MOTHER AND PUP BEHAVIOUR OF THE NEW ZEALAND FUR SEAL, ARCTOCEPHALUS FORSTERI (LESSON)

A.G. McNAB and M.C. CRAWLEY

Department of Zoology, University of Canterbury, Christchurch, New Zealand

ABSTRACT

Descriptions are given of the behaviour of females and pups of the New Zealand fur seal, Arctocephalus forsteri (Lesson 1828), and the early development of mother-pup relations. Twenty births were observed and accurately timed: 12 head presentations had a mean delivery time of 2 min (from 6 s to 6 min) and 8 tail presentations averaged 6.5 min (from 8 s to 19 min). Sniffing of newborn pups by their mothers was frequent and identification was by smell thereafter. Pups were particularly active in the hour after birth, frequently shaking, coughing, calling and looking around. Most pups fed on the first day, but rarely during the first hour. Mothers first left their pups to go swimming at intervals after birth ranging from 45 min to 3 days. The mother's first departure on a feeding trip was 6 to 12 days after giving birth, and pups were not normally left for more than a day or two. When females stayed away for longer periods on subsequent feeding trips, pups more than 21 days old congregated into pods, until their mothers returned. Females fed only their own pups and were hostile to others, but pups attempted to feed from strange females. Pups played with their mothers and had play-fights with other pups. Initially, pups were afraid of the water but all could swim within 20 days. Bulls were indifferent to pups, and trampled or lay on the unwary.

INTRODUCTION

This paper describes the birth process, the behaviour of females and pups, and the early development of mother-pup relations in the New Zealand fur seal, Arctocephalus forsteri (Lesson 1828). This fur seal inhabits the rocky shores of New Zealand, South Australia, and many of the subantarctic islands to the south of them (King 1969, Wilson 1974). Recent studies of the behaviour and ecology of New Zealand A. forsteri have been made by Stirling (1970), Crawley and Brown (1971), Crawley (1972), Miller (1971, 1974, and in press), Wilson (1974) and Crawley and Wilson (in press), and of Australian A. forsteri by Stirling (1971a,b), Stirling and Warneke (1971) and Gentry (1973). Because of the unknown effects on the seal populations of the geographic separation and the climatic differences between New Zealand and South Australia, the papers above refer only to the particular A. forsteri population studied. However, the accumulating evidence indicates that
differences between the populations are minor (Crawley and Wilson in press).

There has so far been no published account of the birth process and mother-pup relations in New Zealand A. forsteri, but Stirling (1971b) has made a preliminary study of these topics in the Australian population. The purpose of our study was to provide descriptive and quantitative information on the behaviour of females immediately before, during, and after parturition, and to trace the early development of pup behaviour and mother-pup relations. This information may be compared directly with that for other species which have been studied, for example the northern fur seal, Callorhinus ursinus, (Bartholomew 1959, Peterson 1968), the South African fur seal, A. pusillus, (Rand 1955, 1967), the South American fur seal, A. australis (Vaz Ferreira 1956), the Amsterdam Island fur seal, A. tropicalis (Paulian 1964), and the South Georgia fur seal, A. gazella (Bonner 1968).

This work forms part of a comprehensive study of the biology of the New Zealand fur seal being carried out by members of the Zoology Department, University of Canterbury, New Zealand.

STUDY AREA AND METHODS

This study was carried out from 28 November 1973 to 7 January 1974 on Taumaka, the larger of the two Open Bay Islands (43°52'S, 168°53'E) which lie 4.5 km offshore from the mouth of the Okuru River, South Westland, New Zealand. There is a large (2000-3000) population of fur seals on the island (Crawley and Brown 1971), some of the characteristics of which have already been described (Miller 1971, 1974, Crawley and Wilson in press). The seals haul out on the fissured limestone shelves on the leeward side of the island. The top of Taumaka is covered with a dense growth of kie-kie, Freycinetia banksii, and a low forest of Hebe elliptica, Schefflera digitata and Fuchsia excorticata borders the limestone shelves. The landward side of the island rises steeply, and only a few caves and large rocks provide resting places for seals. The geology and vegetation of the island were described by Burrows (1972).

The study area chosen for detailed observational work was protected from the sea by large outlying rocks. The inlet thus formed was served by two channels. The seals were observed, without disturbing them, from a cliff-top vantage point beside the inlet. Here up to 200 seals could be seen, at ranges from 10 to 100+ m. Pups of known age, and their mothers, were marked by throwing paint-filled eggs at them as soon after birth as possible, when they were together and dry.

FEMALE BEHAVIOUR BEFORE PARTURITION

Females arrived ashore only a few days before giving birth, but the exact interval was difficult to determine as females were not then marked. For three females which were individually recognizable, the births took place 2.5 days, 1-2 days, and 0.5 days after arrival ashore, which is similar
to the mean figure of 2.1 days for nine females recorded by Miller (1971). There are similar short arrival-birth intervals recorded for other seals, for example 3 days for Callorhinus ursinus (Bartholomew and Hoel 1953), and about one day for the California sea lion, Zalophus californianus (Peterson and Bartholomew 1967).

Most females became restless and aggressive immediately prior to giving birth, frequently changing body and flipper positions. Some females circled about, on and off rocks, and occasionally sniffed the vulva or rocks touched by it. Neighbouring seals, formerly ignored, were threatened during this period. Some females even moved several metres to bite inoffensive wandering pups. Generally, such manifestations of restlessness were evident only during the hour immediately prior to parturition, but one female was noticeably restless 8 h 50 min before giving birth, and two others became restive 4 h 45 min and 1 h 41 min respectively, before parturition. Similar restlessness and irritability have been recorded for Australian A. forsteri (Stirling 1971b), A. gazella (Bonner 1968), Callorhinus ursinus (Peterson 1968) and Zalophus californianus (Peterson and Bartholomew 1967).

**PARTURITION**

Following a period of restlessness, many females showed labour movements. In a typical sequence, the female lay down with her head in the air, and then lowered her head steadily while straining forwards on her foreflippers and lifting her hind-quarters and flippers clear of the ground. The female then relaxed before repeating the procedure. Some females waved their hind-quarters laterally, while others circled and dragged their hind-quarters over the rocks. Periodic sniffing of the vulva, and rocks in contact with it, was common. Occasionally, slight contractions were seen to pass posteriorly down the flanks of some females.

The delivery was timed from when any part of the foetal membranes or pup was seen, to when the pup was completely free. Of the 24 complete births observed, 13 were by head presentation and 11 by tail. The times taken for the births, and the intervals between birth and the appearance of the placenta, are given in Table 1. One female was in labour for the exceptionally long time of 5 h 14 min and delivery took 1 h 39 min. Excluding this individual, the mean delivery time for 8 tail presentations was 6.5 min, and for 12 head presentations 2 min. No twins were born.

During the early stages of delivery, the pup was pushed out slowly by a series of single contractions, and it often slid back when the female relaxed. Once the pup was half out the remainder of the delivery was usually rapid. The amnion usually burst during, or even before, delivery, releasing yellow amniotic fluid. Delivery was aided by adroit use of sloping terrain by some females, but there was no sign of birth being assisted by the mother pulling the pup with her teeth, as was reported for A. australis (Vaz Ferreira 1956), A. pusillus (Rand 1955), and A. gazella (Bonner 1968). For 21 females timed, placentas were expelled an average of
### TABLE 1. DELIVERY TIMES AND INTERVALS BETWEEN PARTURITION AND EXPULSION OF THE PLACENTA FOR 24 OBSERVED BIRTHS OF *A. FORSTERI* PUPS.

<table>
<thead>
<tr>
<th>Delivery time (min)</th>
<th>Presentation</th>
<th>Interval before appearance of placenta (min)</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>Head</td>
<td>35</td>
</tr>
<tr>
<td>0</td>
<td></td>
<td>102+</td>
</tr>
<tr>
<td>0</td>
<td></td>
<td>34</td>
</tr>
<tr>
<td>0</td>
<td></td>
<td>89</td>
</tr>
<tr>
<td>0</td>
<td></td>
<td>25</td>
</tr>
<tr>
<td>2</td>
<td></td>
<td>22</td>
</tr>
<tr>
<td>2</td>
<td></td>
<td>31</td>
</tr>
<tr>
<td>2</td>
<td></td>
<td>80</td>
</tr>
<tr>
<td>3</td>
<td></td>
<td>40</td>
</tr>
<tr>
<td>3</td>
<td></td>
<td>6</td>
</tr>
<tr>
<td>3</td>
<td></td>
<td>74</td>
</tr>
<tr>
<td>6</td>
<td></td>
<td>-</td>
</tr>
<tr>
<td>-</td>
<td></td>
<td>65</td>
</tr>
<tr>
<td>0</td>
<td>Tail</td>
<td>-</td>
</tr>
<tr>
<td>0</td>
<td></td>
<td>43</td>
</tr>
<tr>
<td>2</td>
<td></td>
<td>44</td>
</tr>
<tr>
<td>2</td>
<td></td>
<td>19</td>
</tr>
<tr>
<td>6</td>
<td></td>
<td>60+</td>
</tr>
<tr>
<td>10</td>
<td></td>
<td>163+</td>
</tr>
<tr>
<td>12</td>
<td></td>
<td>8</td>
</tr>
<tr>
<td>19</td>
<td></td>
<td>-</td>
</tr>
<tr>
<td>99+</td>
<td></td>
<td>3</td>
</tr>
<tr>
<td>-</td>
<td></td>
<td>13</td>
</tr>
<tr>
<td>-</td>
<td></td>
<td>18</td>
</tr>
</tbody>
</table>

53 min after the pup was born and detachment occurred about 15 to 20 cm from the umbilicus. The umbilical cord was broken either by the movements of the mother, during or after the birth, or by the pup sliding away after delivery was completed. In the latter situation, the placenta sometimes pulled out and remained attached to the pup (15 of 97 pups born in the study area). Three pups were dead shortly after birth; one was stillborn and the others apparently suffocated in the amnion.

Births have been described for many other seal species, and in all except the grey seal, *Halichoerus grypus* (Boyd et al. 1962) both head and tail presentations have been recorded.
The delivery times for five Australian *A. forsteri* (from 5 s to 4 min, Stirling 1971b) were shorter than those recorded here but the one tail presentation recorded by Stirling took twice as long as the longest head presentation, and this is in agreement with the general trend in this study. Rand (1955) found that tail presentations in *A. pusillus* were only half as frequent, and took twice as long, as head presentations. The placenta-expulsion times recorded by Miller (1971) averaged 65.1 min, and Stirling (1971b) reported that four females passed placentas within 45 min, which is in general agreement with our data.

**BEHAVIOUR OF MOTHERS AND PUPS IMMEDIATELY FOLLOWING BIRTH**

Three mothers and their newborn pups were closely watched for the first hour following birth. Other mother-pup pairs were observed intermittently as opportunity permitted.

Most mothers sniffed their pups immediately after birth. Sniffing was particularly frequent during the first 15 min. Only two mothers were seen to pick at their pups' fur as though attempting to remove membranes (which were absent anyway). No attempts were made by the mothers of the two pups who suffocated to remove the enveloping membranes. Several pups struggled free of foetal membranes unassisted, but most were free when born. No mothers bit the umbilical cord, licked the pup, or ate the placenta. Pup-licking has been recorded for *A. tropicalis* (Paulian 1964), and it is thought that *A. pusillus* occasionally eats the foetal membranes (Rand 1955).

Twenty-three out of 29 mothers observed lifted their newborn pups by the skin of the head and neck, or sometimes the body, with their mouths. They pulled the pup closer, swung it from side to side, or simply held it up and then dropped it. Two of the dead pups were lifted by their mothers, but the third was ignored. Mothers generally attempted to keep their pups close to them during the first hour, but one female left her pup after 45 min, went swimming and returned several minutes later. Wandering pups were pulled back, and pup movements often precluded, intentionally or fortuitously, by the mothers lying on them. One female lay on her pup and made frequent neck movements to keep the pup pinned down.

Females were more placid after parturition than they had been immediately beforehand. They still threatened other seals if they came too close, but generally laid or sat quietly. The three study mothers spent 20, 26 and 45 min respectively, of the first hour lying or sitting still. The pups, on the other hand, were very active during this early period. It may be seen from Table 2 that the three study pups spent an average of only 2% of the first hour with their eyes closed and their bodies still. An average of about 81% of the time was spent looking around, sniffing or nuzzling their mothers, and sniffing the rocks. The remaining 17% of the time was spent coughing, calling, shaking and making such movements as their muscular co-ordination and the attentions of their mothers allowed.
TABLE 2. SUMMARY OF THE BEHAVIOUR OF THREE STUDY PUPS OF A. FORSTERI DURING THE FIRST HOUR AFTER BIRTH.

<table>
<thead>
<tr>
<th>Activity</th>
<th>Pup 1</th>
<th>Pup 2</th>
<th>Pup 3</th>
<th>Average</th>
</tr>
</thead>
<tbody>
<tr>
<td>Eyes closed and body still</td>
<td>2</td>
<td>3</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>Sniffing or nuzzling mother</td>
<td>43</td>
<td>15</td>
<td>10</td>
<td>23</td>
</tr>
<tr>
<td>Looking around</td>
<td>33</td>
<td>42</td>
<td>51</td>
<td>42</td>
</tr>
<tr>
<td>Sniffing rocks</td>
<td>12</td>
<td>5</td>
<td>32</td>
<td>16</td>
</tr>
<tr>
<td>Other activities</td>
<td>10</td>
<td>35</td>
<td>6</td>
<td>17</td>
</tr>
</tbody>
</table>

All pups close enough to be heard coughed during the first hour, and also shook their heads and shoulders. These actions probably rid the throat, nose, ears and fur of amniotic fluid. Older pups shook themselves only when wet, and coughing was otherwise heard only when hungry pups apparently choked on the milk while suckling. Most pups also called within the first 30 min, sometimes within seconds, of birth. Calls were very frequent during the first few hours. The three study pups called 121, 214 and 242 times respectively, during the first hour alone. The calls appeared to be spontaneous, rather than in response to mothers' calls. These calls were termed "mother-attraction calls" by Stirling (1970). They became stronger and deeper as pups grew older.

Mothers gave two kinds of call after parturition: a quiet lowing call, heard only after delivery, and a more frequently used "pup-attraction call" (Stirling 1970). Females generally called far less frequently during the first hour than did their pups; the three study mothers called only 1, 10 and 52 times, respectively.

Although pups spent much of the first hour sniffing and nuzzling their mothers, only one fed during this time. This is characteristic of fur seal and sea lion pups, except for A. pusillus (Rand 1955). Many mothers were uncooperative in exposing their nipples to their pups at first, particularly if they were unsettled because of heat or overcrowding.

MOTHER-PUP INTERACTIONS

LOCATION AND IDENTIFICATION

Most seals ultimately identify their pups by smell, and A. forsteri is no exception. As a result of frequent sniffing of pups during delivery and immediately after birth, it is probable that most mothers can identify their pups with certainty within a few hours.

Mothers who left their pups when they were less than 3 days old always returned to the same spot to renew contact. Pups as young as this seldom moved far, unless chased by other females, and were easily located. Three mothers were seen to return to where they had left their pups, only to find that other mother-pup pairs were in residence. Two of the displaced pups were known to be 2.5 and 3 days old, respectively. The
returning mothers threatened the usurping females and generally behaved as though the new pups were theirs. After mutual threatening, the returned mothers gave up and finally renewed contact with their displaced young. The third mother persisted in her efforts to reach the new pup for 13 min, for 12 of which she was answering the calls of her own pup which was being bitten by another female in the vicinity. Eventually, after being threatened by other females she had disturbed, the displaced mother went for a swim, but she was seen with her own pup 7 min later.

Mothers returning from the sea to pups older than 3 days returned to the general area where they had left them, but did not always look or call for them. Any searching behaviour was often preceded by, and interspersed with, sleeping and grooming. Some mothers appeared to recognize their own pup's call, but the final identification was always made by smell. Only one mother mistook another pup for her own after sniffing it. She went for a swim when her pup was only 45 min old, and on her return picked up a 4-6 h old pup and placed it beside her own. She sniffed both intermittently for 6 min, and then bit the older, foreign pup until it moved away. Similar methods of location and identification have been recorded for other Arctocephalus species (Rand 1955, 1967, Paulian 1964, Stirling 1971b, Vaz Ferreira 1956).

Pups as old as 21 days were unable to recognize their returning mothers. They were wary of wet females moving through the colony and often ran away from their own mothers at first.

FEEDING

During a feeding session, three main types of activity were distinct; nuzzling, suckling and resting. Nuzzling often included a slight biting, as a pup tried to locate a nipple and then stimulate it to become erect so that it could be grasped in the mouth.

Feeding took place in virtually any combination of positions of mother and pup, provided the mother was comfortable and the pup could reach a nipple. Most often mothers lay on their sides with the pups at an angle to them. Newborn pups nuzzled randomly all over the mother's body and often sucked the fur. For five pups observed very carefully at close range, the times of the first feeds were 47 min, 1 h 22 min, 5 h 4 min, 5 h 37 min and 7 h 15 min. One pup had not fed within 5.5 h of birth, although there had been ten nuzzling bouts with an average time of 12.7 min each.

As pups grew older, there was a distinct decrease in nuzzling and resting time, and an increase in suckling time. Suckling became more vigorous; for the first few minutes of each session their heads bobbed up and down and sucking noises were often heard. All pups had to nuzzle for a time to cause the nipple to become erect, but no pup older than 3 days was seen to nuzzle for more than 1 min. Young pups tended to use only one nipple per feeding session, but older pups frequently moved from one nipple to another. There was no apparent diurnal rhythm in feeding activity.
LIFTING PUPS

Mothers commonly lifted their pups with their mouths during the first hour after birth; when pups had moved away; when waves swept round them during storms; or when the mother wanted to swim and had to take her pup with her. One mother was seen to pull her pup out of the shade of a ledge and place her hind-flippers there. The pup immediately climbed back, on top of the mother's flippers. Mothers carrying their young down to the water have also been observed in Australian *A. forsteri*, while pup retrieval over the first day or so is common in *A. australis* (Vaz Ferreira 1956, Stirling 1971b) and *Callorhinus ursinus* (Peterson 1968).

DISCIPLINE AND PLAY

Mothers occasionally disciplined their pups with open-mouth threats (Stirling 1970), growling and even biting. These actions were usually in response to over-rough suckling or biting by pups.

All mother-pup play was initiated by the pup and usually followed feeding. Whisker-mouthing which involved a pup passing the mother's vibrissae through its mouth and over its head and nose, was indulged in by pups only one day old. Slightly older pups often gently bit their mother's nose, mouth and upper neck. The mother usually responded by biting back, so that they were gently mouthing one another. This play was usually terminated by the mother pushing the pup away with her nose and moving her head away. Pups also mouthed their mothers' flippers if these were held up, but the female merely moved the flippers away.

FEMALE BEHAVIOUR

FEMALES AND THE SEA

Females returned to the sea for one or more of five possible reasons: to feed; to cool off; to ride out high seas; to escape annoyance caused by other seals; and to wash and groom.

All the mothers observed went down to the sea when first subjected to a very hot day after giving birth. For 13 mothers timed, the interval from birth to first immersion in the sea ranged from 45 min to 3 days. Another mother, who sheltered in a cave with her pup, first went down to the sea when her pup was 8.5 days old. Australian *A. forsteri* females began going to sea to cool off when their pups were a week old (Stirling 1971b).

Apart from cooling off, the only other reason why females left pups under 3 days old to go to sea was to escape from strong surf. During storms, most mothers and pups moved up the beach out of the splash zone, but in some places cliffs prevented this. Females without pups faced the incoming waves and braced themselves against the wash. Females holding pups faced away from the sea, but waves of 1 to 1.5 m could not be withstood in this position and the mothers had to let the pup go and face the sea or swim off.
Mothers near (< 10 m) the water would sometimes go for a swim immediately after being harassed in some way, either by an over-curious bull or other females. This happened most often on hot days.

When females went to sea they commonly washed themselves by rubbing their bodies with their foreflippers. As they swam away from shore they left a yellow-brown trail in the water as the dirt from the rookery washed off. Sometimes females entered the water apparently only to wash and groom. This was characteristic only of mothers with pups older than 8 days.

THE FEEDING-NURSING CYCLE

The presence or absence of mothers on the days after they had given birth was recorded to try and elucidate the nursing-feeding cycle. Seven mothers for which data are available spent an average time of 8.5 days (range 6-12 days) after birth in the colony. After this period they were absent for varying lengths of time, but not usually for more than 2 days if their pups were less than 21 days old. Miller (1971) found that females first left to feed about 10 days after giving birth, stayed away 3-5 days and then suckled for 2-4 days. In this study, it was found that the females stayed away for only a day or two at first. Sometimes they did not rejoin their pups immediately on their return, but rested in the shallows or near the water's edge.

PUP BEHAVIOUR

PUPS AND WATER

Young pups avoided water, particularly moving water. Sometimes they were unable to escape waves, but even when less than 3 days old they could withstand pounding by waves of up to 1 m high. They held onto the rocks with their flippers until the surge had ended, and then scrambled higher up the rocks. Despite these efforts, however, some pups were swept out to sea and drowned, while others were washed up alive elsewhere on the rookery. One of the latter was washed up 30 m away from its original position and was eventually re-united with its mother, but most who suffered this fate had little chance of being found again. An aversion to water has been noted for pups of *A. pusillus* (Rand 1967), *A. tropicalis* (Paulian 1964) and *Callorhinus ursinus* (Bartholomew 1959).

Pups around the edge of the inlet soon lost their fear of calm water and were the first to start swimming. The youngest pup seen in calm shallows was 7 days old, and it was swimming at 10 days. Another swam at 18 days old, but most were older than this before they first swam. The first swimming strokes were made when a pup found itself out of its depth, and consisted of simultaneous strokes of the fore-flippers, downwards and backwards. The head was held high up out of the water and the hind-flippers were trailed. The hind-flippers were used to change direction. If pups were frightened while swimming, for example by a larger wave or by an adult splashing by, they swam frantically for the shore using fore-flippers only. Pups did put their heads below water but did not keep them there for long. Stirling (1971b) noted that Australian
A. forsteri could swim at birth, but normally this would not happen. Swimming styles appear to be similar for all fur seal pups which have been observed (Vaz Ferreira 1956, Paulian 1964, Rand 1967).

PUPS AND FOREIGN ADULTS

Pups rarely came into contact with females other than their mothers during the first few hours after birth. Thereafter, however, pups were constantly harassed by other females and were often bitten before they could retreat. For protection, pups quickly adopted submissive postures (Stirling 1970), which were evident at 4, 6, 7 and 10 days in four pups observed closely. Young pups made the mistake of gaping submissively at a female and then turning away to retreat, thereby risking being bitten on the rump. Older pups kept their mouths directed towards the female until either they or she moved away. Pups under 28 days old rarely managed to fend off other mothers, but older pups frequently did so.

Bulls treated pups with complete indifference, and the onus was on the pups to keep out of the way to avoid being trampled or sat upon. Most pups quickly learned to avoid bulls, and even pups of only 10 days old would, if cornered, wail, snort aggressively and even bite bulls, until they could struggle free. No deaths due to squashing were observed, although this has been reported for Halichoerus grypus (Coulson and Hickling 1964).

GROOMING

Aimless and uncoordinated scratching with the hind-flippers was carried out even by newborn pups, but directed scratching was not seen until pups were several hours old (2 h 16 min was the earliest). Only the shoulders and stomach could be scratched at all effectively, and only while lying down, by pups up to 2 days old. At 6 days many could scratch the head and back of the neck, but more delicate scratching of the side of the head and nose could not be achieved until pups were 16 to 21 days old. Grooming was most common after feeding and when pups were wet.

PUP-PUP INTERACTIONS

Pups grouped together in pods when the mothers began to stay away at sea for several days. The size and position of pods were affected by external factors such as weather and terrain. On very hot days large pods formed in caves, under ledges, around rock pools and on wet rocks near inlets. In stormy weather, densely packed pods formed on the highest points. The large pods mainly comprised pups of 21 or more days old.

The most common interaction among pups was play-fighting. This consisted of biting each others necks, shoulders and mouths and pushing against one another. A pup of 8 days old was seen to play-fight, and pups of different ages sparred together for example, 14 and 24 days old. Sometimes the older, and stronger, pup bullied the younger, which wailed and scrambled away. Older pups often chased younger ones from preferred shady ledges. Play-fighting is also common in Australian A.
forsteri (Stirling 1971b), A. pusillus (Rand 1967) and A. tropicalis (Paulian 1964).

In addition to playing with their mothers and with other pups, many pups played with their own flippers and inanimate objects such as sticks. Similar play is common in A. pusillus (Rand).

ACKNOWLEDGMENTS

We wish to thank Graham Wilson and Terry Schaeffer for assistance with the study, and Hugh McLellan for transport to and from the island. Transport and food costs were paid from M.C. Crawley’s University Grants Committee seal research grant.

LITERATURE CITED


