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WINTER ECOLOGY OF A BLACK OYSTERCATCHER POPULATION

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Abstract.—The movements and foraging of Black Oystercatchers were studied during winter. Many birds concentrated in mudflats during daytime where they fed on mussels (*Mytilus edulis*). The birds ignored other potential prey but had little impact on the mussel beds. More time was spent foraging in beds with higher densities of mussels and this behavior is discussed in relation to a model of optimal foraging.

Oystercatchers (*Haematopus* sp.) are shorebirds inhabiting most continental sea coasts. They have attracted considerable attention in Europe where they concentrate in large numbers on intertidal flats during winter and pose a significant threat to the cockle fishery (Hancock 1970). The birds feed preferentially on second-winter cockles (*Cardium edule*) just before they reach the size of entering the fishery (Franklin 1972). A single bird concentrating on cockles may remove over three hundred per day (Davidson 1968). The birds feed on mussels (*Mytilus edulis*) as well, and will prey on *Macoma baltica* or other bivales when cockles or mussels are in poor supply (Hancock 1970). According to Dare (1966), oystercatchers tend to concentrate in areas where cockles and mussels occur in sufficient density to sustain the relatively high daily food requirements of the birds. Heppleston (1971a) found that British oystercatchers (*H. ostralegus occidentalis*) were unable to obtain their food requirements from estuarine habitats during winter in spite of extending their foraging time into the night. These birds apparently made up their deficit by feeding at high tide on earthworms in grass fields. In a study of the anatomy of the bill, Heppleston (1970) found many sensory corpuscles which would allow the bird to probe mud or soil for invertebrates. An interesting increase in the use of terrestrial habitats by oystercatchers for feeding and also for breeding has been observed in Britain and New Zealand (Heppleston 1971a, Baker 1974). Nevertheless, the major prey items in the diet of oystercatchers are molluscs and this specialized feeding habit greatly reduced interspecific competition with other waders (Heppleston 1970). A variety of studies has been carried out on the abilities of oystercatchers to open bivalves, especially mussels (Drinnan 1958, Norton-Griffiths 1967, Heppleston 1971b). Norton-Griffiths found that some oystercatchers stabbed mussels when they were submerged and gaping while others hammered the shells open. Studies in New Zealand have indicated other differences occurring in the birds including variations in habitat selection, niche utilization, and breeding biology (Baker 1974). For example, South Island Pied Oystercatchers (*H. o. finschi*) concentrate in large flocks in habitats with soft substrates, such as mudflats. In contrast, the black phase of the Variable Oystercatchers (*H. unicolor*) occurs in smaller flocks along rocky shores. According to Baker, these are generally excluded from mudflats through competition with the South Island Pied form.

On the west coast of North America, a black form of oystercatcher occurs in relatively low numbers along the exposed coast. The Black Oystercatcher is usually regarded as a separate species, *H. bachmani,* although Heppleston (1973)

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has reviewed the systematics of the family Haematopodidae and suggests that the west coast species be regarded as a subspecies, *H. ostralegus bachmani*. However, as he points out, the classification of oystercatchers is a subject of continuing controversy and further studies are required.

Information on the biology of Black Oystercatchers was collected by Webster (1941) and more recently by Hartwick (1974). Studies to date have centered on the behavior and ecology of these birds during the summer breeding season. Their diet at that time consists mainly of mussels (*M. californianus*) and limpets (*Collisella* sp. and *Notoacmea* sp.) although other items such as polychaetes (*Nereis*) and various arthropods are also taken (Hartwick 1976). They inhabit rocky shores although occasionally pairs are seen on sandy beaches. Relatively little information exists on the ecology and behavior of this species during winter in spite of the popularity of their European counterpart. The present study was initiated in order to investigate the movements and feeding patterns of Black Oystercatchers during the period, December 1975 through April 1976. In a previous study (Hartwick 1976), the foraging of the birds was compared to a current model of optimal foraging theory (Royama 1970). This model suggests that predators should allocate their time according to the profitabilities of various prey items, spending most of their time concentrating on items which are more profitable. Another objective of the present study was to investigate this hypothesis for the case of oystercatchers feeding during the winter.

STUDY SITE

Most of the work centered on a large sand and mudflat in Lemmens Inlet near Tofino (lat. 49°N, long. 126°W) on the west coast of Vancouver Island (Fig. 1). Lemmens Inlet is a portion of Clayoquot Sound lying approximately 3 miles from the outer exposed coast and 11 miles from the main breeding site in the area (Cleland Island). During the winter these mudflats serve as feeding and roosting sites for many species and large flocks of oystercatchers were observed to use the flats at that time. The invertebrate fauna of the inlet is a mixture of organisms characteristic of both exposed and semiprotected environments. The dominant organism, at least in terms of numbers, is *Mytilus edulis*, the common bay mussel, which forms extensive beds over much of the area of the mudflats.

METHODS AND MATERIALS

Observation posts were established at four locations in the mudflats, always on the shore of an island. Whenever possible, observations were made over entire tidal cycles (for example, from a high tide through to the next high tide). On each observation day the total number of oystercatchers using the mudflats was recorded. Movement patterns into and out of the mudflats and within the mudflats were also noted. The diet of the birds was recorded from observations made by telescope. It was usually possible to identify a food item directly or by the feeding behavior of the birds. The mussel beds occurred as relatively discrete units and the relative use of the various beds by the birds was estimated by recording the time spent feeding in each bed. Feeding rates were measured for various mussel beds by recording the number of successful attacks in a given time at various stages in the tide cycle. Mussels that had been fed on by the birds were collected for measurement. The obvious tracks of the birds in the mud aided in this process. The total time spent feeding and roosting was also noted.

The primary mussel beds used for feeding by the Black Oystercatcher were surveyed to determine their tidal height, area, and density. Transects were made through the mussel beds and mussels were collected within a 0.5-m square at random intervals along the transects. Mussels in the quadrants were counted and measured. Samples were also taken in mussel bed areas not normally used by the oystercatchers.

Additional counts and observations were made by boat trip to the outer reefs and to Cleland Island, the main breeding site for these birds in this area. These trips have also been made at various times in the year over a 5-year period.

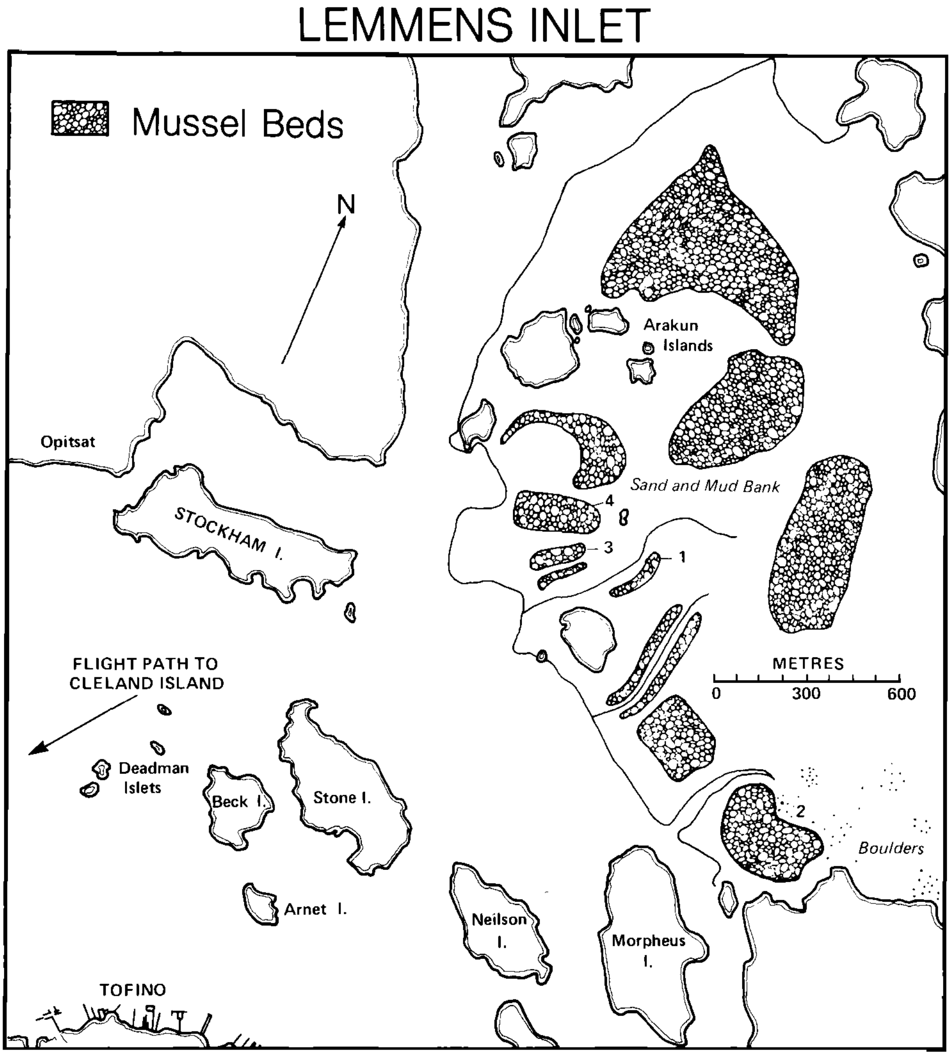

FIGURE 1. Study site at Lemmens Inlet in Clayoquot Sound, Vancouver Island.

OBSERVATIONS AND RESULTS

Distribution and Numbers of Birds

Visits to the area in the fall indicated little or no use of the mudflats at that time with most oystercatchers still out on exposed rocky shores, although sightings of flocks in protected areas have been reported as early as November (D. Hatler, pers. comm.). By December, there is consistent use of the mudflats for feeding and this continues through April after which time most birds again appear on exposed rocky shores. Boat trips to outer reefs indicated use of rocky shores by at least some of the birds throughout the winter, generally occurring as small flocks. Oystercatchers were observed on Cleland Island at various times throughout the winter and in March over 50 oystercatchers were spotted on the island with some showing obvious pairing and territoriality. In October (1976) only small

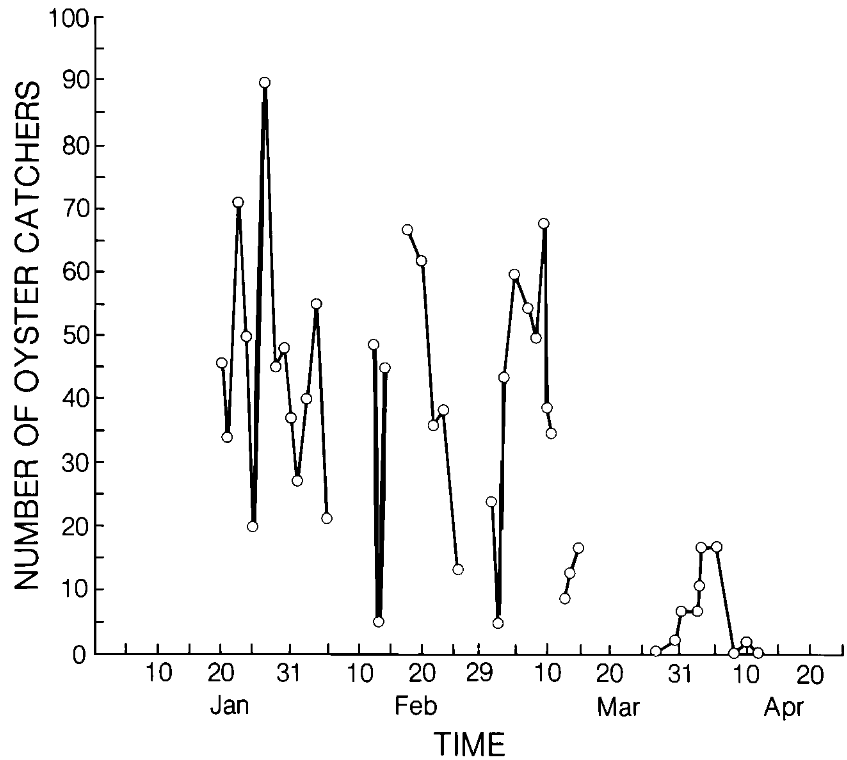

FIGURE 2. The number of oystercatchers observed on the mudflats of Lemmens Inlet.

numbers were observed in the breeding area and these generally left the island for the day, returning to roost at night.

The number of oystercatchers observed on the mudflats varied throughout the season from as many as 90 birds on 27 January to very few or none during observation periods in April. Use of the mudflats by these birds was generally heavy in the period from January to early March with numbers falling off in mid-March and remaining low thereafter (Fig. 2). Aside from this seasonal trend, fluctuations in numbers of birds appeared to be unrelated to tides, times, or general weather patterns although some low counts were associated with stormy weather (13 Feb.).

Movement Patterns of Oystercatchers

Daily Movements to and from Feeding Area

The Black Oystercatchers did not roost in the mudflats overnight, but returned each evening to reefs and roosting sites out in more exposed areas (Fig. 1). Each morning Black Oystercatchers would fly into the feeding area in small groups from a westerly direction. The birds called repeatedly while flying, often being answered by distant birds already in the feeding area. Incoming flocks were frequently observed to land in the vicinity of birds that had been calling.

In the evening or late afternoon the oystercatchers left the feeding area of the mudflats for the open coast as a single large flock. The behavior of the birds getting ready to depart was very distinctive and repeated each day. One bird would begin calling, soon to be joined by all the others in the flock. Flight from the area as a single flock would soon follow once many birds had started calling.

The timing of arrival and departure from the feeding area was influenced by the tidal cycle. Arrival in the feeding area in the morning was usually coordinated with the low tide so that if the tide was high early in the day, the flock would not show up until the late morning or early afternoon. Similarly, once the mussel beds were covered by a rising tide the flock tended to leave the feeding area and fly to the open coast. The flock did not usually remain in the feeding area in late afternoon or evening unless the mussel beds were exposed and in all cases, the birds left the area before dark.

Movements within the Feeding Area

At high tide, Black Oystercatchers in the mudflats usually roosted on the tip of a small, bare rock in the middle of the mudflats. As the tide dropped to the level of *Fucus* growing on rocks in the mudflats, the oystercatchers would leave the roosting site in small numbers and begin foraging in the *Fucus* zone. As the tide drops lower the oystercatchers begin moving into and foraging in the mussel beds as they become exposed. The mussel beds used by the flock for feeding are exposed by a falling tide in this order: Area 4, Area 2, Area 3, Area 1, and the N-S channel beds. The oystercatchers move from bed to bed as they are exposed up to the point where the lower beds are exposed. From that point to low tide the movement into a particular feeding area within the mudflats is less predictable.

A period of roosting as a single flock usually occurs at or near the time of low tide. This is especially true if the birds have been feeding as the tide goes out. The earlier or later in the day the low tide occurs, the less likely the birds are to roost. Roosting invariably occurs at the water's edge and was rarely observed within a mussel bed.

Once low tide is reached and the tide begins to flood the mudflats the birds present usually feed continuously until the last mussel bed is covered. Once again, the movement into the various feeding areas follows the pattern with which they are covered by the tide. Time spent foraging in a feeding area is influenced by rate of flow of the tide, the presence or absence of other oystercatchers in the feeding area, and disturbances from outside sources. On a flooding tide, Black Oystercatchers are observed to forage in mussel beds along the line of the advancing water. Since Area 4 is the highest feeding area available, all the oystercatchers that are present in the mudflats will eventually be forced to forage there when the tide is at a certain level. Once Area 4 is covered the Black Oystercatchers fly to their roosting site in the mudflats. The length of time spent here depends on the time of day and, to some extent, on the weather.

Survey of the Mussel Beds

The survey of the mussel beds used as primary feeding areas indicated that Area 4 was the largest and had the highest density of mussels. Area 2 was roughly the same size but contained considerably fewer mussels (Table 1). Area 3 was half the size of 2 and 4, but had a density of mussels halfway between that of Areas 2 and 4. The North Arakun mussel beds which were not used by the birds to any extent were extensive but had considerable amounts of eel grass associated

TABLE 1
MUSSEL BED CHARACTERISTICS

Location	Area (m^2)	Tidal height (ft.)	Density (mussels/m^2) (range in parentheses)	Time foraging[a] (%)
Area 1	3,606	4.1–5.8	524 (0–1208)	1.9
Area 2	32,000	4.9–6.3	548 (0–888)	18.8
Area 3	17,825	4.7–6.6	800 (244–1720)	28.6
Area 4	36,822	6.9–8.0	1182 (0–2332)	43.4

[a] Based on 55 hours of observations on 15 different days over a 3-month period.

with them. The size distribution of mussels in the North Arakun beds showed a mean size of 51.4 mm, compared to a mean size of 30.83 in Area 4. The density of mussels in the North Arakun beds was roughly 90 mussels/m^2, less than $^1/_{10}$ the density of Area 4. The mean time periods over which each bed was washed by waves were determined. This time of vulnerability varied with a mean of 31.2 min for Area 4, 57.2 min for Area 3, 47.5 min for Area 2, and 56.6 min for Area 1, based on 21 observations.

FORAGING RESULTS

Size and type of prey.—Black Oystercatchers on the mudflats of Lemmens Inlet fed exclusively on the mussel *Mytilus edulis*. Mussels fed on by the birds varied in size from 2.13 cm to 7.23 cm with a mean size of 5.0 cm based on a sample of 1428 mussels from Areas 1, 2, and 3. The size distributions of mussels taken from the various beds were similar in spite of significant differences in the size distributions of mussels in the beds. Figure 3 illustrates the size distribution of mussels taken by the birds for all samples combined. The selection of similar-sized items from beds of varying compostion resulted in a clear selection of relatively large mussels from beds in which the mean size of mussel was relatively small.

Use of the feeding areas.—Since the oystercatchers feed in mussel beds only when they are washed by water it is possible to estimate the amount of time the mussel beds are available to the oystercatcher and compare this with the amount of time the oystercatcher actually spends in the feeding area. Feeding in this area does not occur at night so this estimate is based only on tidal cycles during the

TABLE 2
FEEDING RATES (MUSSELS/MIN)

Tide condition	*Fucus* zone	Area 1	Area 2	Area 3	Area 4	N-S channel
Exposed	.1	.875	1.04	.514	.96	.99
Flooding	–	–	1.058	.428	.97	.85
Ebbing	.38	–	–	1.07	.98	–
No. of birds observed	5	1	9	5	19	8

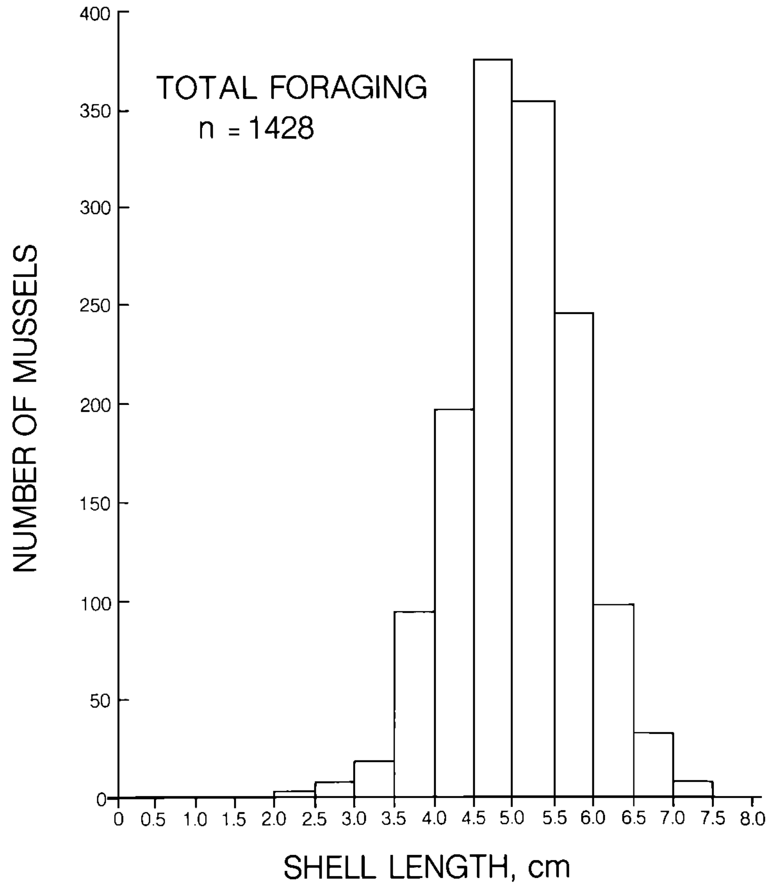

FIGURE 3. Size distribution of mussels taken by oystercatchers.

daylight hours. Of the total amount of time the mussel beds are available to the Black Oystercatcher, the birds spend roughly 53% of this time in the feeding area. A further breakdown of this figure showed that the birds were roosting approximately 52% of the time and feeding for 48% of the time. Thus the Black Oystercatcher uses only 25% of the time that the mussels are vulnerable for actual foraging.

This foraging time is distributed over the various beds. The percentage of time spent feeding in each area varied from a low of 1.9% in the *Fucus* zone to a high of 43.4% in Area 4 (Table 1).

Feeding rates.—The mean feeding rates of birds varied from a low of 0.1 mussels per minute in the *Fucus* zone while that zone was exposed, to a high of 1.06 mussels per minute in Area 2 during a flood tide (Table 2). The overall mean feeding rate for Areas 2, 3, and 4 was 0.9 mussels/min.

DISCUSSION

On the basis of this study and general observations, it would seem that Black Oystercatchers can be found on rocky exposed shores throughout the year but make use of protected mudflats to a varying extent especially in the winter. Since winter storms are common in the area it is surprising that the birds still utilize the exposed areas. The general impression, however, is that they are strongly tied to the breeding area and to nearby reefs. At this point it is difficult to judge the relative importance of protected mudflats. There is considerable variation in the numbers of oystercatchers using the mudflats at Lemmens Inlet. Storms do not appear to drive the birds into the bays and even in rather heavy seas they can be observed in flocks on the lee side of the islands and reefs. Total counts in the area suggest that most birds remain in Clayoquot Sound throughout the year and when they are not in protected inlets like Lemmens Inlet they are on reefs and rocky shores closer to the main breeding area. Several times, birds banded on Cleland Island were observed in the flocks using the mudflats supporting the idea that birds seen on the mudflats breed nearby.

There was no indication that the birds were feeding at night and they followed a consistent pattern of leaving the mudflat in the evening. Whether they fed on exposed shores at night was not determined but it seems rather doubtful under winter conditions.

Some interesting differences exist when the Black Oystercatcher is compared to its European cousin. For example, Black Oystercatchers ignored cockles (*Clinocardium nuttalii*) and other potential food items on the mudflats and concentrated on mussels, *M. edulis,* using the same stabbing method as they do with *M. californianus* on exposed shores. The restricted diet differs considerably from the diet of these birds during the breeding season when they can be observed feeding on a wide variety of items. Such a restriction suggests that food is not in short supply and, indeed, that seems to be the case at least at this time. On the other hand, large numbers of other species of birds including crows, starlings, gulls, and waterfowl use the same mudflat and it may be that diet restriction is somehow related to their presence. However, only gulls have been observed to directly interfere with the foraging of the oystercatchers.

The beds most used by the oystercatchers were those occurring in the open away from the shores of islands, closest to the open water, in the direction of the breeding area, and containing the greatest densities of mussels. The rather limited use of the mudflat area as a whole suggested that the birds would have minimal impact on the mussel beds at this time. Calculations based on their use of particular beds and their observed feeding rates support this impression. For example, an oystercatcher feeds in Area 4 an average of 50 min/day with a mean feeding rate of 0.97 mussel/min, therefore consuming approximately 50 mussels/day from this bed. If the maximum number of 90 birds were present then they would remove 4500 mussels/day from the bed. This is a maximum estimate probably much larger than the actual rate of predation. The estimated number of mussels in Area 4 was 43,523,600 and, since the birds utilized the beds primarily in the winter months, the birds probably had a minimal effect on the mussel populations at their present abundance.

The oystercatchers may even be aiding the survival of the mussel beds by their foraging. The empty shells of the eaten mussels remain within the matrix of the clump and are then available for mussel spat to settle on. In a shifting, loose substrate such as a mudflat, surfaces for settlement are at a premium, and we have observed on many occasions numbers of juvenile mussels growing on or within an empty shell. Thus the removal of the mussel, but not its shell, by the oystercatcher is effectively creating more space for larval settlement.

The relative use of the different mussel beds is of great interest. The percentage of time spent feeding in any bed increases with the density of mussels in the bed. Differences in the sizes of the areas and the lengths of time during which they are washed by waves do not explain the relative use of the beds. Presumably, the birds are responding to profitability differences (Royama 1970) in the beds. Thus, a higher density of mussels would result in a greater biomass return for a given hunting period. On the other hand, the feeding rate estimates do not necessarily support this idea, although the sample size is admittedly relatively small.

The restricted diet is also interesting. Mussels are probably the most profitable of food items available on the mudflats. They are both numerous and accessible. Nevertheless, Royama's model is based on the idea that predators will continually sample other prey in order to compare profitabilities over time and space. The Black Oystercatchers in Lemmens Inlet appear to feed only on mussels without sampling other items. Perhaps relative profitabilities do not change on the mudflat over the winter in which case the observed behavior would represent a most efficient pattern.

Further studies are required to determine how much feeding occurs on rocky exposed shores during winter. The amount of use of the mudflats may depend on feeding conditions in other areas. At present there is no satisfactory explanation for the pattern of variation in numbers using the mudflats and conclusions about the winter diet of the birds may be premature.

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