the Rakaia study area. The principal objective was to obtain data which could be used in linear regressions. During similar data collection, a joint Fisheries Research Division-Ministry of Works and Development-North Canterbury Catchment Board study used 24 technical staff to obtain the information on one day each over a range of discharges (Glova, pers. comm.). Only one field assistant was available in this study and hence it was not possible to collect all the data in one day. An attempt was therefore made to conduct each experiment during a period of relatively stable flows so that the raw data could be collected over a two or maximum, three day period. Natural variations during extended periods of flow recession were assumed to be masked by internal variability which would have occurred during daily flow gaugings.. Under normal conditions discharge measurements are considered to be subject to plus or minus five percent error (Duncan, pers. comm.).

Two reaches within the Rakaia study area were chosen on the basis of braiding hydrology for data collection. Both cross-sections were near sites chosen by the fisheries investigators. Cross-section one was highly unstable and very braided (>15 channels), with cross-section two being dominated by a major braid and a relatively small number of intermediate and minor braids (<10 in total; see Plate 7). The two cross-sections were considered on the basis of aerial photos to be typical of the range of conditions encountered on the lower Rakaia. For the respective cross-sections 10 transects were chosen on each braid covering in equal proportion; pools, runs, and riffles, with backwaters contributing the balance. Each transect was marked for subsequent

PLATE 7: Approximate locations of surveyed cross-sections for the incremental analysis on the Rakaia and Ashley rivers. (Note, the Rakaia photos were taken in late 1983 although the surveys were completed in mid-1982.)

Reach 1
(top left)

Reach 2
(top right)



Cross-section 1
(bottom left)

Cross-section 2
(bottom right)

measurement at a different flow.

A Wolman sampler was used for the determination of substrate size classes, a pygmy meter for water velocity measurement, and a cross-section bed profile gauge (designed by Fisheries Research Division) to measure accurately, water depths and associated widths at each transect over the range of bird use. Following bed profile and substrate composition measurements, the pygmy meter was used to measure water velocity and, with associated depth and channel width measurements, to calculate braid discharge. In very shallow edges, or where the water was fouled with algal growth, a 'pooh stick' was used to calculate water velocity. In this method a short stick is placed on the water, and timed over a distance of one metre. Velocity was then calculated as the average from five runs. With the major channels being ungaugable without a jetboat, it was proposed to sum the discharge from minor and intermediate braids, and then to determine total discharge in the study area by subtraction from daily flow records.

Following the collection of hydrological data it was proposed to follow the approach used by Glova and Duncan (1985) in their determination of weighted usable area calculations on the Rakaia river. Flooding, equipment failure, and logistical problems contributed to the complete failure of the cross-sectional sampling programme in 1981. It was subsequently decided to use the model developed by Glova and Duncan (1985), in association with habitat use data collected in this study.

7.3.2. Habitat use measurements

Although depth and substrate records were kept for feeding wrybills, banded dotterels, pied stilts and South Island pied oystercatchers in both study areas, velocity measurements were obtained only for wrybills on the Rakaia. This was because of the difficulty in obtaining large enough samples of pied stilt and South Island pied oystercatcher observations on the Rakaia, and because banded dotterels show a marked preference for very shallow and slow flowing edge microhabitats which are difficult to model. Moreover, because of other study commitments, there was insufficient time to extend the scope of this part of the project.

Wrybill data were obtained during the collection of spot observation habitat use records (see Section 6.3.1), and following the conclusion of time-budget observations. Due to the concentration needed to obtain time-budget data it was not possible to measure velocity at all feeding stations.

Water velocity was measured by pygmy meter or pooh stick depending on the nature of the water body, with velocity calculated to the nearest 0.1m/s. Depth was observed and recorded as 0-10; 11-20; 21-40; 41-60; 61-80; or > 80mm deep. Substrate classes were defined in Section 3.3.2.

7.3.3. Probability of use curves

Wrybill microhabitat use data must be transformed into weighted probability of use functions before use in the model. A weighted probability of use curve plots probabilities on an ordinal scale to standardise data input into the model. Thus, for water depths, the 0-10 and 11-20mm classes were combined to provide equal ranges over all depth observations. The class with the highest observed frequency was then given a weighted probability of use value of one with other values adjusted accordingly. It is assumed therefore, that the habitat of greatest use is the preferred microhabitat. This method follows that described by Bovee and Cochnauer (1977), and Bovee (1978). Weighted probability of use curves are combined to provide a composite probability of use function for ultimate use in the model. This composite function is produced by multiplying the corresponding probability values from individual use functions.

7.3.4. Hydrological sampling

A joint Fisheries Research Division - Ministry of Works and Development - North Canterbury Catchment Board survey team established two representative cross-sections within the Rakaia study area. Hydrological data from these two transects were collected during the period August 1981 to May 1982. Water depths, velocities and substrate composition were measured on six occasions at flows ranging from 69-176 cumecs (measured at the Gorge). As a means of reducing flows, Coleridge and Highbank power stations were shut down for 12 hours. The methods used are fully explained in Glova and Duncan (1985).

7.3.5. A simplified approach for smaller rivers

A major limitation to the further application to other rivers of the incremental method applied on the Rakaia in this study, is the extensive sampling requirements. In order to provide an approach which is simpler to apply in the field, and easier to calculate the results for, an attempt was made to develop a simplified methodology for use on smaller rivers. It was intended that such a method could be undertaken by a minimum of two people, and that the subsequent results could then be used in the formulation of river management plans.

Two river cross-sections were selected in the area of greatest bird density on the Ashley river study area. No attempt was made to select sites randomly, as it was considered the most critical area is where the greatest bird numbers are present. Both cross-sections were established in a line perpendicular to the direction of principal river form. The following information was collected at each braid in the cross-section:

- (1) Channel width;
- (2) Usable width, defined for wrybills as water <100mm deep, and flowing at a velocity of less than 0.5m/s.

In addition, the number of braids in each cross-section was recorded. Width and depth were measured by tape measure, and velocity by a pooh stick. Daily mean discharge data were obtained from the North Canterbury Catchment Board for the Ashley Gorge recorder and were adjusted according to the recession equation developed for the Rangiora bridge site (see Section 2.3.2). Adjusted flows and other measured parameters were regressed against each other on a cross-sectional basis.

7.4. Results

7.4.1. Probability of use and weighting factor calculations

Records of water depth, velocity, and substrate were collected for waters used by wrybills feeding on the Rakaia (Table 7-1a,b,c). Shallow (0-20mm), slow flowing water (0-0.2m/s) on a shingle substrate was the most frequented aquatic habitat. To smooth out the weighted probability of use functions and simplify computation, water depths were combined to fit 20mm ranges, and velocities to fit 0.2m/s classes. Shingle (2-32mm) and stones (32.1-64mm) were combined in the substrate classification to match the classification defined by Mosley (1982b), and thereby

TABLE 7-1: Probability of use and weighting factor calculations for depth, velocity, and substrate requirements of wrybills on the Rakaia river.

a) Water depth:

Depth (mm)	Frequency	Frequency adjusted to fit equal depth classes	Weighted probability of use for adjusted frequencies
0-10	95	176	1.00
11-20	81		
21-40	74	74	0.42
41-60	22	22	0.13
61-80	7	7	0.04

b) Water velocity:

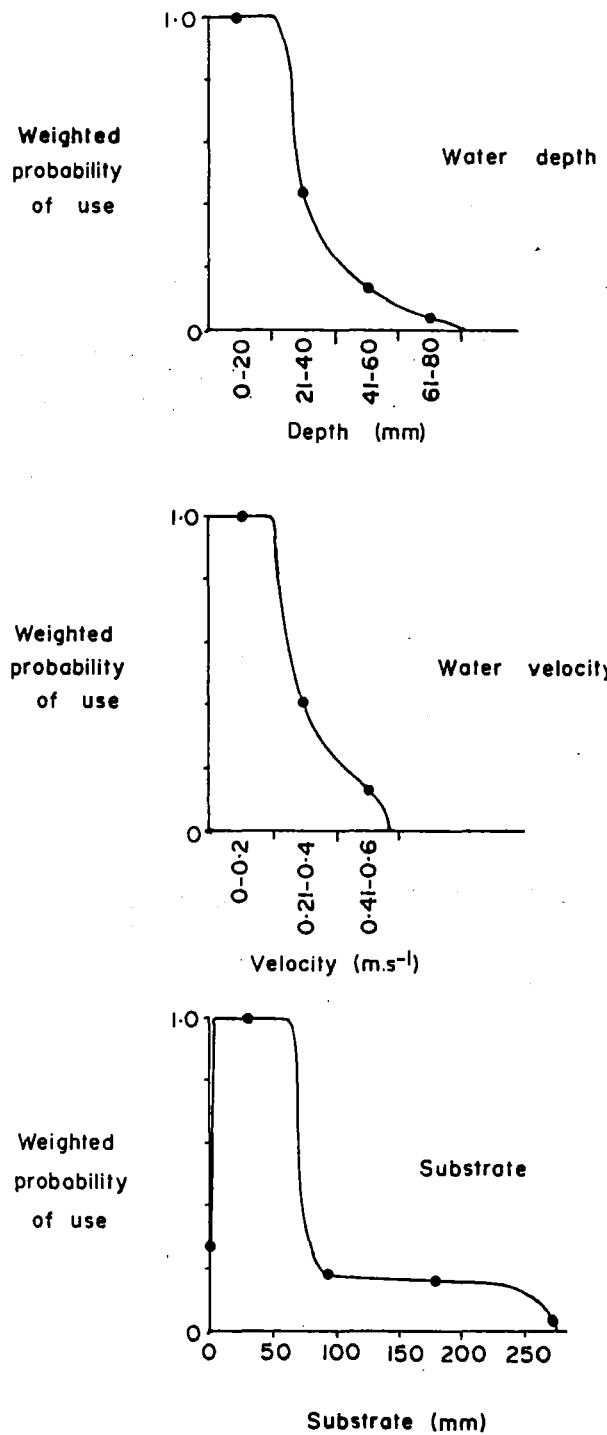
Velocity (m/s)	Frequency	Frequency adjusted to fit 0.2m/s velocity classes	Weighted probability of use for adjusted frequencies
0-0.1	40	61	1.00
0.11-0.2	21		
0.21-0.3	18	25	0.41
0.31-0.4	7		
0.41-0.5	8	8	0.13

c) Substrate:

Size range (mm)	Frequency	Frequency adjusted to fit Mosley's (1982b) substrate classification	Weighted probability of use for adjusted frequencies
< 2	31	31	0.27
2-32	92	113	1.00
32.1-64	21		
64.1-128	20	20	0.18
128.1-256	18	18	0.16
> 256	4	4	0.04

facilitate use in the model. Under the adjusted frequencies a weighted probability of use value of one was accorded to the highest class frequency in each table. Probability of use weighting functions were then graphed (Figure 7-1) and submitted to the Ministry of Works and Development for the calculation of weighted usable areas.

FIGURE 7-1 : Probability of use weighting factors for adult wrybills on the Rakaia River.



Weighted usable area and channel width measurements were provided on a total cross-section (Table 7-2) and individual braid basis (Appendix 5).

TABLE 7-2: Weighted usable area and channel width values for two cross-sections and two flow sets on the Rakaia river.

Reach	Date of measurement	River discharge (m^3/s)	Width (m)	Weighted usable area (m^2/m)
1	6 August 1981	146	450.7	45.83
	7 August 1981	92	374.1	51.65
	18 August 1981	113	393.1	42.66
1	6 April 1982	87	285.1	36.60
	7 April 1982	132	338.9	33.31
	4 May 1982	70	250.7	37.33
2	6 August 1981	146	310.5	29.31
	7 August 1981	89	282.2	33.23
2	6 April 1982	86	218.7	22.92
	7 April 1982	132	250.2	14.66
	4 May 1982	69	204.9	25.03

Flows during both sets of experiments were relatively stable. However, several large floods occurred in the interval between experimental sets (Figure 3-8).

7.4.2. The discharge-width relationship

As discharge declined there was a corresponding decrease in overall channel width ($r^2=0.31$; $P>0.05$; see Figure 7-2). The relationship was much clearer when examined on a reach-flow set basis, but the small sample sizes meant non-significant correlations in all cases ($P>0.05$). Declines in channel width were higher for minor channels than for major braids, and there was also a tendency for width to decline at a greater rate during flows of 69-87 cumecs, than at higher flows in the range 86-146 cumecs (Table 3-3). There was no significant difference for any of these relationships ($P>0.05$).

FIGURE 7-2 : Discharge-channel width relationships for the Rakaia river.

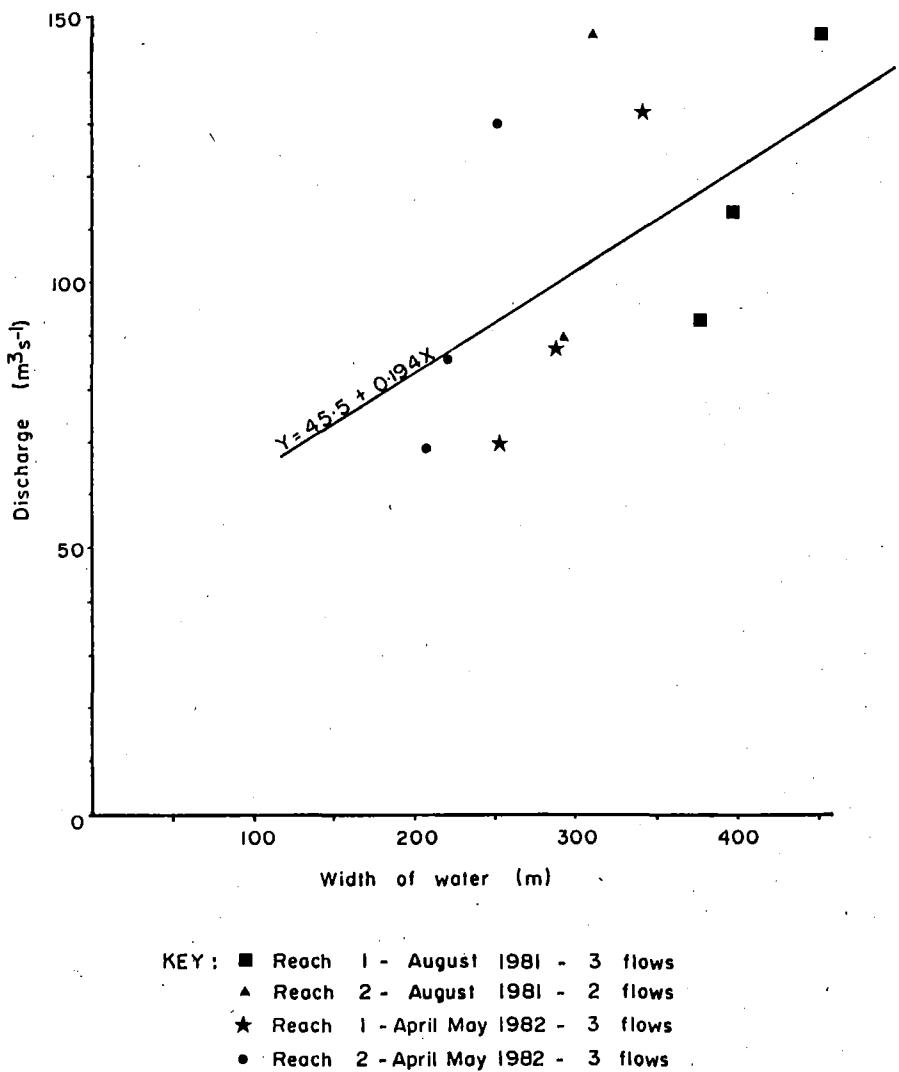


TABLE 7-3: Rates of decline in channel width with falling discharges over two flow ranges on the Rakaia river.

Range of declining flows (m^3/s)	Minor channel (<5 cumecs)	Major channel (>5 cumecs)
146-86 (4 sets)	-0.07 m/cumec (N=37; range= -0.28 to +0.07)	-0.06 m/cumec (N=14; range= -0.20 to +0.008)
87-69 (2 sets)	-0.14 m/cumec (N=15; range= -0.82 to +0.05)	-0.11 m/cumec (N=6; range= -0.24 to -0.006)

7.4.3. The discharge-weighted usable area relationship

Weighted usable area increased with decreasing discharge when examined on a reach-flow set basis (Figure 7-3a,b), although this change was only significant for reach two-flow set two ($r^2=0.995$; $P<0.05$). No meaningful relationship existed when all flows and corresponding weighted usable areas were plotted together. Weighted usable area fell only once with falling discharge. This decline from $45.83m^2/m$ at 146 cumecs to $42.66m^2/m$ at 113 cumecs was followed by a rise to $51.65m^2/m$ at 92 cumecs river discharge.

Minor braids contributed weighted usable area out of all proportion to their relative discharge when compared with major braids. Flows in braids of less than 5 cumecs (minor braids) averaged 10.61% of total discharge (N=11; Range= 7.28-13.54%) but contributed an average of 62.61% of total weighted usable area (N=11; Range= 45.18-73.12%). Weighted usable area tended to increase in both minor and major channels as flows declined, with the mean rate of change rising at lower flows. Rates of increase were lower in minor channels than in major braids (Table 7-4). Mann-Whitney U tests for all relationships were not significant ($P>0.05$).

FIGURE 7-3 : Discharge-weighted usable area relationships for two study cross-sections and two sets of declining flows on the Rakaia river.

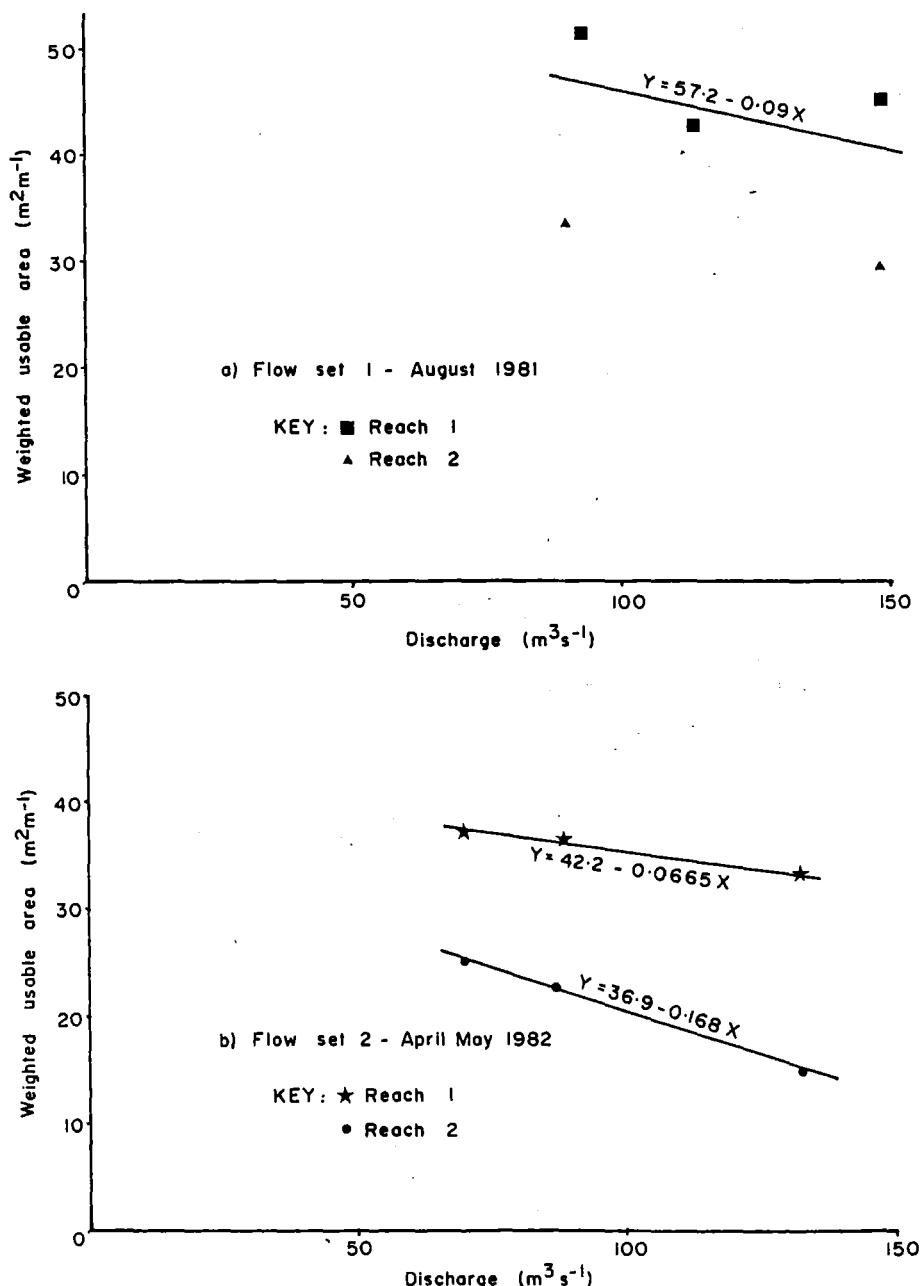


TABLE 7-4: Rates of increase in weighted usable area with declining discharges over two flow ranges on the Rakaia river.

Range of declining flows (cumecs)	Minor channel (<5 cumecs)	Major channel (>5 cumecs)
146-86 (4 sets)	+0.004 m ² /m/cumec (n=37; range= -0.091 to +0.087)	+0.01 m ² /m/cumec (N=14; range= -0.035 to +0.043)
87-69 (2 sets)	+0.008 m ² /m/cumec (n=15; range= -0.154 to +0.32)	+0.04 m ² /m/cumec (N=6; range= -0.058 to +0.191)

7.4.4. Usable width on the Ashley river

Two cross-sections approximately 300m apart were established on the Ashley river (Plate 7). Recordings were made on 7 occasions at cross-section one, and on 6 occasions at cross-section two. Table 7-5 summarises the data.

(a) Discharge-channel number relationships:

Discharge was positively correlated with the number of channels in both cross-sections ($r^2=0.65$; $P<0.05$ for cross-section one, and $r^2=0.97$; $P<0.01$ for cross-section two; Figure 7-4a,b). As flows declined from 21.2 to 5.9 cumecs there was a decline from 7 to 4 channels in cross-section one. As expected the three channels to dry up were all minor braids (flows of less than one cumec). In cross-section two, the number of channels fell from 7 at 21.2 cumecs to 4 at 8.7 cumecs with all losses again being minor braids.

(b) Discharge-usable width relationships:

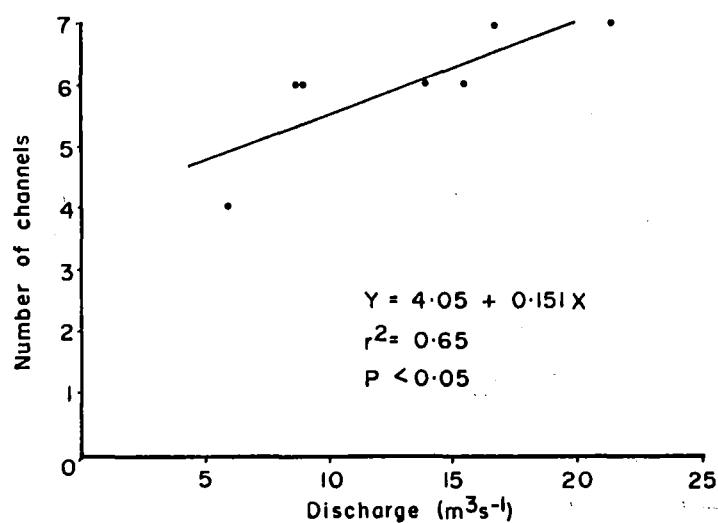
Flow was highly correlated with usable width on both cross-sections ($r^2 =0.90$; $P<0.01$ for cross-section one, and $r^2 =0.91$; $P<0.01$ for cross-section two; Figure 7-5a,b), so that as discharge declined there was a corresponding drop in usable width. It was noticeable that usable width in cross-section two was at consistently higher levels than for corresponding discharges in cross-section one.

TABLE 7-5 : Usable width and other cross-sectional data collected at a range of flows on the Ashley river in 1983.

	Date	Ashley Gorge flow ($m^3 s^{-1}$)	Adjusted flow ($m^3 s^{-1}$)	Number of channels	Width (m)	Usable width (m)
Cross-section one	31/10/83	16.5	21.2	7	83.2	12.5
	5/11/83	13.2	16.5	7	73.3	11.6
	10/11/83	7.8	8.8	6	66.6	5.2
	25/11/83	12.3	15.2	6	75.7	7.6
	29/11/83	11.3	13.8	6	63.5	6.4
	2/12/83	7.7	8.7	6	55.0	5.2
	31/12/83	5.7	5.9	4	53.0	1.9
Cross-section two	31/10/83	16.5	21.2	7	86.9	30.6
	5/11/83	13.2	16.5	6	71.4	24.1
	10/11/83	7.8	8.8	4	59.1	11.9
	25/11/83	12.3	15.2	6	76.0	24.6
	29/11/83	11.3	13.8	5	64.7	15.1
	2/12/83	7.7	8.7	4	57.0	11.3

FIGURE 7-4 : Number of channels-total discharge relationships for two cross-sections on the Ashley river.

a) Cross-section one



b) Cross-section two

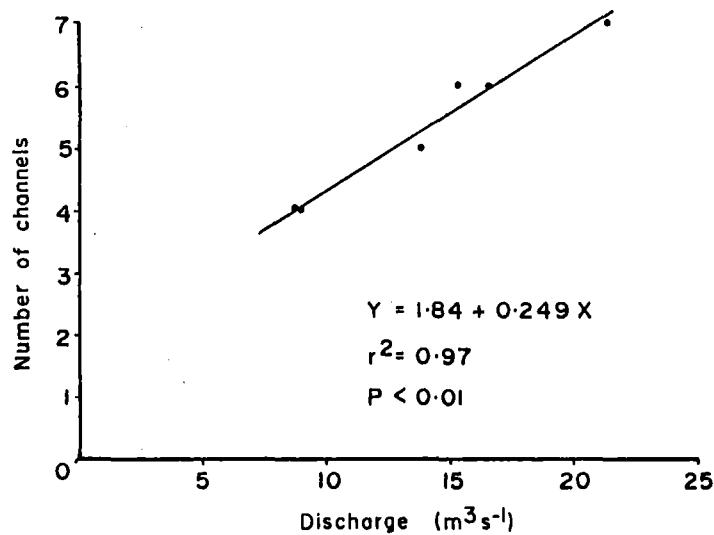
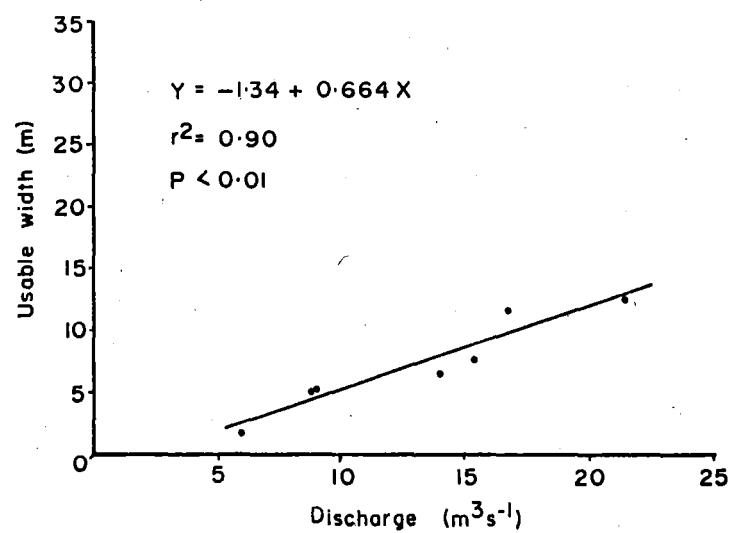
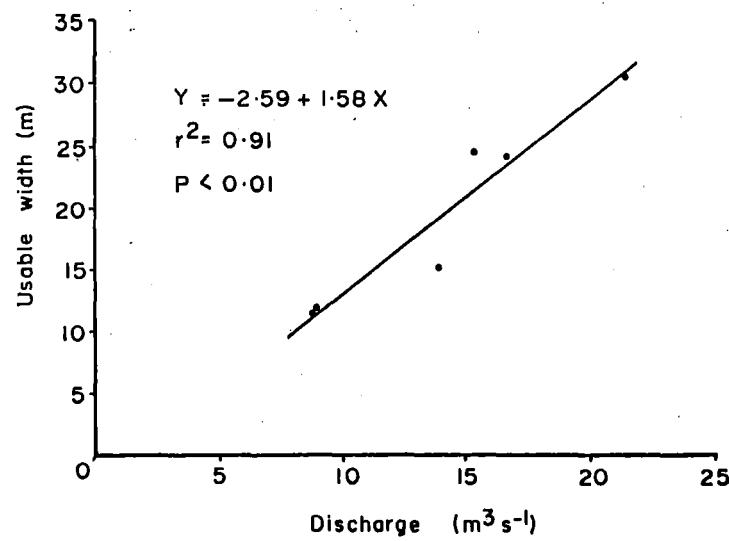


FIGURE 7-5: Total usable width-discharge relationships for two cross-sections on the Ashley river.

a) Cross-section one



b) Cross-section two



(c) Channel number-usable width relationships:

Declines in the number of channels in each cross-section were associated with significant declines in total usable width ($r^2=0.81$; $P<0.01$ for cross-section one, and $r^2=0.91$; $P<0.01$ for cross-section two; Figure 7-6a,b).

(d) Width-usable width relationships:

As total cross-sectional width declined there were corresponding and significant falls in usable width ($r^2=0.78$; $P<0.01$ for cross-section one, and $r^2=0.96$; $P<0.01$ for cross-section two; Figure 7-7a,b) for each cross-section.

(e) Width-discharge relationships:

Discharge was positively correlated with channel width in both cross-sections ($r^2 =0.84$; $P<0.01$ for cross-section one, and $r^2=0.92$; $P<0.01$ for cross-section two; Figure 7-8a,b). There was little difference between channel width in both cross-sections at corresponding discharges.

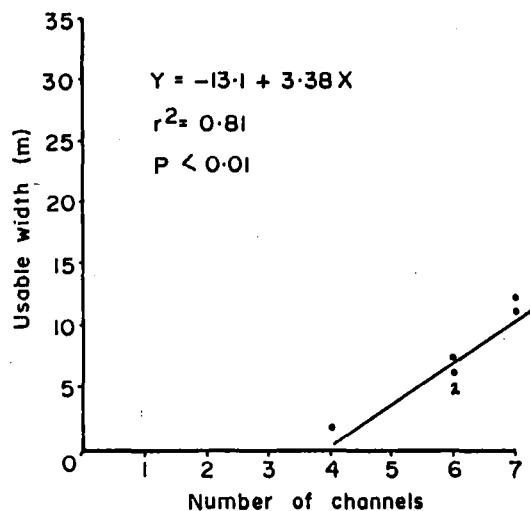
7.5. Discussion

Previous impact assessment studies on braided rivers which have used the incremental approach, or a modified version, have concentrated on the flow requirements of fish, e.g., Jowett (1980), Jowett and Wing (1980), Mosley (1983a), Glova and Duncan (1985). In these studies weighted usable area has generally risen with increasing discharge, e.g., Jowett and Wing (1980), or has remained virtually static over a range of flows, e.g., Glova and Duncan (1985). In contrast, for the range of flows examined, on the Rakaia, weighted usable area for wrybills increases with decreasing discharge.

Glova and Duncan (1985) found that the amount of weighted usable area available for fish in minor braids of the Rakaia declined markedly as river flows decreased. As flows drop, depths and velocities also decline, often outside the range preferred by fish (Glova, pers. comm.). Wrybills, which require slow, shallow water, benefit from such a change. Hence weighted usable area increases in minor braids, even at low flows, as discharge declines. The loss of one or two small braids during these falls in flow did not alter this overall trend. This can be explained in part by the change in status of formerly intermediate

FIGURE 7-6 : Total usable width-number of channels relationships for two cross-sections on the Ashley river.

a) Cross-section one



b) Cross-section two

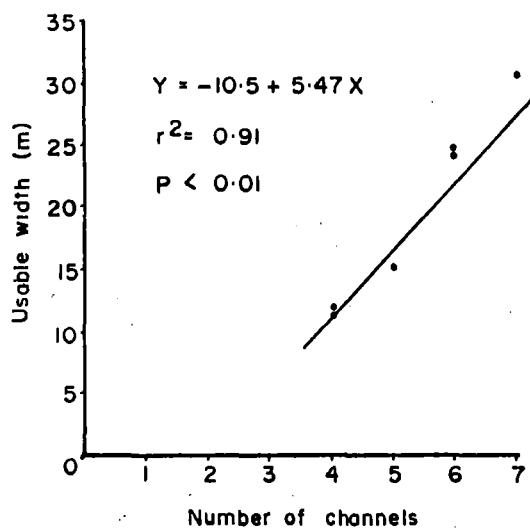


FIGURE 7-7 : Total width-usable width relationships for two cross-sections on the Ashley river.

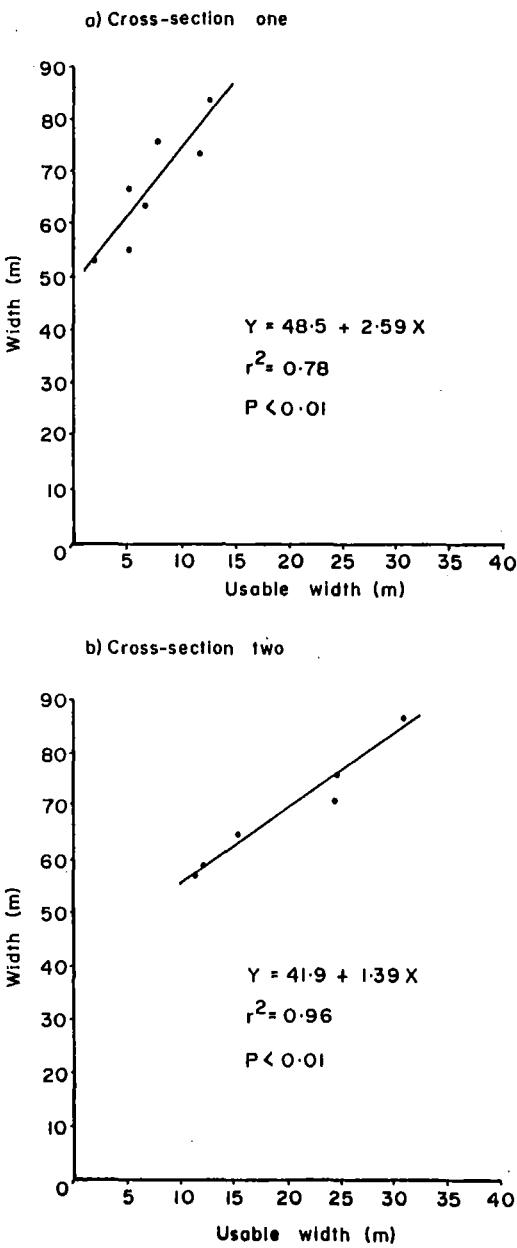
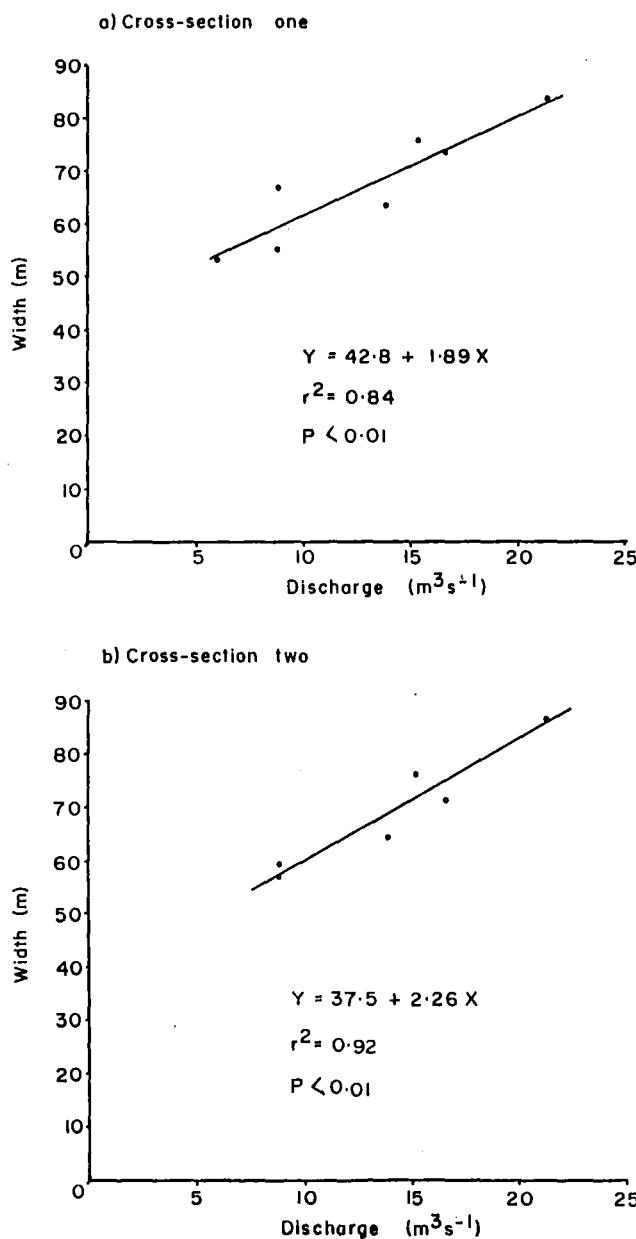


FIGURE 7-8 : Total width-discharge relationships for two cross-sections on the Ashley river.



braids into minor channels as flows dropped. Birds are better equipped than are fish to cope with such changes of preferred habitat. Flight enables rapid movement between patches (braids) to enable the exploitation of newly available resources but fish may be stranded. As channel width declines aquatic invertebrates may be affected in three ways:

- (1) They become stranded on dry land where they are easily preyed upon by edge-feeding birds such as wrybills and banded dotterels;
- (2) They move downslope with the decline in width, thereby increasing invertebrate densities for feeding birds; and
- (3) They move downslope with the decline in width, but densities are such that the carrying capacity is exceeded, thus leading to catastrophic drift. Invertebrates in the drift are often washed into backwaters and eddies where they again fall easy prey to birds.

Any, or all of these events, appear likely to be advantageous to feeding wrybills.

Fish biomass and numbers were greater on a per unit area basis in minor braids than in intermediate or major channels (Glova and Duncan, 1985). Wrybills showed a preference for feeding in minor braids (see Figure 6-1) which is supported by the extensive provision of weighted usable area in these habitats. Furthermore, the density of wrybill breeding pairs was greater in the vicinity of reach one than in reach two (see Figures 4-1 and 4-2). The former was more unstable and highly braided, and provided higher levels of weighted usable area than the latter, over the full range of study flows.

As flows declined, weighted usable area for wrybills, rose at a faster rate during very low flows than when flows were dropping from median to low levels. At the same time, the rate of decrease in channel width also increased. When combined, these events provide some insight into the likely effects of reducing discharges below the levels experienced in this study. Increasing rates of width decline indicate that at some flow channels will dry up, and weighted usable area in those channels will fall to zero. This occurred in one or two minor braids over the range of study flows, but did not affect total weighted usable area, because of compensatory rises in usable area in other channels. If flows were to decline further and result in more channel

losses, then weighted usable area increases in remaining channels would have to occur at faster rates to compensate for these additional losses. It does not appear that such rises can continue to occur indefinitely as flows decline further and further. Therefore, although weighted usable area for feeding wrybills increased over the range of flows studied, it seems likely that at some lower flow it will decline rapidly. This minimum has not been determined.

It should be emphasised that weighted usable area only provides a measure of the amount of physical habitat available for feeding wrybills over a range of discharges. However, assessments based on individual channels do provide some detail about the likely impact of flow modification. A major criticism of the method is that changes in weighted usable area may underestimate the effects of flow modifications on food availability (Cowie, 1983). Wrybills are opportunists, and although they feed primarily on, or at the water's edge, their diet consists mainly of invertebrates of terrestrial origin which dwell in this area or have been caught within the water body and drift downstream (see Section 6.4.2). Studies of foraging behaviour support these results and indicate that on the lower Rakaia, wrybills are more able to survive the impact of flow modification than birds which breed on high country catchments. The high breeding success rates recorded on the Ashley river during periods of declining flows (see Section 3.4.4.1) provide additional support for this conclusion. Consequently, it is doubtful that declines in flows over the range examined here will have much, if any, negative effect on wrybill feeding.

The development of a simplified approach aimed at minimising labour input and the complexity of statistical analysis, yet still retaining some predictive value, was attempted on the Ashley in 1983. In constructing the method it was necessary to remove several of the major components incorporated within the full incremental approach:

- (1) Weighting factors were not calculated and it was assumed water depths less than 100mm and velocities slower than 0.5m/s would provide for the microhabitat needs of wrybills. This was justifiable on grounds of expediency and from recognition of the fact that the channel bottom generally slopes quickly to much shallower and slower flowing water closer to the channel edge. Furthermore, the method is designed only as an indicator of the trend of changes occurring to microhabitat provision

with changes in discharge;

(2) A representative sample of microhabitats was not examined as it was considered important to concentrate on the most important areas for wildlife. This meant that the most braided section of the study area was chosen for the establishment of the two cross-sections. Consequently, study findings should not be used to infer changes over the whole river system, but rather as indicators of likely occurrences in areas of prime bird habitat;

(3) Each channel was sampled only once under this method in order to reduce the time involved in collecting field measurements. On average it took two people approximately one hour to complete each cross-section, whereas use of the full incremental methodology took 24 people one day to complete two cross-sections on the Rakaia. Admittedly, the Rakaia is a much bigger and more difficult river to sample, but it would still require a large labour and time input to undertake the same study on a smaller river like the Ashley. As a result, it was possible to allocate more time to undertake further sampling on other days. More sample days provided the opportunity to examine a wider range of flows, and to gather sufficient information to develop significant relationships. Because of the sampling problems associated with applying the full methodology to braided rivers, it has not been feasible to devote the labour and time necessary for establishing this data base;

(4) The measurement of only one transect at each channel over the width of the cross-section meant that weighted usable area values could not be calculated. Usable width, which is simply the proportion of channel width of potential foraging use to birds, is simpler to understand than weighted usable area, and was therefore used to present the study results.

Despite these changes this new approach is warranted where short term studies are to be undertaken. However, because of the exclusion of weighting factors, interpretation of the usable width data should probably be restricted to inference at index levels only. Thus, cross-sectional differences in usable width at corresponding flows should not be directly compared when this approach is used.

Results from the Ashley were only consistent with the Rakaia for the width-discharge relationship. This was not surprising, but the fact that usable width and the number of channels in each cross-section declined almost linearly with discharge, contrasted markedly with the Rakaia study findings. There was also a consistent relationship between declines in usable width, and a drop in the number of channels in a cross-section. With declining flows on the Rakaia, the drying up of one or two channels was more than compensated for by the provision of additional area in other small to medium braids as their flows also declined. On the Ashley, the number of braids in each cross-section was lower than the Rakaia. Consequently, as each dried up there was less opportunity for modifications in the others to compensate for the loss of another channel. As flows declined further, the problem became worse. This observation provides some indirect evidence to show that at some stage on the Rakaia, a further drop in discharge will result in a weighted usable area decline. Furthermore, it follows that for smaller braided rivers like the Ashley, Ashburton, and Opihi, declining discharges may also mean a drop in weighted usable area for birds. If this study has shown anything, it has indicated how difficult it can be to generalise about aspects of impact assessment on different river systems.

7.6. Summary and conclusions

The incremental approach to impact assessment is one means of objectively quantifying the effects of flow reduction on the provision of preferred wrybill feeding microhabitat. Although the method has been extensively used for fish, this is the first application for birds. In spite of criticisms, weighted usable area measurements provide an indication of physical changes likely to occur in rivers, and as such can be used in association with other habitat considerations and behavioural information, to determine those flows necessary to conserve bird habitat. For feeding at least, it appears that abstraction within the natural low to medium flow range will not adversely affect wrybills on the lower Rakaia river. However, the simplified usable width approach developed and applied to the Ashley in this study, indicates that for some rivers at least, usable habitat appears to decline with discharge. Similar assessments for other species and on other river systems should be undertaken to see whether such conclusions are valid on a community basis.

The fact that weighted usable area increased with declining discharge on the Rakaia in this study must not though, be taken to mean that wrybill conservation will necessarily be enhanced by lower than natural river flows. Other factors related to space use, nest site provision, and protection from predators, mean that higher flows than those determined for feeding may well be required.

8. CONCLUSIONS AND MANAGEMENT IMPLICATIONS

8.1. Summary

In New Zealand, and particularly along the eastern side of the South Island, the presence of wide, unstable braided rivers, is associated with the presence of a diverse riverbed bird fauna. Many of these species are introduced, others are recent migrants from Australia, some are endemic and breed on a range of habitats, while a few, notably the wrybill, nest only on these rivers. There are now considerable threats to these rivers from existing and planned water resource developments. As a consequence it is now necessary to quantify habitat needs and possible development impacts so that appropriate conservation measures can be incorporated within river management planning.

8.1.1. The study approach

Most previous research concerning riverbed birds has concentrated on behavioural matters rather than on quantifying habitat needs and predicting instream flow requirements. Even the work of Robertson *et al.* (1983) concerning the habitat requirements of birds in the Ahuriri river catchment merely addresses aspects of habitat use without determining fine grained microhabitat preferences, or attempting to quantify changes in habitat likely to occur with changes in river flow.

This lack of research directed toward quantifying these relationships necessitated recourse to related disciplines as a means toward establishing a research approach. Fisheries scientists have in recent times been faced with similar problems on the same rivers. Apart from identifying particular physical parameters and relating these to specific biological requirements, they have attempted to model, by means of the incremental approach, changes in habitat which occur as a function of river discharge. In brief, the approach as applied in New Zealand has involved the measurement of species-specific depth, velocity and substrate preferences, the development of weighted probability of use curves, and the calculation of weighted usable area over a range of measured river flows.

The incremental approach was assessed in light of the logistical constraints imposed on a study of this nature, and in relation to the range of potential study species and river systems. As a result it was

decided to use the approach as a quantitative measure for impact assessment. Two riverbed nesting species, the wrybill and black-fronted tern, were then selected for intensive study as indicator species. Both were chosen because of their restricted distribution and reliance on riverbed habitats and it was further assumed that providing for these species would at the same time safeguard most other riverbed birds. To check this assumption, a study of banded dotterels, pied stilts and South Island pied oystercatchers was also made. Since most riverbed nesting species are migratory and use the riverbed primarily during the spring and early summer breeding season, most work was confined to this period.

Having chosen the study species, it then became necessary to select study areas occupied by each species which were representative of a range of river systems, and likely to provide results of benefit to the future management of these river types. Since previous researchers had studied high country catchments, study areas were located on the lower reaches of the Rakaia and Ashley rivers, so that contrasts with high country areas could then be made. Rivers with contrasting flow regimes were chosen in order that these, too, may be used as indicators of habitat requirements, and to choose reaches where other associated work was occurring so that the results from concurrent studies could be used to complement one another.

It was initially proposed to develop a model encompassing the behaviour of braided river hydrology, and then to relate this to specific habitat needs for feeding and breeding by riverbed birds. Data collection for this work began on the lower Rakaia in 1981, but floods and logistical problems completely destroyed this aspect of the project. During 1982 and 1983 more specific data were collected relating to breeding success, physical and botanical factors concerned with home range and nest site selection, and hydrological parameters associated with foraging behaviour. In all cases these measurements used standard hydrological classifications, a point normally overlooked in other studies of riverbed birds, but important if competitive resource demands are to be assessed objectively. In addition, a time-budget study of wrybills on both rivers was carried out and related to changes in river flow and seasons, so that critical periods and limiting factors could be identified. Wrybill habitat use data collected during time-budget research and spot observations of foraging were incorporated within an

existing weighted usable area model developed for the lower Rakaia, and a simplified usable width measure which was developed and tested on the lower Ashley river. The latter studies were expected to provide quantitative assessments of changes in usable habitat which occur with variations in flow.

8.1.2. The study findings

In broad terms the findings reflected the contrasts between the two study areas. Thus, the Ashley, characterised by declining discharges as the breeding season progressed, had greater bird densities and higher levels of breeding success than the Rakaia where flows fluctuate wildly throughout the breeding season, particularly from October onwards. Because of greater flow stability, food availability is considered to be higher on the Ashley and is probably correlated with the smaller home range sizes for banded dotterels on this river.

Frequent and large floods on the Rakaia appeared to affect the ability of wrybills to lay repeat clutches. Time-budget studies supported this argument, and indicated that conditions on the Ashley were more conducive to successful breeding. These findings were backed up by the much higher level of wrybill breeding success on the Ashley in 1983. There is apparently little flexibility in wrybill time-budgets. This was shown by the early departure of many birds from the river in 1983, probably as a result of flooding which limited the availability of food, so that it was more economic to forage elsewhere.

Nest site selection in all of the study species is closely related to the presence of water. Nest sites were usually less than 50m from water on both rivers, and large areas of otherwise suitable riverbed without water were not used for breeding. On the Rakaia wrybills tolerated vegetation cover around the nest of up to approximately 5%, but above this there appeared to be a shift to other less vegetated sites. Lupin, the dominant plant type on the Rakaia, is a rapid coloniser of shingle substrate, being most successful at high points where the impact of flooding is least. Due to the wrybill's intolerance of vegetative ground cover, their nests were occasionally located at suboptimal cross-section heights. This resulted in an increased likelihood of nests being washed away by only medium-sized floods.

Vegetated islands also provided cover for mammalian predators which had a greater impact on breeding success on these lower reaches than they had in a previous wrybill breeding study on the upper Rakaia (Hay, 1984). Predation was higher on the Ashley river study area. This appeared to be related to the reduced protection provided by the braiding pattern on the Ashley where flows were much smaller and in fewer channels than on the Rakaia. Flooding is the only natural control on the encroachment of exotic vegetation. This was graphically demonstrated on the Rakaia between 1982 and 1983 when extensive flooding reduced the area of dense-mature vegetation by approximately 30%.

Studies of foraging concentrated on the determination of microhabitat preferences, whereas previous research has recorded habitat use only. Most species showed a distinct preference for minor channels on both rivers, where food availability is greatest. It was shown from weighted usable area calculations that the greatest areas of preferred habitat, in terms of depth, velocity and substrate, are present in these channels. Wrybills foraged almost exclusively in or along the edge of aquatic habitats, while banded dotterels and South Island pied oystercatchers spent much of their time foraging on terrestrial substrates. In contrast, pied stilts were only observed feeding in water and, along with South Island pied oystercatchers, were seen at much greater depths than wrybill s or banded dotterels. Microhabitat overlaps were generally moderate or high at the broadest level of analysis, but for the wrybill-banded dotterel relationship, were reduced considerably by extending the assessment to more detailed levels including depth and substrate considerations.

Studies of wrybill and banded dotterel diet were made by faecal analysis for both study areas. Both species are opportunist feeders, consuming a variety of prey from terrestrial and aquatic sources. Mayfly larvae were the dominant items in wrybill faeces from the Rakaia, but still contributed only about 30% of the total identifiable diet. Previous research on the upper Rakaia had concluded that wrybills were reliant on mayfly larvae (Pierce, 1979). Inter-specific diet overlap was low on both rivers. The diet of wrybills on the two rivers differed because whereas on the Rakaia mayfly larvae were the dominant aquatic insects, these were replaced by caddisfly larvae on the Ashley river. This difference is caused by the greater flow stability on the Ashley. In contrast the inter-basin overlap between banded dotterel diets was

very high, largely because the food was of terrestrial origin which differed little between rivers.

Pitfall trapping indicated that food availability was greater on the Ashley, and probably greater downstream, than in high country areas. Pitfall traps located near the water collected many more invertebrates than those located away from water, and beetles dominated most returns. An index of aquatic invertebrate density was established for the Rakaia, and was based on the published findings of Sagar (1983a, 1983b). In general there was an inverse relationship between density and flow instability. This was demonstrated most noticeably in the latter half of the 1982 breeding season, and during 1983 when invertebrate densities were considered to be low. The index appeared to relate well to bird breeding successes in both seasons.

Predictions concerning habitat changes with variations in flow were related to vegetation encroachment and foraging requirements. If nest site needs are to be maintained then the flood regimes must remain substantially unmodified. Weighted probability of use curves based on depth, velocity and substrate needs of wrybills were developed, and then incorporated within the weighted usable area calculations undertaken for the lower Rakaia river by the Ministry of Works and Development, and Fisheries Research Division of the Ministry of Agriculture and Fisheries. Over the range of flows studied there was an increase in weighted usable area as discharge declined. However, at some lower flow beyond the natural low flow limit of the river, weighted usable area will begin to decline. Indirect support for this contention came from a simplified usable width approach tested on the Ashley river. Although inter-basin comparisons of this nature are difficult to make, the smaller number of braids was seen as a reason for the decline in usable width which occurred as a function of discharge on this river. The latter method could be used on a number of rivers with minimal time and labour input, and the results then used as an indicator of likely changes in the provision of foraging habitat.

Of the five species studied, the wrybill was considered the greatest habitat specialist. The others were considered generalists, although the black-fronted tern should be classed as a restricted generalist and managed accordingly. Habitat generalists appear best equipped for life on Ashley flow-type rivers with declining breeding

season discharges. Wrybills also appear well suited to life on these systems, but at the same time have a number of adaptations which equip them for Rakaia flow-type rivers. Where habitat on these rivers is largely unmodified, especially by vegetation encroachment, there are high wrybill densities. As the extent of vegetation encroachment increases, so wrybill density appears to decline.

The indicator species approach was most applicable to factors related to breeding season habitat requirements. Wrybills appeared to have the most restricted and narrowest range of needs, but these generally fell within the ranges also used by other species. Recommendations based on wrybills would therefore provide for the generalist needs of most other riverbed nesting species. However, black-fronted terns nested on a broader range of microhabitats and defining other species needs on the basis of black-fronted tern requirements is not justified. When applied to feeding needs the approach had only limited success. For instance, the greater depth requirements of aquatic feeding pied stilts and South Island pied oystercatchers are not catered for when applying weighted usable area calculations made for wrybills. Moreover, because black-fronted terns spent considerable, albeit, an unknown amount of time foraging over adjacent farmland, it was not possible to study their overall feeding needs within the context of this study.

8.2. Management recommendations

The study provides a framework in which to assess the likely impacts of man-induced changes to the flow regime on riverbed nesting birds. At present the lower reaches of Canterbury braided rivers are most likely to be affected, so the results of this study are particularly relevant. This study shows it is not sufficient to conserve only one riverbed system. Concentrating conservation measures on the Rakaia would tend to neglect species other than the wrybill which are not well suited to breeding on this river. Conversely, protecting the Ashburton or Ashley at the expense of the Rakaia would place wrybills at risk because at present they occur in very low numbers on these other rivers. It would also be unwise to disregard completely lowland sections of rivers by claiming that high country areas occupied by the same species, often at greater densities, would fulfill this conservation role. Subtle changes in climate which affect food

availability means it is risky to further restrict the range of a species such as the wrybill. Clearly, there is a need to protect representative river types, and there are good reasons (see O'Donnell and Moore, 1983) for suggesting that the lower Ashley and Rakaia should be to the fore in this respect.

It seems likely that major irrigation development adjacent to the Rakaia will cause a massive increase in the population of black-backed gulls. Colonies of this species can cover large areas of riverbed and are avoided by most other riverbed species. Should this happen on the lower Rakaia then wrybill numbers will probably decline. Thus, a population control programme aimed at reducing black-backed gull numbers should be instituted.

A high rate of nest predation on the lower Rakaia compared for the upper river is associated with vegetation encroachment, and associated high rabbit and mustelid numbers. Pest destruction boards should be urged to fulfill their management functions and reduce rabbit numbers drastically. This may lead to a subsequent fall in predator numbers active on the riverbed but more work is still needed on this predator-prey relationship.

Direct development impacts can be broadly divided into two classes:

- (1) Those modifying the flow regime, viz., water abstraction for irrigation, and damming for hydro electric power;
- (2) Those changing the channel morphology, viz., river stabilisation works.

Study results can be used to predict the impacts these developments may have on specific wildlife values on individual river systems.

(a) Water abstraction

Water abstraction for irrigation occurs during spring and summer in Canterbury. On Ashley flow-type rivers this tends to correspond with declining flows, while on the Rakaia it is associated with high discharges. Peak irrigation requirements generally occur in February with another important period being late November to early December (Maidment *et al.*, 1980). Consequently, the highest demand normally does not occur during the breeding season. Furthermore, irrigators generally

demand water of high quality with a low silt load. Floods are therefore normally left substantially untouched. The most significant threats to bird conservation therefore occur with abstraction from medium to low flows which may lead to reduced food availability, loss of preferred foraging microhabitats, and by reducing the number of braids may lead to greater predator impact on breeding birds. For the Rakaia it appears all three possibilities would have only slight, if any, impact on breeding wrybills. Weighted usable area measurements indicated that, for the range of flows studied, there was an increase in the area of preferred habitat as discharge declined. These declines in flow did not result in major changes to the braiding pattern, and it appears that any overall decline in food caused by greater flow variability would be less likely to affect wrybills, than it would the fish species in the river. On the basis of these considerations it appears that minimum flows recommended to meet the needs of fish, will also meet the needs of wrybills.

Higher levels of predation on the Ashley appear to be associated with a much smaller braiding pattern than exists on the Rakaia. A significant relationship existed between declining flows and a drop in the number of channels in the most highly braided cross-section of the study area. This was also the reach with the greatest density of breeding birds. At the same time the amount of usable width also declined. Since October to November was the period of most intense breeding activity, it would seem logical to establish minimum flows on discharges sustained at the 90 percentile level during this time. This equates to a breeding season mean daily flow of approximately 6.5 cumecs at the Ashley Gorge.

(b) Water storage

Damming, whether for hydro or irrigation, has the most disastrous and immediate impacts on riverbed birds. By storing floodwaters, the capacity of the river system to limit the encroachment of vegetation onto the bare shingle areas needed for breeding, is reduced. This is amply demonstrated on the lower Waitaki river where willows have now stabilised large areas of riverbed to the detriment of species like wrybills and banded dotterels.

Even with a multiple objective planning strategy which includes wildlife needs as an integral component, it is difficult to see how pre-development values can be sustained. Despite this it may be possible to sustain the existing community structure, but at reduced species' population levels. For instance, the proposed residual river on the lower Waitaki may be designed in such a way as to provide a braided river environment suitable for riverbed nesting birds. A strategy incorporating suitably spaced flood events to clear the riverbed of exotic vegetation growth, and medium to low flows during the breeding season, may result in an Ashley type community developing. On this sort of system this appears preferable to a Rakaia flow regime which results in much lower bird densities.

(c) River stabilisation

The stabilisation of a river can occur by the encroachment of vegetation or by the actions of man, e.g., stopbanking and tree planting. Almost invariably they reduce the riverbed width and often result in greater bed stability. Either is bad for the riverbed nesting bird community. Stopbanking will tend to confine the riverbed and reduce its carrying capacity for the existing bird populations. Thus, high bird numbers on rivers like the Rakaia are a function of river size as well as habitat quality. Reductions in size will therefore reduce numbers by diminishing available area, providing of course, that other control factors remain the same. In addition, there is some likelihood that eventually these activities could stabilise the braiding process by restricting potential channel movement. This would also restrict the availability of suitable habitat. As a result it is essential to maintain natural riverbed width and instability.

8.3. Conclusions

This is the first work to have quantitatively determined the likely impacts of different forms of water resource developments on riverbed nesting birds. The study has:

- (1) described the habitat use-hydrology relationship for a range of species on two hydrologically distinct braided river systems;
- (2) quantified breeding and feeding habitat requirements and assessed the likely impact of development on these needs; and

(3) developed predictive tools for impact assessment which can be applied to other species in other systems.

There have been a number of important research findings. It was shown that contrasting flow regimes lead to characteristic community structures and population densities consistent with these discharge patterns. The first quantitative assessment of banded dotterel and wrybill diets has been made, the results conflicting with previously held beliefs, and the first full time-budget study of a riverbed bird completed. Wrybill time-budgets lack flexibility and as a consequence management decisions likely to affect their habitat must be assessed carefully. To this extent the determination of relationships between declining discharge and the area of foraging habitat provided the first quantitative evaluation of these impacts on riverbed nesting birds. In association with other aspects of this study it is now possible to plan better for the conservation of riverbed nesting birds in New Zealand, particularly where multiple use of water is planned.

ACKNOWLEDGEMENTS

As with all research projects there are many people to whom I am greatly indebted.

The following assisted with nest finding, surveying, or banding on the Ashley and Rakaia rivers: Malcolm Anderson, Bryan Bates, Mike Bowie, Lindsay Dell, Jane Ensor, John Fennell, Geoff Hancock, Rod Hay, Chris Hughey, Stu Moore, Kevin McGrath, Ian Morrison, members of the Ornithological Society of New Zealand, Colin O'Donnell, Brian Ross, Dave Teulon, Professor Gordon Williams, Graham Wilson, and Graham Wragg; thank you all.

My special thanks to Peter Tillson who gave up many weekends to help in nest searching and surveying. In addition he drafted several diagrams for the thesis. For all this help I am extremely grateful.

I would like to thank John Bethell who assisted me with nest finding and surveying for much of the 1983 breeding season, and Dave Rogers who helped for a time in 1981. Their assistance is appreciated.

I gratefully acknowledge the assistance received under the Department of Internal Affairs Wildlife Scholarship, and am thankful for a Lincoln College Research Grant in 1983. However, without the generous financial support provided by my parents it is doubtful whether this thesis could have been completed.

John Early and Dr Rowan Emberson of the Department of Entomology, Lincoln College, were of great assistance during the identification of invertebrates collected in pitfall traps. These two and Dr Mike Winterbourn of the Zoology Department, University of Canterbury, helped unravel the mysteries entangled in the banded dotterel and wrybill faeces. I also thank Paul Sagar for useful insights into the invertebrate 'problem'. The assistance of Helen Harman and Dave Teulon in sorting invertebrates was greatly appreciated.

I am grateful to the Ministry of Works and Development for the loan of a pygmy meter, and to the Geography Department, University of Canterbury, and the Agricultural Engineering Department, Lincoln College, for the use of surveying equipment. Thanks also, to John Fenwick and Graham Davenport, hydrologists at the Ministry of Works and Development, Christchurch, for patiently supplying me with considerable

river flow data. I would also like to thank Maurice Duncan for agreeing to, and then running wrybill probability of use curves through the weighted usable area model developed for the Rakaia river.

Dr Kelly Duncan from the Zoology Department, University of Canterbury, helped solve several statistical problems and provided a useful 'stats' package for subsequent computer work. Alison Lister from the Centre for Computing and Biometrics, Lincoln College, also solved a couple of sticky problems. I am particularly grateful for this assistance.

I would also like to thank Jane Ensor for typing many of the tables, figure headings, and appendices for the thesis. Thanks are also due to the Geography Department, University of Canterbury, for providing the space and equipment to undertake my drafting needs.

My parents, Dave and Mary Hughey, apart from being a source of great encouragement, gave considerable assistance in the field. They found many nests, and Dad braved deep channel crossings and often uncertain weather conditions to help with surveying.

To Dr Brent Cowie, Dr Ray Pierce, Dr Ralph Powlesland and Graham Wilson who commented on different sections of the thesis, and to Mark Sadler who read and commented on the text, go my sincere thanks.

I wish now, to extend my sincere thanks to those involved with the supervision of this work. The late Professor Gordon Williams was my original supervisor. I remain grateful for his encouragement and logistical support. Upon his untimely death in mid-1983, Dr Eric Scott took over my supervision. I was thankful for the help of Dr Scott, with outside support from Dr Malcolm Crawley, Wildlife Service, Department of Internal Affairs, Wellington, and Dr Ian Owens, Geography Department, University of Canterbury.

Finally, I would like to thank Wanda and W. Bill Plover for making my stays on the Rakaia, which were so often interrupted by nor'west gales, dust storms and floods, so very enjoyable.

REFERENCES

- ANON.; 1976. The Rakaia. Brochure produced for the New Zealand Water Conference 1976 by the Conference Organising Committee, Christchurch.
- ANDERSON, D.J. 1982. The home range: a new nonparametric estimation technique. Ecology 63: 103-112.
- ANDERSON, S.H.; SHUGART, H.H.JR. 1974. Habitat selection of breeding birds in an East Tennessee deciduous forest. Ecology 55: 828-837.
- ASHKENAZIE, S.; SAFRIEL, U.N. 1979. Time-energy budget of the semi-palmated sandpiper Calidris pusilla at Barrow Alaska. Ecology 60: 783-799.
- BAKER, A.J. 1972. Systematics and affinities of New Zealand oystercatchers. Thesis, Ph.D. Christchurch: University of Canterbury, New Zealand.
- BAKER, M.C.; BAKER, A.E.M. 1973. Niche relationships among six species of shorebirds on their wintering and breeding ranges. Ecological Monographs 43: 193-212.
- BEER, C.G. 1966. Adaptations to nesting habitat in the reproductive behaviour of the black-billed gull Larus bulleri. Ibis 108: 394-410.
- BLOKPOEL, H.; CATLING, P.M.; HAYMES, G.T. 1978. Relationship between nest sites of common terns and vegetation on the Eastern Headland, Toronto Outer Harbour. Canadian Journal of Zoology 56: 2057-2061.
- BOMFORD, M. 1978. The behaviour of the banded dotterel, Charadrius bicinctus. Thesis, M.Sc. Dunedin: University of Otago, New Zealand.
- BOVEE, K.D. 1978. The incremental method of assessing habitat potential for coolwater species, with management implications. American Fisheries Society Special Publication 11: 340-346.
- BOVEE, K.D.; COCHNAUER, T. 1977. Development and evaluation of weighted criteria, probability-of-use curves for instream flow assessments: Fisheries. Cooperative Instream Flow Service Group. Fort Collins: United States Fish and Wildlife Service, Colorado.
- BOWDEN, M.J.; et al. 1982. The water resources of the Ashley catchment. Christchurch: North Canterbury Catchment Board.
- BOWDEN, M.J. 1983. Water resources. p1-60. In: Bowden, M.J.; coordinator. The Rakaia river and catchment - a resource survey. Christchurch: North Canterbury Catchment Board.

- BROWN, J.L. 1969. Territorial behaviour and population regulation in birds. Wilson Bulletin 81: 293-329.
- BROWN, J.H.; ORIANS, G. 1970. Spacing patterns in mobile animals. Annual Review of Ecology and Systematics 1: 239-262.
- BUCKLEY, F.G.; BUCKLEY, P.A. 1979. Do aleutian terns exhibit extraordinary anti-predator adaptions? p99-107. In: Proceedings. Conference of the Colonial Waterbird Group. Southwestern Louisiana University, Lafayette, Louisiana.
- BUDGEON, L. 1977. Aspects of the biology of the black stilt (*Himantopus novaezealandiae*. Gould) in the Upper Waitaki River Basin. Thesis, B.Sc. Honours. Christchurch: University of Canterbury, New Zealand.
- BULL, P.C.; GAZE, P.D.; ROBERTSON, C.J.R. 1978. Bird distribution in New Zealand, a provisional atlas 1969-1976. Wellington: Ornithological Society of New Zealand.
- BURGER, J. 1976. Nest density of the black-headed gull in relation to vegetation. Bird Study 23: 27-32.
- BURGER, J. 1984. Colony stability in least terns. Condor 86: 61-67.
- BURGER, J.; LESSER, F. 1980. Nest site selection in an expanding population of herring gulls. Journal of Field Ornithology 51: 270-280.
- CHARNOV, E.L.; ORIANS, G.H.; HYATT, K. 1976. Ecological implications of resource depression. American Naturalist 110: 247-259.
- CHILD, P. 1983. Decline of the pied stilt in Central Otago. Notornis 30: 243-244.
- CHILD, P.; CHILD, M. 1984. The Alexandra black-fronted dotterels: 1982/83 season. Notornis 31: 31-39.
- CHOW, V.T. 1964. Handbook of applied hydrology. New York: McGraw-Hill.
- CHUTTER, F.M. 1972. A reappraisal of Needham and Usinger's data on the variability of a stream fauna when sampled with a surber sampler. Limnology and Oceanography 17: 139-141.
- CHUTTER, F.M.; NOBLE, R.G. 1966. The reliability of a method of sampling stream invertebrates. Archiv fur Hydrobiologie 62: 95-103.
- CLIFFORD, H.F. 1966. The ecology of invertebrates in an intermittent stream. Investigations of Indiana Lakes and Streams 7: 57-98.

- COWIE, B. 1983. Fisheries and wildlife. p111-248. In: Bowden, M.J.; coordinator. The Rakaia river and catchment - a resource survey. Volume 3. Christchurch: North Canterbury Catchment Board.
- COWIE, R.J. 1977. Optimal foraging in great tits (Parus major). Nature 268: 137-139.
- dA PRATO, S. 1981. The effect of spates on the feeding behaviour of dippers. Bird Study 28: 60-62.
- DAVIES, N.B. 1976. Food, flocking and territorial behaviour in the pied wagtail, Motacilla alba yarrellii in winter. Journal of Animal Ecology 45: 235-253.
- DAVIES, N.B. 1977. Prey selection and social behaviour in wagtails (Aves: Motacillidae). Journal of Animal Ecology 46: 37-57.
- DAVIES, N.B. 1981. The economics of territorial behaviour in birds, p63-74. In: Klomp, H.; Woldendorp, J.W.; editors. The integrated study of bird populations. Symposium proceedings. Amsterdam: North-Holland.
- DAVIS, S.F. 1979. Fish and fishery values of the Rakaia river - a preliminary report. Internal Report. Christchurch: Fisheries Research Division, Ministry of Agriculture and Fisheries.
- DAVIS, W.J. 1982. Territory size in Megaceryle alcyon along a stream habitat. Auk 99: 353-362.
- DINGWALL, P.R. 1982. New Zealand: saving some of everything. Ambio 11: 296-301.
- DOWNING, J.A. 1979. Aggregation, transformation, and the design of benthos sampling programs. Journal of the Fisheries Research Board of Canada 36: 1454-1463.
- DUNCAN, M. 1984. Personal communication. Hydrologist. Christchurch: Ministry of Works and Development.
- DUNNE, T.; LEOPOLD, L.B. 1978. Water in environmental planning. San Francisco: Freeman.
- ELLIOT, J.M. 1977. Some methods for the statistical analysis of samples of benthic invertebrates. Freshwater Biological Association Scientific Publication 25.
- EVANS, R.M. 1982. Foraging-flock recruitment at a black-billed gull colony: implications for the information center hypothesis. Auk 99: 24-30.
- FAHNESTOCK, R.K. 1963. Morphology and hydrology of a glacial stream - river, Mount Rainier Washington. Geological Survey Professional Paper 422-A. Washington: United States government printing

- office.
- FALLA, R.A.; SIBSON, R.B.; TURBOTT, E.G. 1978. The new guide to the birds of New Zealand and outlying islands. Auckland: Collins.
- FORD, R.G. 1979. The analysis of space use patterns. Journal of Theoretical Biology 76: 125-155.
- GIBSON, F. 1978. Ecological aspects of the time budget of the American avocet. American Midland Naturalist 99: 65-82.
- GIGER, R.D. 1973. Streamflow requirements of salmonids. Project AFS-62-1, Oregon Wildlife Commission.
- GILL, F.B.; WOLF, L.L. 1975. Economics of feeding territoriality in the golden-winged sunbird. Ecology 56: 333-345.
- GLOVA, G.J. 1982. Fishery impact evaluation - application of the incremental method. p16-27. In: McColl, R.H.S.; editor. River low flows: conflicts of water use. Water and Soil Miscellaneous Publication 47. Wellington: Water and Soil Division, Ministry of Works and Development.
- GLOVA, G.J. 1982. Personal communication. Scientist. Christchurch: Fisheries Research Division, Ministry of Agriculture and Fisheries.
- GLOVA, G.J.; DUNCAN, M. 1985. Potential effects of reduced flows on fish habitats in a large braided river, New Zealand. Transactions of the American Fisheries Society 114: 165-181.
- GOSS-CUSTARD, J.D.; JONES, R.E.; NEWBERY, P.E. 1977. The ecology of the Wash. 1. Distribution and diet of wading birds (Charadrii). Journal of Applied Ecology 14: 681-700.
- GREEN, R.F. 1977. Do more birds produce fewer young? A comment on Mayfield's measure of nest success. Wilson Bulletin 89: 173-175.
- GRIFFITHS, G. 1985. Personal communication. Hydrologist. Christchurch: North Canterbury Catchment Board and Regional Water Board.
- HARRIS, M.P. 1967. The biology of oystercatchers Haematopus ostralegus on Stockholm Island, S. Wales. Ibis 109: 180-193.
- HARRIS, M.P. 1970. Territory limiting the size of the breeding population of the oystercatcher (Haematopus ostralegus) - a removal experiment. Journal of Animal Ecology 39: 707-713.
- HAY, R. (sic). 1979. The wrybill - one of the world's ornithological oddities. Forest and Bird 214: 13-17.
- HAY, J.R. 1984. The behavioural ecology of the wrybill plover. Thesis, Ph.D. Auckland: University of Auckland, New Zealand.

- HEATHER, B.D. 1973. The black-fronted dotterel (Charadrius melanops) in the Wairarapa. Notornis 20: 251-261.
- HEATHER, B.D. 1977. Foot-trembling by the black-fronted dotterel. Notornis 24: 1-8.
- HENSLER, G.L.; NICHOLS, J.D. 1981. The Mayfield method of estimating nesting success: a model, estimators, and simulation results. Wilson Bulletin 93: 42-53.
- HERRON, S.K. 1981. Influence of physical factors on riparian carabid beetles (Bembidion and Actenonyx). Thesis, B.Sc. Honours. Christchurch: University of Canterbury, New Zealand.
- HIGGINS, K.F.; KIRSCH, L.M.; BALL, I.J.JR. 1969. A cable-chain device for locating duck nests. Journal of Wildlife Management 33: 1009-1011.
- HILDEN, O. 1965. Habitat selection in birds: a review. Annales Zoologici Fennici 2: 53-75.
- HOCKEY, P.A.R. 1984. Growth and energetics of the African black oystercatcher Haematopus moquini. Ardea 72: 111-117.
- HOLLAND, P.K.; ROBSON, J.E.; YALDEN, D.W. 1982. The breeding biology of the common sandpiper Actitis hypoleucus in the Peak District. Bird Study 29: 99-110.
- HOLMES, R.T.; BONNEY, R.E.JR.; PACALA, S.W. 1979. Guild structure of the Hubbard Brook bird community: a multivariate approach. Ecology 60: 512-520.
- HORN, H.S. 1966. Measurement of "overlap" in comparative ecological studies. American Naturalist 100: 419-424.
- HUGHEY, K.F.D. 1980. Hydrological aspects of brown trout management in the Selwyn river system, Canterbury, New Zealand. Thesis, M.Sc. Christchurch: University of Canterbury, New Zealand.
- HUGHEY, K.F.D. 1983. Protecting the habitat of our braided river wildlife. Soil and Water 19(2): 13-18.
- HUGHEY, K.F.D. 1985. The relationship between riverbed flooding and non-breeding wrybills on northern feeding grounds in summer. Notornis 32:42-50.
- HUXLEY, J. 1942. Evolution: the modern synthesis. London: Allen and Unwin.
- JACKSON, R.; JACKSON, J. 1980. A study of lapwing breeding population changes in the New Forest, Hampshire. Bird Study 27: 27-34.

- JAMES, F.C. 1971. Ordinations of habitat relationships among breeding birds. Wilson Bulletin 83: 215-236.
- JENNICH, R.I.; TURNER, F.B. 1969. Measurement of non-circular home range. Journal of Theoretical Biology 22: 227-237.
- JOHNSON, D.H. 1979. Estimating nest success: the Mayfield method and an alternative. Auk 96: 651-661.
- JORGENSEN, C.D.; TANNER, W.W. 1963. The application of the density probability function to determine the home ranges of Uta stansburiana stansburiana and Cnemidophorus tigris tigris. Herpetologica 19: 105-115.
- JOWETT, I.G. 1980. Residual river Luggate-Queensberry development. Power Division Report. Wellington: Ministry of Works and Development.
- JOWETT, I.G. 1982. The incremental approach to instream flow needs: New Zealand case studies. p9-15. In: McColl, R.H.S.; editor. River low flows: conflicts in water use. Water and Soil Miscellaneous Publication 42. Wellington: Water and Soil Division, Ministry of Works and Development.
- JOWETT, I.G.; WING, S.J. 1980. Evaluation of flow requirements for the Tekapo river fishery. Power Division Report. Wellington: Ministry of Works and Development.
- KREBS, J.R. 1971. Territory and breeding in the great tit, Parus major L. Ecology 52: 2-22.
- KREBS, J.R. 1981. Optimal foraging, predation risk and territory defence. p83-90. In: Klomp, H.; Woldendorp, J.W.; editors. The integrated study of bird populations. Symposium proceedings. Amsterdam, North-Holland.
- KROGER, R.L. 1972. Underestimation of standing crop by the surber sampler. Limnology and Oceanography 17: 475-478.
- LACK, D. 1944. Ecological aspects of species-formation in passerine birds. Ibis 86: 260-286.
- LACK, D. 1949. The significance of ecological isolation. p299-308. In: Jepsen, G.L.; Mayr, E.; Simpson, G.G.; editors. Genetics, paleontology, and evolution. Princeton: Princeton University.
- LACK, D. 1954. The natural regulation of animal numbers. Oxford: Clarendon.
- LALAS, C. 1977. Food and feeding behaviour of the black-fronted tern, Chlidonias hybrida albostriatus. Thesis, M.Sc. Dunedin: University of Otago, New Zealand.

- LALAS, C. 1979. Seasonal movements of black-fronted terns. Notornis 26: 69-72.
- LALAS, C.; HEATHER, B.D. 1980. The morphology, moult and taxonomic status of the black-fronted tern. Notornis 27: 45-68.
- LEOPOLD, L.B.; WOLMAN, M.G.; MILLER, J.P. 1964. Fluvial processes in geomorphology. San Francisco: Freeman.
- LINDROTH, C.H. 1976. Genus Bembidion Latreille (Coleoptera: Carabidae) in New Zealand: a revision. New Zealand Journal of Zoology 3: 161-198.
- MacARTHUR, R.; LEVINS, R. 1967. The limiting similarity, convergence, and divergence of coexisting species. American Naturalist 101: 377-385.
- MACINNES, C.D. 1980. Comment: observer-induced predation is real. Journal of Wildlife Management 44: 222-224.
- McCONKEY, B.F. 1971. Bionomics of the pied stilt (*Himantopus leucocephalus*) in New Zealand with special reference to breeding behaviour. Thesis, M.Sc. Palmerston North: Massey University, New Zealand.
- MCNICHOLL, M.K. 1975. Larid site tenacity and group adherence in relation to habitat. Auk 92: 98-104.
- MAIDMENT, D.R.; LEWTHWAITE, W.J.; HAMBLETT, S.G. 1980. Rakaia water use and irrigation development. Water and Soil Miscellaneous Publication 19. Wellington: Water and Soil Division, Ministry of Works and Development.
- MAYFIELD, H. 1961. Nesting success calculated from exposure. Wilson Bulletin 73: 255-261.
- MAYFIELD, H.F. 1975. Suggestions for calculating nest success. Wilson Bulletin 87: 456-466.
- MERTON, J.M. 1977. Feeding habitats of the black stilt, *Himantopus novaezealandiae*, in the Upper Waitaki Basin. Thesis, B.Sc. Honours. Christchurch: University of Canterbury, New Zealand.
- MILLER, H.W.; JOHNSON, D.H. 1978. Interpreting the results of nesting studies. Journal of Wildlife Management 42: 471-476.
- MINSHALL, G.W.; WINGER, P.V. 1968. The effect of reduction of stream flow on invertebrate drift. Ecology 49: 580-582.
- MOORE, S. 1981. Wildlife survey of the Ashley river. Internal report. Christchurch: New Zealand Wildlife Service, Department of Internal Affairs.

- MOORE, S. 1983. Personal communication. Wildlife Officer. Christchurch: New Zealand Wildlife Service, Department of Internal Affairs.
- MORISITA, M. 1959. Measuring of interspecific association and similarity between communities. Memoirs of the Faculty of Science, Kyushu University, Series E. (Biology) 3: 65-80.
- MORRIS, R.D.; KIRKHAM, I.R.; CHARDINE, J.W. 1980. Management of a declining common tern colony. Journal of Wildlife Management 44: 241-245.
- MOSLEY, M.P. 1982a. Analysis of the effect of changing discharge on channel morphology and instream uses in a braided river, Ohau River, New Zealand. Water Resources Research 18: 800-812.
- MOSLEY, M.P. 1982b. A procedure for characterising river channels. Water and Soil Miscellaneous Publication 32. Wellington: Ministry of Works and Development.
- MOSLEY, M.P. 1982c. Critical depths for passage in braided rivers, Canterbury, New Zealand. New Zealand Journal of Marine and Freshwater Research 16: 351-357.
- MOSLEY, M.P. 1983a. Prediction of changes in the physical character of braided rivers in response to changing discharge. Journal of Hydrology (N.Z.) 22: 18-67.
- MOSLEY, M.P. 1983b. The effect of reduced flows on temperatures in the Rakaia river. Internal Report WS 788. Christchurch: Water and Soil Science Centre, Ministry of Works and Development.
- MOSLEY, M.P. 1984. Hydrological evidence on the Rakaia River. Presented to the Planning Tribunal chaired by Judge Skelton into the Rakaia National Water conservation Order, Christchurch.
- MOSLEY, M.P.; GLOVA, G.J. 1983. Instream uses of New Zealand rivers. p8-39. In: Proceedings.; Workshop on residual streamflow and damming in small streams. Auckland: Auckland Regional Authority.
- NATIONAL WATER AND SOIL CONSERVATION AUTHORITY COMMITTEE. 1984. Recommended draft Water Conservation Order: Rakaia river. Wellington: National Water and Soil Conservation Authority.
- NETHERSOLE-THOMPSON, D.; NETHERSOLE-THOMPSON, M. 1979. Greenshanks. Calton: Poyser.
- NEWTON, I. 1981. The role of food in limiting bird numbers. p11-30. In: Klomp, H.; Woldendorp, J.W.; editors. The integrated study of bird populations. Symposium proceedings. Amsterdam: North-Holland.

- NEWTON, I.; et al. 1977. Spacing of sparrowhawk nesting territories. Journal of Animal Ecology 46: 425-441.
- NORTH CANTERBURY CATCHMENT BOARD. 1974. Rakaia river management plan. Christchurch.
- ODUM, E.P. 1971. Fundamentals of ecology. Philadelphia: Saunders.
- O'DONNELL, C.F.J. 1983. Personal communication. Scientist. Christchurch: New Zealand Wildlife Service, Department of Internal Affairs.
- O'DONNELL, C.F.J.; MOORE, S.M. 1983. The wildlife and conservation of braided river systems in Canterbury. Fauna Survey Unit Report 33. Wellington: New Zealand Wildlife Service, Department of Internal Affairs.
- OLIVER, W.R.B. 1955. New Zealand birds. Second edition. Wellington: Reed.
- ORIANS, G.H. 1961. The ecology of blackbird (Agelaius) social systems. Ecological Monographs 31: 285-312.
- ORIANS, G.H. 1966. Food of nestling yellow-headed blackbirds, Cariboo Parklands, British Columbia. Condor 68: 321-337.
- ORIANS, G.; HORN, H.S. 1969. Overlaps in foods of four species of blackbirds in the potholes of Central Washington. Ecology 50: 930-938.
- PHILLIPS, R.E. 1980. Behaviour and systematics of New Zealand plovers. Emu 80: 177-197.
- PIERCE, R.J. 1971. Black-fronted dotterels nesting near Timaru. Notornis 18: 133.
- PIERCE, R.J. 1976. The feeding ecology of wrybills in Canterbury. Thesis, Dip.Sci. Dunedin: University of Otago, New Zealand.
- PIERCE, R.J. 1979. Foods and feeding of the wrybill (Anarhynchus frontalis) on its riverbed breeding grounds. Notornis 26: 1-21.
- PIERCE, R.J. 1982a. A comparative ecological study of pied and black stilts in South Canterbury. Thesis, Ph.D. Dunedin: University of Otago, New Zealand.
- PIERCE, R.J. 1982b. A good nesting season for black stilts. Forest and Bird 14(2): 30-32.
- PIERCE, R.J. 1985. Personal communication. Scientist. Dunedin: University of Otago.
- PITELKA, F.A. 1958. Timing of molt in stellar jays of the Queen Charlotte Sounds, British Columbia. Condor 60: 38-49.

- POSSARDT, L.D.; DODGE, W.E. 1978. Stream channelisation impacts on songbirds and small mammals in Vermont. Wildlife Society Bulletin 6: 18-24.
- POTTS, T.H. 1882. Out in the open. Reprinted 1976, Christchurch: Capper.
- POWLESLAND, R.G. 1981a. Comparison of time-budgets for mainland and outer Chetwode Island populations of adult male South Island robins. New Zealand Journal of Ecology 4: 98-105.
- POWLESLAND, R.G. 1981b. Riverbed birds and their vulnerability to development schemes on rivers. Internal Report. Wellington: New Zealand Wildlife Service, Department of Internal Affairs.
- RATCLIFFE, D.A. 1976. Observations on the breeding of the golden plover in Great Britain. Bird Study 23: 63-116.
- RESH, V.H. 1979. Sampling variability and life history features: basic considerations in the design of aquatic insect studies. Journal of the Fisheries Research Board of Canada 36: 290-311.
- ROBERTSON, C.J.R.; O'DONNELL, C.F.J.; OVERMARS, F.B. 1983. Habitat requirements of wetland birds in the Ahuriri river catchment, New Zealand. Occasional Publication 3. Wellington: New Zealand Wildlife Service, Department of Internal Affairs.
- SAGAR, P.M. 1983a. Benthic invertebrates of the Rakaia river. Fisheries Environmental Report 36. Christchurch: Ministry of Agriculture and Fisheries.
- SAGAR, P.M. 1983b. Invertebrate recolonisation of previously dry channels in the Rakaia river. New Zealand Journal of Marine and Freshwater Research 17:377-386.
- SAGAR, P.M. 1984. Personal communication. Scientist. Christchurch: Fisheries Research Division, Ministry of Agriculture and Fisheries.
- SAGAR, P.M.; ELDON, G.A. 1983. Food and feeding of small fish in the Rakaia river, New Zealand. New Zealand Journal of Marine and Freshwater Research 17: 213-226.
- SCHOENER, T.W. 1965. The evolution of bill size differences among sympatric congeneric species of birds. Evolution 19: 189-213.
- SCHOENER, T.W. 1968. Sizes of feeding territories amongst birds. Ecology 49: 123-141.
- SEASTEDT, T.R.; MacLEAN, S.F. 1979. Territory size and composition in relation to resource abundance in Lapland longspurs breeding in Arctic Alaska. Auk 96: 131-142.

- SHUGART, H.H.; PATTEN, B.C. 1972. Niche quantification and the concept of niche pattern. In: Patten, B.C.; editor. Systems analysis and simulation in ecology 2. New York: Academic Press.
- SIBSON, R.B. 1963. A population study of the wry-billed plover (Anarhynchus frontalis). Notornis 10: 143-153.
- SIBSON, R.B. 1975. Some thoughts on the diet of the South Island pied oystercatcher. Notornis 22: 66-67.
- SMITH, A.E. 1975. The impacts of lowland river management. Bird Study 22:249-254.
- SMITH, K.G. 1977. Distribution of summer birds along a forest moisture gradient in an Ozark watershed. Ecology 58: 810-819.
- SOIKKELI, M. 1967. Breeding cycle and population dynamics in the dunlin (Calidris alpina). Annales Zoologici Fennici 4: 158-198.
- SOKAL, R.R.; ROHLF, F.J. 1981. Biometry. Second edition, San Francisco: Freeman.
- SOUTHWOOD, T.R.E. 1978. Ecological methods with particular reference to the study of insect populations. London: Methuen.
- STEAD, E.F. 1932. The life histories of New Zealand birds. London: Search.
- STRANG, C.A. 1980. Incidence of avian predators near people searching for waterfowl nests. Journal of Wildlife Management 44: 220-222.
- SVARDSON, G. 1949. Competition and habitat selection in birds. Oikos 1:157-174.
- SWALES, S. 1982. Environmental effects of river channel works used in land drainage improvement. Journal of Environmental Management 14: 103-126.
- TENNANT, D.L. 1972. A method for determining instream flow requirements for fish, wildlife, and the aquatic environment. p3-9. In: Transcript of Proceedings.; Instream flow requirement workshop. Portland, Oregon.
- TUCKER, V.A. 1969. The energetics of bird flight. Scientific American 220: 70-78.
- TURBOTT, E.G. 1969. Native birds. p426-434. In: Knox, G.A.; editor. Natural history of Canterbury. Wellington: Reed.
- TWYDLE, M.; TWYDLE, W.; 1983. South Island pied oystercatchers nesting in Hawkes Bay. Notornis 30: 197-198.
- VAN WINKLE, W.JR.; MARTIN, D.C.; SEBETICH, M.J. 1973. A home-range model for animals inhabiting an ecotone. Ecology 54: 205-209.

- VERNER, J. 1965. Time budget of the male long-billed marsh wren during the breeding season. Condor 67: 125-139.
- VERNER, J. 1977. On the adaptive significance of territoriality. American Naturalist 111: 769-775.
- WARD, R.C. 1975. Principles of hydrology. Second edition. London: McGraw-Hill.
- WATT, J.C. 1980. Notes on pitfall trapping on Headlong Peak, Mount Aspiring National Park. New Zealand Entomologist 7: 184-191.
- WESCHE, T. 1978. Minimum stream flows. Wyoming Wildlife 42(11): 6-10.
- WEST, G.C. 1968. Bioenergetics of captive willow ptarmigan under natural conditions. Ecology 49: 1036-1045.
- WIENS, J.A. 1969. An approach to the study of ecological relationships among grassland birds. Ornithological Monographs 8.
- WILLIAMS, D.D.; HYNES, H.B.N. 1974. The occurrence of benthos deep in the substratum of a stream. Freshwater Biology 4: 233-256.
- WILLIAMS, G.R.; GIVEN, D.R. 1981. The red data book of New Zealand. Wellington: Nature Conservation Council.
- WINNETT-MURRAY, K. 1979. The influence of cover on offspring in western gulls. p33-43. In: Proceedings.; Conference of the Colonial Waterbird Group. Southwestern Louisiana University, Lafayette, Louisiana.
- ZARET, T.M.; RAND, A.S. 1971. Competition in tropical stream fishes: support for the competitive exclusion principle. Ecology 52: 336-342.

APPENDIX 1

THE BRAIDED RIVER ENVIRONMENT

1. Introduction

The characteristic pattern of riverbed use by birds is related to a number of physical parameters associated with particular river forms and flow regimes. These features are described in this chapter, and then assessed in terms of habitat use by the range of riverbed nesting birds in New Zealand.

2. The riverbed environment

Aquatic and terrestrial environments are the two main riverbed components with the latter being further subdivided into active riverbed and riparian environments. These subdivisions occur in most river systems, although the relative proportions vary in accordance with the hydrology and geomorphology of the particular waterway. The variation in the occurrence of these features can have direct and subtle effects on riverbed use by birds.

2.1. Channel form

River shape is the complex result of two classes of interacting factors: those relating to the debris load, its size, lithology, amount, and depositional forms; and those related to water flow (Dunne and Leopold, 1978). Different combinations of these factors lead to the two main channel forms: braided and single thread rivers. Braided rivers separate around islands, with individual channels being divided by gravel bars which change rapidly in size and shape, resulting in a constantly varying distribution of channels and bars (Fahnestock, 1963).

Single channel systems can be further subdivided into meandering or straight streams. Rivers meander because this pattern is a closer approach to minimum uniformly distributed work than are alternative shapes (Dunne and Leopold, 1978). In nature there are no continuously straight rivers but irregular non-meandering channels which are more or less straight. These channel types are characterised by regular pool-riffle sequences, with successive riffle bars occurring on alternate sides of the channel.

Riffles and pools provide the essential character of a stream system, with riffles typified by greater than average slope, and consequently streamflow velocity. In riffles, water depth is less than average, and the gravel substrate is cleaner and of larger particle size than that found in pools. The physical habitat in riffles is well suited to the growth and development of many common aquatic invertebrates, including species of mayfly (Order *Ephemeroptera*), stonefly (Order *Plecoptera*) and caddisfly (Order *Trichoptera*). This habitat suitability can be attributed to the larger substrate size which provides protection from the direct force of the current, while at the same time maintaining relatively high current velocities through the substrate (Wesche, 1978). The latter produces turbulence, thus preventing the build-up of a thin layer of stagnant water about the insect's body, which facilitates oxygen and nutrient uptake (Wesche, 1978). Riffles form as a result of deposition and the subsequent maintenance of gravel bars.

Pools are deeper, slower flowing, and have predominantly sand and silt substrates. Consequently, most invertebrates inhabiting pools are burrowing species. The decreased turbulence, which reduces the ability of aquatic insects to make efficient use of the available nutrients and oxygen, restricts many aquatic insects to riffles.

2.2. Flow regime

Streamflow is considered to be the critical factor in a lotic (flowing) environment (Giger, 1973). Obtaining an understanding of the dynamic hydrology of river flow is therefore important when relating bird behaviour and habitat use to the physical features of the riverbed environment.

Runoff, that part of the precipitation as well as other flow contributions which appears in surface streams of either perennial or intermittent form (Chow, 1964), consists of three components (Ward, 1975):

- (1) Subsurface runoff, which is the sum of interflow and groundwater flow, and is usually equal to the total flow of water arriving at the stream as saturated flow into the stream bed itself, and as percolation from the seepage faces on the stream bank;
- (2) Baseflow, which is the sustained or fair weather runoff, and is the

sum of groundwater runoff and delayed interflow;

(3) Quickflow or direct runoff, which is the sum of channel precipitation, surface runoff, and rapid interflow. This component represents the major runoff contribution during storms, and is therefore the largest contributor to most floods.

Baseflow and quickflow appear to have the most significant impacts in terms of fisheries and wildlife management. In general terms, streamflow reaches a maximum during wet seasons and at times of snow melt, and declines slowly as the relative importance of baseflow increases during the dry season and at times of snow and ice accretion. In the short term, flows peak sharply during storms but decline relatively slowly after rainfall ceases. The long term, sustained, dryweather runoff or baseflow is therefore closely associated with the feeding behaviour and successful nesting of most riverbed birds. In contrast, quickflow flooding has immediate impacts on nesting success and the provision of food.

The long term relationship between baseflow and quickflow determines the principal character of a stream or river (Ward, 1975):

- (a) Ephemeral streams which comprise quickflow only, and which therefore flow only during, and immediately after, rainfall or snowmelt;
- (b) Intermittent streams which flow during wet seasons, but dry up during droughts. Riverflow consists mainly of quickflow, but baseflow makes some contribution during the wet season, when the water table rises above the streambed; and
- (c) Perennial rivers, which flow throughout the year, so that even during the most prolonged dry spell the water table is always above the stream bed. Groundwater flow can make a continuous and significant contribution to total runoff in perennial streams.

All three streamflow types are represented, although disproportionately, in Canterbury rivers. The small and mainly single channel Selwyn river has upper and lower reaches of perennial flow, a large central area of intermittent flow, and tributaries with ephemeral flow patterns (Hughey, 1980). The identification and mapping of these zones on a single channel river is simple, but becomes much more complicated on a braided river. Flow in the Rakaia as a whole is

perennial, but in any one braided cross-section all three streamflow types are represented. During medium to large floods most channels contain flowing water, but as the flow recedes the ephemeral nature of many channels quickly occurs. Other channels are sustained for extended periods of time by gravel bank seepage and underflow, but during long periods of dry weather runoff or baseflow, even some of these channels dry up, thereby displaying an intermittent flow pattern. A further complication arises because of the unstable nature of the bed in a braided river. After large floods, which can cause large scale bed profile modification, even those channels considered to be of perennial type may have been abandoned and the flow contained within a previously defined ephemeral or intermittent channel. In general, those channels most closely approaching a perennial flow classification will provide the most reliable food supplies for fish and birds..

2.3. Bird habitat provision

River form and the flow regime can be related to various aspects of the breeding and feeding ecology of riverbed birds. However, only those species which breed on the 'active riverbed', defined as that section of the river floodplain geomorphologically influenced by flows less than the bankful discharge (which is the flow equalling or exceeding the bank to bank capacity of the river), were assessed in this study. On most rivers the active riverbed is bordered by the riparian zone and berm land, which are typically more stable areas. In New Zealand, shags (Phalacrocorax spp.), white-faced herons (Ardea novaehollandiae Latham), blue ducks (Hymenolaimus malacorhynchos Gmelin) and New Zealand kingfishers (Halcyon sancta Vigors and Horsfield) are species which breed in riparian habitats, and in some cases are highly reliant on the active riverbed for feeding.

When the available bird habitat and use of braided and single channel rivers are compared, braided rivers have higher densities and a greater range of species using the active riverbed (pers. obs.; see Table 1). The essential conditions for braiding are provided by sediment transport and a low threshold of bank erosion (Leopold *et al.*, 1964). Channel morphology changes rapidly and there are many islands of variable stability. Where erosion and deposition are occurring rapidly, mid channel islands may be only sparsely vegetated, or not vegetated at all. Depending on preferred nest site requirements, these islands

provide large areas of potential breeding habitat which has been occupied by a range of bird species in New Zealand. However, although deposition ultimately produces these mid channel islands, subsequent erosion may make them very transitory. The timing of these events may involve minutes or days (Fahnestock, 1963), or months or seasons on rivers subject to periodic or seasonal floods (Leopold, et al., 1964). Extreme short term channel variations are typical of Alaskan braided rivers. Such conditions have not favoured exploitation by riverbed birds. Conversely, the periodicity of these events on Canterbury braided rivers must, on average, be sufficiently long to allow for successful breeding to maintain the population of each species.

TABLE 1: Habitat provision for birds nesting on braided and single channel rivers, assuming equal flows (Hughey, 1983).

Habitat consideration	Braided river	Single channel river
Nest site provision	Numerous shingle islands and banks often clear of vegetation. Active riverbed is very wide.	Limited backwater areas and higher banks often heavily vegetated - the riparian zone is used extensively by tree nesters.
Breeding success	Islands are protected from feral predators by the moat effects of braiding. Floods can contribute to very high mortalities.	The close proximity of vegetated areas and the lack of protective waterways exposes nests to the attention of feral predators.
Feeding	Large areas of edge habitat to suit the preferred depths and other hydrological needs of waders. Actual usable area related to braiding index. Instability can contribute to relatively low aquatic productivity.	Channel is often very stable and productive with suitable habitat for birds like waders restricted to backwaters. Steep banks and vegetated margins restrict usable area.
Carrying capacity	Larger riverbed area and channel pattern lead to greater habitat area and carrying capacity. A range of species can occupy a single cross-section.	Relatively small areas of open riverbed available. Total numbers and diversity usually low. Territorial behaviour plays an important role.

Single channel systems are typically narrow and stable, in marked contrast to the width and instability of braided rivers. Both features contribute to the limited availability of suitable habitat for riverbed breeding birds on single channel rivers where there are few mid-channel islands and the mainstream edge or banks are the only potentially usable riverbed habitat. This edge or bank habitat is of two forms:

- (1) The depositional point bar found on the convex bank of river bends or meanders; and
- (2) The steep erosive bank on the concave bend.

For riverbed breeding birds the recent deposits on convex banks appear to be the only clear gravel or other substrate available as potential ground nesting sites (pers. obs.). Stability in these systems is also reflected in the enclosed, and often heavily vegetated riverscape, which favours a different bird community to that typically recorded on the wide braided rivers. Moreover, aquatic habitat use for feeding may be restricted by steep, vegetated banks and again favours a different species use pattern from that on braided rivers. Generally though, the overall carrying capacity for riverbed nesting birds is lower than on braided rivers of comparable discharge.

3. The geographical distribution of riverbed breeding birds

Geographical aspects of the distribution of riverbed nesting birds and published material concerning general habitat use patterns are presented in this section. Species reviewed include only those considered commonly to occupy active riverbeds for breeding purposes. Common species such as paradise shelducks (Tadorna variegata Gmelin) and spur-winged plovers (Lobibyx novaehollandiae Stephens) are excluded because they usually nest on the more stable berm lands or riparian zones. Two other species, Caspian terns (Hydroprogne caspia Pallas) and white-fronted terns (Sterna striata Gmelin), which commonly breed in coastal habitats, are occasionally recorded nesting in riverbeds. However, since these occurrences are relatively uncommon, and are not considered to be critical in the population dynamics of each species, they are not included in this study. The red-capped dotterel (Charadrius rubricollis Gmelin), which was believed to be colonising several Canterbury riverbeds including the Ashley, but which has not been recorded breeding in recent years, is similarly excluded. Blue

ducks, which inhabits forested, single channel, mountain catchment rivers, is adapted to feeding on aquatic insects, but nests on vegetated bermlands near streams. While it is correctly regarded as a river bird it is not a riverbed nester, and as such is omitted from this study. By definition and exclusion the following list of riverbed nesting birds was established:

- Banded dotterel
- Black-backed gull
- Black-billed gull
- Black-fronted dotterel
- Black-fronted tern
- Black stilt
- Pied stilt
- South Island pied oystercatcher
- Wrybill

The generalised breeding season distribution of each species is shown in Table 2. Four of the nine species nest only in the South Island, and while none is restricted totally to the North Island, black-fronted dotterels are presently more numerous there. Six species use riverbeds as their sole or principal breeding habitat. A breeding season preference for braided river habitats is shown by six species.

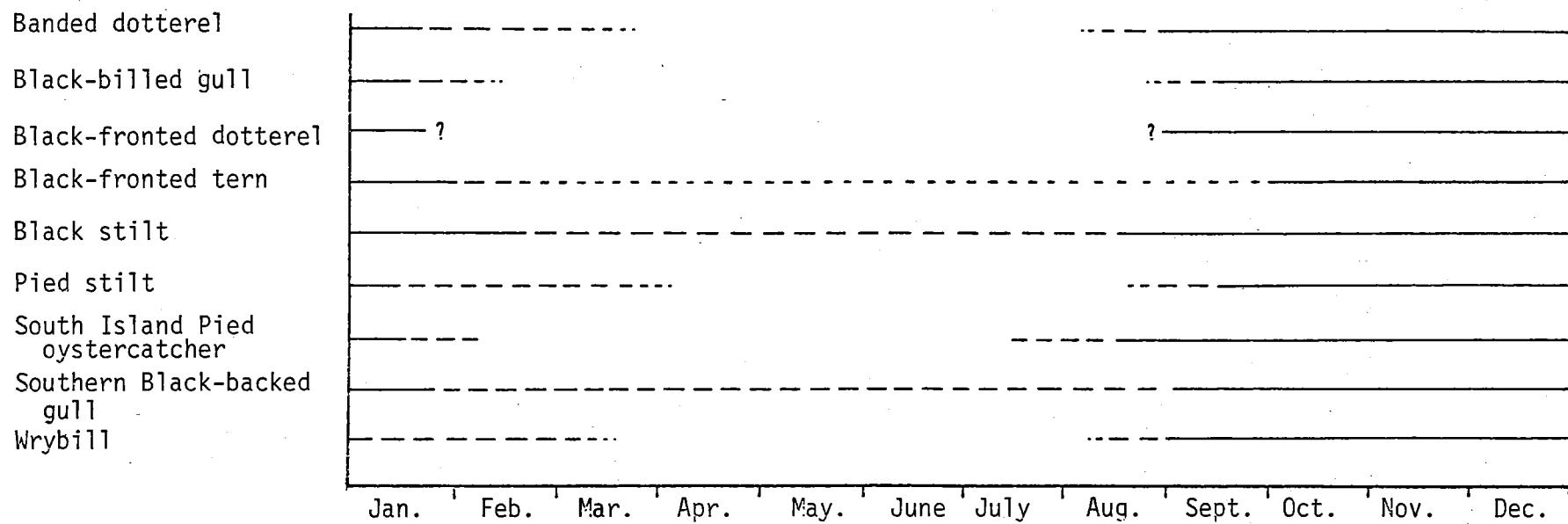
After breeding most species migrate from riverbeds to harbours and estuaries around New Zealand, or, for banded dotterels, to Australia. The greatest period of potential competition occurs during the late August to early January breeding season when all species are present on the rivers (see Figure 1). Black-fronted terns, black-backed gulls and black stilts are the only species which occupy rivers on a year-round basis. However, depending on species-specific behaviour, a portion of each of these species' populations undertakes some form of migration within New Zealand. The research implications of this migratory behaviour made it important to concentrate study during the breeding season, i.e., the period late August to early January.

3.1. Banded dotterel

TABLE 2 : The spatial distribution of riverbed nesting birds during the breeding season.

	Nationwide distribution	North Island		South Island		Breeding on active riverbeds			River system preferences			All systems
		Only	Mainly	Only	Mainly	Only	Mainly	Often	Mainly braided	Mainly single channel		
Banded dotterel	✓				✓			✓	✓			
Black-billed gull	✓				✓		✓					✓
Black-fronted dotterel	✓		✓			✓				✓		
Black-fronted tern				✓		✓			✓			
Black stilt				✓				✓	✓			
Pied stilt	✓				✓			✓	✓			
South Island pied oystercatcher				✓			✓		✓			
Southern black-backed gull	✓						✓					✓
Wrybill				✓		✓			✓			

FIGURE 1 : Periods of greatest riverbed use by riverbed nesting birds.



Banded dotterels (Order Charadriiformes: Family Charadriidae) are the most numerous and widespread of the smaller plovers (see Table 3 for tarsus and bill lengths of each species) breeding in New Zealand (Falla *et al.*, 1978). Distribution is more coastal in the North Island than in the South Island (Bull *et al.*, 1978), a feature probably attributable to a seasonal variation in distribution associated with post-breeding migration. Banded dotterels are present on all major river systems in Canterbury (O'Donnell and Moore, 1983).

TABLE 3: Tarsus and bill lengths of riverbed nesting bird species in New Zealand.

Species	Tarsus (mm)	Bill length (mm)
Banded dotterel	30-32	16-18
Black-billed gull	43-44	37-38
Black-fronted dotterel	25	15
Black-fronted tern	15-17	25-28
Black-stilt	85-95	69-76
Pied stilt	108-110	61-66
South Island pied oystercatcher	45-56	70-96
Southern black-backed gull	58-71	46-58
Wrybill	27-30	30-32

Data source: Oliver (1955)

The widespread distribution of banded dotterels is also reflected in the range of nest sites chosen for breeding. Nests are simple cups or scrapes in the sand, shingle, drift, or turf, and are found on riverbeds, terraces, lake shores, beaches and pasture. After breeding, banded dotterels migrate to coastal areas, or to Australia.

Banded dotterels forage over a variety of substrates. Shingle, sand, and muddy areas are preferred feeding habitats, although birds are often observed wading in the water over the same substrates. For all seasons on the Ahuriri river most feeding occurred in terrestrial locations with significant use of aquatic habitats also being made (Robertson *et al.*, 1983). Oliver (1955) recorded banded dotterels feeding on the fruits of Coprosma petreie, and Muehlenbeckia axillaris growing on the riverflats of inland Canterbury, but the species is

generally regarded as being insectivorous (Bomford, 1978). On the riverbeds of inland Canterbury, Pierce (1976) found that terrestrial and sub-benthic invertebrates were eaten with foraging behaviour divided between pecks and probes depending on the nature of the substrate. Although the generalised features of habitat use on the Ahuriri river were extensively studied by Robertson *et al.* (1983), no determinations of habitat preferences in relation to occurrence have been carried out.

3.2. Black-billed gull

Although small numbers of the endemic black-billed gulls (Order Charadriiformes: Family Laridae) regularly breed in the North Island, this species is essentially an inland gull of the larger river systems and lakes of the South Island (Falla *et al.*, 1978). Black-billed gulls breed on all of the larger Canterbury rivers (O'Donnell and Moore, 1983). They arrive on their breeding grounds in August and September, and after breeding they begin a coastward and northward migration. This movement off the riverbed is not synchronised, and may continue until April.

Shingle islands and the beaches of braided rivers are the sites typically chosen by colonies of black-billed gulls for nesting (Beer, 1966). Changes in vegetation status of their preferred non-vegetated or only sparsely vegetated sites from one year to the next are reported to affect black-billed gull site tenacity (Beer, 1966).

Black-billed gulls are omnivorous opportunist feeders (Powlesland, 1981b). Aquatic and terrestrial insects contribute a large portion of the diet (Falla *et al.*, 1978). Foraging behaviour associated with colonial leadership and flocking leads the species to rich resources over farm land (Evans, 1982). A shift to riparian terrestrial habitats was also observed on the Ahuriri (Robertson *et al.*, 1983). This behaviour makes it difficult to determine precise feeding habitat needs in relation to river hydrology.

3.3. Black-fronted dotterel

Black-fronted dotterels (Order Charadriiformes: Family Charadriidae) were first recorded in Hawkes Bay in 1954. Since then, this self-introduced Australian species has become strongly established on the riverbeds of Hawkes Bay and the Wairarapa in the North Island. The presence of breeding pairs on the Opihi river in South Canterbury

was observed in 1970 (Pierce, 1971). Further records have recently been noted on the Ashburton, Ashley and Rakaia rivers (O'Donnell and Moore, 1983).

In Hawkes Bay, black-fronted dotterel nests have been found on river shingle which is usually a few metres from the waters edge (Falla *et al.*, 1978). A nest on the Opihi river described by Pierce (1971) was a shallow depression formed of pebbles, small chips of wood, and sheep dung located on a large shingle island. While no published information regarding site selection and vegetation tolerance exists, it seems likely that riverbed preferences will be similar to those of other small plovers. Birds remain on their summer quarters for as long as river conditions remain suitable (Heather, 1977). Small flocks assemble during winter (Falla *et al.*, 1978) but little is known about migratory tendencies.

On the Opihi river, black-fronted dotterels were seen feeding in a small muddy backwash alongside banded dotterels (Pierce, 1971). The birds fed exclusively on the riverbed and showed a preference for muddy pools (Pierce, 1971). Similar observations were made on Wairarapa riverbeds by Heather (1973) who concluded that black-fronted dotterels are freshwater feeders which prefer the fine silty mud, freshly exposed by falling river and pond levels. Foraging behaviour is split between pecks and probing, but the only prey identified has been worms (Heather, 1973). Child and Child (1984) attributed the decline of banded dotterels on the Manuherikia river near Alexandra to displacement by black-fronted dotterels. The implications of this require research to determine which conditions are favourable to either or both species so that conservation of banded dotterels can be achieved.

3.4. Black-fronted tern

The endemic black-fronted tern (Order Charadriiformes: Family Laridae) is found predominantly along the eastern South Island, and in Canterbury they breed on all of the medium to large river systems (O'Donnell and Moore, 1983). Black-fronted tern move locally within New Zealand; after breeding most individuals disperse to coastal regions and some go to the North Island (Lalas, 1979). Lalas (1979) also found that most terns had left the Upper Waitaki river system by late March but that in the Tasman Valley dispersal was not complete until late May. This report can be contrasted with observations on lower sections of

Canterbury's rivers where some terns overwinter each year (pers. obs.).

Black-fronted tern nests are generally shallow scrapes on bare shingle (Lalas and Heather, 1980). They breed in loose colonies, often in association with black-billed gulls (Falla *et al.*, 1978). Colonies are typically located in areas of bare shingle with little or no vegetation present (Robertson *et al.*, 1983). The abandonment of one colony located near dense vegetation on the Ahuriri river was attributed to the spring growth of lupins (Robertson *et al.*, 1983).

Terns are primarily insectivorous feeders during spring and summer, feeding in swallow-like fashion on emerging aquatic insects on or above the surface of shingle-bed rivers and streams (Lalas, 1977). Oliver (1955) recorded terns picking up invertebrates exposed during farm tillage. During tern mating displays small fish are caught by the male and presented to the female. However, it has not been determined whether fish comprise an important portion of diets. Robertson *et al.* (1983) found that throughout the year terns predominantly use on-river aquatic habitats for feeding, particularly main channels and riffles. Unfortunately, the relationship between on-river and adjacent farmland feeding has not been determined, and, as for black-billed gulls, this makes it difficult to determine precise feeding habitat needs and how these are affected by braided river hydrology.

3.5. Black stilt

Black stilts (Order Charadriiformes: Family Recurvirostridae) have the most restricted breeding season distribution of the riverbed nesting birds, and are classified as an endangered species in New Zealand (Williams and Given, 1981). The only breeding wild populations of this species are found in the MacKenzie Basin of inland South Canterbury, where birds frequent a range of habitats including riverbeds, swamps, lake edges, and tarns. The black stilt has been intensively studied, e.g., Budgeon (1977), Merton (1977), Pierce (1982a), Robertson *et al.* (1983), and a wide ranging conservation programme is being implemented (see Pierce, 1982b).

Black stilt nests are found on shingle riverbeds, sidestreams with vegetated banks, swamps with emergent vegetation, and tarns (Pierce, 1982a). Unlike most other riverbed nesting species they show some propensity to nest near emergent vegetation (Pierce, 1982a). Most of

the breeding population overwinters in the MacKenzie Basin but some localised shifts occur (Pierce, 1982a), and some immature birds migrate to coastal harbours and lagoons in the North Island (Falla et al., 1978).

Habitat use for feeding varied seasonally on the Ahuriri river, with flowing water habitats being used most in spring and least in summer (Robertson et al., 1983). Pierce (1982a) concluded that black stilt feeding was closely adapted to riverine habitats, whereas pied stilts used ponds and lakes more heavily. Riffles were the most heavily used river habitats. Food on the Cass river included mayfly larvae (Ephemeroptera: Leptophlebidae), caddisfly larvae (Trichoptera) and midge larvae (Diptera: Chironomidae) (Pierce, 1982a).

3.6. Pied stilt

The pied stilt (Order Charadriiformes: Family Recurvirostridae) is the most common of the larger waders breeding in New Zealand (Falla et al., 1978), being found throughout the country (Bull et al., 1978) over a wide range of habitats including rivers, lakes, swamps, farmland, and the seashore. Many pied stilts are found on rivers such as the Ashburton and Ashley, with fewer on the large Canterbury rivers (O'Donnell and Moore, 1983).

Pied stilts breed on the seashore, boulder banks, saline lagoons, swampy paddocks, lakeshores and riverbeds (Falla et al., 1978). McConkey's (1971) study of nest record cards showed that pied stilts prefer to nest on riverbeds. Nests are usually placed near water (Oliver, 1955; Pierce, 1982a). In the North Island breeding occurs from June to January (Falla et al., 1978), but in the South Island it does not begin until late September or early October (Pierce, 1982a). There is little in the literature to determine nest site vegetation tolerance, however Child (1983) suggested that vegetation encroachment was one reason for a decline in pied stilt numbers in Central Otago.

Pied stilts feed on adult and larval insects, worms, shellfish, and other small invertebrates (Oliver, 1955). Budgeon (1977) showed that they seldom feed close to dense cover, preferring relatively open areas. Both Pierce (1982a) and Robertson et al. (1983) have shown pied stilts rely on pools and backwaters while feeding on braided river systems. In none of these studies has this claimed reliance been tested against the

occurrence of microhabitats to assess habitat preference.

3.7. South Island pied oystercatcher

The total population of South Island pied oystercatchers (Order Charadriiformes: Family Haematopodidae) has been estimated at 49000 (Baker, 1972). However, recent winter survey counts indicate the population may now be closer to 80000 birds (Sagar, pers. comm.). South Island pied oystercatchers breed in inland South Island areas (Falla et al., 1978). They are common on the Canterbury riverbeds (O'Donnell and Moore, 1983), and are numerous around the edges of lakes and other wetlands. Furthermore, their range seems to be broadening with a recent record on a Hawkes Bay river (Twydle and Twydle, 1983).

The South Island pied oystercatcher nests mainly on riverbeds and lake shores up to 1000m (Falla et al., 1978), although increasing numbers are nesting on farmland and high country tussock grasslands (Baker, 1972). When breeding on riverbeds South Island pied oystercatchers choose nest sites which are free of vegetation (O'Donnell and Moore, 1983), or bare gravel with sparse vegetation and a cobble substrate (Robertson et al., 1983). After breeding, large flocks congregate on coastal estuaries and mudflats in the North and South Islands. The northward and coastal migration begins in December (Falla et al., 1978) while the inland and southward movement begins in July.

On the Ahuriri river, the South Island pied oystercatcher was observed feeding in a wide variety of terrestrial and aquatic microhabitats (Robertson et al., 1983). During all seasons most feeding was in terrestrial locations, including terraces and flats, while aquatic feeding occurred in minor braid riffles and pools (Robertson et al., 1983). Feeding on pastures was also important (Robertson et al., 1983), but, as for black-billed gulls and black-fronted terns, this makes it difficult to determine the hydrology-feeding ecology relationship. Little is known about the breeding season diet of South Island pied oystercatchers, but Sibson (1975) suggested that it probably includes worms, slugs, snails, insects, and possibly tadpoles, frog spawn, and larval fish.

3.8. Southern black-backed gull

This large gull (Order Charadriiformes: Family Laridae) is distributed throughout New Zealand (Bull et al., 1978) where it frequents coastal areas, outlying and offshore islands, rivers, lakes, and alpine tarns. It is very common on all of the medium to large Canterbury rivers (O'Donnell and Moore, 1983).

Riverbeds are only one of a number of breeding habitats for southern black-backed gulls. It nests in colonies which may exceed 1000 birds (Moore, 1981), covering a wide area of riverbed. Most colonies are located amongst areas of medium vegetative cover (O'Donnell and Moore, 1983), although peripheral nests are often located on clear shingle areas some distance from the main colony (pers. obs.). Although there is a general coastward movement following breeding, many overwinter on lowland sections of rivers (pers. obs.).

On the Ahuriri river, Robertson et al. (1983) found that feeding occurred equally on terrestrial habitats and flowing aquatic habitats in autumn; mainly on mid channel bars with wetland turf habitat in winter; on both flowing and terrestrial habitats in spring; and mainly on farmland habitats in summer. Many birds are found near supplies of offal (Falla et al., 1978), hence the large numbers on the Waimakariri river near the rubbish tips of Christchurch. Scavenging is also important over farmland, so it seems likely that the very large numbers on the Waitaki river (O'Donnell and Moore, 1983) reflect the intensified pastoralism associated with irrigation along both banks of this river.

3.9. Wrybill

In the breeding season, the small, endemic wrybill (Order Charadriiformes: Family Charadriidae), is restricted to a limited number of Canterbury, South Canterbury, North and Central Otago riverbeds (Hay, 1984). Recent surveys have recorded very low numbers on the Ashley and Ashburton rivers, approximately 100 on the Waimakariri, and a large but as yet unquantified population on the upper Rangitata river (O'Donnell and Moore, 1983). Approximately 100 wrybills have been located on the Ahuriri river (Robertson et al., 1983) with a similar number thought to be breeding on the Cass, Dobson, and Tasman rivers, in the Mackenzie Basin (Pierce, pers. comm.). The largest population is believed to occur on the Rakaia river (O'Donnell and Moore, 1983).

Wrybills are most numerous in areas with a highly braided, unvegetated gravel riverbed (O'Donnell and Moore, 1983).

Sibson (1963) estimated the total population at 5000, a figure thought to be conservative. Hay (1984) has recently confirmed this estimate, but riverbed surveys have failed to record numbers which approach this figure (see O'Donnell and Moore, 1983). Survey counts should therefore be used cautiously when determining conservation priorities. After breeding wrybills migrate north to the large harbours and estuaries near Auckland.

Hay (1984) found wrybill nests to be located near water on wide areas of bare shingle, clear of vegetation cover. This study, like many others on riverbed birds, e.g., Pierce (1976, 1982a), Robertson *et al.* (1983), occurred where bare shingle is the dominant habitat type. In other areas, such as the lower Rakaia, where there is large scale encroachment of exotic vegetation, tolerance of, and preference for, particular levels of vegetation density and ground cover have not been studied. This aspect of wrybill breeding ecology requires further research.

Pierce (1979) found that wrybills prefer feeding in shallow water where they obtain their main food, the mayfly, *Deleatidium* spp. Aquatic feeding in shallow riffles was most important during periods of 'normal' flow in the Ahuriri river, with terrestrial foraging becoming important during floods (Robertson *et al.*, 1983). Shingle in either terrestrial or aquatic habitats is the preferred feeding substrate (Pierce, 1979). Other aspects of the feeding ecology, including preferences for certain braid sizes and channel forms have not been determined but are important in water management considerations.

4. Summary and conclusions

Braided rivers of the type found in New Zealand are rare. These wide, unstable, shingle-bedded, multi-channelled rivers, provide a combination of physical conditions which facilitate their use for breeding by a diverse range of bird species. Some of these birds are totally restricted to riverbeds, and therefore rely on braided rivers for their survival. The most suitable conditions for their habitat needs are found on the braided rivers of Canterbury and the MacKenzie Basin. In the North Island the single channel rivers provide marginal

habitats for most species, and consequently some are absent or present in comparatively low numbers.

Of the nine species defined as riverbed nesting birds the black stilt is listed as an endangered species. Apart from this species, which is restricted to the MacKenzie Basin, all others breed on rivers flowing over the Canterbury Plains. Considerable behavioural research has been carried out for many of these species. However, a quantitative assessment of habitat needs and the impacts of flow modification on these requirements for birds nesting on Canterbury Plains' rivers has not been made.

NOTE: References cited in this Appendix are included in the main list of references.

APPENDIX 2

**THE RELATIONSHIP BETWEEN RIVERBED
FLOODING AND NON-BREEDING WRYBILLS
ON NORTHERN FEEDING GROUNDS IN
SUMMER**

By K. F. D. HUGHEY

ABSTRACT

I investigated the relationship between floods on the riverbed breeding grounds of Wrybills (*Anarhynchus frontalis*) and the number of Wrybills censused on northern harbours the following summer. For the purposes of the study I assumed that most birds oversummering on northern harbours are first-year non-breeders and that flood flows of the Rakaia River are representative of most other Wrybill breeding rivers. A highly significant negative correlation ($r^2=0.69$; $p<0.01$) existed for the 1968-1982 period. The study's findings provide some support for the observation that by the early 1960s the Wrybill population, after many years of growth, had begun to stabilise. Serious flooding in the 1982 and 1983 breeding seasons may have again destabilised the population structure.

INTRODUCTION

Several bird species breed only on the braided rivers of the eastern South Island, and recently there has been considerable research into these birds' behavioural ecology (Lalas 1977, Pierce 1979, 1982, Hay 1984) and habitat needs (Robertson *et al.* 1983, Hughey, in prep.). As many of these rivers are subject to existing or planned hydroelectric or irrigation development, we need to know how well these birds cope with natural hazards before we can try to assess the impact of human intervention.

The endemic Wrybill (*Anarhynchus frontalis*) relies on the braided rivers of Canterbury and the MacKenzie Basin (Fig.1) for breeding. If these rivers go on being developed by man, the entire population of about 5000 (Hay 1984) will be at risk. Most of these rivers have their headwaters in the main divide of the Southern Alps. They are partly glacially fed but also receive westerly storms that cause large floods in most of the Wrybill's spring and early summer breeding seasons. Flows in these rivers are highly variable during the breeding season, when average discharges are greater than at other times of the year. In contrast, the smaller rivers such as the Ashburton and Ashley, which drain eastern foothill catchments, do not receive the full effects of these storms and so are characterised by declining flows during the breeding season (Fig.2).

Wrybills, like most other riverbed nesting birds, require large areas of bare shingle for their nesting. The actively changing riverbeds of most high-country catchments are largely free of vegetation, but the lowland sections

1985

NON-BREEDING WRYBILLS

43

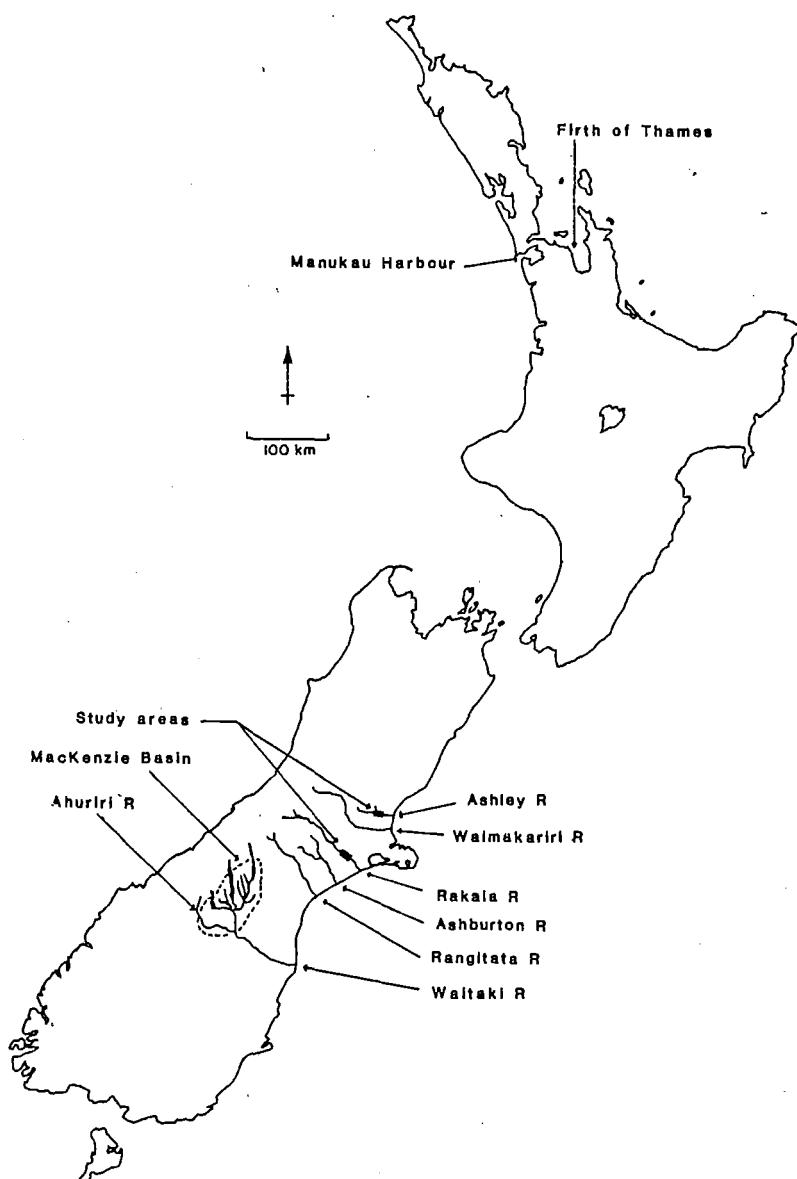


FIGURE 1 — Location map of the main Wrybill breeding areas (South Island) and winter feeding sites (North Island) discussed

of many rivers have been greatly modified by the invasion of exotic plants, including broom (*Cytisus scoparius*), gorse (*Ulex europaeus*), lupin (*Lupinus* spp.), and willow (*Salix* spp.). Stead (1932) thought that these modifications had reduced Wrybill numbers on the lower Rakaia River. However, the scouring action of floods helps maintain vegetation-free nesting areas.

The Rakaia River is the most important Wrybill river (O'Donnell & Moore 1983, Hughey, in prep.) with 1000-1500 breeding Wrybills (Cowie 1983). Only about 100 have been found on the whole Ahuriri River (Robertson *et al.* 1983), and similar numbers breed on several other MacKenzie Basin rivers (Pierce, pers. comm.). Although the Rangitata River has not been thoroughly surveyed, Wrybill numbers appear to be high on the upper reaches (Wragg, pers. comm.).

Wrybills depend on aquatic and riparian habitats for their invertebrate food (Pierce 1979, Robertson *et al.* 1983). However, flooding causes a temporary but spectacular decline in available food (Pierce 1979, 1982, Sagar 1983), which affects breeding success (Hughey, in prep.). Furthermore, Hay (1984) considered floods to be the major cause of nest and egg losses. A flood on 7 December 1976 destroyed almost every Wrybill nest in his upper Rakaia study area. The peak instantaneous discharge (the absolute flood peak) on this date ($2271 \text{ m}^3\text{s}^{-1}$) was slightly above the estimated bankful discharge (i.e. the flow equalling or exceeding the bank-to-bank capacity of the river) of $2200 \text{ m}^3\text{s}^{-1}$ (Hughey, in prep.) that is predicted to flood all riverbed nests.

After breeding, Wrybills migrate northward to wintering grounds, mostly in the northern half of the North Island. At two especially important areas, Manukau Harbour and the Firth of Thames, summer and winter counts of Wrybills have been made annually since 1961. After their late summer and winter stay on these northern places, most Wrybills migrate south for riverbed breeding. Hay (1984) found a mixture of first- and second-year birds, and even some adults, among remaining oversummering Wrybills. Proportions of each varied, but it seems likely that birds spending the summer on northern harbours are predominantly first-year non-breeders, although this has yet to be proven. If so, summer counts are likely to reflect the breeding success of the previous nesting season. The object of my study was to see if summer counts of non-breeding Wrybills and the flood regime of the previous breeding season were related.

METHODS

I used the summer counts of Wrybills in the Manukau Harbour and the Firth of Thames, from the Ornithological Society of New Zealand records cited in O'Donnell & Moore (1983), and peak instantaneous flow data for the Rakaia and Ahuriri Rivers, from the Ministry of Works and Development. All the important Wrybill rivers, except the Ahuriri, have their headwaters within the 'Eastern Alps' hydrological region (Toebes & Palmer 1969). I therefore assumed that the flooding of these rivers would be similar in relative size, frequency, and timing. This assumption is supported by Waugh (pers. comm.), who found a generally good correlation between the Rangitata and Rakaia Rivers. Since the Rakaia is the most important Wrybill breeding river, I decided

1985

NON-BREEDING WRYBILLS

45

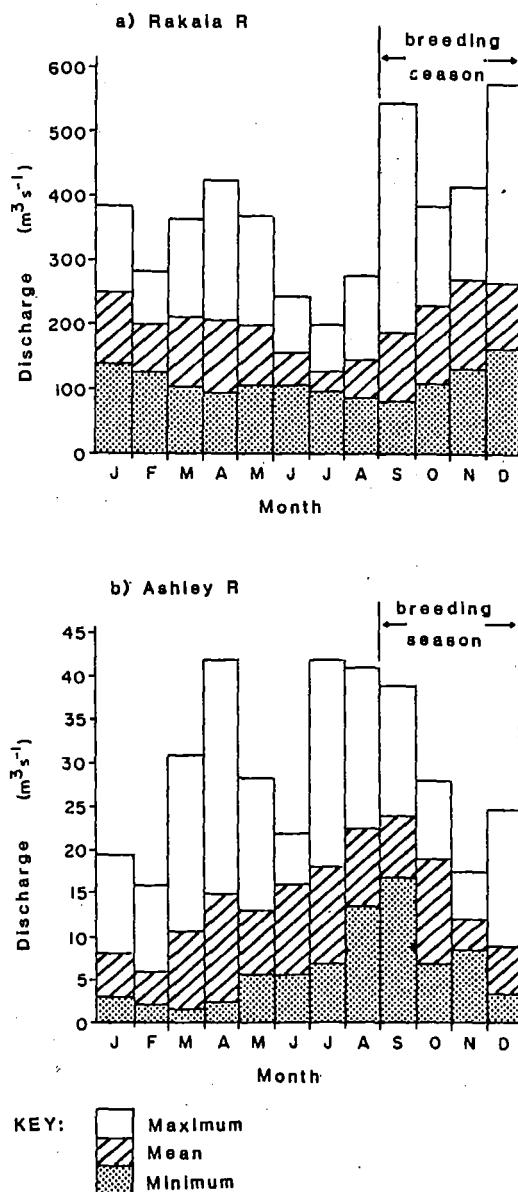


FIGURE 2 — Annual variations in the flow regime of a mountain catchment river (the Rakaia) compared with a foothill catchment river (the Ashley)

to use the flood flow data from this river as representative of all other major Wrybill rivers. To test this assumption I compared the flood regime of the Rakaia with that of the Ahuriri River by plotting the flows of both rivers for the 1980 season (Fig. 3). This comparison shows only minor variations in the pattern of flows. Using only Rakaia River flow data for the rest of this analysis is therefore reasonable.

I attempted to correlate summer counts of non-breeding Wrybills against the Rakaia River's peak instantaneous discharge of the previous breeding season. I selected the seasonal floods as follows:

1. I included floods that occurred only between 10 September and 10 November, when most first clutches are laid, incubated, and reared (Hay 1984, Hughey, in prep.).
2. If no medium to large floods ($> 700 \text{ m}^3\text{s}^{-1}$) occurred between 10 September and 10 November, I assumed that most breeding would be successful. To allow some margin for late-chick growth, I extended this period to 20 November. Moreover, because Hay (1984) found that only about 20% of pairs attempt to rear two broods and because I did not record any Wrybills trying to rear two broods, I omitted flood peaks after 20 November.
3. If large flood peaks occurred between 10 September and 10 November, I extended the period for flooding to 20 December to allow time for attempted renesting.

Although Wrybills have been counted in each summer since 1960, I included only the 1968–1982 counts in this analysis for the following reasons:

1. The Wrybill population on northern harbours is considered to have risen markedly from 1940 to the late 1950s or early 1960s (Sibson 1963).
2. The early 1960s seem to mark the beginning of a population plateau, perhaps because the population was nearing the capacity of its breeding habitat. The spread of Wrybills into Otago in the 1960s (Child 1971, 1973) seems to support this view.
3. After two years of non-breeding status, Wrybills have a breeding life of around five years (Hay 1984). If the population did reach the capacity of its breeding habitat in 1961, it would have taken until 1968 for each year class to adjust to this plateau level and for the age structure of the population to become stable.
4. When the population reached this stable structure, its migratory behaviour was also likely to stabilise within the limits of natural population fluctuations. We have to be confident that the annual migratory events were consistent before we can establish any long-term relationship between flooding and birds spending the whole summer on northern harbours.
5. 1982 and 1983 are the first years since 1966–1968 with summer counts in the north of fewer than 100 birds. The low numbers in 1982 and 1983 may be associated with a population decline caused by large and frequent flooding, which is supported by a low Wrybill fledgling success rate on the Rakaia River for the 1982 season at least (Hughey, in prep.) Such a decline may change existing patterns of migration. Thus, the apparently stable population plateau in 1968–1982 is the best period to study.

1985

NON-BREEDING WRYBILLS

47

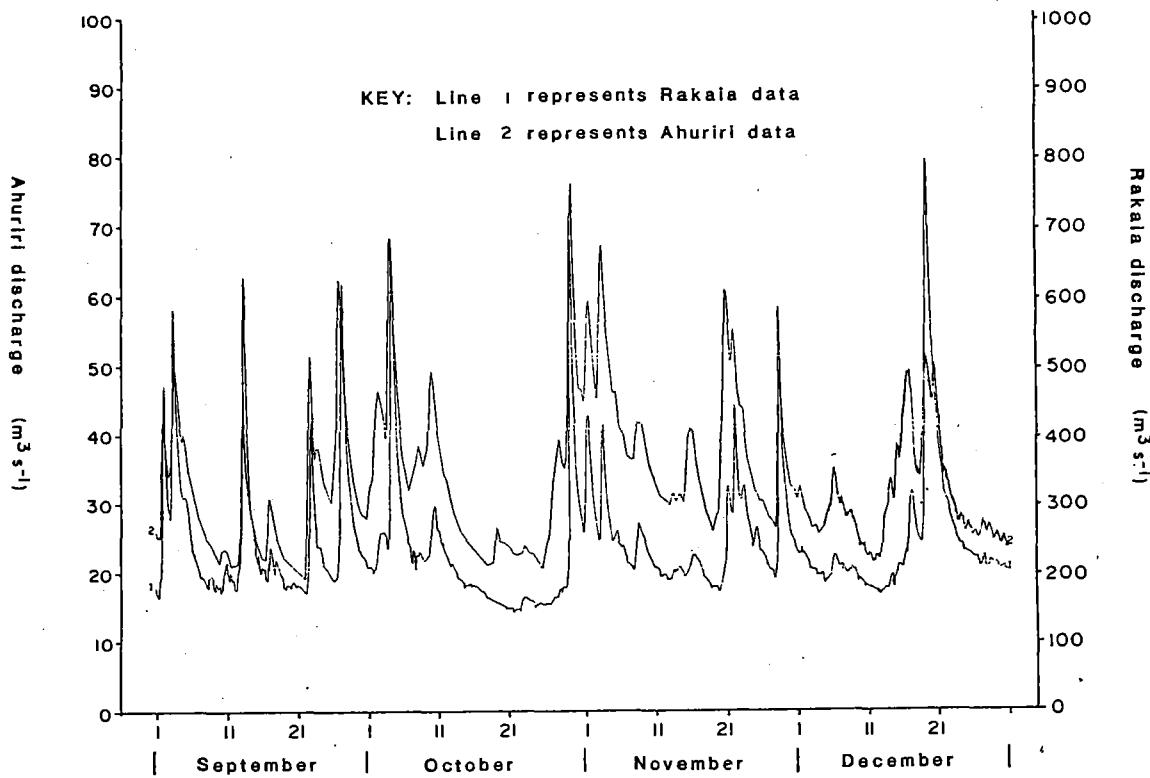


FIGURE 3 — Instantaneous discharges of the Ahuriri and Rakaia Rivers compared for the 1980 breeding season

RESULTS AND DISCUSSION

I found a highly significant negative correlation ($r^2 = 0.69$; $p < 0.01$) between summer Wrybill counts on northern harbours and the peak instantaneous discharge for the Rakaia River from the previous breeding season (Fig. 4). As the Rakaia is representative of most other Wrybill breeding rivers, it appears that over the period 1968–1982, summer counts of Wrybills were high whenever only small floods had occurred in the previous breeding season but were low whenever large floods had occurred.

These findings provide important clues to population changes of Wrybills, but these clues can be misleading. With breeding success being inversely correlated with flooding, development projects such as damming or irrigation, which harvest or level out flood peaks, might be expected to improve Wrybill breeding success and so lead to a higher population. Certainly, on the Ashley River, where flows characteristically decline in late spring and summer, Wrybill breeding success was very high in 1983 (6 pairs produced at least 6 fledglings) whereas on the flood-dominated Rakaia it was very low (30 pairs produced 2 fledglings — Hughey, in prep.). Thus, development projects that stabilise flow might also be expected to lead to an increased number of Wrybills on the river.

Although floods do limit Wrybill breeding success, they also keep the river shingle free of vegetation, which Wrybills require for suitable nest sites. Without these floods, exotic vegetation would soon spread over many Wrybill habitats (Hughey, in prep.), jeopardising the survival of the species.

The bankful flow of the Rakaia (about $2200 \text{ m}^3\text{s}^{-1}$) occurs about once in every 2.2 breeding seasons (Hughey, in prep.). If this flow occurs between early September and early November, it destroys many first clutches. Furthermore, if these flows were to occur in several successive seasons and more than once each season, Wrybill numbers could be seriously reduced.

Wrybill rivers are, hydrologically, broadly classified into

1. Rivers with their sources in mountain catchments such as the Ahuriri, Rakaia, Rangitata and Waimakariri, which have high breeding-season flows and are where most Wrybills breed; and
2. The smaller and less braided rivers of the eastern foothills such as the Ashburton and Ashley, which have flows that decline during the breeding season and are where only a few Wrybills breed.

However, if conditions such as the Southern Oscillation which influenced the New Zealand climate in 1982, resulting in more westerly storms, were to continue for several years, conditions on rivers like the Rakaia might become marginal for Wrybills. In the meantime, flows in rivers like the Ashley seem to have remained suitable for successful breeding. Thus, concentrating conservation efforts only on rivers that at present support large numbers of Wrybills may not be wise. The habitats of secondary rivers should also be conserved.

An important assumption of this study relates to the age structure of the Wrybills that remain for the whole summer on northern harbours. Hay

1985

NON-BREEDING WRYBILLS

49

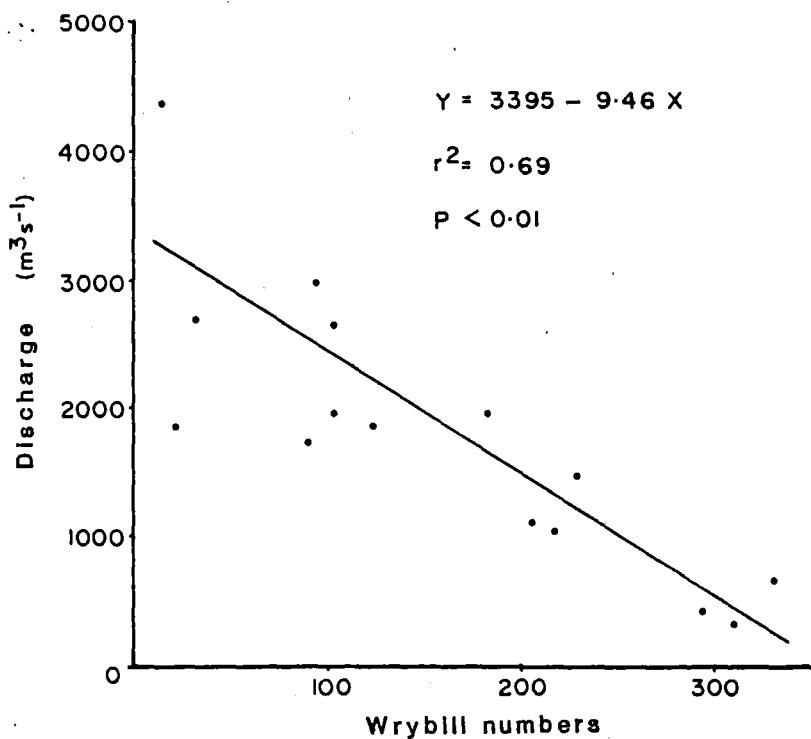


FIGURE 4 — The relationship of each summer count of Wrybills in the Manukau Harbour and the Firth of Thames to the peak instantaneous Rakaia River discharge of the previous breeding season (1968-1982)

(1983) found that about 90% of overwintering Wrybills leave the harbours for their South Island breeding grounds in August and that most of the rest leave later. This second departure appears to be of immature non-breeders, some of which return to their natal areas midway through the breeding season (Hay 1983). However, even after this second migration, some Wrybills remain on the northern harbours for the whole summer. In addition, Wrybills probably do not breed until their third year (Hay, pers. comm.). Therefore, the birds remaining in the north after the main migration are probably mostly first- and second-year non-breeders. It seems logical to expect that the secondary migration reported by Hay (1983) is mainly of second-year non-breeders, perhaps in association with a few first-year and adult birds, and that any birds staying in the north are mostly first-year birds. The high correlation between the numbers of Wrybills spending the summer on northern harbours and flood events from the previous breeding season supports this last suggestion. If the apparent relationship between flood events and birds summering in the north is true, summer counts may eventually be a useful warning of any population decline of Wrybills.

ACKNOWLEDGEMENTS

I thank Graham Davenport from the Ministry of Works and Development, Christchurch, for discharge data for the Ahuriri and Rakaia Rivers and John Waugh of the South Canterbury Catchment Board, Timaru, for comments on the relationship between Rakaia and Rangitata river flows. I thank Eric Scott, Graham Wilson, Paul Sagar, Ian Stewart, Rod Hay and Judy Grindell who read and commented on drafts of this paper, Barrie Heather for final editing, Peter Tillson for drafting several of the diagrams, and Jane Ensor for typing. Finally, I acknowledge the encouragement of the late G. R. Williams.

LITERATURE CITED

- CHILD, P. 1971. A Wrybill in Central Otago. *Notornis* 18: 252.
 CHILD, P. 1973. Wrybills in Central Otago: further records. *Notornis* 20: 77-78.
 COWIE, B. 1983. Fisheries and wildlife. Pages 111-248 in M. J. Bowden, "The Rakaia River and catchment — a resource survey." Vol 3. Christchurch: North Canterbury Catchment Board and Regional Water Board.
 HAY, J. R. 1979. The Wrybill — one of the world's ornithological oddities. *Forest and Bird* 214: 13-17.
 HAY, J. R. 1983. Shore birds of the Miranda coastline. *Tane* 29: 15-30.
 HAY, J. R. 1984. The behavioural ecology of the Wrybill Plover. PhD thesis, University of Auckland.
 LALAS, C. 1977. Food and feeding behaviour of the Black-fronted Tern, *Chlidonias hybrida albostriatus*. MSc thesis, University of Otago, Dunedin.
 O'DONNELL, C. F. J.; MOORE, S. M. 1983. The wildlife and conservation of braided river systems in Canterbury. Fauna Survey Unit Rep. 33. Wellington: Wildlife Service, Dept. Internal Affairs.
 PIERCE, R. J. 1979. Foods and feeding of the Wrybill (*Anarhynchus frontalis*) on its riverbed breeding grounds. *Notornis* 26: 1-21.
 PIERCE, R. J. 1982. A comparative ecological study of Pied and Black Stilts in South Canterbury. PhD thesis, University of Otago, Dunedin.
 ROBERTSON, C. J. R.; O'DONNELL, C. F. J.; OVERMARS, F. B. 1983. Habitat requirements of wetland birds in the Ahuriri River catchment, New Zealand. Occ. Publ. 3. Wellington: Wildlife Service, Dept Internal Affairs.
 SAGAR, P. M. 1983. Benthic invertebrates of the Rakaia River. Fish. Env. Rep. 36. Christchurch: Ministry of Agriculture and Fisheries.
 SIBSON, R. B. 1963. A population study of the Wry-billed Plover (*Anarhynchus frontalis*). *Notornis* 10: 143-153.
 STEAD, E. F. 1932. The life histories of New Zealand birds. London: Search.
 TOEBES, C.; PALMER, B. R. 1969. Hydrological regions of New Zealand. Misc. Hydr. Publ. No. 4. Wellington: Water and Soil Division, Ministry of Works and Development.

K. F. D. HUGHEY, Department of Entomology, Lincoln College. Present address: Wildlife Service, P.O. Box 1308, Christchurch.

APPENDIX 3 : Composition of wrybill and banded dotterel faeces
collected on the Ashley and Rakaia rivers.

[A] WRYBILL

(i) Rakaia river

Collection date	FOOD ITEM																	
	Diptera	Adult	Coleoptera	Larvae	Hemiptera	Adult	Lepidoptera	Larvae	Hymenoptera	Thysanoptera	Arachnida	Adult	Ephemeroptera	Larvae	Trichoptera	Adult	Plecoptera	Larvae
14/09/83	1	1			1			1			1	1			1	1		
15/09/83			1											2				
19/09/83	1			1					1			1						
20/09/83	1	6			6													
28/09/82	1	2			1					1	1			8				
5/10/83													7					
8/10/82	1	1	2	1									1					
11/10/82	1	1											1					
13/10/83			1							1			8			1		
14/10/82	2	1			1							1	2	20			4	
15/10/82	1	2			1					1			3			1		
16/10/82	1	4			3			1	1					2				
19/10/83	10	3			2	1			1	2	1	6			1			
19/10/82	1	1											1	8			4	
19/10/82	1	1	2							1			8			2		
20/10/83			1			4												
20/10/83	2	3			2									13			1	
3/11/82	5	4			2					1	1	4			1			
4/11/82	1	2			1							1	11			1		
17/11/82	1	1			1							1	21					
4/12/82	1	2	1	1									1					
7/12/82	2	6			77					1								
23/12/82	1	4			1									8			2	

(ii) Ashley river

2/10/83	1	3			2					1			1	4	15			1
15/10/83	1	2			1					1			1			5		
1/11/83			1											2			1	

APPENDIX 3 : Continued

[B] BANDED DOTTEREL

(i) Rakaia river

FOOD ITEM

Collection date	Diptera	Adult	Coleop- tera	Larvae	Hemiptera	Adult	Lepidop- tera	Larvae	Hymenoptera	Arachnida	Adult	Ephemeroptera	Larvae	Trichoptera	Adult	Plecop- tera	Larvae
	Diptera	Adult	Coleop- tera	Larvae	Hemiptera	Adult	Lepidop- tera	Larvae	Hymenoptera	Arachnida	Adult	Ephemeroptera	Larvae	Trichoptera	Adult	Plecop- tera	Larvae
15/09/83	1	2			3							1					1
15/09/83	1	4	1	1			4										
20/09/83	1	7	1	4						1							
20/09/83		2		1						1							
20/09/83			7	1	1			1	1								
4/10/83		2	1	1													
4/10/83		1				1	2										
6/10/82		3	6	1								8					
7/10/82	2	4		1			1	1									
15/10/82	2	7		2					1	1							
15/11/82	1	4	2	1			1	2	1								

(ii) Ashley river

16/09/83		5		16				1				2					
16/09/83		3		1							1	5	1				
23/09/83	1	2	1	1		1			1								
24/09/83	1	4		4		1	1	1			4	4			2		
24/09/83	1	17	1	1		1					1		1	1	1	1	
10/10/83	1	17	1	1	1	4			1								
20/10/83		1	1														
21/10/83	1	12	1	32	2	1			1								
25/10/83		3	1	1		1				1							
28/10/83		4	1	1		1											
1/11/83	1	4		1		1											
1/11/83	1	13	1	7		1	1	1				1					
1/11/83		2	1	1													
1/11/83		4	1	1			1			1							

APPENDIX 4 : Numbers of invertebrates caught in pitfall traps located at three sampling sites (4 traps per site) on the Ashley and Rakaia rivers.

[A] ASHLEY RIVER		Collection date	Microhabitat sampled	Diptera	Hymenoptera	Lepidoptera	Hemiptera	Arachnida	Trichoptera	Plecoptera	Staphylinidae	Circulionidae	Actenonyx bembidooides	Bembidion charile	Bembidion spp.	Other Coleoptera	Coleoptera
																Larvae	
2/09/83	Near water	38					7	1			8		38	129	165		
	Shingle	1					1	10			2	38	11	135			
	Vegetation	3					3	5			1	1	4	17			
8/09/83	Near water	10					3			24		58	180	194			
	Shingle	2	1				6			1		20	6	51			
	Vegetation	10					4	7		6	1	2	3	21	2		
16/09/83	Shingle	2					3					12	16	48		5	
	Vegetation	11					2	19		1		6	16	21	2		
23/09/83	Near water	84					27	4		5	3	107	144	88	1		
	Shingle	12					4	6				59	13	133		1	
	Vegetation	13					3	8		1		2	2	3	2		
30/09/83	Shingle	5					2	5				12	2	11		4	
	Vegetation	3		1			5			1		9	11	1			
8/10/83	Near water	30					55	7	1	2	9		28	176	153		
	Shingle	311		1	12	10						67	25	193		1	
	Vegetation	19	1			1	9					33	9	1			
15/10/83	Shingle	23	1			5	6			2		45	29	155		2	
	Vegetation	3	1				10			1		15	1	1			
21/10/83	Shingle	15				4	11			1		70	1	30		1	
	Vegetation	6					10			1		2	1		2	2	
28/10/83	Shingle	15	1			2	18	1		1		63	10	29	3	5	
	Vegetation	6		1		1	13					16	1		1	2	
5/11/83	Near water	164		1	21	14	7			25	1	370	365	419			
	Shingle	25				2	17			3		28	17	10	8	22	
	Vegetation	10	1		4	50						4	2		9	7	
12/11/83	Near water	25				7	33	26		6	1	97	41	57	2	5	
	Shingle	15	1			4	11					6	4	9	6	11	
	Vegetation	7				2	26					3	1	6		5	
18/11/83	Shingle	2		1	1	8						12	4	5		8	
	Vegetation	7			3	7						14		4	1	3	
25/11/83	Near water	80	1	1	17	189	47			22		242	123	107	3	7	
	Shingle	8			3	9	1			1		33			15	7	
	Vegetation	9	1	1	3	145	1					1	6	1		5	

APPENDIX 4 : Continued.

[A] ASHLEY RIVER Continued

Collection date	Microhabitat sampled	Coleoptera												
		Diptera	Hymenoptera	Lepidoptera	Hemiptera	Arachnida	Trichoptera	Plecoptera	Staphylinidae	Circulionidae	Actenonyx bemboides	Bembidion charile	Bembidion spp.	Other Coleoptera
2/12/83	Near water	33			9	44	57	10		40	133	382		5
	Shingle	32			12	13		1		19	1	42	4	12
	Vegetation	8			5	12				3		8	2	3
24/12/83	Shingle	10	7		7	9				4	1	1	4	2
31/12/83	Near water	1		1	14	11				53	4	33		
	Shingle	3			6	13				8	1	2	1	2
	Vegetation				3	18				2		1		
7/01/84	Shingle	5			2	79	1	1		5	1	1	1	2
	Vegetation	3	2	1	5	13		1			1	1		1

[B] RAKAIA RIVER

2/09/83	Near water	118			33			1	5	1	5	194	10	
	Shingle	11			3	10			1		12	83		1
	Vegetation	5			3	5					2	1		
7/07/83	Near water	76			45	3		1		23	108	71	1	
	Shingle	15			12			47		107	68	9		
	Vegetation	3			1	4			3	1	4			
16/09/83	Shingle	22			2	7		1		33	46	2		1
	Vegetation	13			3					8	10	7	7	
21/09/83	Near water	97			33	1		1	5		56	350	29	2
	Shingle	4			1	4		2		72	72			
	Vegetation	2			4			1		2	5		1	
30/09/83	Shingle	41			8	1		1	1	48	14	2		
4/11/83	Near water	132		1	12	2	1		3		98	129	100	
	Shingle	44						2		294	61			
2/12/83	Near water	100			22	2	1	2		227	50	47		
	Shingle	15			1	1		1		158	14			2

APPENDIX 5 : Wrybill weighted usable area, channel width and channel discharge data for individual branch channels on the Rakaia river.

[A] Reach 1 - flow set 1.

CHANNEL	6 AUGUST 1981			7 AUGUST 1981			18 AUGUST 1981		
	CHANNEL FLOW (m ³ s ⁻¹)	CHANNEL WIDTH (m)	WEIGHTED USABLE AREA (m ² m ⁻¹)	CHANNEL FLOW (m ³ s ⁻¹)	CHANNEL WIDTH (m)	WEIGHTED USABLE AREA (m ² m ⁻¹)	CHANNEL FLOW (m ³ s ⁻¹)	CHANNEL WIDTH (m)	WEIGHTED USABLE AREA (m ² m ⁻¹)
1	2.915	9.97	0.39	2.245	9.63	0.64	2.508	9.73	1.80
2	13.88	27.17	0.87	9.33	13.47	1.70	10.88	27.57	2.44
3	0.054	3.82	0.97	0.104	7.42	0.75	0.051	4.04	0.92
4	0.346	7.55	0.88	0.104	7.42	1.29	0.159	7.45	1.21
5	14.16	45.0	1.32	9.19	44.43	2.10	10.23	43.7	1.66
6	0.19	5.3	0.81	0.081	4.57	1.27	0.12	4.99	1.29
7	N O D A T A			0.012	4.07	0.86	0.033	6.03	1.06
8	0.617	23.2	4.94	0.115	23.2	8.57	0.273	23.65	7.74
9	40.47	60.0	2.45	27.45	57.4	1.52	36.22	58.88	1.44
10	48.53	110.1	12.18	33.93	100.1	11.81	40.04	101.5	8.82
11	1.89	34.17	1.02	0.881	24.17	0.58	1.018	23.37	0.70
12	0.439	27.8	4.54	0.04	16.65	6.93	0.052	14.2	5.49
13	0.92	18.7	8.45	0.004	4.5	3.83	0.123	7.15	1.48
14	0.369	4.55	0.49	0.012	2.35	0.68	0.088	3.1	0.42
15	0.285	4.8	0.69	0.004	2.15	1.50	0.039	3.4	1.26
16	5.728	19.57	1.94	2.967	16.8	2.95	4.7	15.7	0.84
17	6.532	21.1	1.14	3.475	19.17	2.10	3.46	19.3	1.44
18	2.08	15.9	0.89	0.852	12.62	1.58	1.57	14.82	1.79
19	0.307	12.0	1.86	0.13	8.07	1.85	0.115	10.55	1.92

APPENDIX 5 : Continued

[B] Reach 1 - flow set 2.

CHANNEL	6 APRIL 1982			7 APRIL 1982			4 MAY 1982		
	CHANNEL FLOW (m ³ s ⁻¹)	CHANNEL WIDTH (m)	WEIGHTED USABLE AREA (m ² m ⁻¹)	CHANNEL FLOW (m ³ s ⁻¹)	CHANNEL WIDTH (m)	WEIGHTED USABLE AREA (m ² m ⁻¹)	CHANNEL FLOW (m ³ s ⁻¹)	CHANNEL WIDTH (m)	WEIGHTED USABLE AREA (m ² s ⁻¹)
1	0.28	10.13	1.24	1.74	15.02	2.12	0.802	10.97	0.65
2	29.1	83.43	3.02	44.2	86.2	0.85	19.1	82.1	6.27
3	48.3	139.0	12.28	64.2	43.2	14.05	46.3	38.9	14.19
4	1.0	10.7	2.40	3.46	15.77	1.24	0.685	10.47	1.54
5	2.4	14.1	0.52	4.96	19.25	1.47	1.914	13.77	0.51
6	0.068	7.38	0.87	0.137	11.38	2.51	0.019	6.75	0.96
7	0.261	14.0	0.75	1.6	26.72	0.74	N O F L O W		
8	6.26	38.7	1.23	10.0	41.36	0.76	2.673	35.24	2.31
9	0.032	10.62	2.62	0.102	14.88	1.48	N O F L O W		
10	0.223	20.13	4.93	0.37	22.7	5.29	0.065	19.03	6.41
11	1.61	20.77	2.56	3.02	23.0	1.16	0.897	19.27	3.05
12	0.697	16.12	1.18	1.93	19.4	1.64	0.307	14.24	1.44

APPENDIX 5 : Continued

[C] Reach 2 - flow set 1.

CHANNEL	6 AUGUST 1981			7 AUGUST 1981		
	CHANNEL FLOW (m ³ s ⁻¹)	CHANNEL WIDTH (m)	WEIGHTED USABLE AREA (m ² m ⁻¹)	CHANNEL FLOW (m ³ s ⁻¹)	CHANNEL WIDTH (m)	WEIGHTED USABLE AREA (m ² m ⁻¹)
1	0.472	11.45	0.52	0.072	9.65	0.86
2	32.9	77.9	4.80	20.45	72.67	5.38
3	0.029	7.63	2.14	0.04	4.5	1.64
4	0.075	10.87	2.42	0.1	10.43	2.24
5	INADEQUATE DATA			INADEQUATE DATA		
6	48.3	69.75	5.39	38.7	64.5	6.59
7	0.234	15.85	2.08	0.092	10.65	1.45
8	2.63	60.75	4.71	1.458	59.85	8.4
9	1.29	14.97	2.56	0.59	13.1	1.72
10	3.82	22.67	2.36	1.476	19.0	1.96
11	2.35	12.82	1.56	0.958	11.5	1.81
12	0.383	6.37	0.77	0.098	6.3	1.18

APPENDIX 5 : Continued

[D] Reach 2 - flow set 2

CHANNEL	6 APRIL 1982			7 APRIL 1982			4 MAY 1982		
	CHANNEL FLOW (m ³ s ⁻¹)	CHANNEL WIDTH (m)	WEIGHTED USABLE AREA (m ² m ⁻¹)	CHANNEL FLOW (m ³ s ⁻¹)	CHANNEL WIDTH (m)	WEIGHTED USABLE AREA (m ² m ⁻¹)	CHANNEL FLOW (m ³ s ⁻¹)	CHANNEL WIDTH (m)	WEIGHTED USABLE AREA (m ² m ⁻¹)
1	8.312	23.18	2.64	16.2	23.5	0.13	3.4	19.06	1.65
2	N O F L O W			0.15	12.2	1.34	N O F L O W		
3	50.3	53.5	1.15	64.9	56.0	1.58	45.1	51.8	1.60
4	2.3	18.15	0.38	4.38	18.55	0.35	1.88	17.17	0.31
5	0.707	7.85	0.33	0.974	7.77	0.20	0.222	7.47	0.70
6	1.85	17.5	1.39	3.2	19.25	1.06	1.11	15.2	1.14
7	17.7	41.77	2.81	23.6	43.9	2.23	14.8	40.9	2.01
8	1.15	29.4	8.87	2.91	37.8	5.32	0.729	28.5	14.31
9	0.054	7.62	2.11	0.198	8.98	1.35	0.01	7.48	2.34
10	1.15	19.77	2.24	3.14	22.22	1.10	0.665	17.3	0.97