

Feeding Behaviour and Diet of the White-faced Heron *Ardea novaehollandiae* in Westernport Bay, Victoria

KIM W. LOWE

White-faced Herons *Ardea novaehollandiae* were studied in Westernport Bay between 1977 and 1982. Herons were present throughout the year but most moved away from the coast during the breeding season. Some herons returned to the same areas of mudflat from year to year. Herons fed in a wide variety of habitats: intertidal mudflats, saltmarsh, freshwater marsh, cultivated pastures and drainage depressions, residential lawns and intertidal rocky shores on the oceanic coastline. Herons fed in both intertidal and terrestrial habitats throughout the year but took most of their food from the intertidal habitat in summer and autumn and from the terrestrial habitat in winter and spring. On mudflats, herons usually foraged alone and occasionally defended feeding territories. They consumed a large range of prey species and prey sizes on the mudflats. Two species of caridean prawn and one species of crab dominated the stomach contents of eight herons that had fed on mudflats. The stomach contents of six herons that had fed in terrestrial habitats also contained a large range of prey species. The White-faced Heron used feeding methods that were energetically inexpensive and appeared to have low capture rates. The feeding strategy of the White-faced Heron may be described as a "habitat generalist".

The distribution of the White-faced Heron extends over most of the Australian continent. Although a common and widespread bird little has been published on the biology of the species — feeding ecology is not an exception. Lea and Gray (1935) summarised previous records of stomach contents and added further records. Sharland (1926) observed feeding of adult herons on tidal mudflats and feeding of young at the nest. Hobbs (1957) saw herons employing "foot stirring" and feeding on "yabbies" in the Murray River. Vestjens (1977) presented a summary of the stomach contents of nine herons at an inland freshwater lake. These anecdotal records were superseded by Carroll's (1967) study of the stomach contents of 89 White-faced Herons collected in New Zealand. The present study investigated the feeding behaviour and diet of the White-faced Heron at a site in coastal Victoria. Most data were collected while carrying out an intensive study of the biology of the Sacred Ibis *Threskiornis aethiopica* and are of necessity somewhat limited. Nevertheless, the lack of published information on the biology of the White-faced Heron prompted me to collect data as I was able.

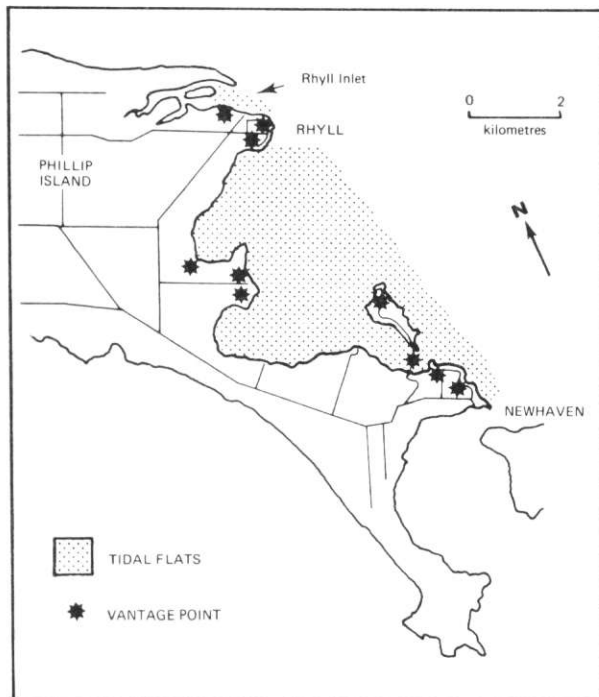
Study Area

From September 1977 to May 1982 I observed the feeding behaviour of White-faced Herons in Westernport Bay and the near-shore pastures. Observations were made throughout the area to indicate whether the behaviour observed at the main study area near Rhyll, Phillip Island (38°28' S., 145°18' E.) was typical of that shown throughout Westernport Bay. The study area near Rhyll was described in Lowe (1982).

Methods

The study area was visited for one to three days at least each fortnight. The distribution of herons near Rhyll was observed from a car driven around the eastern part of Phillip Island and from vantage points over-looking intertidal habitats (Fig. 1). As they fed, herons were observed from the car, hides in the mangroves fringing the intertidal habitat and boats driven or anchored between the mudflats. The feeding movements were observed with 10 x 50 and 16 x 50 binoculars and with a x20 telescope.

The horizontal distribution of birds feeding on mudflats was recorded on four occasions: 25 September 1977, 2 and 3 March 1978 and 27



● Figure 1. The location of tidal flats, vantage points and roads at the main study site near Rhyll.

June 1978. The number of birds feeding in each of six arbitrary zones was counted fifteen minutes before and on the hour for each hour of the low tide period. The zones are defined as:

- (A) dry substrate;
- (B) shallow film of water over substrate;
- (C) interface between zones (B) and (D);
- (D) water depth less than $\frac{1}{3}$ tarsal length;
- (E) water depth $\frac{1}{3}$ to 1 tarsal length; and
- (F) water depth greater than 1 tarsal length.

During the study, six herons were collected from pastures as they fed, two herons from intertidal habitat as they fed and six herons as they arrived at a roost after feeding in intertidal habitat. Immediately after the bird was shot a 70% ethanol solution was injected into the bird's stomach using a hypodermic syringe. Within two hours of collection the stomach was removed and preserved in a solution of 4% formaldehyde for later analysis. Prey taxa were identified and counted and blotted wet weight was recorded.

Most prey items were not significantly digested and whole animals were counted and weighed. Two heron nestlings regurgitated food when they were handled for banding*. These food samples were preserved in 4% formaldehyde and prey taxa were identified later.

White-faced Herons were difficult to census on the intertidal feeding habitat because their grey plumage was indistinct from the colour of the background. Herons could only be censused accurately on the near-shore intertidal areas. The Rhyll Inlet (Fig. 1) provided suitable conditions for censusing and the number of herons feeding there was counted sixteen times from 7 December 1978 to 11 January 1980. Herons were counted from the cliff on the southern shore of the inlet. This vantage point was elevated approximately 20 m above the intertidal habitat and provided an unobstructed view of the 32.7 ha area. Approximately 60% of this area was lightly covered (<50% cover) with eelgrass *Zostera marina*, 17% with heavy cover (> 50% cover) of eelgrass *Z. marina* and *Heterozostera tasmanica* and the remainder was bare muddy sands.

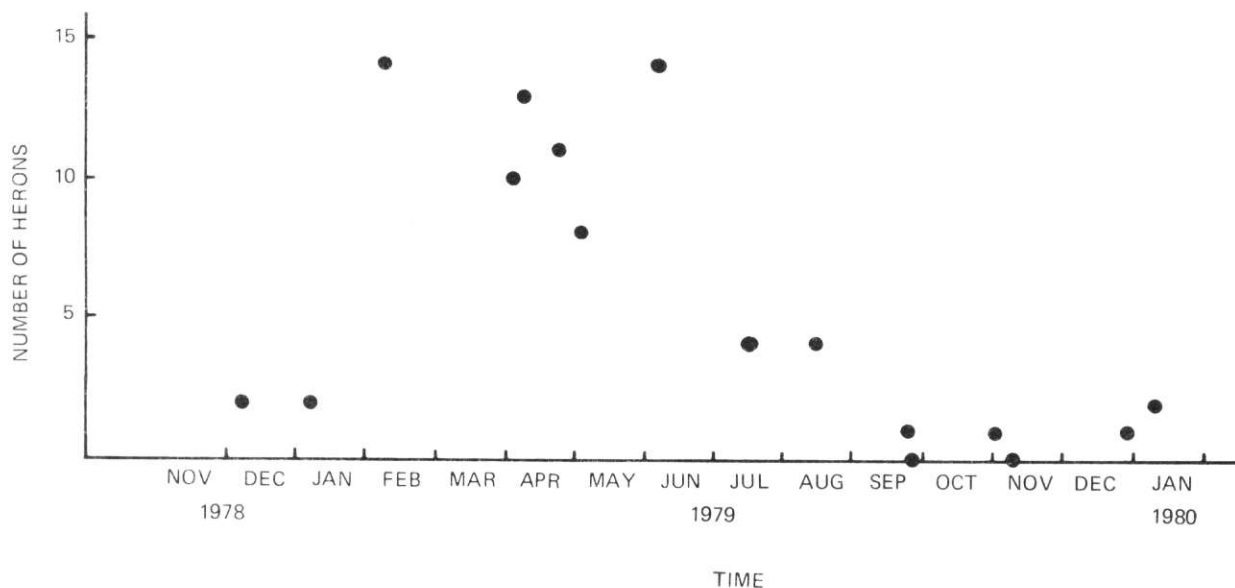
Results

White-faced Herons occurred in the study area throughout the year. The herons fed in a wide variety of habitats; intertidal mudflats, salt marsh, freshwater marsh, cultivated pastures and drainage depressions, residential lawns and intertidal rocky shores on the oceanic coastline of Phillip Island. Herons fed only during daylight and they used mainly visual cues to locate prey. During the non-breeding season, they roosted communally in mangroves, coppices of trees (eucalypts, cypresses) on pastoral land and in freshwater marshes, e.g. Rhyll Swamp. Herons left the roost soon after dawn and fed nearby usually moving further from the roost as the day progressed.

Intertidal feeding

On the mudflats, herons were most numerous from late summer to early winter (Fig. 2). At this time up to 14 herons fed in Rhyll Inlet, a maximum density of 0.43 herons per ha, if all of the intertidal habitat is considered. For the rest of the year few herons fed intertidally. On the mudflats, herons were usually well-spaced except when aggressive interactions occurred. In April 1979 two herons foraged within 30 m of each other for most of the low-tide period and

* Bands used were provided by the Australian Bird-banding Scheme, Division of Wildlife and Rangelands Research, CSIRO.



• Figure 2. Counts of herons feeding at low tide at Rhyll Inlet.

approached to within three metres of each other for brief periods on several occasions. They showed no obvious reaction to each other and no aggressive behaviour occurred. However, this was a most unusual happening and most herons fed alone.

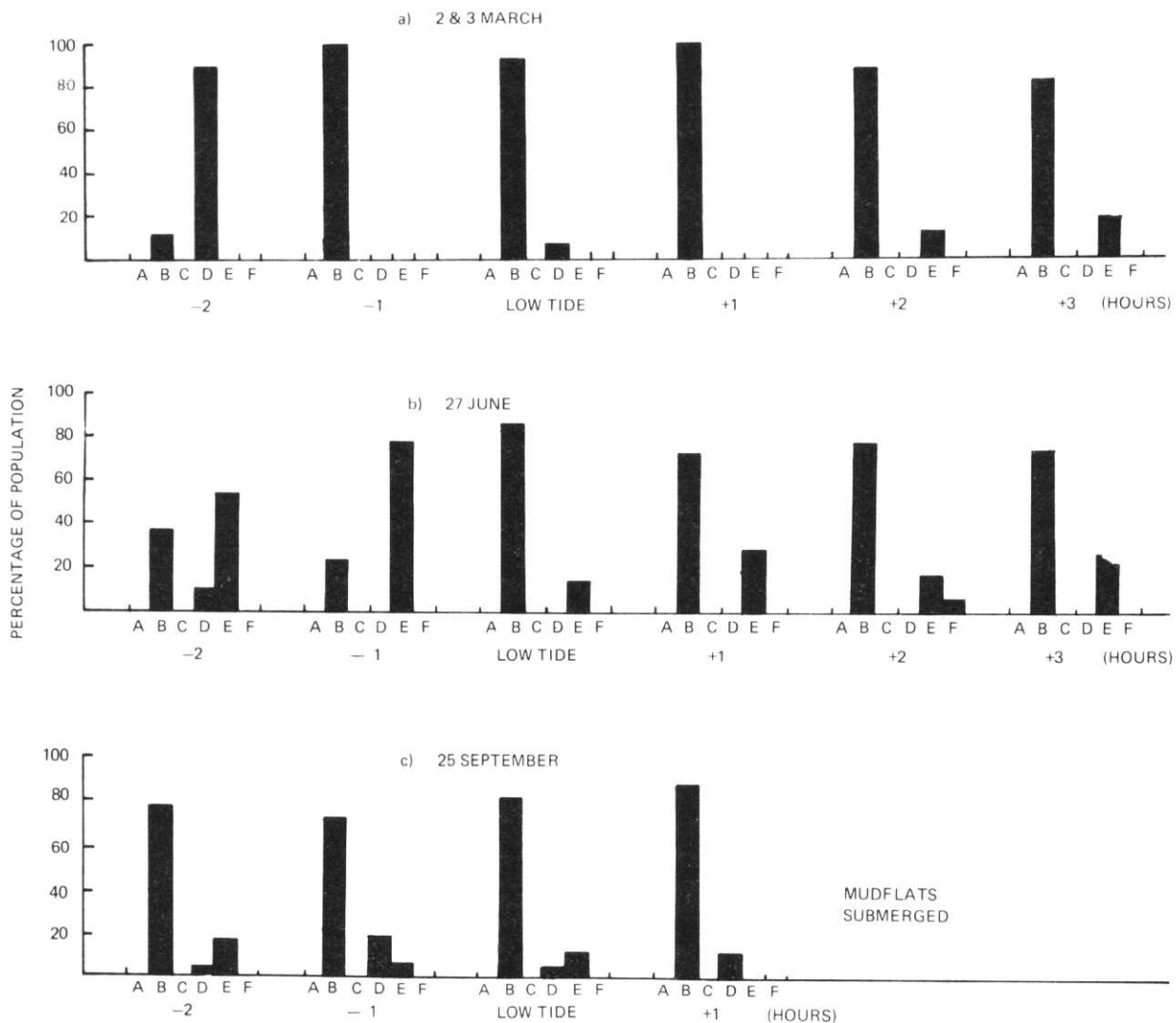
Aggressive interactions between herons feeding on the mudflats were rather infrequent. The most obvious aggressive interactions were of single herons that stopped foraging and flew in the direction of another heron. Often the flying heron called; this call was never heard in situations other than aggressive interactions. The call consisted of a grating "graak" sound lasting approximately one second. When the flying heron called, the heron it approached usually took flight immediately and was chased for two or three seconds. The chased heron usually landed at a new feeding site nearby and soon resumed foraging; occasionally it flew well away from the site of the interaction. The chasing heron usually returned to the site where it last was foraging. Single aggressive interactions of this type were seen throughout the study period.

Repeated interactions during the same low tide were observed on only four occasions: once in February and March 1978, and twice in June 1978. These interactions all occurred in the same

part of Rhyll Inlet. The most extensive sequence of aggressive interactions was recorded on 27 June 1978 in Rhyll Inlet during 216 minutes of observation centred on low tide. Six adult herons aggregated on an area of approximately 6.25 ha near the southern shore of the Inlet. During the observation period 12 separate aggressive interactions occurred involving all six herons. In 11 of the 12 interactions the aggressor chased a heron from the feeding site. In the remaining interaction the aggressor landed within three metres of another heron, the aggressor fed as it moved back towards the sites of the other interactions and the other heron moved along the shoreline in the opposite direction. One heron acted as aggressor in 10 or 11 of the interactions and chased all other herons. This heron appeared to be defending a feeding territory. On a map of the Inlet straight lines drawn between the sites of the 11 interactions and enclosing all of the area in which the aggressive heron had fed, encompassed an area of approximately 2 ha. The territory included zones B, C, D, E (see Methods) during the slack tide period. As the tide came in the area of Zone E increased to include all the territory. Seagrass covered all of substrate in the territory and most coverage was >50%. The territorial heron fed throughout the entire area and showed no preference for any

part. Another heron that was aggressor on one occasion chased a heron from within the presumed territory and was immediately chased by the territory holder. In all but one aggressive interaction the territorial heron responded to a heron wading (and feeding) into the defended area. The remaining interaction followed the flight of a heron into a defended area. There may have been more subtle interactions between

the herons as they waded but these interactions and their results were impossible to assess. The incoming tide covered the territory within 20 minutes of the last interaction and the territorial heron moved to a patch of heavily grassed mudflat that was still exposed. The heron fed there alone until the water was too deep for the heron to feed. On the 29 June 1978, no aggressive interactions were observed during the entire low



● Figure 3. Percentage of total population of White-faced Heron in Rhyll Inlet feeding in Zones A to F on: a) 2 and 3 March 1978; b) 27 June 1978; and c) 25 September 1977.

tide period. In fact, no herons fed within the area defended two days previously and only three herons foraged simultaneously in Rhyll Inlet. The weather on both 27 and 29 June was very similar; sunny, cool with 10-15 knot NE winds.

Herons fed throughout Rhyll Inlet except for the sand bar on the northern side. They fed almost exclusively in Zones B, D and E (see Fig. 3). Herons used the simple feeding methods typically found in herons. That is, the basic "stand and wait" or "wade or walk slowly" (Meyerriecks 1962). When employing the "stand and wait" method, herons rarely used "head tilting" (*sensu* Krebs and Partridge 1973). "Foot stirring" was observed infrequently in herons feeding intertidally although it was observed throughout the year. When prey were captured they were never speared but were always gripped between the mandibles, usually crushed and swallowed within a few seconds. Infrequently, the heron moved out of the water onto exposed substrate before manipulating and swallowing prey.

Herons began feeding as soon as the mudflats were exposed and continued feeding until the water was too deep to feed in. They fed for approximately five hours each low tide. In summer, and early autumn, herons roosted communally on rocky headlands or at farm dams with Sacred Ibis and Royal Spoonbills *Platalea regia* after they had fed intertidally. Mudflats were abandoned on very windy days especially when temperatures were low. Birds left the mudflats when the weather became cold and windy. This frequently happened in autumn and winter. In mid-summer when air temperature is high herons left intertidal feeding grounds when blustery winds of 20 knots or greater occurred. The major cause of herons abandoning intertidal feeding grounds appeared to be strong wind which may be re-inforced by cold temperatures. Often strong winds are associated with rainfall which presumably increases the availability of terrestrial prey making terrestrial habitat more profitable for feeding.

Seasonal use of feeding habitat

Herons fed in terrestrial habitats throughout the year. In summer, they fed preferentially on intertidal habitats (the exceptions discussed previously) during the low tide. Before and after low tide herons fed in pastures especially from late summer onwards. In autumn they first regu-

larly fed throughout the day in terrestrial habitats and did not feed on mudflats. In winter and spring herons fed almost exclusively in terrestrial habitats. However, at any time of the year herons foraged on mudflats in the daytime if the weather was calm and mild.

Terrestrial feeding

Most of the available terrestrial habitat in the Westernport Bay region is pasture grazed by cattle. Lone herons were observed throughout the year in pastures but groups of herons were more common. Up to 60 herons formed feeding flocks and the largest flocks were observed in May and June. The number of herons feeding in terrestrial habitats was too difficult to estimate. However, herons were uncommon in August, September and October of each year. Despite regular and intense searches at this time few herons were located near the shores of Westernport Bay.

Breeding

The searches did locate nesting pairs. Attention was directed then towards nest finding especially in 1978 and 1979. In 1978 four active heron nests were located. All four nests were in eucalypt trees; two were on the edge of farm dams, one near a water storage reservoir and one remote from any water source. In all four nests eggs were laid in late August or early September and young fledged in October. The nesting pairs were solitary and well spaced, i.e. over 2 km between the closest two nests. Solitary feeding herons were watched on the pastures in an attempt to follow birds to the nest sites. This aim was not achieved because birds fed well away from the nest site and were difficult to track. Nest relief was infrequent (one change over from dawn to 13:00 hr at one nest with eggs) and hence tracking opportunities were infrequent. All four nest sites were checked in 1979, 1980 and 1981. None were re-used for nesting nor were new sites located.

Prey capture

It was obvious when a heron attempted to capture a prey but sometimes difficult to determine if it was successful. Sometimes after striking at the surface of the mudflat the heron would rapidly shake its head laterally once or twice in a short arc. No prey was visible in the bill and this suggested that the heron may have been

shaking mud from its bill. Herons sometimes shook the bill in this manner when they were known to have captured a fish or a crab. Presumably this movement shook mud from the bill but may also have aided in killing the prey. With care it was possible to be confident when a prey was captured.

Capture rate varied from a mean of 0.4 captures per minute (15 min. observation) to 2.14 capture per minute (14 min. observation) on the same day in November 1977. Preliminary records indicated that capture rate varied with time in the tidal cycle at the same place, between places at the same time and between herons at the same place and time. Attempts to limit the observations to particular herons failed because they could not be recognised individually and it was unprofitable to continuously watch single birds —

they were rather mobile and waded throughout the study area. It was also not profitable to record at one site the feeding behaviour of any heron that moved into and fed there. The scope of this study prevented further observation of capture rates. The preliminary records did show that herons usually captured prey infrequently, i.e. approximately one per minute. No attempt was made to record feeding rate in terrestrial habitats.

Food

The contents of eight stomachs of adult White-faced Herons that were collected as or after they fed in intertidal habitat are listed in Table 1. Eighteen species were represented in the stomachs with from three to 12 species present in each stomach (mean \pm S.D. = 6.8 ± 3.0).

TABLE 1

Prey species from stomachs of eight adult White-faced Herons that fed in intertidal habitats. Numerals in ordinary type are numbers of each prey taxon per stomach and in parentheses are percentage composition (wet weight) of each stomach. Birds are identified by the date of collection (X < 0.1%).

Prey Taxon	Herons								All Herons	Σ Wt. (g)
	A 25.2.81	B 8.4.80	C 9.4.80	D 12.4.78a	E 12.4.78b	F 26.5.78	G 14.7.79a	H 14.7.79b		
CRUSTACEANS										
CARIDEA (shrimps)										
<i>Macrobrachium intermedium</i>	0(0)	4(5.0)	1(0.2)	2(4.0)	11(8.8)	10(10.9)	34(35.1)	136(58.0)	198 (23.1)	44.10
<i>Chlorotocella leptorhynchus</i>	0(0)	0(0)	0(0)	1(X)	0(0)	1(X)	43(23.8)	123(16.7)	168 (8.0)	15.27
<i>Pontophilus intermedius</i>	0(0)	0(0)	0(0)	0(0)	5(4.7)	19(21.9)	34(17.1)	13(3.8)	71 (5.2)	9.88
<i>Alpheus euprosyne</i>	0(0)	0(0)	0(0)	0(0)	3(2.9)	7(15.1)	0(0)	—	10 (1.2)	2.30
BRACHYURA (crabs)										
<i>Halicarcinus ovatus</i>	0(0)	0(0)	0(0)	25(38.0)	3(0.6)	0(0)	0(0)	1(0.1)	29 (1.1)	2.06
<i>Nectocarcinus tuberculosus</i>	1(13.1)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	—	1 (1.3)	2.38
<i>Pilumnus fissifrons</i>	3(6.8)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	—	3 (0.7)	1.24
<i>Litocheira hispidosa</i>	0(0)	0(0)	0(0)	1(2.0)	1(1.2)	0(0)	0(0)	—	2 (0.2)	0.30
<i>Paragrapsus</i> sp.*	0(0)	0(0)	0(0)	0(0)	4(48.2)	2(2.5)	0(0)	1(1.9)	7 (5.0)	9.52
<i>Brachynotus spinosus</i>	0(0)	0(0)	0(0)	2(8.0)	14(7.1)	0(0)	0(0)	1(0.2)	7 (0.9)	1.73
<i>Macrophthalmus latifrons</i>	40(52.0)	8(70.8)	47(51.7)	19(30.0)	13(13.5)	34(41.2)	0(0)	4(2.7)	165 (26.4)	50.66
AMPHIPODA										
<i>Orchestia</i> sp.	0(0)	0(0)	0(0)	50(18.0)	0(0)	0(0)	0(0)	0(0)	50 (0.5)	0.90
ISOPODA										
<i>Crabzys</i> sp.	1(0.6)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	1 (X)	0.10
MOLLUSCS										
Sepiolidae (squid)	0(0)	0(0)	7(43.8)	0(0)	4(6.5)	0(0)	0(0)	1(1.0)	12 (13.2)	25.14
FISH										
Syngnathidae (pipefish)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	2(1.6)	2(1.6)	4 (0.7)	1.27
Gobiidae (gobies)	6(27.5)	2(24.2)	8(4.3)	0(0)	10(6.5)	13(8.4)	10(18.9)	6(5.0)	55 (9.5)	18.17
Clinidae (weedfish)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	1(3.5)	1(1.7)	2 (0.9)	1.81
Monocanthidae (leatherjackets)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	1(7.3)	1 (2.1)	3.99

* Either *P. gaimardi* or *P. laevis*.

The most numerous prey species were the prawns, *Macrobrachium intermedium* and *Chlorotocella leptorhynchus* and the crab, *Macrophthalmus latifrons*. Prawns *M. intermedium* and crabs *M. latifrons* dominated the weight of the stomach contents. Prawns *M. intermedium*, crabs *M. latifrons* and fish of the family Gobiidae (mainly *Arenigobius bifrenatus* and specimens too far digested to be identified) each occurred in seven out of the eight stomachs.

Most of the shrimps, *M. intermedium*, *C. leptorhynchus* and *Pontophilus intermedius* were taken by the two herons (G and H, Table 1) collected as they fed on a dense stand of sea-grass in July. These stomachs contained few *M. latifrons* in contrast to the other six stomachs that all had large numbers of this crab. Most of the weight of squid came from a single heron (C).

The contents of six stomachs of adult herons collected as they fed in pastures are listed in Table 2. At least 11 taxa were represented. The two herons collected in April had taken only crickets and grasshoppers. The heron collected in June had consumed mainly adult flies and earth-

worms but the earthworms comprised the bulk of the weight of the stomach contents. The herons collected in August had taken mainly beetles, notostracans, earthworms and molluscs.

Two nestling herons regurgitated dipterans when they were banded in September 1978. One nestling regurgitated 28 larvae of the family Tipulidae and the other regurgitated 26 adult *Odontomyia* sp.

Discussion

The data indicate that some White-faced Herons were present in Westernport Bay throughout the year but most herons moved away from the coast during spring; presumably they bred inland and maintained feeding and breeding territories. Herons fed in both intertidal and terrestrial habitats throughout the year but took most of their food from the intertidal habitat in summer and autumn and from the terrestrial habitat in winter and spring. A heron, colour-banded as a nestling in September 1978, was resighted feeding in Rhyll Inlet at low tide in May 1981, January 1982 and March 1982. The bird had adult plumage when first resighted and was never seen in pastures. This indicates that

TABLE 2

Prey species from stomachs of six adult White-faced Herons that fed in pastures. See Table 1 for explanation of numerals (ad = adult; l = larvae).

Prey Taxon	Herons					
	19.4.78	21.4.78	26.6.79	3.8.78	11.8.78	25.8.78
ARTHROPODA						
INSECTA						
COLEOPTERA (beetles)						
Scarabaeidae	—	—	—	—	—	1ad (0.2)
Dytiscidae	—	—	—	7ad 1l (2.2)	2ad (0.9)	7ad (1.2)
Hydrophilidae	—	—	—	4ad (1.0)	2ad (1.1)	2ad (0.3)
DIPTERA (flies)	—	—	13ad (2.4)	1l (0.2)	1l (0.3)	—
LEPIDOPTERA (motahs)	—	—	1l (X)	—	—	—
ORTHOPTERA						
Gryllidae (crickets)	7 (100.0)	23 (94.0)	—	—	—	—
Tettigonidae	—	8 (6.0)	1 (0.4)	—	—	—
CRUSTACEA						
Notostraca (shield shrimps)	—	—	—	c.150 (58.3)	c.150 (34.8)	c.450 (98.3)
ARACHNIDA (spiders)	—	—	4 (0.8)	—	—	—
Lycosidae (immatures)	—	—	—	—	—	—
ANNELIDA						
Oligochaeta (earthworms)	—	—	12 (96.4)	—	18 (63.0)	—
MOLLUSCA						
Gastropods (snails)	—	—	—	21 (38.3)	—	—

some herons do return to the same areas of mudflats from year to year following the spring dispersal from the coast. Also, some herons remain near their birth place for extended periods, e.g. over three years. This observation challenges the suggestion that the White-faced Heron is nomadic throughout its range (see Hancock and Elliot 1978). The banded heron was never seen feeding at the same site on consecutive days and it probably changed feeding site frequently and certainly did not maintain a permanent feeding territory on the mudflats. Occasionally one heron maintained a feeding territory in Rhyll Inlet. Herons appeared to forage over an area of several hectares on the mudflats and this area changed from day to day.

Herons usually foraged alone and seemed to abandon feeding on mudflats during strong winds. Both situations relate to the use of visual cues to locate prey. Further, all of the prey taken by herons are usually found on the surface of or above the sub-stratum. The prey occur over a broad range of intertidal microhabitat types; from areas of bare sandy mud (e.g. *M. latifrons*) to mudflats covered by shallow water (e.g. gobies) to permanently water covered (shallow) seagrass beds (e.g. shrimps, squid). Prey from all of these microhabitats occurred in all stomachs (Table 1) indicating that herons foraged in a variety of microhabitats during the same low tide. There was no indication that herons preferred particular microhabitats (and prey species). Herons consumed a large range of prey sizes from amphipods and dipterans (3 mm long; 0.01 g wet weight) to fish and squid (60 mm; 10 g wet weight). The White-faced Heron is well described by Recher and Recher (1980) as a "habitat generalist". They suggested that herons that have a diverse diet are typically "searchers" and are large herons. The White-faced Heron certainly is a "searcher" but is small to medium size.

Herons used feeding methods that were energetically inexpensive and appeared to have very low capture rates. They attempted to minimise their intake of inorganic material when they swallowed a prey. Presumably this improves the efficiency of digestion of food which may be critical considering their low consumption rates.

The feeding ecology of the White-faced Heron is in striking contrast with that of the Royal Spoonbill with which it shares feeding grounds.

The Royal Spoonbill employs very active tactile feeding methods, has a higher prey consumption rate and takes a smaller range of prey species and sizes (Lowe 1982). The specialised feeding ecology of the spoonbill differs greatly from the generalist feeding of the heron.

This preliminary study of the feeding ecology of the White-faced Heron describes one facet of the diverse life-style of this common and successful heron. Much more study and reporting is called for.

Acknowledgements

I am most grateful to Peter Dann and Kaye MacRae for assistance in the field. Rob Howard, Bruce Rigby and Al Robertson kindly assisted in identifying some of the marine prey. Arthur Neboiss identified insects eaten by the herons and I thank him. Graeme Watson provided helpful comments on the manuscript.

References

- Carroll, A. L. K. (1967), 'Foods of the White-faced Heron', *Notornis* 14: 11-17.
- Hancock, J. and H. Elliot (1978), 'The Herons of the World', London: London Editions.
- Hobbs, J. N. (1957), 'Feeding habits of some water-birds', *Emu* 57: 216.
- Krebs, J. R. and B. Partridge (1973), 'Significance of head tilting in the Great Blue Heron', *Nature* 242: 533-535.
- Lea, A. M. and J. T. Gray (1935), 'The food of Australian birds', *Emu* 34: 275-292.
- Lowe, K. W. (1982), 'Feeding behaviour and diet of Royal Spoonbills *Platalea regia* in Westernport Bay', *Emu* 82: 163-168.
- Meyerriecks, A. J. (1962), 'Diversity typifies heron feeding', *Nat. Hist.* 71: 48-59.
- Recher, H. F. and J. A. Recher (1980), 'Why are there different kinds of herons?', *Trans. Linn. Soc. (NY)* 9: 135-158.
- Sharland, M. S. R. (1926), 'In the haunts of the heron', *Emu* 26: 40-44.
- Vestjens, W. J. M. (1977), 'Status, habitats and food of vertebrates at Lake Cowal', CSIRO Division of Wildlife Research Technical Memorandum 12. Canberra: CSIRO.

Kim W. Lowe,
Department of Zoology,
University of Melbourne,
Parkville, Victoria 3052.