THE PREDATORY BEHAVIOUR AND IMPACT OF RED FOXES (VULPES VULPES) ON THE SEABIRD COLONIES OF BACCALIEU ISLAND, NEWFOUNDLAND

BOHDAN OLAF SKLEPKOVYCH

THE PREDATORY BEHAVIOUR AND IMPACT OF RED FOXES (*Vulpes vulpes*) ON THE SEABIRD COLONIES OF BACCALIEU ISLAND, NEWFOUNDLAND

BY

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Dedication

To the memory of
David Whritenour and *Ruth Price*,
whose friendship and love
will always be remembered

ABSTRACT

The predatory behaviour of red foxes (*Vulpes vulpes*) in relation to a large multi-species seabird community was studied on Baccalieu Island, Newfoundland, from 1983-1986. Fox diet was assessed by examining faecal composition, avian prey remains and larder hoarded prey. Leach's Storm-Petrels (*Oceanodroma leucorhoa*) made up 75% of scat by wet weight, 89% of remains, and 95% of prey items in and scattered about larders. Black-Legged Kittiwakes (*Rissa tridactyla*), Atlantic Puffins (*Fratercula arctica*), Common Murres (*Uria aalge*), Northern Gannets (*Sula bassanus*) and Herring Gulls (*Larus argentatus*) formed 19% of scat by wet weight and 11% of remains. Comparisons are drawn between seasons and different methods of analysis.

The Leach's Storm-Petrel population was estimated at 3,360,000 ± 317,000 adult breeding pairs. Based on harvest levels and the estimated energy requirements of the resident fox population, 31,000 ± 3,000 adult storm-petrels would be taken annually. Factors which tend to keep predatory impact at low levels are (1) the massive size of the storm-petrel colony and (2) the scarcity or lack of winter food for the foxes. The high availability of Leach's Storm-Petrels also appears to hold impact on each of the other seabird species nesting on Baccalieu Island at < 1% of their adult breeding populations. The presence of foxes on Baccalieu Island may also deter ground-nesting avian predators (i.e. Herring Gulls and Great Black-Backed Gulls (*Larus marinus*)) from nesting and from preying extensively on the resident burrow-nesting seabirds on the island.

Experiments on the scatter hoarding behaviour of red foxes were conducted in a semi-natural enclosure at Salmonier Nature Park. At low levels of food deprivation, increased levels of prey abundance were found to decrease the time spent in search of a cache site by foxes. Increased levels of food deprivation and prey abundance were also suggested to increase the motivation to hoard as evidenced in the decrease in mean time of prey pickup to cache initiation interval. The time spent caching and subsequent return to the prey patch were not significantly altered by the manipulations and possible reasons for the lack of experimental effect are discussed. Ninety-seven percent of all prey items set out were cached, of which, 75% were later recovered. On average, 54% of the available caches were recovered within 192 h of being set out, at a mean rate of 9.3% recovery/day. These present findings are considered in light of optimal foraging theory.

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throughout this project were worth a co-authorship. In return, I leave these important words of advice: "there are no tree monsters; at least on Baccalieu Island!"

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Foremost, I express loving thanks to my parents, who provided support, encouragement and a substantial proportion of funds necessary for the completion of this project. They deserve a page all to themselves.

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Chapter 1

INTRODUCTION

The introduction (Kadlec, 1971; Bailey, 1982) or chance occurrence (Norman, 1971; Maccarone and Montevecchi, 1981; Petersen, 1982; Quinlan and Lenhausen, 1982) of mammalian predators to predator-free seabird islands is often considered a major threat to seabird populations (Nisbet, 1979). Many studies have shown that fox predation can adversely effect small seabird colonies (Kadlec, 1971; Patton and Southern, 1977), but little is known of their impact on larger, well-established island populations. The present thesis attempts to assess the role of the red fox (*Vulpes vulpes*) as a predator of a large seabird community.

1.1. BACKGROUND

By nesting in areas inaccessible to terrestrial predators (e.g. coastal or oceanic islands) many seabird species are free from mammalian predation (Braestrup, 1941; Fay and Cade, 1959; Lack, 1968; Buckley and Buckley, 1980; Perrins and Birkhead, 1983). When predators gain access to seabird islands, they often have dramatic effects on seabird mortality, especially among the more vulnerable ground- and burrow-nesting species (e.g., gulls, terns, petrels, auklets, Bent, 1922; Fisher and Lockley, 1954; Jones and Byrd, 1979). The lack of effective anti-predator behaviour among many seabirds (Buckley and Buckley, 1980) and their apparent vulnerability to introduced predators have led some avian ecologists and conservationists to contend that seabirds cannot successfully coexist on islands with mammalian predators (Errington, 1948; Ashmole, 1971; Bailey, 1982; Lensink, 1984).

Why are colonial nidicolous seabirds particularly vulnerable to mammalian predation? The life-history pattern of many of these long-lived species involves low adult mortality, delayed breeding, production of a single small clutch per year and low annual productivity (Ashmole, 1963; Lack, 1968; Dunn, 1979; Moors and Atkinson, 1984). Although increased longevity may assure higher reproductive success (Murphy, 1968; Hairston, Tinkle and Wilbur, 1970; Maiorana, 1976), mammalian predators are not restricted to preying on eggs and young of seabirds, as avian predators often are (Fisher and Lockley, 1954; Hatch, 1970; Evans and Nettleship, 1985) and adult mortality greatly increases predatory impact (Moors and Atkinson, 1984). Furthermore, seabirds synchronize breeding effort and concentrate in number, space and time, attracting predators (Moors and Atkinson, 1984; Wittenberger and Hunt, 1985). Although synchrony is thought to occur in response to an optimal food supply (Immelmann, 1971), it may provide partial protection (Curio, 1976; Perrins and Birkhead, 1983; Wittenberger, 1984) by swamping predators (Wittenberger and Hunt, 1985). Because a limit exists on the number of individuals a predator can kill, a lower proportion of total prey are taken during peak breeding periods (Patterson, 1965; Nisbet, 1975; Taylor, 1984).

Synchrony however, is not always effective, as certain mammalian predators (i.e. foxes, rats) kill beyond their immediate needs (i.e surplus killing, caching; Novikov, 1962; Kruuk, 1964, 1972; Tinbergen, 1965).

During the late 1800's and early 1900's, foxes were released on 201 Alaskan islands for purposes of commercial fur-farming (Murie, 1959; Jones and Byrd, 1979; Bailey, 1982). These introductions are believed to have caused some population declines (Lensink, 1984) and extirpations (Bailey, 1982) of seabird colonies. However, because historical information regarding seabird colonies, numbers and the consequence of predator introductions is rarely well documented, these suggestions are often anecdotal (Jones and Byrd, 1979; Manuwal and Campbell, 1979; Moors and Atkinson, 1984). Furthermore, resultant reductions in seabird numbers would more accurately reflect the effects associated with unnatural abundances of foxes, considering the basic intentions of commercial farming (Murie, 1959) and that foxes were often provided with supplementary food supplies (Novikov, 1962). Moreover, past changes in seabird populations may also have resulted from multiple causes such as: overexploitation of fisheries (Murie, 1959; Straty and Haight, 1979), human exploitation of seabirds (Fisher and Lockley, 1954; Cline, Wentworth and Barry, 1979;), the occurrence of additional predators (i.e. rats, otters, bears, Barabash-Nikiforov, 1938; Fay and Cade, 1959) and natural fluctuations in seabird numbers resulting from changes in food supply, climatic conditions, general movements or epizootic disease, (Fisher and Lockley, 1954; Tuck, 1960; Ashmole, 1971; Bailey and Davenport, 1972; Sekora, Byrd and Gibson, 1979; Drury, 1979).

Studies on the impact of foxes (e.g. *Vulpes vulpes* and *Alopex lagopus*) on island-nesting seabirds have principally focused on small seabird populations (Kadlec, 1971; Patton and Southern, 1977) and/or on the temporary effects immediately following an introduction (Petersen, 1982; Quinlan and Lenhauser, 1982). Under these conditions predatory losses are without exception high and with regards to smaller colonies lead to large reductions in colony size, decreased reproductive success or desertion (Patton and Southern, 1977). Larger colonies also experience high predatory losses. For example, after two red foxes reached Shiak Island by crossing over pack ice, many adult Tufted Puffins (*Lunda cirrhata*) and Glaucous-winged Gulls (*Larus glaucescens*) were killed and breeding success was drastically reduced in five of the seven species nesting on the island (Petersen, 1982). The following year however, the foxes were no longer present and the number of breeding birds "appeared similar" to that in prior years. Although such accounts confirm prey vulnerability and define the temporary effects accompanying a chance occurrence, they do not clearly quantify the predators' role in population declines. Predator presence may govern the location and success of nest sites and thus, influence colony shape and size (Bertram and Lack, 1938; Larson, 1960), however, a species or population can only be considered endangered when predatory losses, no matter what their size, consistently cause adult mortality to exceed annual recruitment (Moors and Atkinson, 1984).

Few studies have successfully demonstrated a relationship between predation and the decline of a large seabird population (Moors and Atkinson, 1984). Norman (1971) examined the effects of fox predation on Short-tailed Shearwaters (*Puffinus tenuirostris*) nesting on two large coastal islands in Australia. On Philip Island, where rabbits were available as alternative prey to foxes, the effect of predation on shearwaters was found to be of minimal importance. On Benison Island however, where alternative prey was unavailable, predation was directed at pre-breeding adults, indicating a possible decline in recruitment to the breeding population. Aside from suggesting the possibility of long-term influences on a large seabird population, this study reveals the role of alternative prey in altering predatory effects. In this case, the presence of rabbits acted to decrease predatory pressure on the seabirds (see also Bergerud, 1967, 1983). In some situations however, the presence of alternate prey may act to increase the size of the predator population and direct greater pressure on the principal prey species (Odum, 1975).

Although a large seabird community provides predators with an abundant food supply, predators on islands are often confronted with an equally dramatic period of prey scarcity during non-nesting months (Freuchen, 1935; Ricklefs, 1969; Stephenson, 1970). Osgood, Preble and Parker (1915) contended that additional food supplies were needed to maintain the resident fox population on the Pribilofs during winter (see also Kadlec, 1971). It appears then, that the lack of alternative prey on seabird islands often precludes predatory mammals from establishing resident populations (Patton and Southern, 1977). Of the 201 Alaskan islands on which foxes were released for fur-farming, foxes remain on only 82 of them (Bailey, 1982). Many reports further confirm, that the occurrence of foxes on islands is often temporary (Bergman, 1966; Bailey and Faust, 1981; Petersen, 1982; Quinlan, 1982), and even if foxes survive, decreased reproductive success has been reported (Berns, 1969).

By hoarding food, an animal may help ensure adequate nutrition during periods of prey scarcity or uncertainty (Morse, 1980). Food hoarding is highly developed and clearly adaptive for species relying on prey that show large temporal fluctuations in abundance (Ewer, 1968; Sherry, 1985). Red and arctic foxes both hoard food, but the method of caching differs. The red fox scatter hoards (Morris, 1962); that is, it conceals each individual load of prey separately and scatters these caches over a large area (Murie, 1936; Scott, 1943; Kruuk, 1964; Tinbergen, 1965; Henry, 1976; Macdonald, 1976, 1977). On the other hand, the arctic fox most commonly larder hoards; that is, prey are stored together in one or a few large holes often located near or within the den site (Hewitt, 1921; Gibson, 1922; Braestrup, 1941; Pedersen, 1962). These differences, often regarded as species typical, appear to be a result of environmental circumstance, because arctic foxes also scatter hoard (Osgood et al., 1915; Hersteinsson and Macdonald, 1982), and red foxes have been found to hoard in larders (Maccarone and Montevecchi, 1981).

The arctic fox is endemic to northern climes where abrupt changes in prey availability are common. Curiously, most reported larders contain large numbers of seabirds (Gibson, 1922; Freuchen, 1935; Braestrup, 1941; Pedersen, 1962) and occasionally microtine rodents are also stored (Feilden, 1877; Stephenson, 1970). The red fox is commonly studied in temperate climates where only scatter hoarding has been reported. Therefore, although a number of factors may influence the type of hoarding method used (Ewer, 1968), larder hoarding among foxes typically occurs when prey are temporarily available in large numbers (i.e. seabird colonies, good lemming years).

Knowledge of predator-seabird interactions is far from complete and often, local circumstances dictate the influence and impact of an introduced predator on a seabird population. The numbers and behaviour of both predator and prey and the availability of alternative foods for the predator are important factors in this interaction (Holling, 1959). Some of these factors were investigated in the present thesis.

1.2. STUDY AREA

Baccalieu Island (~6.3 x 1 km, 48°07'N, 54°12'W) is situated off the northernmost tip of the Avalon Peninsula of Newfoundland and is separated from the mainland (~3.2 km) by the Baccalieu Tickle (Figures 1-1 and 1-2). The island's flora is locally diverse, with coastal heath, coniferous forest and grassy slopes and meadows composing the predominant habitat types. The surrounding climate is typical of coastal Newfoundland with cool, foggy summers and relatively mild winters, frequently interspersed with strong winds and harsh conditions (Banfield, 1983).

Figure 1-1: Map of Baccalieu Island showing place names. Inset shows the islands' location in relation to Newfoundland.

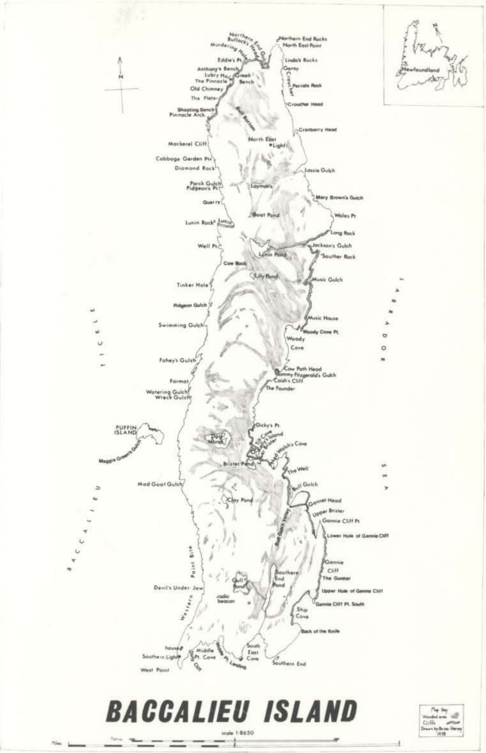

N
Newfoundland
N
Northern End Gulch
Bullock's Head
Murdering Hole
Eddie's Pt.
Anthony's Bench
Lubry Hole
Green Bench
The Pinnacle
Old Chimney
The Flats
Shooting Bench
Pinnacle Arch
Northern End Rocks
North East Point
Linda's Rocks
Ganty
Croucher
Parrats Rock
Croucher Head
Bull Bottom
Cranberry Head
North East Light
Mackerel Cliff
Cabbage Garden Pt.
Diamond Rock
Lassie Gulch
Porck Gulch
Pidgeon's Pt.
Layman's
Mary Brown's Gulch
Quarry
Boat Pond
Wales Pt.
Lunin Rock
Lunin
Long Rock
Well Pt.
Jackson's Gulch
Lunin Pond
Souther Rock
Cow Rock
Lilly Pond
Tinker Hole
Music Gulch
Pidgeon Gulch
Music House
Swimming Gulch
Woody Cove Pt.
Woody Cove
Fahey's Gulch
Cow Path Head
Tommy Fitzgerald's Gulch
Coish's Cliff
The Founder
Farmat
Watering Gulch
Wreck Gulch
BACCALIEU TICKLE
LABRADOR SEA
PUFFIN ISLAND
Maggie Green's Gulch
Dicky's Pt.
Dog Marsh
Old Tilt Cove
Kelly's Island
Lower Brister
Ned Walsh's Cove
Brister Pond
The Well
Mad Goat Gulch
Bull Gulch
Clay Pond
Gannet Head
Upper Brister
Gannie Cliff Pt.
Bull Gulch Valley
Lower Hole of Gannie Cliff
Western Point Bite
Gannie Cliff
Southern End Pond
The Gunner
Gull Pond
Devil's Under Jaw
Upper Hole of Gannie Cliff
radio beacon
Gannie Cliff Pt. South
Ship Cove
Back of the Knife
house
Southern Light
West Point
Dirty Cliff
Middle Pt. Cove
Middle Pt. Landing
South East Cove
Southern End
BACCALIEU ISLAND
scale 1:8650
Miles
Metres
Map Key
Wooded area
Cliffs
Drawn by Brian Harvey 1978

Figure 1-2: Southern view of Baccalieu Island and nearby Puffin Island.

Seabirds breed on Baccalieu Island from about April to October. The major colonies are located on the eastern side of the island where cliff-nesting species such as Black-legged Kittiwakes (*Rissa tridactyla*: ~13,000 pairs), Common Murres (*Uria aalge*: ~4,000 pairs), Northern Gannets (*Sula bassanus*: ~600 pairs), and Thick-billed Murres (*Uria lomvia*: ~180 pairs) nest on precipitous cliffs (population estimates based on Montevecchi and Tuck, 1986). Atlantic Puffins (*Fratercula arctica*: 30,000 prs) nest in areas of grass and talus slope, principally from Dickey's Point to Woody Cove and along the northern end of the island (Montevecchi and Tuck, 1986). The Leach's Storm-Petrel (*Oceanodroma leucorhoa*) colony is massive in size, but has largely gone unrecognized as an important colony (Brown, et al., 1975; Nettleship, 1980) and has never been censused. Storm-Petrels nest over the entire island (with the exception of areas lacking necessary drainage) and are found in densest concentration in the grassy slopes and meadows from Gannie Cliff to The Founder and in the steeper slopes from Croucher to Green Bench. Razorbills (*Alca torda*), Black Guillemots (*Cepphus grylle*), Northern Fulmars (*Fulmaris glacialis*), Common Ravens (*Corvus corax)* and numerous passerine species (see Wells and Montevecchi, 1984) also nest on the island. With the exception of Common Ravens, the most common avian predators are Herring Gulls (*Larus argentatus*) and Great Black-Backed Gulls (*Larus marinus*) whose nesting is largely restricted to nearby Puffin Island (Figure 1-2).

During late winter and spring, southwardly flowing pack ice drifts along the eastern coast of Newfoundland and in some years may settle between the

Figure 1-3: Southern view of Baccalieu Island and the extent of ice occurrence; April 1984.

mainland and Baccalieu Island (Figure 1-3). Foxes are known to scavenge on off-shore sea ice (Freuchen, 1935; Andriashek, Killiaan and Taylor, 1985) and are believed to have reached Baccalieu Island by crossing over an ice bridge (Maccarone and Montevecchi, 1981) probably formed of close to compact or consolidated pack ice (Markham, 1980). Ice floes that would permit crossing (>6/10 coverage concentration) have occurred in the vicinity a total of 10 - 13 years from 1959 - 1984 (Davidson, 1985). Although foxes were first noticed by the lighthouse-keepers ca. 1959 (P. Rice, pers. comm.), they most probably inhabited the island prior to ~~this~~ date; a local resident requested permission to trap foxes on Baccalieu Island in 1914 (Newfoundland Fish and Game Commission Records).

The only other mammals to have been recorded on Baccalieu Island in recent years are otters (*Lutra canadensis*, A. Macfarlane; C.W.S. unpubl. data), but their presence is infrequent and temporary. House mice (*Mus musculus*) were found in a shed near the southern lighthouse in 1960, but were exterminated that same year after the dwelling had been destroyed (R. Hyde and L. Walsh, pers. comm.). Hence, the lack of mammalian prey limits the diet of resident foxes to seabirds, some landbirds, berries and occasional refuse discarded by the lighthouse-keepers. As well, there are no beaches *per se* on Baccalieu Island, as steep cliffs form most of the island's shoreline, severely limiting the foxes' opportunity to scavenge on marine foods.

1.3. STUDY PROBLEMS

The predatory behaviour of a well-established red fox population was examined in relation to a large, multi-species, seabird island from 1983 - 1986. An effort was made to gain an understanding of fox-seabird interactions in order to provide a sound foundation on which to base management decisions with regard to seabird conservation.

In Chapter 2, the diet and predatory behaviour of the resident foxes is reviewed on the basis of prey remains, carcasses found at larder sites and scat analyses. Preliminary investigation revealed that the smallest, most abundant and highly vulnerable of the island's seabirds, the Leach's Storm-Petrel, experienced the highest levels of depredation and therefore, special consideration was directed to assessing the foxes' relationship to this species. The habitat distribution, burrow occupancy and size of the Leach's Storm-Petrel colony on Baccalieu Island was also examined (Chapter 3). Using this information, seabird harvest levels and the foxes' food requirements, an attempt was made to assess the foxes' impact of foxes on each of the island's breeding seabird species. To gain an insight into the the proximate factors influencing caching behaviour, experiments were conducted on captive foxes in a semi-natural environment at Salmonier Nature Park. An optimal foraging approach was used to examine the effects of hunger state and prey abundance on the components of caching behaviour (Chapter 4).

Chapter 2

PREDATORY BEHAVIOUR OF RED FOXES ON BACCALIEU ISLAND

2.1. INTRODUCTION

This chapter examines the predatory behaviour and diet of red foxes on Baccalieu Island. The objective was to assess the foxes' relationship to the island's major seabird species. The foxes' harvest of Leach's Storm-Petrel was the subject of primary focus, because this smallest and most abundant seabird species was found to experience the greatest depredations and, as shown in chapter 3, the resident breeding population is an important one, being the largest known Leach's Storm-Petrel colony in the North Atlantic, and possibly in the world.

2.2. METHODS

The general field routine consisted of keeping in constant contact with the resident foxes. During the course of this study, the entire island was traversed by foot at least once every two weeks. At other times, daily efforts were directed in areas of major fox/seabird activity along the southeastern coast of the island.

To confirm the absence of mammalian prey species (e.g. *Microtus pennsylvanicus, Mus musculus*) on Baccalieu Island, one live-trap and 2 household mouse traps were set at 12 different stations and 3 different habitats. Traps were checked at ~3 day intervals over a 2 month period.

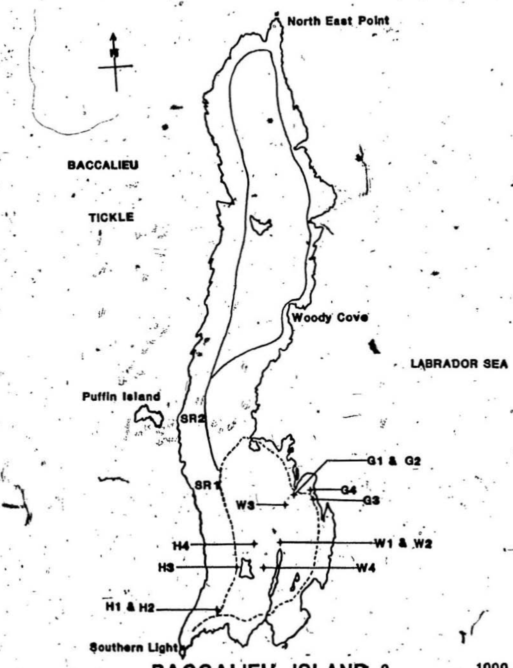
2.2.1. Examination of Nest Predation

The high burrow density region (from about Upper Brister to Old Tilt Cove) was checked daily for signs of storm-petrel burrows at which predation had occurred. Sites with substantial excavation (>4 adjacent burrows) were examined and measured in an effort to understand the possible cues associated with predatory attacks. Percent ground covered by each of the general vegetation types (e.g. grass, fern), burrow density, ground slope and percent canopy (tree) cover were recorded. Equivalent sized, adjacent plots were marked in random compass directions and similar microhabitat features were recorded. Data collection took place from May 31 - August 22, 1983. Because of the violations of normality and homogeneity of variance assumptions, data were tested with the Mann-Whitney U.

2.2.2. Collection of Prey Remains

On 42 occasions, a standard route along the southeastern portion of the island and a standard route leading to its northeastern tip were systematically searched for prey remains (Figure 2-1). The species of avian prey taken and the type of damage inflicted on each was recorded. No other (significant) mammalian predators inhabit the island and all damaged remains that could not be attributed to avian predation were assumed to be the result of fox

Figure 2-1: Map of Baccalieu Island showing standard routes (SR1, SR2) and location of storm-petrel occupancy plots (G - Grass; W - Woods; H - Heath).


N
North East Point
BACCALIEU
TICKLE
Woody Cove
LABRADOR SEA
Puffin Island
SR2
SR1
G1 & G2
G4
G3
W3
H4
W1 & W2
H3
W4
H1 & H2
Southern Light
BACCALIEU ISLAND
0
1000
metres

predation. Evidence of egg predation was also noted, though eggshell remains may have been discarded by avian predators, such as Common Ravens (*Corvus corax*, e.g. Montevecchi, 1979).

2.2.3. Scat Analyses

Fox scats were collected along two standard routes (Figure 2-1) from May-August 1983, in October 1984 and February 1985. Summer droppings were examined in the field and frequency of occurrence by prey type recorded. This method provided an estimate of prey taken during the seabird nesting period. After analyses of the first seasons data it became apparent that a more accurate method of faecal examination was desirable. Therefore, fall and winter droppings were collected in the field and taken to the laboratory where they were analyzed using the weight of undigested matter method (Lockie, 1959). Faecal samples were sterilized by autoclave at temperatures exceeding 130° C (Kennedy and Carbyn, 1981). Scats were individually weighed and measured and then thoroughly washed in warm water, broken up and floated in a plastic sieve (with 2 mm perforations) to remove extraneous detrital matter. After drying at 70° C, droppings were individually separated into prey components, which were weighed using a Mettler (model AE100) balance. This technique is more precise than the frequency of occurrence measure and also permits the estimation of the original wet weight of prey represented in scat (Lockie, 1959; see also Floyd, Mech and Jordan, 1978).

Avian remains in scat were identifiable to species when body parts such as beaks or legs were recovered. Feathers and bones provided additional means by which to differentiate gulls from storm-petrels and puffins. In the laboratory, the fine structure of downy barbules was examined under microscope (at 100 and 250X) to determine avian order (Chandler, 1916; Day, 1966), however, the similar feather morphology among seabirds as a result of their similar phylogeny (Cracraft, 1981, 1985; Strauch, 1985) and the fact that digestion often destroyed the barbs and barbules required for identification (Scott, 1941; Lever, 1958) rendered this method frequently unsuccessful. Therefore, a combination of methods and characteristics were used to identify and separate avian components into 5 conservative categories: positive storm-petrel, probable storm-petrel (~90% accurate), passerine, large seabird (e.g. gull, puffin, murre), and unknown aves. In addition, vegetable matter (e.g. grass, berries), insect, eggshell and marine organisms were examined and weighed.

2.3. RESULTS

2.3.1. The Red Fox Population and Denning Sites

Fox tracks and signs of predation were useful in determining areas of activity and fox numbers. In conjunction with direct sightings and resightings of distinguishable individuals, an impression of the population size was gained (Table 2-1).

In summer 1984, I was able to identify 7 individual foxes on the basis of pelage markings, size and area of encounter. Three family groups appeared to

Table 2-1: Summary of estimated fox numbers and denning sites.

DATE	INDIVIDUALS KNOWN (POSSIBLE)	DENS KNOWN (POSSIBLE)
SUMMER 1978 (a)	- -	2 (-)
SUMMER 1983	5 (3)	2 (1) number cubs unknown
SUMMER 1984	7 (2)	3 (1) 5,0,4 cubs
OCTOBER 1984	6	-
FEBRUARY 1985	7 (4)	2 freshly dug den sites
JUNE 1985	8	1 (1) no cubs sighted

(a) Maccarone and Montevecchi (1981)

live south of Woody Cove (Figure 1-1). Tracking in the snow during February 1985, suggested that 9 individuals were present on the island. The two most northern residents (1 at Lunin Pond, 1 on the northern end) however, were tracked for only 1 day due to inclement weather, making it impossible to conclude whether they were lone foxes, a pair, or distinct family groups.

The scarcity of field signs and the rarity of fox sightings north of Woody Cove (only 3 times during the entire study) suggested that fox activity during the nesting season was generally focused around the areas of greatest seabird activity (along the eastern coast). Although field signs were also found along the western side of the island, this area appeared peripheral to major fox activity except along the wooded ravines which transect the island (east to west) and during the winter months when foxes extend or fully utilize home ranges as a result of food scarcity (Sheldon, 1950).

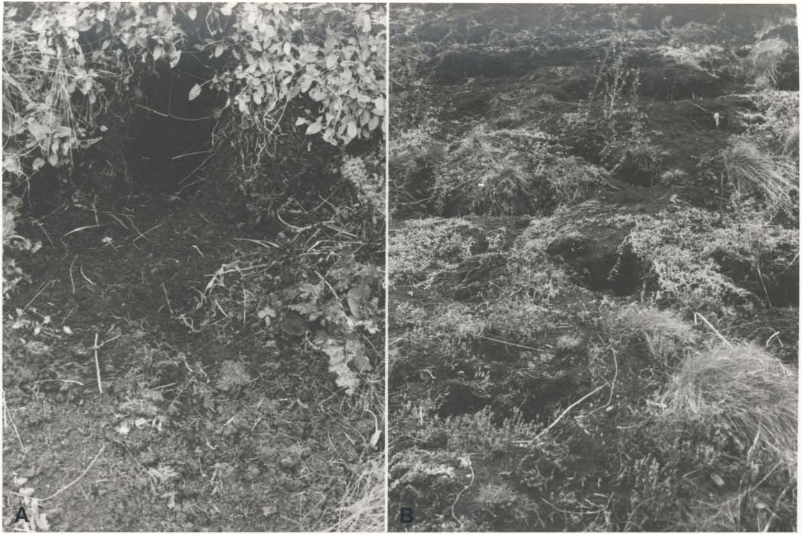
The number of dens and the extent of their use was difficult to assess due to the island's large size and because many boulder strewn areas form natural cavities which are used by foxes as temporary shelters. Of the four possible dens found in 1984, two contained cubs. The fate of these cubs was also difficult to determine, because adults moved young to alternate dens after being disturbed (see also Sheldon, 1949; Douglas, 1965; Sargeant, 1972).

2.3.2. Digging Sites

Foxes preyed on storm-petrels in two ways: by (1) excavating nesting burrows and (2) capturing adults returning to burrows. In the latter, both predator and prey behaviour was difficult to observe accurately since storm-petrels arrive after dark. The digging out of nests, on the other hand, was quite conspicuous (Figure 2-2) and could easily be monitored along the grassy sloped regions where burrow density was high. The foxes although principally nocturnal, were often active during twilight hours making direct observations of nest predation possible.

When excavating burrows, foxes generally dug directly into burrow entrances using their forepaws to widen the opening enough to thrust their heads into the tunnel. If an adult, young or egg was not reached, digging was resumed until prey capture. Typically, from one to a few consecutive burrows were checked and scent appeared to play an important role in determining whether a burrow was dug or not. If a burrow was not dug, the fox urine-marked the entrance (Figure 2-3) and travelled ~5-15 m before checking another. That burrows were scent marked after each investigation or successful predation suggested that foxes used this system to identify burrows previously checked or emptied, in order to decrease the amount of time spent foraging during a future visit (see Henry, 1976). Of 20 burrows checked and ignored by the fox, only 4 had been occupied (1-egg, 1-adult and 2-egg and adult), whereas 20 actively dug burrows, resulted in 13 successful captures (7 were unoccupied) (X_1^2=4.94, $p<.05$).

Figure 2-2: Close-up (A) and distant (B) view of depredated storm-petrel nests dug by red foxes at Ned Walsh's Cove.



A
B

Figure 2-3: A fox scent marking a storm-petrel burrow entrance after an unsuccessful attempt at prey capture.

Though less frequently observed, foxes at times dug down directly into the storm-petrel nest chamber, a method commonly used by foxes digging up rabbit stops (Myers and Parker, 1965; Mulder and Wallage-Drees, 1979). The fox, attracted by the call of an adult storm-petrel, would laterally turn its head many times in an effort to localize the nest chamber. If unsuccessful within a short while, the fox often alternated between digging above the nest and at the nearby burrow entrance.

The foxes were not always successful in excavating prey and on some occasions, burrows were dug for extended periods without success. For example, one individual spent $\geq$30 min excavating a burrow located in a bank, until finally a hole $\sim$.5 m^2 in diameter was dug directly through ($\sim$3m) to the other side of the bank. Although the extent of avian predation was not examined during this study, Common Ravens were observed occasionally digging storm-petrel burrows and were successful in capturing adult birds. A similar observation was made for Northwestern Crows (*Corvus caurinus*; Bent, 1922) and has also been suggested for Bald Eagles (*Haliaeetus leucocephalus*) (DeGange and Nelson, 1982). Digging of storm-petrel nests by ravens appeared to be limited and was always separable from red fox predation.

Digging by foxes was typically focused at one or a few burrows or within a relatively small area, although several larger areas were found at which extensive digging had been done. For example, on the eastern slope of Ned Walsh's Cove in an area of $\sim$1800 m^2 which was estimated (a grid was laid over the dug area and 1 - 3 m^2 sub-plot was randomly sampled within each 10 m vertical strip) to contain 5,508 burrow holes, 55.1 ± 21.3% of the burrows were dug out by the foxes. This excavation was located ~30 m from an active den and may have resulted from a few years of seasonal digging (W.A. Montevecchi, pers. comm.).

The extent of burrow damage also varied. In 37 surveyed plots, 28.1% (182/647) of burrow entrances were heavily dug, 55.3% (358/647) showed minor signs of digging and 16.5% (107/647) were untouched by foxes. A minimum of 53 kills were found at these sites of which 96% were associated with heavily dug burrows. Seventeen percent of the heavily dug burrows contained young or young and adults, indicating that captures did not always occur at extensively dug burrows and that partial excavation does not in all cases lead to burrow abandonment. Extensive digging disturbed surrounding vegetation and in some areas caused soil erosion and burrow deterioration.

Table 2-2 summarizes the features associated with excavated and adjacent unexcavated plots. Digging sites appeared to be non-randomly selected. Burrow density was higher and the percentages of tall vegetation and dead ferns was significantly lower at excavated sites.

Table 2-2: Comparison of features (% = % cover) of areas dug by foxes and adjacent nondug control plots; analysed using the Mann-Whitney U Test.

PLOT FEATURES	EXCAVATED N = 49		CONTROL N = 49		TWO-TAILED P
	MEAN	± S.E.	MEAN	± S.E.	
SIZE (M^2)	5.4	1.0	5.4	1.0	-
NO. BURROWS	24.4	3.1	19.6	3.3	0.03
% GRASS	39.4	4.7	34.5	4.5	N.S.
% SHORT PLANT	26.2	5.1	15.7	3.3	N.S.
% TALL PLANT	21.7	3.6	36.7	4.3	0.01
% DEAD FERN	5.5	2.2	5.9	2.5	0.02
% MOSS	3.8	2.2	3.3	2.1	N.S.
% DIRT	3.7	1.1	3.9	1.1	N.S.
% CANOPY COVER	6.8	3.1	4.3	2.0	N.S.
SLOPE (DEG.)	29.2	2.5	30.4	2.7	N.S.

N.S. = Nonsignificant difference

2.3.3. Prey Remains

Avian remains (Figures 2-4, 2-5) collected during the summer and fall are summarized in Table 2-3. Leach's Storm-Petrel made up 76.7 to 97.6% of all remains (mean = 89.0 ± 7.6%). The highest proportions of non-storm-petrel remains were found in May, the onset of nesting for many of the species. In light of the fact that not all seabird species (e.g. puffins, kittiwakes and murres) were present in April and October, an overview of fox predation from May to August seems comparatively more informative. During this period the following proportions were taken: Leach's Storm-Petrel 86.9 (N=324), Atlantic Puffin 4.3 (N=16), Black-legged Kittiwake 5.0 (N=19), Herring Gull 2.5 (N=9), Northern Gannet 1.1 (N=4) and Common Murre 0.3 (N=1).

Adult mortality due to fox predation on storm-petrels was high, however, egg loss appeared similar to that found in gulls (Figure 2-6). Possibly, the movement of adult storm-petrels in their nests distracts foxes from taking the eggs; alternatively, storm-petrel eggs, because of their small size, are ingested whole by foxes, leaving few noticeable remains and/or the foxes prefer the adults over less profitable eggs. Puffin eggshells were similarly, infrequently found. This may reflect the deeper, more protective nature of their burrows (pers. obs.), being commonly located in areas of boulder scree. Though murres and gannets suffered relatively high egg loss, adult predation was low. Murres nest on sheer portions of cliff and appeared more sensitive to disturbances (i.e. fox activity). The gannets' large size may limit the extent of predation (Nelson, 19[illegible]), however, adults may occasionally be blown into Bull Gulch Valley where they are vulnerable to fox attacks (pers. obs).

Figure 2-4: Three types of Leach's Storm-Petrel remains encountered: A - surplus kill (arrow indicates punctures inflicted by canid teeth); B - carcass minus head; C - wing set.

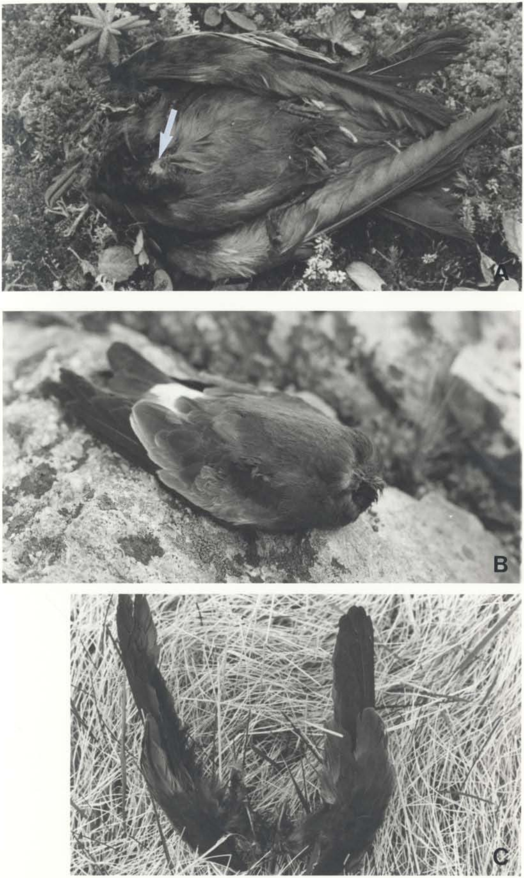

A
B
C

Figure 2-5: Herring Gull (A) and Atlantic Puffin (B) remains.

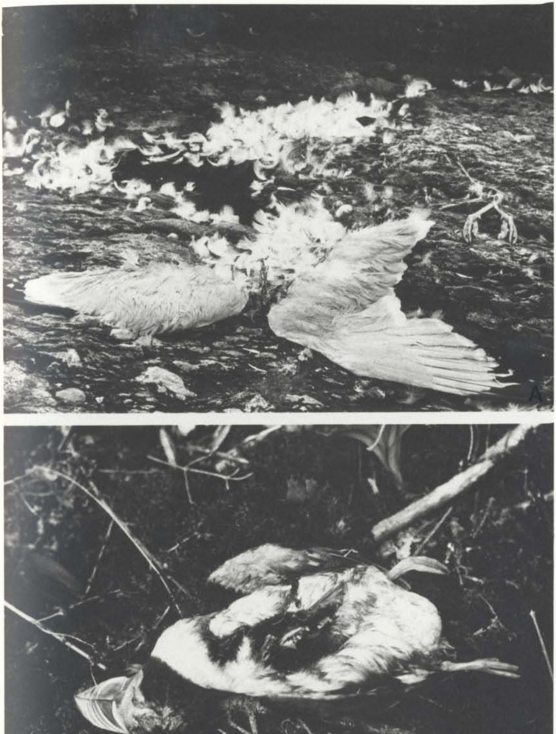

A
B

Table 2-3: Percent (no.) of avian remains collected during different months on Baccalieu Island.

SPECIES	APRIL	MAY	JUNE	JULY	AUGUST	OCTOBER	MEAN % OF TOTAL
STORM-PETREL	(a) 84.9(45)	76.7(112)	92.6(88)	97.6(83)	87.2(41)	(b) 94.7(195)	89.2(564)
PUFFIN	--	5.5(8)	3.2(3)	1.2(1)	8.5(4)	0.5(1)	2.7(17)
KITTIWAKE	--	4.8(7)	1.1(1)	1.2(1)	2.1(1)	--	1.6(10)
HERRING GULL	1.9(1)	2.1(3)	1.1(1)	--	2.1(1)	0.5(1)	1.1(7)
UNKNOWN GULL	9.4(5)	8.2(12)	1.1(1)	--	--	3.9(8)	4.1(26)
GANNET	1.9(1)	2.1(3)	1.1(1)	--	--	0.5(1)	0.9(6)
MURRE	--	0.7(1)	--	--	--	--	0.2(1)
UNKNOWN	1.9(1)	--	--	--	--	--	0.2(1)
SUM	100 (53)	100 (146)	100 (95)	100 (85)	100 (47)	100 (206)	100 (632)

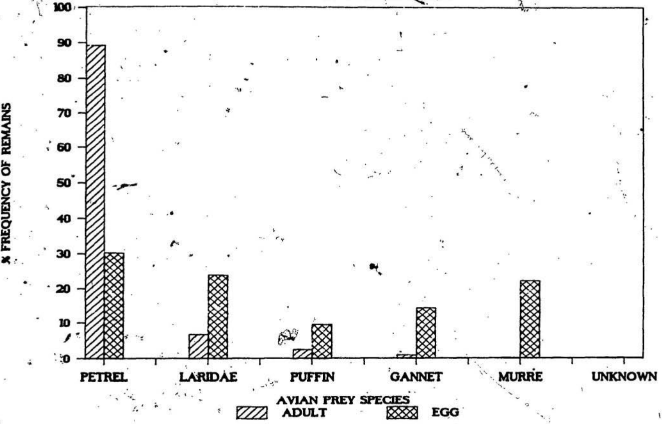
(a) A small proportion of these may have been left by avian predators (see text)

(b) A small proportion may be fledgelings; similar in appearance to adults at this time

Figure 2-6: Percent of remains of different avian prey species (Adult N = 632, Egg N = 63)

AVIAN (ADULT AND EGG) REMAINS

ATTRIBUTED TO FOX PREDATION



Only 12 signs of predation were found during the 30 days spent on the island in February-March. Identifiable remains were from two storm-petrels, a Common Eider (*Somateria mollissima*) an Iceland (*Larus glaucoides*) or Glaucous (*Larus hyperboreus*) Gull (2nd winter), an unidentified (1st winter) gull, four unknown completely white feather patches from either gulls or sea ducks and one possible alcid. The rarity of remains during the winter may have been due to three nonexclusive reasons: (1) fresh snowfall covering predatory signs, (2) low food availability and/or (3) many kills are completely eaten or cached.

2.3.4. Surplus Killing

Kruuk (1972) defined surplus killing as "the killing of prey by a predator, without the killing individual or its offspring or members of the same social unit eating any-thing from the carcass, although there is free access to the carcass, and usually the particular prey species would be eaten by that predator." On Baccalieu Island surplus killing was restricted to Leach's Storm-Petrels, with the only evidence of predation being that of canine teeth marks generally found at the base of a bird's neck. Eleven percent (65/614) of all avian remains or 12.0% (65/555) of all storm-petrels were left as surplus. The condition in which avian remains were found is summarized in Table 2-4.

The majority of storm-petrel remains and carcasses (excluding feathers) were found in the wooded areas of the island. As well, the proportion of surplus kills was higher when the birds arrived at the colony (April and May)

Table 2-4: Condition of avian remains attributed to red fox predation on Baccalieu Island during different months.

CONDITION	APRIL	MAY	JUNE	JULY	AUGUST	OCTOBER
WHOLE	13.2(7)	13.1(16)	8.4(8)	3.5(3)	10.6(5)	13.1(27)
CHEST BITE	--	4.1(5)	2.1(2)	--	2.1(1)	--
BODY ONLY	--	3.3(4)	1.1(1)	--	23.4(11)	2.9(6)
HEAD ONLY	5.7(3)	0.8(1)	1.1(1)	--	--	0.5(1)
HALF CONSUMED	--	4.1(5)	4.2(4)	--	6.5(3)	1.0(2)
LEG(S) (a)	--	1.6(2)	--	--	--	--
WINGS AND LEGS (a)	--	0.8(1)	--	--	--	--
WINGS (a)	18.9(10)	13.1(16)	23.2(22)	11.8(10)	25.5(12)	29.6(61)
FEATHER (a, b)	62.3(33)	59.0(72)	60.0(57)	84.7(72)	31.9(15)	52.9(109)
TOTAL	100 (53)	100 (122)	100 (95)	100 (85)	100 (47)	100 (206)

(a) A small proportion of these may have been taken by avian predators (see text)
(b) Only large numbers of feathers or feather clumps (often blood stained) were considered signs of predation

and at fledging (October) than during the summer (June-August) (x_1^2=6.5, $p<.02$). Vulnerability appeared to be an important factor in determining which species and/or individuals were surplus killed (cf. Kruuk, 1964). During arrival, when petrels were re-establishing nest sites, burrows were often snow covered or ice jammed (~10 - 15 cm deep), and adults were commonly found crushed into burrow entrances. Similarly at fledging, young were particularly vulnerable (and weak toward the latter part; pers. obs.). having to travel a great distance on foot before reaching a clearing (A. Hartenist, pers. comm.). These individuals appeared to constitute a significant portion of surplus kills.

2.3.5. Caching Behaviour

In addition to scatter hoarding, red foxes on Baccalieu Island have been found to larder hoard prey (Maccarone and Montevecchi, 1981). Although rarely seen near larders, on one occasion I observed a fox enter a larder area carrying two storm-petrels in its mouth. A small larder hole was entered for approximately 5 sec after which the fox came out and travelled ~10 m to a larger larder hole where both prey items were deposited. The fox then returned to the first hole sniffed for a while and left in the same direction from which it came. After less than 5 min, the fox returned with another storm-petrel. This one however, the fox ate, leaving the uneaten remains above ground.

During this study, seven larder sites were found; of these five were located at dens (Table 2-5). The largest hoard was located in area 7 (Figure 2-7) where eight separate larders contained a total of 320 avian carcasses

Table 2-5: Number of carcasses found in larders (and scattered above ground within 3 m^2 of each larder hole).

LARDER	DATE	STATUS	NO. OF	AVIAN SPECIES						
			CACHES	PETREL	PUFFIN	KITTIWAKE	UNKNOWN GULL	GANNET	MURRE	TOTAL
1(a)	JUNE/78	ˆ	1	302	15	2	--	--	1	320
2(b)	JUNE/79	ˆ	1	30	3	3	--	--	1	37
3(b)	AUG/80	*	2	42	38	1	--	--	1	82
4	MAY/83	x	1	4(2)	--	--	--	--	--	4(2)
5	JUNE/83	+	2	12(3)	5(-)	3(-)	--	1(-)	1(-)	22(3)
6	JULY/83	ˆ	1	5(-)	1(-)	--	--	--	--	6(0)
7	MAY/84	*	3	41(60)	1(-)	1(2)	--	1(-)	--	44(62)
8	OCT/84	+	2	10(15)	--	--	--	--	--	10(15)
9	OCT/84	x	1	7(16)	3(1)	--	-(1)	--	--	10(18)
10	JUNE/85	+	8	285(71)	5(1)	1(4)	--	--	--	
	JUNE/85	(c)	8	29(-)	--	--	--	--	--	320(76)
SUM (THIS STUDY ONLY)			26	393(167)	15(2)	5(6)	-(1)	2(-)	1(-)	416(176)

(a) Montevecchi, unpubl. data (almost all below ground; very few above)

(b) Maccarone and Montevecchi, 1981 (almost all below ground; very few above)

(c) Eight smaller caches found nearby (see text)

*: Den with cubs

+: Den - no cubs present

ˆ: Possible den - some apparent activity

x: No den within 100 m

Figure 2-7: Photograph taken of larder hole and hoard at larder site no. 10 (see table 2-5).

(range = 18 - 161) and eight smaller caches contained a total of 27 items (range = 2 - 7). Ninety-three percent (297/320) of carcasses found in the eight principal larders were mostly intact.

Storm-Petrels formed 94.5% (393/416) of carcasses found at all seven major larders and 94.9% (167/176) of items found scattered within 3 m^2 of each larder hole. The proportion of storm-petrels found at larder sites (94.6% (560/592)) was significantly higher than field remains (89.2%(561/629); x_1^2=4.7, $p<.05$) or that found in scat (82.1% (134/163); x_1^2=9.73, $p<.01$). The proportion of storm-petrels found in scat and as remains did not differ (x_1^2=0.2, $p>.05$). It is clear that the foxes hoarded more storm-petrels than they ate.

2.3.6. Scat Analysis

Table 2-6 summarizes the frequency of occurrence of prey found in scat during summer. Storm-petrels comprised 82.1 ± 9.9% of all remains, ranging over 81-91% in May through July and dropping to 67-70% in August. Though the peak period of storm-petrel utilization appeared to be in July (90.5 ± 0.7%), the occurrence of larger seabirds in scat was highest in May (16.0 ± 4.2%), gradually decreasing to 0% in August. The overall decline of avian prey in scat during August coincides with an increase in berry intake (e.g. blueberry, bilberry, bakeapple). The absence of larger seabirds in the diet may also reflect that some species (e.g. puffins, murres, kittiwakes) leave the island in August and are no longer available. Insect and eggshell remains occur in

Table 2-6: Percent frequency (no.) of occurrence of avian remains found in summer scat.

SPECIES	MAY 2	MAY 21	JUNE 7	JULY 19	JULY 21	AUGUST 12	AUGUST 17	TOTAL %(N)
STORM-PETREL	78.6(33)	66.7(16)	71.9(23)	85.0(17)	82.0(9)	70.0(7)	62.5(15)	73.6(120)
STORM-PETREL (a)	2.4(1)	20.8(5)	15.6(5)	5.0(1)	9.1(1)	--	4.2(1)	8.6(14)
LARGE SEABIRD	19.0(8)	12.5(4)	12.5(4)	10.0(2)	9.1(1)	--	--	11.0(19)
PASSERINE	--	--	3.1(1)	--	--	--	--	0.6(1)
EGGSHELL	--	--	--	5.0(1)	--	--	--	0.6(1)
PLANT MATTER	--	20.8(5)	--	15.0(3)	18.2(2)	--	8.3(2)	7.4(12)
BERRY	2.4(1)	8.3(2)	6.3(2)	5.0(1)	--	60.0(6)	37.5(9)	12.9(21)
INSECT	--	--	--	10.0(2)	--	--	--	1.2(2)
NO. OF SCAT	4[illegible]	24	32	20	11	10	24	163

(a) Avian remains that could not be identified positively, but were almost certainly storm-petrels minute proportions in scat and therefore, unless found in noticeable quantities, may have been overlooked.

Tables 2-7 and 2-8 summarize the diet of foxes in the fall and winter seasons based on dry weights and the estimated total intake of prey calculated using Lockie's (1959, 1961) correction factors. Based on the total proportion of estimated wet weight ingested, storm-petrels formed 75.1% of the diet in the fall and 53.0% in the winter. The intake of large seabirds however, increased from 18.9% in the fall to 42.9% in the winter. Seaducks (Figure 2-8) and gulls are abundant during the non-nesting period and undoubtedly constitute an important part of fox diet. One winter scat contained the beak of a dovekie (*Alle alle*). Although landbirds were available to foxes during the winter, no remains were found in scat. Murie (1959) and Stephenson (1970) have similarly noted that passerines are rarely taken.

Non-avian prey formed 6.6% and 14.1% by dry weight of fall and winter scat, respectively. Marshberries (*Vaccinium oxycoccus*), blueberries (*Vaccinium angustifolium*), tundra bilberries (*Vaccinium uliginosum)*, crackerberries (*Cornus canadensis*), bakeapples (*Rubus chamaemorus*), and crowberries (*Empetrum nigrum*) are frequently taken by foxes and constitute a major source of carbohydrate (Lindstrom, 1983). Marshberries, which are available in the fall and spring, might be important to the foxes during lean periods. Periwinkles (*Littorina spp.*) and mussel (*Mytilus sp.*) fragments were found in small quantity in fall scat. In comparison, winter scat contained a

Table 2-7: Analysis of scat collected in October 1984 (N=166); based on dry weight, estimated wet weight and frequency of occurrence.

SPECIES	DRY WT.		EST. WET WT. (a)		FREQ. OCC.
	(g)	(%)	(g)	(%)	(%)
STORM-PETREL	106.3	43.9	8178.1	75.1	81.3
STORM-PETREL (b)	75.4	31.2			
NON-STORM-PETREL	33.5	13.8	2040.6	18.7	9.6
PASSERINE	2.8	1.2	125.8	1.2	1.2
UNKNOWN AVES	8.0	3.3	421.7	3.9	7.8
EGGSHELL	1.7	0.7	24.8	0.2	27.7
VEGETATION	6.0	2.5	6.0(c)	0.1	74.7
BERRIES	5.1	2.1	70.8	0.6	27.1
INSECT	2.0	0.8	24.1	0.2	35.5
MARINE	0.6	0.2	0.6(c)	<0.1	3.6
ROCK	0.6	0.2	0.6	<0.1	4.2
MISC.	0.2	0.1	0.2	<0.1	3.0
TOTAL WT.	242.0	100.0	10,893.3	100.0	-

(a) All corrections based on Lockie (1959;1960)
(b) Avian remains that could not be identified positively, but were almost certainly storm-petrels.
(c) No correction available

Table 2-8: Analysis of scat collected in February 1985 (N=52); based on dry weight, estimated wet weight and frequency of occurrence.

SPECIES	DRY WT.		EST. WET WT. (a)		FREQ. OCC.
	(g)	(%)	(g)	(%)	(%)
STORM-PETREL	18.0	25.2	1685.3	53.0	63.0
STORM-PETREL (b)	19.4	27.1			
NON-STORM-PETREL	22.2	31.0	1354.4	42.6	29.6
PASSERINE	0.0	0.0	0.0	0.0	0.0
UNKNOWN AVES	1.9	2.7	101.6	3.2	7.4
EGGSHELL	<0.1	<0.1	0.1	<0.1	3.7
VEGETATION	2.2	3.0	2.2(c)	0.1	92.6
BERRY	1.9	2.6	26.5	0.8	33.3
ARTHROPODA	<0.1	<0.1	0.1	<0.1	11.1
MARINE	5.7	7.9	5.7(c)	0.2	29.6
ROCK	0.1	0.1	0.9	<0.1	14.8
MISC.	0.2	0.3	0.2	<0.1	7.4
TOTAL WT.	71.7	100.0	3,177.1	100.0	-

(a) All corrections based on Lockie (1959;1961)

(b) Avian remains that could not be identified positively, but were almost certainly storm-petrels

(c) No correction available

Figure 2-8: Large flock of Common Eiders off the eastern coast of Baccalieu Island (February, 1985); through January - March flocks of > 1,000 birds are not uncommon.

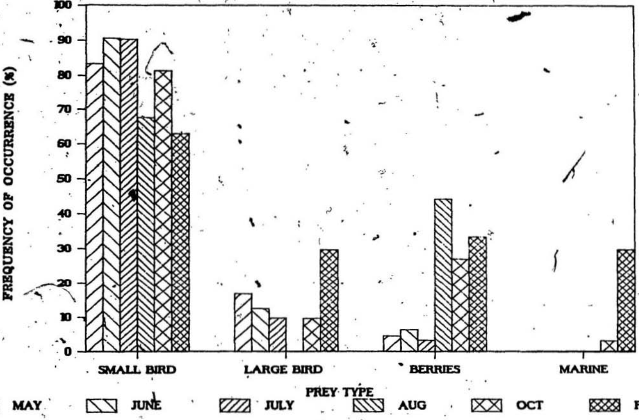
high proportion of sea urchin (*Strongylocentrotus* fragments (8% dry wt.) and no other marine invertebrate species were found. Grasses, *Empetrum* leaves, balsam needles and lichens were frequently present in scat, but in small proportion and were probably ingested accidentally while capturing prey or foraging on berries (Lloyd, 1980), although certain grasses act as diuretics (Lever, 1958) and are sometimes eaten in large quantity (Bezeu and Gallant, 1950). Insect remains (<1% by dry or wet wt.) included Coleoptera (principally *Nicrophorus marginatus*), unidentifiable Diptera, Hymenoptera (*Megabombus pennsylvanicus*) and Siphonaptera (*Ctenocephalides spp.*). Dead maggots (Dipteran larvae) were also found in scat suggesting the use of scavenged or cached foods. Only one winter scat contained Isopoda (two sowbugs).

Seabirds were the principal prey of foxes during nesting (summer/fall) and non-nesting (spring) periods. Berries and marine invertebrates were also taken and may be important in supplementing fox diet. Figure 2-9 summarizes the pattern of monthly changes in the 4 major prey groups of fox diet on Baccalieu Island.

2.4. DISCUSSION

Red foxes are opportunistic predators and eat a wide variety of foods, with availability acting as a primary determinant of diet (Errington, 1935; Scott, 1943; Korshgen, 1959; Englund, 1965). On Baccalieu Island, avian prey made up ~86-93% (winter and fall dry wt., respectively) of fox diet, of which,

Figure 2-9: Summary of the monthly changes in the 4 major prey groups in fox diet; based on the frequency of occurrence in red fox scats (N = 381). Small Bird = Storm-Petrel, Passerine; Large Bird = Larids, Alcids; Marine = Marine Invertebrates.



MONTHLY ANALYSIS OF RED FOX SCATS

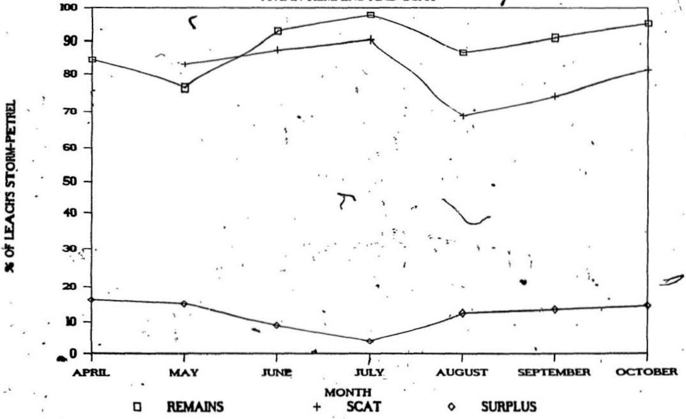
COLLECTED ON BACCALIEU ISLAND

Leach's Storm-Petrels constituted the bulk (89.0 ± 7.6% remains). Three factors which increased storm-petrel susceptibility to high depredations were: (1) their relative abundance, (2) their vulnerability when arriving at the colony, fledging and adult feeding and brooding/incubation shift changes (especially in the wooded areas), and (3) their accessibility in nesting burrows (especially in the grass region). Predator efficiency is increased due to the foxes nocturnal nature and the fact that both hearing and scent are well-developed as distance receptors for locating subterranean prey (Osterholm, 1964).

The three methods used to determine prey utilization were consistent in showing that storm-petrels composed 89-95% of kills and 75% of ingested wet weight. The highest proportion of storm-petrel was found in July (scat, 90.5%; remains, 97.6%) which coincides with either: (1) the peak of egg-laying, since scat collected in July may have been deposited in late June or (2) during early chick rearing, when adults would be making frequent foraging trips. Nevertheless, these factors suggest that storm-petrels were either at peak abundance on land or highly vulnerable. However, because surplus killing was at its lowest (Figure 2-10), the former may actually be the case. On the other hand, during the nesting season large seabird species were found in highest proportion in May (scat, 16.7%; remains, 23.3%). While establishing nest sites, cliff-nesters (e.g kittiwakes, gannets) are exposed to predation when gathering nesting material on the grassy slopes (pers. obs.), suggesting that vulnerability rather than availability may be the cause.

Figure 2-10: Monthly changes in the proportion of surplus killing compared to to that of avian remains and scat (Remains $N = 632$; Scat $N = 329$; Surplus $N = 564$).

COMPARISON OF SURPLUS KILLING TO
AVIAN REMAINS AND SCAT



The resident red fox population of Baccalieu Island consisted of up to 9 individuals (excluding young), comprising 3 or 4 family groups. Seabirds were a highly abundant food source from April through October and the scarcity of food in winter may limit the fox population.

Foxes fully utilized home ranges during the winter (see also Sheldon, 1950; Ables, 1975). This was apparent in that tracks were highly noticeable along the western half of the island where, during other periods of the year, little activity occurred. Scavenging along the limited beaches and on both stable and flowing pack ice was also common and there, foxes may have occasionally found an injured or trapped murre or eider (Freuchen and Solomonsen, 1958; Tuck, 1960; R. Hyde and L. Walsh, pers. comm.). As well, large flocks of seaducks (i.e. Common Eider, Oldsquaw) were commonly observed feeding in leads in the pack ice close to shore (Figure 2-11) and attracted foraging foxes (pers. obs.). The behaviour of one fox in particular exemplified food scarcity. On two separate occasions this individual was observed foraging in the trees and during 1 hr had eaten as many as four balsam fir (*Abies balsamea*) cones (Figure 2-12). Murie (1959) also noted that during periods of prey scarcity foxes will eat food items that appear to have little value, although coniferous cones may provide some nutrients (A. Diamond, pers. comm.). The relative increase of marine invertebrates in the diet, the low occurrence of prey remains and increased cache use, provided additional evidence of food scarcity during the winter.

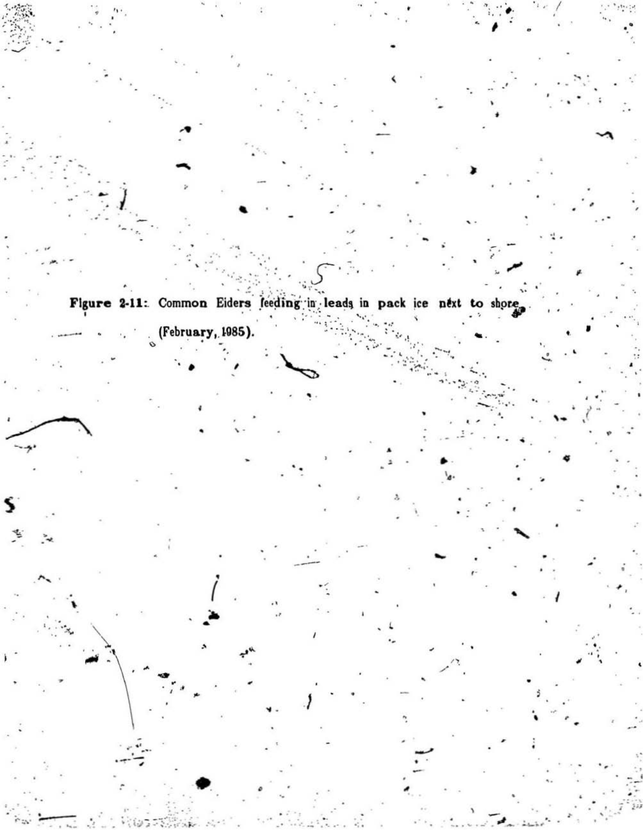
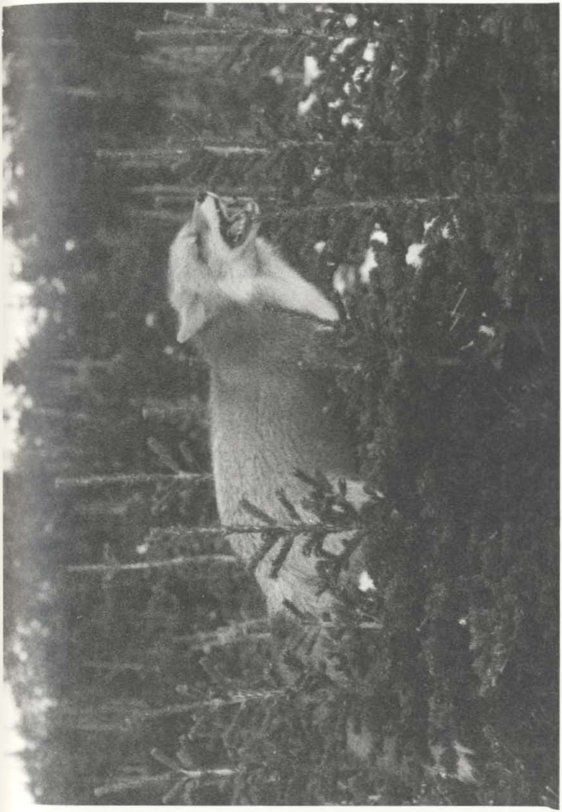


Figure 2-11: Common Eiders feeding in leads in pack ice next to shore (February, 1985).

Figure 2-12: Fox eating a balsum fir cone in the trees (February, 1985), suggesting prey scarcity.



Periods of low prey availability may act to stabilize fox populations by decreasing: (1) reproductive success, (2) postpartum survival of cubs and/or (3) juvenile survival during the first winter. Chircova (1941) found that female red foxes as a consequence of poor nutrition, may not come into estrus, ova may not be fertilized, reabsorption of embryos takes place and females may fail to lactate; in general, the proportion of barren females increases under conditions of food scarcity (Englund, 1970). On Baccalieu Island one pair failed to produce offspring in two separate years, even though a den site was occupied and their behaviour reflected that of a mated pair. Because breeding in foxes takes place in early February and young are born in April (Ables, 1975), the lack of food would not be an important factor in decreasing postpartum survival of cubs on Baccalieu Island, since seabirds begin breeding at this time. On the other hand, young or juvenile foxes probably experience high levels of mortality during their first winter on the island. Although the fox population on Baccalieu Island appears limited, it has maintained itself for more than 25 years.

One behaviour with apparent survival value for the foxes is caching prey for future use (Figure 2-13) and the ability to cache enough food for the winter may be more important in determining the size of the fox population on the island than the scarcity of winter prey. Larders have been found in five years (see Maccarone and Montevecchi, 1981), indicating that this method of hoarding is not uncommon and may be adaptive by increasing reproductive success. Cache use was verified in that storm-petrels composed 47 - 53% of

Figure 2-13: Cache utilization in winter: A - tracks leading to and from a cache suggesting a fox recovered food from a cache below the snow; and B - direct observation of cache recovery.


A


B

fresh scat collected in February. Though seaducks, gulls and passerines may be taken during the winter, cached prey and scavenged surplus kills may provide additional nutrition.

In view of the existing literature, the caching behaviour of red foxes on Baccalieu Island is unusual in that prey are both scatter and larder hoarded. Arctic foxes typically larder hoard when near seabird colonies and scatter hoard in non-seabird areas (Braestrup, 1941). These findings suggest that environmental circumstance determine the method of hoarding. Caching behaviour by red foxes may be more flexible than previously described. Larder hoarding may actually be an effective (or safe) strategy in areas of low population density and/or in areas lacking interspecific competitors (see Ewer, 1968), where the hoarder would be more likely to recover its own food items (Andersson and Krebs, 1978). Although Common Ravens may occasionally steal lardered prey from foxes (pers. obs.), foxes tend to avoid one another and even family members (outside the breeding season), which also decreases the likelihood of intraspecific theft (Sargeant, 1972; Storm et al., 1976).

The greater occurrence of storm-petrels in larders than as field remains can be explained in at least four ways: (1) Field collections were not limited to one area or habitat and may therefore reflect greater prey variety than that found at larders. (2) Cubs may assist adults in hoarding during denning and because most dens are located away from the seabird cliffs, only storm-petrels would be available to them. (3) Species that maintain well-delineated (effective) territories can hoard a maximum amount of food by gathering items near the larder first (Smith and Reichman, 1984). (4) Hoarded prey (storm-petrel in this case) may constitute a non-preferred food, which is stored for future use in the event that nothing better is found (Macdonald, 1976; see also Errington, 1935; 1967).

In summation, it appears that the red fox population on Baccalieu Island is well-established though small owing to the scarcity of winter food. Red foxes prey mostly on Leach's Storm-Petrels, reflecting their availability, accessibility and vulnerability.

Chapter 3

PREDATORY EFFECTS OF RED FOXES ON THE LEACH'S STORM-PETREL POPULATION OF BACCALIEU ISLAND

3.1. INTRODUCTION

To assess the impact of red fox predation on the Leach's Storm-Petrel population of Baccalieu Island, knowledge of both harvest levels and storm-petrel population size are needed. Although Baccalieu Islands large area precludes direct and total counts of nesting storm-petrels, the method of systematically censusing burrows in sample plots in different habitats can provide information regarding relative densities, and along with data on habitat area, may be used to estimate populations of breeding birds (Nettleship, 1976; Bull, 1981). The objectives of this chapter are to estimate on Baccalieu Island: (1) the major nesting habitats of Leach's Storm-Petrel and their areas, (2) burrow occupancy levels in the different habitats, (3) the storm-petrels' nesting population, (4) the foxes' impact on the storm-petrels and on (5) all other major breeding seabird species.

3.2. METHODS

3.2.1. Habitat Description and Classification

Leach's Storm-Petrels nest in a variety of habitats on Baccalieu Island. The three principal habitats are: barren heaths, boreal forest and grassy-hummocked slopes (Figure 3-1). The densest concentrations of breeding storm-petrels occur in the grassy areas on the eastern side of the island from Gannie Cliff to Dickey's Point (Figure 3-2). Medium and low density concentrations are found in wooded and heath regions, respectively. Smaller areas composed of herbaceous plants, grass meadow mixed with heath, and grass and herb mixed with heath are also used for nesting. A description of the three major and three sub-habitat types is given below.

Barren (coastal) heaths - Northern and southern portions of the island's barren regions (Figure 3-3) are principally soft ground or *Empetrum* heaths (Meades, 1973, 1983) dominated by ericaceous shrubs (*Vaccinium spp.*, *Empetrum spp.*, *Ledum groenlandicum*, *Rubus chamaemorus*, *Myrica sp.*). Mountain Alder (*Alnus cris*[illegible]) and small, scattered stands of dwarfed spruce (Picea sp.) are also found. The central portion of the island's barrens (Figure 3-4) (with exception of Dog Marsh), although similar in species composition, has a low peat accumulation and is typical of hard ground heath (Meades, 1973, 1983), containing species which have high light requirements and are unable to survive under shrub or forest canopy (Damman, 1964). Bare bedrock, lichens (*Cladonia spp.*) and mosses (*Rhacomitrium sp.*, *Sphagnum sp.*) predominate in this area.

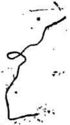


Figure 3-1: Map showing principal habitats on Baccalieu Island.

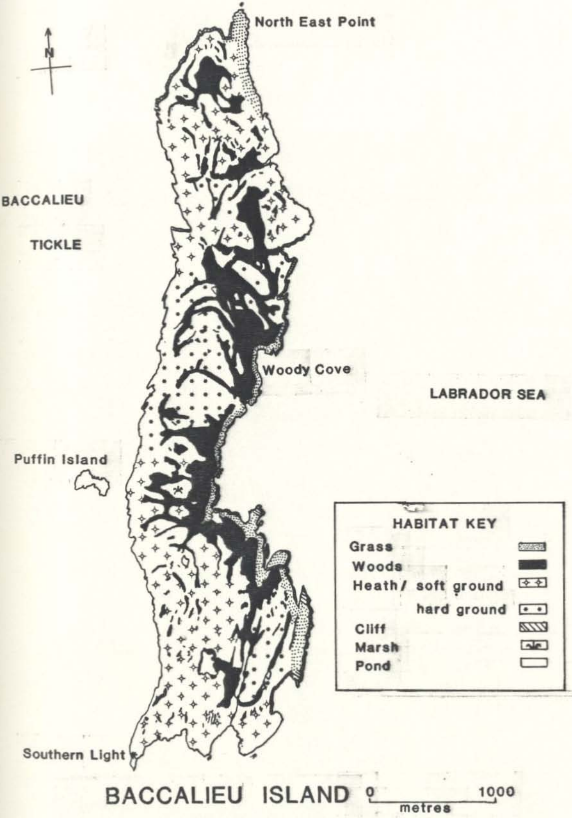
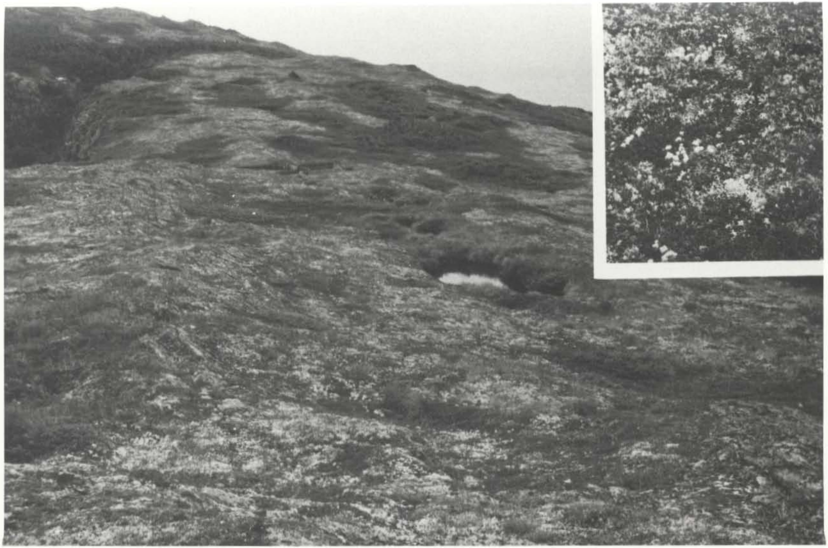

N
North East Point
BACCALIEU
TICKLE
Woody Cove
LABRADOR SEA
Puffin Island
HABITAT KEY
Grass
Woods
Heath / soft ground
hard ground
Cliff
Marsh
Pond
Southern Light
BACCALIEU ISLAND
0
1000
metres

Figure 3-2: View of southeastern cliffs and grassy slopes; the latter is principally occupied by Leach's Storm-Petrels.

Figure 3-3: Photograph taken in the southern *Empetrum* heaths; showing distant (A) and close-up (B) views (storm-petrel burrows are indicated by arrows in A).


A
B

Figure 3-4: Hard ground or coastal heath; the inset provides a close-up of the characteristic vegetation.



Boreal forest - a coniferous forest (Figures 3-5 and 3-6) composed principally of Balsam Fir (*Abies balsamea*) and White Spruce (*Picea glauca*). Deciduous species, such as American Mountain Ash (*Sorbus americanus*), White Birch (*Betula papyrifera*) and Chokecherry (*Prunus virginianica*), form minor forest components. A variety of mosses (*Pleurozium schrabari, Polytrichum sp., Sphagnum sp.*) and herbaceous plants (*Aralia nudicaulis, Clintonia borealis, Ribes glandulosum, Maianthemum canadense, Viola sp.*) form a dense understory, but in some areas, the forest canopy excludes light to the point where the substrate is largely bare.

Grassy hummocked slopes - This habitat is principally composed of mixed grasses (*Poa pratensis, Scirpus caespitosus, Deschampsia flexuosa*) and sedges (*Carex sp.*) often in the form of tussocked slopes and meadows (Figure 3-7). In some portions of this habitat, grasses are mixed with a variety of herbaceous plants (*Cornus sp., Prenanthes sp., Rumex acetosella, Rubus pubescens, Dryopteris austriaca, Osmunda austriaca, Ranunculus sp.*).

Herbaceous plant - Dominated by fern (*Dryopteris austriaca, Osmunda cinnamomea*), this habitat may also consists of a variety of (often tall) herbaceous plants (*Ribes glandulosum, Epilobium angustifolium, Streptopus amplexifolius, Trientalis borealis, Moneses uniflora, Prenanthes sp.*) and is most commonly found in a transition zone between the grass and wooded habitats. Although differentiated, this habitat lies in close association with the grass habitat.

Figure 3-5: Distant view of the wooded habitat.

Figure 3-6: Close-up of the wooded habitat; arrows indicate storm-petrel burrows.

Figure 3-7: Grassy habitat; showing distant (A) and close-up (B) views (storm-petrel burrows are indicated by arrows in B).


A
B

Meadow and Mixed - In the present investigation two additional sub-habitats which are found within the heath habitat were differentiated. The meadow sub-habitat refers to areas of grass meadow (*Deschampsia sp.*) and ericaceous shrub common along the northern end of the island. The mixed sub-habitat similarly contains grasses and *Empetrum*, however, short herbs predominate. Although differentiated here, these sub-habitats are highly heterogeneous, sharing characteristics of heath, grass and herb habitats in varying proportion, making them difficult to delineate.

3.2.2. Habitat Area Analysis

Two methods were used to determine the habitat components of Baccalieu Island. Both complement one another and provide a framework for comparison.

Aerial Photograph Method: Three aerial photographs (1:25,000, Can. Dept. Energy, Mines, and Resources) comprising the southern, central and northern portions of Baccalieu were used. The island's land mass was overlayed by a grid composed of 150 full quadrats. Each quadrat was examined under a magnifying lamp and/or stereoscopic glasses and the percentage of each habitat type was estimated. Aerial photographs were primarily useful in differentiating woods, rocky areas, cliffs, barren and grass habitat. When combined with a knowledge of general habitat characteristics obtained from ground survey, relative area estimates of herb, meadow and mixed sub-habitats could be made.

Map (Digitizer) Method: A Numonics digitizer (model 1210-1) was used to trace a 1:8650 map of Baccalieu Island and compute its flat surface area in ha. Additionally, areas known to be homogeneous (i.e. woods, ponds, etc...) were calculated. Although aerial photographs could have been used, angle and height inconsistencies between plates would have produced greater error (H. Butler, pers. comm.). Additionally, the larger scale of the map (1:8650) provided for greater accuracy with area calculation. This method is absolute and results in an objective two dimensional analysis of island and habitat areas.

3.2.3. Ground Survey of Possible Burrows

A general measure of the density of holes or possible storm-petrel burrows was needed to evaluate the overall number of storm-petrels nesting in each habitat. In order to cover all areas of the island, plot sites were prechosen on a map (with relatively equal distances between sampling sites) prior to examination. Randomness of plots and transects within heath, wooded, mixed and meadow habitats was assured by travelling a random distance (determined by a table of random numbers; 100-500 m in the heath, 50-100 m in the woods and, 25-50 m in both mixed and meadow habitats) and compass direction (N,S,E,W) from the prechosen site. Estimates of grass and plant habitat densities were obtained from data collected in association with fox hunting strategy (Chapter 1).

Both forest and grass regions seemed to differ in burrow density relative to slope. Therefore, plots were categorized into three slope classes of: 0-29, 30-59 and 60-89°. The number of plots per category (since randomly chosen) were assumed to represent the total proportion of area within each habitat occurring at that slope and obtained percentages were used in estimating storm-petrel numbers.

Exploratory surveys also suggested large regional differences in burrow density within barren habitat. The central area of the island approximately 1 km north of Dog Marsh to Cow Rock (Figure 1-1) contained a lower density of burrows apparently due to shallower soil as indicated by a greater proportion of exposed bedrock and beds of moss. In order to assess these differences in burrow density, data were collected in northern, southern and central locations.

3.2.4. Determination of Burrow Occupancy in Three Primary Habitats

During May - June 1984, occupancy plots were established in grass, forest and *Empetrum* heath habitats south of Brister Pond. Eight sites typical of wooded (n=4) and grassy (n=4) habitats were selected. The exact location of each plot was determined by marking a 5 x 10 m area and subdividing it into four equal quadrats of which one was randomly chosen. This procedure was maintained in selecting four 12.5 m^2 plots per habitat of which two were in areas with $\geq 30°$ slope and two were on approximately level ground (0-5° slope). Grass habitat is composed of either grass tussock or grass mixed with herbs, two plots were placed at Gannet Head (grass tussock) and two at Bull Gulch (grass/herb) (Figure 2-1) to account for possible subhabitat differences. In the heath habitat, the density of holes (or possible burrows) was very low and variable. Therefore, two 100 m^2 plots (H1 and H2; Figure 2-1) were set up in high burrow density heath habitat (most common along the island's periphery), and two 4 X 100 m transects (H3 and H4) were set out randomly in typical heath habitat.

Diagrams of plots were drawn relating hole position and distance to neighboring holes. A protractor and level were used to determine slope. Within each plot, connections between burrows, burrow length, the presence of nest material, adults, chicks, eggs and the general characteristics of vegetation were recorded. Nests were examined between 12 - 22 July 1984, in early chick rearing approximately 4 to 5 weeks post egg-laying (Morse and Buchheister, 1979) and re-checked from 17 - 20 October for nesting success (1-2 wks after estimated first fledging - access to the island was not available until this time).

3.3. RESULTS

3.3.1. Physical Habitat Characteristics

Baccalieu Island has a total two-dimensional surface area of 523 ha of which, 303 ha are at an elevation of greater than ~75 m above sea level. Table 3-1 summarizes the areas (ha) of the island's habitats. Non-nesting regions such as ponds, bedrock, cliffs and marshes comprise 87 ha, leaving approximately 437 ha (84% of the total) as potential nesting habitat for the Leach's Storm-Petrels.

Table 3-1: Habitat area estimates using aerial photographic and mapping methods.

HABITAT TYPE	AERIAL METHOD (ha)	AERIAL METHOD (%)	MAP METHOD (ha)	MAP METHOD (%)
HEATH	208.1	40.6	273.7	52.3
WOODS	167.8	32.7	180.0	34.4
GRASS	38.8	7.6	32.8	6.3
MEADOW	6.2	1.2	6.8	1.3
HERB	9.5	1.9	(c)	(c)
MIXED (a)	9.0	1.8	(c)	(c)
MARSH	(b)	(b)	3.4	0.6
POND	(b)	(b)	6.7	1.3
ROCK	55.8	10.9	(c)	(c)
CLIFF	17.8	3.5	19.7	3.8
TOTAL	513.0	100.0	523.1	100.0

(a) For a description see text
(b) Excluded from count
(c) Included in heath count

The aerial photographic and mapping methods differed in estimating the percentage of heath area. This discrepancy was a result of the map method including plant, mixed and rock sub-habitats in the count. Therefore, when these sub-areas are extracted, barren habitat equals 37.9% of the total area or 198 ha., which is similar (2.7% difference) to that of the aerial method. The slight difference between the grass habitat estimates may be attributed to either: (1) a subjective overemphasis (in method 1), since this region is highly sloped or (2) an inaccurate approximation in defining the absolute dimensions of this habitat. The calculated areas of forest, meadow and cliff regions were similar between methods.

Lunin (1.9 ha), Gull (1.8 ha) and Southern End Ponds (1.5 ha) are the largest fresh water bodies on the island. These as well as Boat, Lilly, Clay, Brister and Island Ponds were included in the map analysis. Dog Marsh near the center of the island measured 2.7 ha (method 2) and was excluded from the aerial count as were ponds, since invariably, no petrels nest there. The aerial method was used to estimate the amount of exposed bedrock at 10.9%.

3.3.2. Burrow Density of Plots

Burrow characteristics of grass, forest and heath plots are presented in Tables 3-2, 3-3 and 3-4. Holes which terminated at ≤ 20 cm from the surface were typically inactive and were not considered burrows. Nest chambers with multiple entrances were counted only once (number of nests measure). The number of known nests equalled the actual number of confirmed nests

Table 3-2: Summary of burrow characteristics associated with four grass habitat plots (2.5 x 5 m).

PLOT LOCATION	SLOPE	NUMBER (OF)						
		HOLES	PARTIAL	CONNECTED	INACCESSIBLE	BURROW ENTRANCES(a)	TUNNELS(b)	KNOWN NESTS(c)
G1	0	36	1	6 3 nests	1	35	32	31
G2	40	45	0	8 7 nests	3	45	44	41
G3	0	49	8	11 5 nests	3	41	35	32
G4	45	55	2	8 5 nests	8	53	50	42
Total	--	185	11	33	15	174	161	146
Mean	--	46.3	2.8	8.3	3.8	43.5	40.3	36.5
S.D.	--	8.0	3.6	2.1	3.0	7.5	8.3	5.8

(a) # holes - # partial
(b) # burrows entrances - # additional entrances (see connected category)
(c) # tunnels - # inaccessible

Table 3-2: continued

	NO. OF HOLES/M^2	ESTIMATED NO. TOTAL NESTS(d)	% NESTS(d,e)	NO. OF NESTS/M^2	% OCCUPIED NESTS(f)	NO. OCCUPIED/M^2
	2.88	32.0	88.9	2.56	77.4	1.98
	3.60	43.9	97.6	3.51	61.0	2.14
	3.92	34.5	70.4	2.76	75.0	2.07
	4.40	49.5	90.0	3.96	73.8	2.92
MEAN	3.70	40.0	86.7	3.20	71.8	2.28
S.D.	0.64	8.2	11.6	0.65	7.4	0.43

(d) Extrapolated to include the number of inaccessible burrows
(e) Estimated no. total nests/no. holes
(f) No. occupied/no. known nests

Table 3-3: Summary of burrow characteristics associated with four forest habitat plots (2.5 x 5 m).

PLOT LOCATION	SLOPE	NUMBER (OF) HOLES	PARTIAL	CONNECTED	INACCESSIBLE	BURROW ENTRANCES (a)	TUNNELS (b)	KNOWN NESTS (c)
W1	0	10	0	4 3 nests	3	10	9	6
W2	30	28	3	7 4 nests	8	25	22	15
W3	0	12	1	2 1 nests	2	11	10	8
W4	32	25	0	6 3 nests	9	26	23	14
Total	--	75	4	19	22	72	64	43
Mean	--	18.8	1.0	4.8	5.0	18.0	16.0	10.0
S.D.	--	9.1	1.4	2.2	3.5	8.7	7.5	4.4

(a) # holes - # partial

(b) # burrows entrances - # additional entrances (see connected category)

(c) # tunnels - # inaccessible

Table 3-3: continued

NO. OF HOLES/M^2	ESTIMATED NO. TOTAL NESTS(d)	% NESTS(d,e)	NO. OF NESTS/M^2	% OCCUPIED NESTS(f)	NO. OCCUPIED/M^2
0.80	8.6	85.7	0.69	66.7	0.46
2.24	20.6	73.6	1.65	73.3	1.21
0.96	9.8	81.5	0.78	75.0	0.59
2.00	21.3	85.2	1.70	71.4	1.21
MEAN 1.50	15.1	81.5	1.20	71.6	0.87
S.D. 0.73	6.8	5.6	0.55	3.6	0.40

(d) Extrapolated to include the number of inaccessible burrows
(e) Estimated no. total nests/no. holes
(f) No. occupied/no. known nests

Table 3-4: Summary of burrow characteristics associated with two plots and two transects in the heath habitat.

PLOT LOCATION	PLOT SIZE	SLOPE	NUMBER (OF)						
			HOLES	PARTIAL	CONNECTED	INACCESSIBLE	BURROW ENTRANCES (a)	TUNNELS (b)	KNOWN NESTS (c)
H1	100	0	10	2 1 nest	2	1	8	7	6
H2	100	30	19	1	0	6	18	18	12
Total	200	--	29	3	2	7	26	25	18
Mean	---	--	14.5	1.5	1.0	3.5	13.0	12.5	9.0
S.D.	---	--	6.4	0.7	1.4	3.5	7.1	7.8	4.2
H3	400	0-5	11	0	0	1	11	11	10
H4	400	0-20	14	1	0	2	13	13	11
Total	800	--	25	1	0	3	24	24	21
Mean	---	--	12.5	0.5	0	1.5	12.0	12.0	10.5
S.D.	---	--	2.1	0.7	0	0.7	1.4	1.4	0.7

(a) # holes - # partial

(b) # burrows entrances - # additional entrances (see connected category)

(c) # tunnels - # inaccessible

Table 3-4: continued

	NO. OF HOLES/M^2	ESTIMATED NO. TOTAL NESTS(d)	% NESTS(d,e)	NO. OF NESTS/M^2	% OCCUPIED NESTS(f)	NO. OCCUPIED/M^2
	2.88	32.0	88.9	2.56	77.4	1.98
	0.10	6.9	68.6	0.07	50.0	0.03
	0.19	18.0	94.7	0.18	58.3	0.11
MEAN	0.15	12.4	81.7	0.13	54.2	0.07
S.D.	0.06	7.9	18.5	0.08	5.9	0.06
	0.028	11.0	100.0	0.028	50.0	0.014
	0.035	13.0	92.9	0.033	54.5	0.028
MEAN	0.032	12.0	96.5	0.031	52.3	0.021
S.D.	0.007	1.4	5.0	0.004	3.2	0.010

(d) Extrapolated to include the number of inaccessible burrows
(e) Estimated no. total nests/no. holes
(f) No. occupied/no. known nests

excluding burrows that were possible nests but were inaccessible (Tables 3-2-3-4).

Burrow density was significantly different among habitat types ($x_2^2 = 126.6$, $P < .001$) and was also greater at sloped than at level sites ($x_1^2 = 16.6$, $P < .001$). Within habitat comparisons, however, revealed that burrow density was greater in sloped plots only within grass and forest habitats (grass $x_1^2 = 6.12$, $p < .02$; woods $x_1^2 = 11.6$, $p < .001$; heath $x_1^2 = 2.2$, $p > .05$). No significant difference in burrow density between Bull Gulch (grass/plant) and Gannet Head (grass) was found ($x_1^2 = 2.6$, $p > .05$), however, grass habitat contained 2.7 times as many nests/m^2 as did forest. In addition, no significant difference in the length of occupied burrows between sloped and level plots within grass ($t = .02$, $df = 125$, $p > .05$; overall mean $= 38.4 \pm 10.0$ cm) or wooded ($t = 1.15$, $df = 25$, $p > .05$; overall mean $= 37.5 \pm 12.0$ cm) habitats was found.

3.3.3. Assessment of Physical Habitat Features

The percentage of inaccessible holes in grass, forest and barren habitats was 8.1, 29.3 and 18.5%, respectively. Root systems and the amount of bedrock account for the higher proportion found among the latter types and may reflect certain protective (anti-predatory) benefits asociated with nesting in these habitats (Figure 3-8; see also Myers and Parker, 1965). The higher burrow densities and root systems may also account for the greater proportion of inter-connected burrows in grass (17.8%) and wooded (25.3%) habitats (barren = 3.7%). The percentage of holes less than 20 cm long was 5.9% (grass), 5.3% (forest) and 7.4% (heath).

Figure 3-8: Burrow entrances protected by root system (indicated by arrows).

In Table 3-5, certain physical, competitive and predatory characteristics associated with nesting in the three major habitats are assessed. Based on physical factors (e.g. burrow erosion, flooding, freezing), grass habitat appears high in quality, with forest and barren regions being intermediate and low, respectively. This concurs with degree of habitat use in relation to density. Benefits associated with positive physical features however, may be offset by costs associated with overcrowding and/or vulnerability to predation. The intermediate status of the wooded habitat within each category may therefore reflect why it is more utilized than the heath habitat.

3.3.4. Burrow Occupancy

Sixty-eight percent (155/228) of all accessible nests were occupied by either an adult, egg or chick. Percent occupancy (Table 3-6) was similar between grass and forest habitats at 70.5 and 72.1% and lower within heath plots and transects at 53.8%. No significant difference however, was found ($\chi^2_2 = 4.3$, $p > .05$). The presence of an egg or a chick was used to confirm that a nest was occupied by a breeding pair (≥ 3 yr), the percentage being relatively equal in each habitat (grass, 91.3%; woods, 90.3%; heath 95.2%; combined mean = 91.6% (142/155)). Therefore, a minimum of 62.3% (% occupancy x % breeding) of all known nests were estimated to be occupied by breeding pairs.

Table 3-5: Subjective relative assessment of qualitative habitat features with reference to nesting, competition and predation. Rating Scale: 1 - poor (negative), 2 - fair (neutral), 3 - good (positive) quality.

PHYSICAL HABITAT FEATURES FOR NESTING BY LEACH'S STORM-PETREL	HABITAT		
	GRASS	WOODS	HEATH
BURROWING EASE (a)	2	3	1
TUNNEL EROSION	2	3	1
FLOODING	3	2	1
FROZEN/SNOW BLOCKED (b)	3	1	2
PROXIMITY TO SEA	3	2	2
OBSTACLES (e.g. trees) (c)	2	1	2
OVERALL RATING	15	12	9

(a) Based on soil softness; lack of roots, rocks, etc.
(b) With reference to burrows during colony arrival
(c) With reference to arrival at burrows (i.e. as a possible source of natural mortality)

INTRA- AND INTER-SPECIFIC ASPECTS OF HABITAT OCCUPANCY	HABITAT		
	GRASS	WOODS	HEATH
SUBSTRATE AVAILABILITY (d)	1	2	3
BURROW AVAILABILITY (e)	2	2	3
INTRA-SPEC. COMPETITION	1	2	3
BURROW PROTECTION (f)	1	3	3
OTHER SEABIRDS PRESENT (g)	1	3	2
OVERALL RATING	6	12	14

(d) Based on burrow density (conspecifics)
(e) Based on % occupancy in major habitats
(f) From predators (e.g. foxes, ravens) as a result root systems, bedrock, etc.
(g) As predators (gulls) and competitors (puffins)

Table 3-6: Burrow occupancy in grass, forest and heath habitat plots checked during 12 - 22 July, 1984 (A - Adult; C - Chick; E - Egg).

HABITAT TYPE	PLOT TYPE	PERCENT OCCUPIED (# OCCUPIED / # NESTS)		BURROW OCCUPANT(S)						
				2A,1E	1A,1C	1A,1E	2A	1A	1C	1E
GRASS	Level	74.6	(47/63)	1	-	40	1	2	-	3
	Slope	67.5	(56/83)	1	-	48	2	4	-	1
	Total	70.5	(103/146)	2	-	88	3	6	-	4
WOODS	Level	71.4	(10/14)	-	-	7	1	2	-	-
	Slope	72.4	(21/29)	-	-	20	-	-	-	1
	Total	72.1	(31/43)	-	-	27	1	2	-	1
HEATH	Plots	55.6	(10/18)	-	1	6	-	1	-	2
	Transects	52.4	(11/21)	-	-	8	-	-	-	3
	Total	53.8	(21/39)	-	1	14	-	1	-	5
GRAND MEAN (SUM)		68.0	(155/228)	2	1	129	4	9	-	10

3.3.5. Fox Predation and Reproductive Failure

Nest predation or burrow damage as a result of fox digging was apparent at two grass habitat plots and therefore, if extrapolation is made to all plots, 1.3% (4/314) of all holes checked or 1.5% (4/274) of all confirmed nests would have been dug out by foxes. An adult was killed at each of two nests, one of which also contained an intact (dead) egg. In the other plot, no evidence of kills was found at the two nests (one of which was only slightly dug), suggesting that they had either been unoccupied or were abandoned. Two of the 141 eggs found, were cracked suggesting that egg loss was approximately 1.4%.

3.3.6. Nesting Success

Through the 17 - 20 of October 1985, 129 occupied and unoccupied burrows were re-examined to estimate fledging success and to establish possible error associated with the previous intervention. One previously unoccupied burrow contained a large nest and egg fragments, suggesting that it had been occupied during the first intervention or was established afterwards. No evidence of young or nest material was found in the 13 (8.4%) nests occupied only by adults in July, substantiating their non-breeding status. Seventy-four percent (55/74) of all previously occupied nests were empty, the percentages being similar between grass (78.2% (43/55)) and barren (80.0% (8/10)) habitats, but lower in the wooded habitat (44.4% (4/9)). Based on the proportion of eggs resulting in live young at last visit it can also be estimated that 88-94% (14/16 or 15/17) survived to fledging. No additional predation had taken place at any of the plots since the first intervention.

3.3.7. Ground Survey

Sample plots varied in size and number within and between habitats and therefore, two measures were calculated: (1) the grand mean of holes, in order to obtain a variance estimate and (2) the mean number of holes based on the total number of holes encountered/total area sampled. In the former measure, each plot regardless of size was weighted equally and therefore, plots ≤ 2 m^2 were excluded from the analysis in an effort to increase the homogeneity of plot sizes and decrease the bias towards small plots. This measure (grand mean) is reported in the text (below) only as a comparison with the mean number of burrows, which is believed to provide a more accurate density estimate, treating each plot according to area sampled, and is used to determine storm-petrel numbers.

Grass habitat contained the highest grand mean density of holes (4.2 ± 0.2/m^2). The mean number of burrows was similar between areas of low (0 - 29°) and intermediate (30 - 59°) slope at 4.3 ± 0.4/m^2 and 4.2 ± 0.3/m^2, respectively, and lower (3.6 ± 1.2/m^2) within highly sloped (60 - 90°) areas. Areas with more than 60% fern or tall plant also contained high burrow density (3.8 ± 0.3/m^2) an expected result, because fern habitat is often closely associated with grass habitat. The mean density of possible burrows was 1.2 ± 0.3 holes/m^2 in the forested regions and burrow density increased with slope (shown below). Northern (0.036 ± 0.013/m^2) and southern (0.050 ± 0.008/m^2) heath regions were found to have from four to six times the density of holes as the central region (0.008 ± 0.003/m^2) along the rock backbone of the island.

The barrens also offer suitable nesting substrate along the island's periphery (plots H1 and H2; Figure 2-1) however, this sub-habitat is hard to differentiate from the typical *Empetrum* heath and therefore, its percentage of area is unknown.

Table 3-7 summarizes the number of plots, total area sampled and the number and density of holes/area sampled within each habitat. The sampling scheme was stratified according to slope or geographic location to provide greater flexibility (or precision) in the overall population estimate. Table 3-8 breaks down total area into sub-habitat type and summarizes the density of occupied burrows which was calculated by multiplying the density of holes, by the proportion of holes known to be nesting burrows, by the occupancy rate. For habitats which were sampled (heath, woods and grass) the exact values of occupancy were used in calculating density. For all other sub-habitat estimates (e.g. herb, meadow and mixed), the grand mean occupancy and proportion of actual nesting burrows (of the three sampled habitats) were used to calculate a basic estimate of the breeding population (in nesting pairs) of Leach's Storm-Petrel on Baccalieu Island.

3.3.8. Population Estimate

The total size of the Leach's Storm-Petrel population calculated in Table 3-8 at 2,113,000 pairs is based on a two-dimensional perspective. Analysis of island contour (summarized in Appendix 1) reveals a 31 to 100% increase in area (mean = 1.59 ± 19%) due to topography, suggesting that the total

Table 3-7: Density of holes in different habitat/geographic locations based on a stratified sampling scheme.

HABITAT TYPE	SUB-HABITAT TYPE/ AREA	NO. OF PLOTS	TOTAL AREA OF PLOTS (M^2)	NO. OF HOLES ENCOUNTERED	DENSITY OF HOLES/M^2
HEATH	southern	7	1300.0	59	0.045
	central	5	700.0	6	0.009
	northern	8	800.0	29	0.036
	high dens.(a)	3	300.0	50	0.167
	overall	23	3100.0	144	0,047
WOODS	0 - 29	16	435.0	302	0.694
	30 - 59	6	113.0	180	1.593
	60 - 89	2	29.0	61	2.100
	overall	24	577.0	543	0.941
GRASS	0 - 29	33	154.5	573	3.709
	30 - 59	41	178.8	859	4.806
	60 - 89	3	13.5	50	3.700
	Croucher(b)	6	31.8	95	2.987
	overall	83	378.6	1577	4.166
HERB	0 - 44	14	64.5	306	4.744
	45 - 89	7	61.2	198	3.235
	overall	21	125.7	504	4.010
MEADOW	variable	7	700.0	100	0.143
MIXED	variable	3	62.5	44	0.704

(a) High density - estimated at 5% of total heath habitat

(b) Slope was not measured; estimate based on area only

Table 3-8: Hypothetical population estimate (nesting pairs) of Leach's Storm-Petrels on Baccalieu Island, based on a two-dimensional configuration (for actual estimate, see text).

HABITAT TYPE	SUB-HABITAT TYPE/ AREA	AREA (M^2)	DENSITY OF OCCUPIED BURROWS ($/M^2$)	ESTIMATED NO. OF PAIRS
HEATH	northern and southern	1,231,000	0.0212	26,000
	central	684,000	0.00433	3,000
	high density(a)	65,000	0.0794	5,000
	totals	1,980,000		34,000
WOODS	0 - 29	1,200,000	0.413	496,000
	30 - 59	450,000	0.912	410,000
	60 - 89	150,000	1.21	182,000
	totals	1,800,000		1,088,000
GRASS	0 - 29	87,000	2.21	192,000
	30 - 59	108,000	3.03	327,000
	60 - 89	8,000	2.28	18,000
	Croucher(b)	87,000	1.86	162,000
	non-nesting(c)	38,000	--	--
	totals	328,000		699,000
HERB	0 - 44	65,000	2.78	181,000
	45 - 89	32,000	1.90	61,000
	totals	97,000		242,000
MEADOW	-	68,000	0.0838	6,000
MIXED	-	92,000	0.413	44,000
MARSH, POND BEDROCK AND CLIFF		866,000	--	--
GRAND SUM		5,231,000		2,113,000

(a) Estimated at 5% of total heath habitat

(b) Slope not measured; estimate based on area only surface area of Baccalieu Island is actually 832 ha. This procedure will tend to overestimate habitats common on flatter ground (e.g. heath) and underestimate habitats common on slopes (e.g. grassy areas), but will result in a more conservative estimate. Therefore, the estimated increase attributed to this factor, assuming all habitats are similarly affected, results in a population estimate of 3,360,000 pairs, with lower and upper limits (set at 99% confidence) being 3,043,000 to 3,677,000, respectively.

3.4. DISCUSSION

The colonies of Leach's Storm-Petrel in Newfoundland are vastly larger than any other known colonies in the Atlantic. For this reason Huntington (1963) contended that they may greatly influence other colonies through the interchange of individuals and that destruction of one, may indirectly influence recruitment in another (see also Huntington and Burtt, 1972). Based on the results obtained above, Baccalieu Island supports the largest of all known Leach's Storm-Petrel colonies and could play a significant role in influencing nearby and distant populations. Therefore, it is of utmost importance to identify the role and impact of red foxes, as well as the selective pressure they may impose on the storm-petrel population of Baccalieu Island.

3.4.1. Nest Site Competition, Burrow Occupancy and Habitat Use

Storm-Petrels nest in a variety of habitats on Baccalieu Island. Occupation of sub-optimal or less preferred areas is generally a result of high intraspecific competition (Lack, 1968), which typically occurs at the center of a species' breeding range (Buckley and Buckley, 1980). Eggs outside burrow entrances have also been suggested to reflect conditions of high nest site competition (Huntington, 1963). Thirty-two percent (72/228) of all (well-developed) burrows checked were empty. This suggests, in agreement with Huntington's (1963) findings, that availability of nest sites is not a critical factor at central colonies. Eggs outside burrow entrances were also more commonly found in the forest habitat, where burrow density was intermediate, suggesting that other factors may actually be responsible for this.

Sixty-eight percent (155/228) of all accessible storm-petrel nests were occupied by either an adult, chick or egg, and this result concurs with the 68.5% (50/73) for Baccalieu Island recorded by Grimmer (1981). As well, 62% of all known nests were estimated to be occupied by breeding pairs, which falls within the 53-83% range found by Morse and Buchheister (1979) on Matinicus Rock. Wilbur (1966), suggested that the rarity of dead eggs or chicks in burrows indicates a high survival rate among young storm-petrels between hatching and fledging. Although based on a small sample size, the proportion of eggs resulting in live young near fledging was 88-94%, similar to other studies which have reported fledgling success rates of 87-99% (Wilbur, 1969) 66-82% (Morse and Buchheister, 1979), 73-87% (Grimmer, 1981).

On the basis of burrow density, the grass region appears to be preferred nesting habitat, most likely a factor related to its coastal location and relatively soft nesting substrate. Overall however, most storm-petrels nested in the woods, a result of this habitat's large area and moderately dense nesting concentrations. Storm-petrels burrow easily into the forest floor, especially around the root systems of trees. The rate of burrow occupancy was similar between these two habitats. In contrast, the relatively insignificant number of burrows and lower occupancy levels within the barren heaths probably reflect that this habitat is sub-optimal or newly occupied, possibly due to a hard burrowing substrate and/or lack of drainage (e.g. Storey and Lien, 1985).

3.4.2. Selective Pressures Associated with Predation

Predation imposes selective pressures on the storm-petrel population in at least two ways. First, foxes prey heavily on storm-petrels in the grass habitat. The high nesting density may act to attract predators (Krebs, 1971; Fretwell, 1972), although the relative (vulnerability) risk to any one nest may actually be lower (Hamilton, 1971). Second, the seasonal flux of a prey population in relation to the constant demands of a predator population may direct selective pressures against early and late breeders (Ashmole, 1963; Patterson, 1965; Nisbett, 1975; Montevecchi, 1977). This situation is apparent on Baccalieu Island, where surplus killing is most evident early and late in the breeding season (and most pronounced in the wooded habitat; see Chapter 2). This suggests that early breeding adults and fledglings of late breeders are at greatest risk. Therefore, predation pressure may operate for the selection of safer habitat sites, as well as having a synchronous effect on the breeding phenology of the storm-petrel population of Baccalieu Island (see also Gochfeld, 1980).

3.4.3. Predatory Impact on the Leach's Storm-Petrel Population

The average daily food intake of a red fox has been calculated at 1 lb (Scott, 1941), 378 g (Lockie 1959) and 223 kcal/kg body weight/day (Vogtsberger and Barrett, 1973; see also Sargeant, 1978). Based on a population of 12 foxes (increased to provide for a conservative estimate; see Chapter 2 for actual numbers) over a 832 ha area, and assuming a mean weight of 5.2 kg (Northcott 1974), red fox biomass would be .075 kg of fox tissue/ha. At a mean weight of 50 g (Montevecchi, et al., 1983; see also Gross, 1935; Palmer, 1962) and an adult population size of 6,720,000 individuals, adult storm-petrel biomass approximates 403.85 kg of bird tissue/ha. At an energy density of 12.13 kJ/g for storm-petrel (Montevecchi et al., 1983), 4,898,652 kJ/ha of storm-petrel are available. Based on the fox biomass calculated above and an average prey intake of 934 kJ/kg body weight/day (equivalent to 223 kcal/kg; Vogtsberger and Barrett, 1973), 70.1 kJ/ha/day of storm-petrel would be taken. Therefore, it is estimated that if the foxes of Baccalieu Island utilize storm-petrels exclusively, they would consume 25,587 kJ/ha/yr (21,288,384 kJ/yr), which is equal to 0.5% of the available adult storm-petrel tissue. This is equivalent to 35,100 adult storm-petrels per year.

Natural mortality experienced by adult Procellariiformes is suggested to be ~10% (Morse and Bucheister, 1979). Thus, 672,000 recruited breeders would be required annually to maintain the adult nesting population on Baccalieu Island. Assuming that 92% (3,091,000 pairs) of storm-petrels found in burrows were breeding adults (Table 3-6), that 66% (a minimum) of the chicks fledged (Morse and Buchheister, 1979), and that at least 37% (estimated minimum for shearwaters calculated by Serventy, 1966; see also Harris, 1973; Perrins et al., 1973) of the fledglings reach breeding age (3 years or more), then 755,000 young of the year would survive to breed. In view of the many years of adult reproductive viability (J. Lien, unpubl. d~~ata)~~, this level of recruitment would maintain or increase the current population level in the face of resident fox predation, which would be 5.2% of natural adult mortality at most.

The above estimate of predatory impact assumes that foxes eat only storm-petrels during the whole year and therefore, is probably high because: (1) other avian species (e.g. puffins, kittiwakes) are taken, (2) energy available in the form of eggs and young was not included in the estimate of biomass, (3) other foods are available (e.g. berries, insects) and (4) storm-petrels are present on the island for only 6 - 7 months (late April to early November) of the year; however, caching and surplus killing may account for this difference. In an effort to account for factors 1 and 3, data collected on the predatory behaviour of red foxes (Chapter 2) were incorporated into the estimate of impact. Table 3-9 shows the weight, energy density and energy value/individual of the different avian prey. Based on field remains, lardered prey and scat analysis, the number of individuals taken per species was calculated (Table 3-10).

Table 3-9: Wet weight, energy density and energy value of different avian prey species.

SPECIES	WEIGHT (g)	ENERGY DENSITY (kJ/g)	ENERGY WORTH (kJ/bird)
LEACH'S STORM-PETREL	50 (a)	12.13 (h)	606.5
ATLANTIC PUFFIN	445 (b)	11.75 (i)	5228.8
BK-LEGGED KITTIWAKE	440 (c)	11.75	5170.0
HERRING GULL	1115 (d)	11.75	13101.3
NORTHERN GANNET	3130 (e)	11.75	33777.5
COMMON MURRE	965 (f)	11.75	11338.8
PASSERINE	50 (g)	10.93 (j)	546.5

SOURCE:

(a) Montevecchi et al. (1983)
(b) Montevecchi (unpubl. weights for Baccalieu Island)
(c) Combined mean weights (Belopol'skii, 1957; Swartz, 1964)
(d) Threlfall and Jewer (1978)
(e) Montevecchi (unpubl. weights for Baccalieu Island)
(f) D. Cairns (pers. comm.)
(g) Assumed
(h) Calculated from Ricklefs, White and Cullen (1980)
(i) Calculated from Montevecchi, et al. (1984)
(j) Brisbin (1968)

Table 3-10: Estimated numbers of avian prey taken annually by red foxes on Baccalieu Island; based on the energetic requirements of 12 adult foxes (21,288,384 kJ/yr), calculated using the proportions of field remains, lardered prey and scat/remains.

SPECIES	REMAINS	LARDERED PREY	SCAT(a)
LEACH'S STORM-PETREL	31,380	33,205	27,451
ATLANTIC PUFFIN	110	118	202
BLACK-LEGGED KITTIWAKE	164	86	304
HERRING GULL	45	--	84
NORTHERN GANNET	6	2	11
COMMON MURRE	4	4	6
PASSERINE	--	--	484

(a) Based on corrected wet weight; the unknown/large seabird (scat) categories were broken down relative to known proportions found as avian remains

Table 3-11: Estimated predatory impact on the principle avian breeding populations of Baccalieu Island.

SPECIES	NUMBER TAKEN (a) (Mean ± S.D.)		POPULATION SIZE (No. of Indiv.)	IMPACT (%)
LEACH'S STORM-PETREL	30,679	2940	6,720,000	0.5
ATLANTIC PUFFIN	143	51	59,000 (b)	0.2
BLACK-LEGGED KITTIWAKE	185	110	26,000 (b)	0.7
NORTHERN GANNET	6	5	930 (b)	0.6
COMMON MURRE	5	1	7,052 (b)	0.1

(a) Mean ± S.D. of number taken; based on lardered prey, field remains and scat/remains (Table 3-10)

(b) Montevecchi and Tuck (1986)

Estimates of impact are summarized in Table 3-11. Fox predation appears to account for losses of $\leq$ 1% of the adult breeding component of each seabird species on Baccalieu Island.

Fox predation on the storm-petrels of Baccalieu Island is considered of minimal importance. The foxes may have been in relatively constant association with the seabirds since 1914, and it is possible that predator and prey share a stable ecological relationship. The large size of the storm-petrel population and the growth limitation of the fox population due to the lack of alternative prey during winter months are two factors which may keep predatory impact in check.

Chapter 4

STUDIES ON THE CACHING BEHAVIOUR OF CAPTIVE RED FOXES

4.1. INTRODUCTION

The basic assumption of theoretical models of optimal foraging is that organisms which feed efficiently obtain maximum fitness, because efficient foraging behaviour may increase the time and energy available for other activities such as territorial defence and reproduction (Emlen, 1966; MacArthur and Pianka, 1966; Schoener, 1971; Pearson, 1974; Pyke, Pulliam and Charnov, 1977; Andersson and Krebs, 1978). Many predictions about foraging patterns on the basis of net energy gain per unit time can be made from these models (Pyke, et al. 1977; Hainsworth and Wolf, 1979).

Schoener (1969) differentiated energy maximization and time minimization as two alternative strategies with which to maximize foraging efficiency. Energy maximizers seek to gain the greatest amount of energy possible within a given time period, whereas time minimizers seek to minimize the time necessary to obtain a given amount of food (Morse, 1980). Although both strategies lead to a maximization of food intake while foraging, a time minimizer will quit once its needs for the day are met, whereas an energy maximizer will continue foraging. This latter strategy is used by animals that hoard or cache food. Energy maximization may increase predator efficiency by helping to ensure an adequate food supply during times of shortage.

The red fox is known to hoard food in small, multiple caches, each containing from one to a few items (Kruuk, 1964; Fox, 1971; Henry, 1976; Macdonald, 1977a) and food availability appears to be an important determinant of caching (Kruuk, 1964; Henry, 1976). Food preference (Macdonald, 1977b) and the quality of the food item encountered (Henry, 1977) also affect whether and to what degree an item will be cached.

The act of caching begins when a fox carries off a prey item while searching for an appropriate burial site. Once a spot is chosen, the fox digs a hole with its forepaws while holding the prey item in its mouth (Figure 4-1). The item is then pushed into the hole, which the fox covers and packs down with dirt, leaves or other nearby litter using its muzzle (Figure 4-2). Each component of this hoarding sequence may be considered in view of its possible function. Prey pickup to caching initiation is a measure of travel time and the distance a fox travels until caching. Caching time is related directly to the quality of a food item (Henry, 1976) and may reflect the depth or degree to which an item is hidden. Time to subsequent pickup probably reflects a fox's motivation to return for more prey.

Figure 4-1: Fox digging a cache while holding the prey item in its mouth.

Figure 4-2: Fox camouflaging the cache with dirt and nearby organic litter using its muzzle.

The present study investigated the effects of short term food fluctuations on the different components of caching behaviour. The general question posed was: does the fox make different decisions about the immediate consumption and caching of food as functions of hunger state and food availability? Although other factors may effect hoarding behaviour (see Curio, 1976), food abundance and hunger state should be major external and internal variables that determine on what or how an organism feeds (Hainsworth and Wolf, 1979).

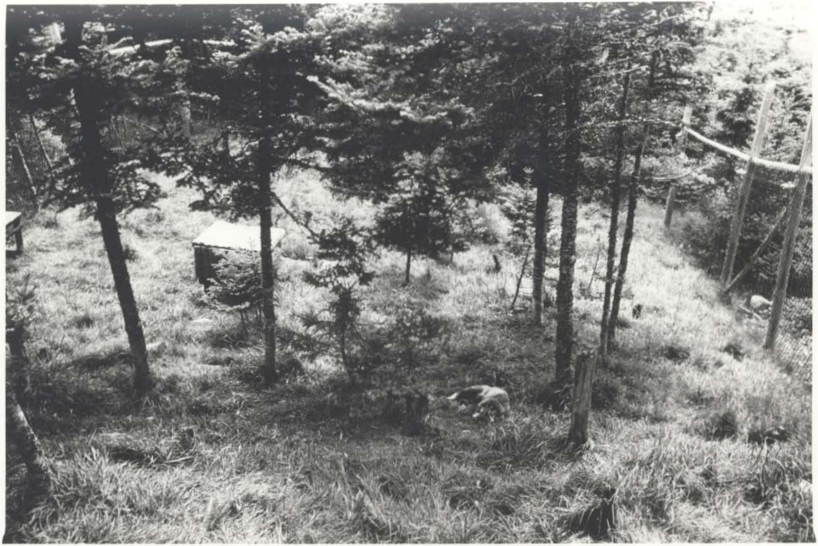
4.2. MATERIALS AND METHODS

Research was carried out at Salmonier Nature Park (47° 15' N, 53° 18' W) located 65 km SW of St. John's, Newfoundland. A hand raised male and female red fox were used, and experiments were conducted in a semi natural 10 x 16 m enclosure (Figure 4-3). Observations were made from an elevated wooden platform at the N end of the compound.

4.2.1. Procedure

Experiments at Salmonier involved placing hens' eggs into the enclosure and monitoring the foxes' behaviour. Handling, caching times and cache locations were recorded. Foxes were food deprived for 1, 3, 24 or 48 hr before testing, and prey abundances of 3, 6, 12 and 24 eggs were randomly run at different levels of food deprivation. By keeping prey type constant the introduction of an additional variable (e.g. prey quality; Henry, 1976) into the experiment was avoided. Thus, changes in behaviour were more likely to be

Figure 4-3: Enclosure used in caching experiments at Salmonier Nature Park.



due to the independent variables. Recovery of cached eggs was assessed by examining the enclosure for discarded eggshells 1-3 hr after the test run and afterwards, on a daily basis.

4.2.2. Design

Hoarding behaviour was partitioned into three categories: 1) pickup, carry and search for a cache site, 2) time spent caching and 3) latency to subsequent food pickup within a trial. These measures reflect the natural hoarding sequence of foxes (see Henry, 1976). Individuals sometimes returned to continue caching, or relocated and reburied food at the end of a trial (after all eggs were cached or eaten which usually required < 45 min.); these times were not recorded, since around the clock observation would be necessary to note all such behaviour.

Correlations between pickup, caching and latency to subsequent pickup measures were low suggesting independence (highest correlation revealed 8% variation in common). Therefore, each time measure, as well as total time, was analyzed separately using a within subject completely crossed 4 x 4 x 6 x 2 way repeated measures design with abundance and hunger state having four levels each, observation number (accounting for an order effect) having six and two subjects.

4.3. RESULTS

4.3.1. Partitioning of Hoarding Components

When foraging on the same patch of food each fox secured about half the items (female 49.4% (84/170), male 50.6% (86/170)). Carrying, caching and latency to subsequent pickup times ranged from 0 to 65 sec (Figures 4-4, 4-5 and 4-6). Modal (and mean ± S.D.) pickup time was 5-10 sec (12.9 ± 8.5 sec), caching time 20-25 sec (23.2 ± 11.9 sec) and subsequent pickup time 5-15 sec (14.6 ± 10.2 sec), respectively. A greater proportion of time was allocated to prey caching than to other component behaviours. Overall hoarding effort ranged from 10 to 110 sec (mean = 50.5 ± 19.9 sec). A tendency for the female to hoard food items faster than the male (mean overall hoarding time: female = 44.6 ± 20.6; male = 56.7 ± 17.2; N = 64) was suggested (Figure 4-7).

The mean carrying (M1), caching (M2), latency to subsequent prey pickup (M3) and overall hoarding times (M0) under each of the abundance and hunger state manipulations are presented in Table 4-1. Neither hunger state nor food abundance significantly altered total hoarding time (M0), though an abundance effect was almost realized ($F_{(3,3)} = 7.16$, $p < .10$). Increased hunger state ($F_{(3,3)} = 260.40$, $p < .001$) and increased abundance ($F_{(3,3)} = 81.13$, $p < .005$) significantly decreased time spent in search of a cache site (M1)(Figures 4-8 and 4-9). Additionally, their interaction (Figure 4-10) was significant ($F_{(9,9)} = 4.57$, $p < .025$). However, no significant effect on the time

Figure 4-4: Frequency distribution of prey pickup to onset of caching time intervals; 5 = 0-5 sec., 10 = 5-10 sec., etc...

PICKUP TIME

FREQUENCY DISTRIBUTION

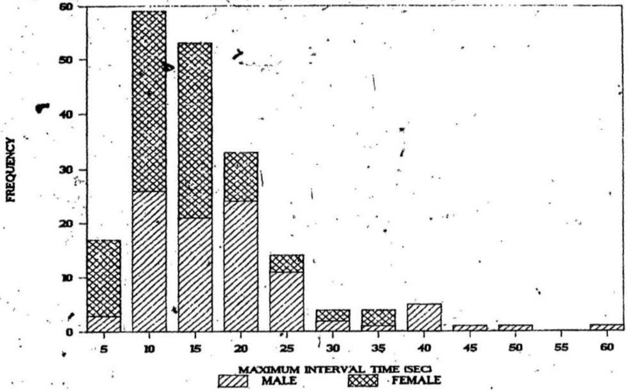


Figure 4-5: Frequency distribution of caching times; 5 = 0-5 sec., 10 = 5-10 sec., etc...

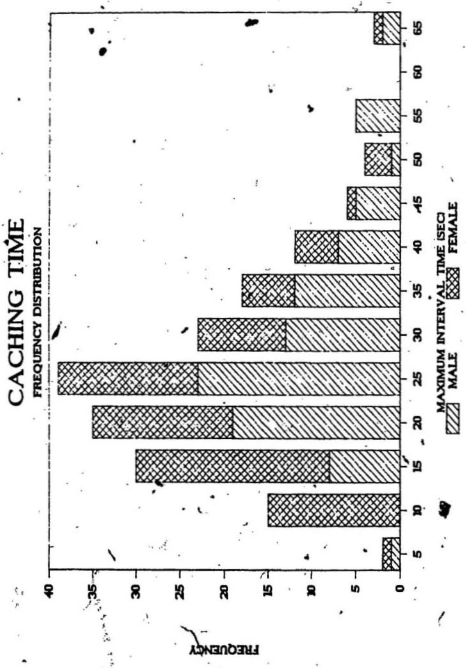

CACHING TIME
FREQUENCY DISTRIBUTION
FREQUENCY
0
5
10
15
20
25
30
35
40
5
10
15
20
25
30
35
40
45
50
55
60
65
MAXIMUM INTERVAL TIME (SEC)
MALE
FEMALE

Figure 4-6: Frequency distribution of caching time to subsequent prey pickup time intervals; 5 = 0-5 sec., 10 = 5-10 sec., etc...

LATENCY TO SUBSEQUENT PICKUP TIME

FREQUENCY DISTRIBUTION

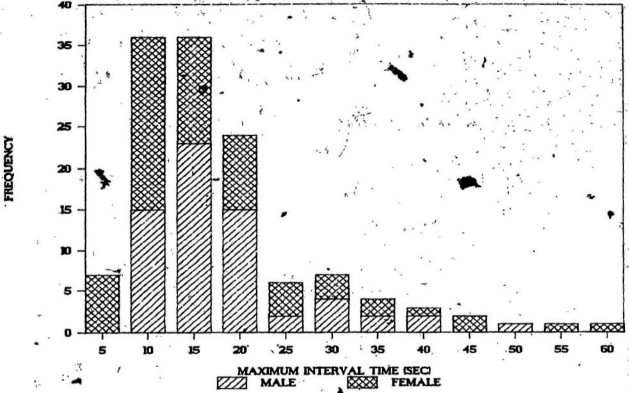


Figure 4-7: Frequency distribution of overall hoarding time; 5 = 0-5 sec., 10 = 5-10 sec., etc...

OVERALL HOARDING TIME

FREQUENCY DISTRIBUTION

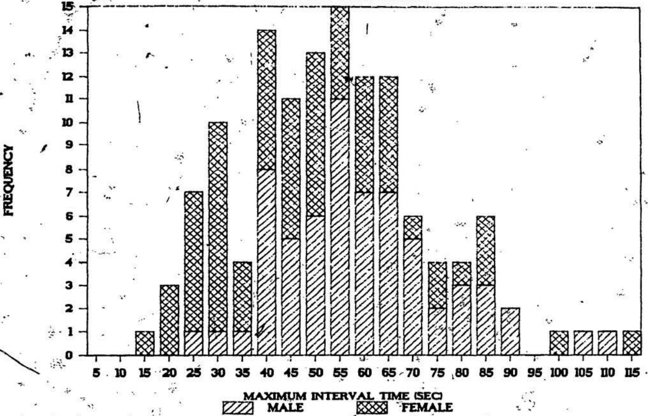


Table 4-1: Overall hoarding time (sec); Mean ± S.D. times during hunger (H) and abundance (A) manipulation.

		ABUNDANCE (NO. OF EGGS)															
		3				6				12				24			
		FOOD DEPRIVATION (HR)															
		1	3	24	48	1	3	24	48	1	3	24	48	1	3	24	48
Pickup to Begin Caching *	$\bar{X}$	12.6	19.3	12.1	13.2	22.8	21.3	16.1	12.2	10.0	11.8	14.3	11.9	8.0	6.8	8.2	7.4
	S.D.	9.0	7.5	4.7	7.1	12.9	12.5	9.4	8.9	4.9	5.2	6.2	4.8	3.7	3.8	4.1	5.8
Caching	$\bar{X}$	19.5	27.[illegible]	24.2	29.2	26.6	32.7	27.3	22.5	22.4	21.0	24.4	25.9	13.9	18.4	18.8	16.3
*	S.D.	13.2	10.9	14.5	13.3	14.1	15.0	14.4	10.3	14.2	9.2	6.6	8.9	7.2	7.8	10.0	6.8
Latency to Next Pickup **	$\bar{X}$	10.5	21.8	10.9	10.5	12.9	18.8	16.4	14.4	14.3	11.6	16.0	12.8	18.6	13.0	22.3	10.8
	S.D.	9.2	11.2	5.6	5.2	10.1	9.0	9.2	17.4	6.0	3.7	6.0	5.0	16.7	7.6	16.8	8.4
Total	$\bar{X}$	36.0	65.3	47.8	49.5	60.1	79.1	61.9	54.9	45.5	45.0	57.1	47.5	38.1	39.6	48.5	32.5
**	S.D.	8.8	22.3	16.2	12.6	17.0	23.3	19.1	15.9	17.2	11.8	11.9	10.7	24.1	14.9	20.0	17.8

COMPILED ACROSS LEVEL C
* 12 OBSERVATIONS/CELL
** 8 OBSERVATIONS/CELL

Figure 4-8: Mean hoarding time (partitioned into pickup, caching and latency to subsequent pickup components) vs hunger state manipulation.

MEAN HOARDING TIME VS HUNGER STATE

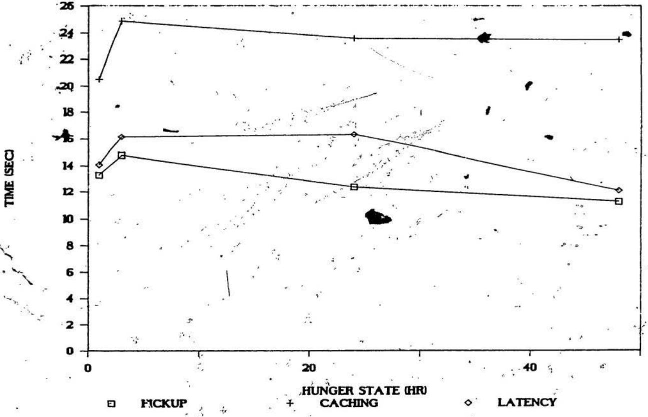


Figure 4-9: Mean hoarding time (partitioned into pickup, caching and latency to subsequent pickup components) vs prey abundance manipulation.

MEAN HOARDING TIME VS ABUNDANCE

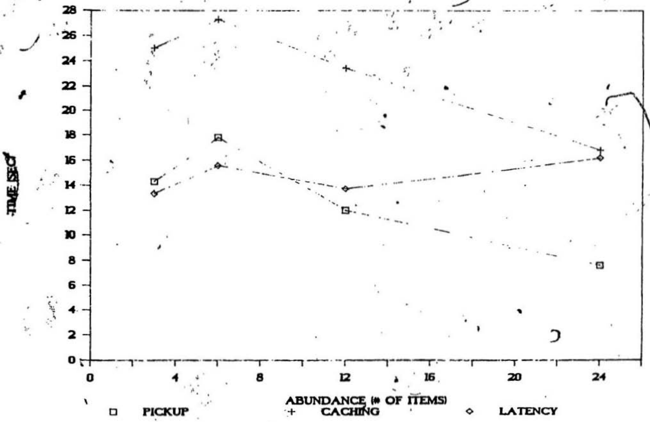
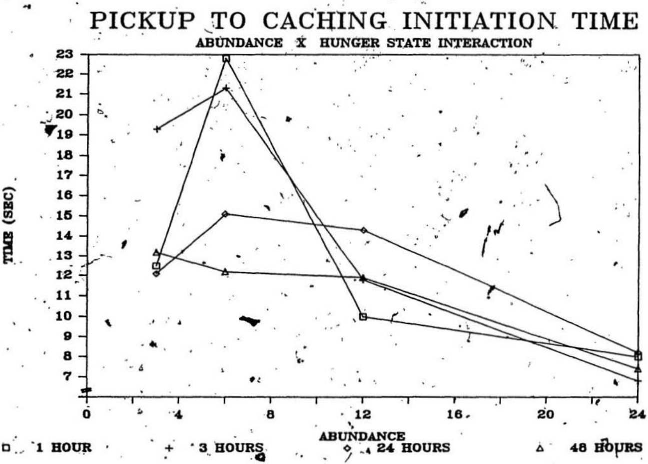


Figure 4-10: Hunger state vs prey abundance interaction



PICKUP TO CACHING INITIATION TIME

ABUNDANCE X HUNGER STATE INTERACTION

spent caching (M2) or the latency to subsequent pickup (M3) was found. Similarly, no sequential effects were found due to the order in which eggs were taken on any of the measures tested (see Table 4-2).

4.3.2. Analyses of Interaction and Simple Main Effects for Measure 1: Pickup Time

Analyses of simple main effects were performed in order to isolate possible sources of the interaction effect (Winer, 1971; Keppel, 1973). Although these tests failed to identify the locus of significance, the effects of A at H1 and H2 were almost realized ($p < .10$ especially in the former). The interaction was then partitioned into independent trend components. The linear component was significant ($F_{(1,9)} = 11.10$, $p < .01$) accounting for 52.6% of the interaction sum of squares. Trend analysis on simple main effects further revealed that the linear trend of factor A at H2 (6 h) was significant in itself ($F_{(1,9)} = 8.23$, $p < .025$), reflecting an overall negative slope (Figure 4-10). Therefore, pickup to caching initiation time intervals decreased with increased levels of abundance at 3 h food deprivation.

Although an interaction was found, the main effects of abundance and food deprivation were significant and because the experimental design was completely balanced (each measure being independent of the other), differences between means within significant trends of main effects were evaluated post-hoc, using the Student-Newman-Keuls test (Sokal and Rohlf, 1969). Mean pickup to caching initiation time intervals were found to differ significantly

Table 4-2: Analysis of variance summary table.

SOURCE	SS	df	MS	F	P
A (ABUNDANCE)	2654.89	3	884.96	81.13	<.005
AxS	32.72	3	10.90		
H (HUNGER)	339.80	3	113.26	260.40	<.001
HxS	1.30	3	0.43		
C (ORDER)	561.96	5	112.39	1.45	N.S.
CxS	387.54	5	77.50		
AxH	1115.67	9	123.96	4.57	<.025
AxHxS	244.00	9	27.11		
AxC	377.64	15	25.17	1.87	N.S.
AxCxS	201.56	15	13.43		
HxC	805.97	15	53.73	0.71	N.S.
HxCxS	1124.83	15	74.94		
AxHxC	1543.67	45	34.30	0.50	N.S.
AxHxCxS	3046.58	45	67.70		

N.S. = Nonsignificant difference

between hunger states 1 hr ($p < .05$), 3 hr ($p < .01$) and 24 hr ($p < .05$) relative to 48 hr, and 3 hr relative to 1 hr and 24 hr ($ps < .01$) (see Figure 4-9). Mean travel time to cache sites were also significantly altered ($p < .05$) between abundance levels of 6 and 24 prey items (see Figure 4-8). These results suggest a possible decrease in the time spent searching for a cache site with increased hunger or prey abundance.

4.3.3. Cache Recovery

Foxes cached 97% (298/307) of the eggs set out. Successful recovery and use of cached food averaged 75.2% (N $\doteq$ 224) varying from 41% (5/12) to 95% (23/24) (Table 4-3). On average, 54% of the available caches were recovered within 192 hr of being set out, at a mean rate of 9.25% recovery/day (Figure 4-11).

4.4. DISCUSSION

Foxes exhibited an increased motivation to cache with increased hunger levels and food item abundance. Primarily, the time spent in search of a suitable cache site decreased with increased prey abundance at an intermediate level of food deprivation. A similar effect however, was almost realized at the lowest level of food deprivation, suggesting that at low levels of hunger, foxes are more motivated to begin caching when presented with higher levels of prey abundance. By doing so, foxes may act to minimize travel time (or distance travelled), which in turn, may maximize the amount of time available for foraging (Macdonald, 1976, 1977a). This strategy is primarily advantageous and occurs when foraging for food available for a limited period of time (e.g. in

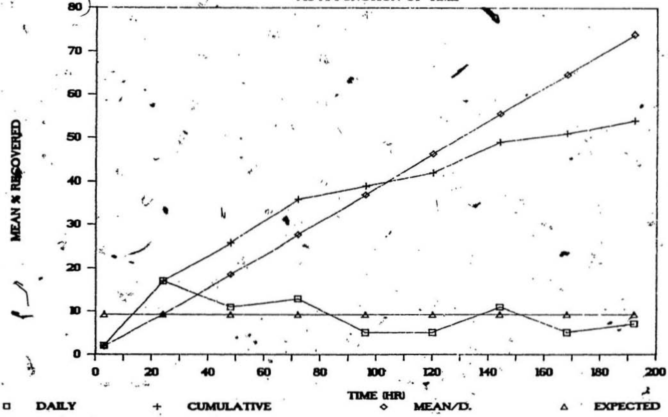
Table 4-3: Results showing that cached food is recovered and eaten (see also Macdonald, 1976).; Lines = combined recovery.

	NUMBER OF EGGS	
SET OUT	CACHED	RECOVERED AND EATEN
12	11	8
12	12	6
6	6	13
12	12	
12	12	23
14	13	10
24	24	15
36	35	30
12	12	5
14	14	12
12	11	
10	10	
3	3	20
24	24	6
12	12	
8	8	
12	12	
6	6	
24	23	
18	16	61
24	22	15
N = 307	298	224
% = -	97	75

Figure 4-11: Mean recovery of cached prey/day; Daily = observed proportion recovered/time period, Cumulative = cumulative proportion recovered, Mean/D. = cumulative mean/day based on the observed overall mean of 9.25%, Expected = expected daily cache recovery based on 9.25%

MEAN PERCENT CACHE RECOVERY

AS A FUNCTION OF TIME



the presence of competitors). After depletion of a food source, an individual may return to rebury or relocate cached prey more securely, and some individuals in the wild have been observed doing so (Errington, 1967; Henry, 1976; pers. obs.). This may be related to why an abundance effect was almost realized in overall hoarding time.

General inspection of main effects (Figures 4-8 and 4-10) reveals a sharp initial increase in caching initiation time with both hunger (1 - 3 hr) and abundance (3 - 6 items) states. Yet, only the hunger difference was significant. Possibly, some motivational equilibrium is reached, after which, slight increases in motivation occur, which is reflected in the lower mean cache initiation times at 24 hr and 48 hr of food deprivation. Significant effects of food item abundance were found only between 6 and 24 item levels, suggesting that only relatively large differences in prey availability will trigger differential responses in travel time to caching. The interaction between hunger and abundance suggested that intermediate levels of hunger (or abundance) may be more important than originally expected in influencing caching behaviour.

Foxes allocated approximately twice as much time to the caching prey (M2) than to searching for a cache site (M1) or their subsequent return to a prey patch (M3). This is probably a consequence of the small size of the enclosure. Caches took on average 23.2 ± 11.9 s (N = 192) to complete, similar to the times recorded by Henry (1976) for wild foxes (24.0 ± 16.5 s, N = 77). By keeping food type constant, it was expected that the effects of manipulating hunger or abundance would be more clearly recognized. However, no significant differences were found, suggesting that caching time (M2) was independent of prey availability and hunger. As proposed by Henry (1976), prey quality may determine the intensity (e.g. depth) at which individuals bury prey.

No general conclusion can be drawn about the foxes' return time to a prey patch, and enclosure size may have contributed largely to the nonsignificance of this measure. Although foxes would wait or travel around the enclosure for some time before returning, as with the caching initiation measures, their paths were generally more direct. Under natural conditions, return times are probably a function of distance originally travelled (pers. obs.) and therefore, would be expected to vary with travel distance.

Between subject variation in all measures may have resulted from individual, sex or hierarchical differences. These factors are not mutually exclusive. In this study, the female was both timid and subordinate, suggesting that these factors may have been responsible for her faster hoarding times.

The recovery of 75% of the caches in this study was lower than the 96% cache recovery level found by Macdonald (1976). This discrepancy is probably due to two factors: prey preference (Macdonald used mice; see Macdonald, 1977b) and inaccessibility (due to frozen or inaccessible caches). In the American Kestrel (*Falco sparverius*), Mueller (1974) noted that retrieval of cached food remained constant, even during food deprivation. Experiments at Salmonier also suggest that cache recovery is relatively constant at a mean rate of 9.25%/day. The number of caches recovered, however, does decrease over time (Figure 4-11). This pattern may be due to conservative cache use or a decrease in encounter rate as the number of caches utilized increases. In either case, caching is an efficient predatory strategy ensuring prey availability for future utilization.

From the foregoing experiments and discussion it seems reasonable to conclude that certain aspects of hoarding behaviour (i.e. pickup to caching initiation interval) in foxes may be governed by food availability. However, further testing using a larger number of subjects is necessary to clarify this relationship. Hunger state and prey abundance may also act as proximate signals influencing certain responses within the hoarding sequence. The adaptive significance of such a mechanism would be in monitoring the environment for fluctuations in prey availability, while at the same time motivating individuals to act accordingly. In this way, an individual's competitive ability and chances of survival could be enhanced.

Chapter 5

GENERAL DISCUSSION

5.1. PREDATOR-PREY CONSIDERATIONS

The introduction or incidental occurrence of terrestrial predators to predator-free seabird islands can potentially alter the stability of local populations. As with all predator-prey relations however, the impact of predation is dependent upon the interaction of a series of behavioural, ecological and geographic variables and therefore, the influence of an introduced predator on its prey varies widely according to specific circumstance (Moors and Atkinson, 1984). While the effects of predation on the dynamics of prey populations are poorly understood, their influence is principally dependent on: the densities of the predator and prey populations, the characteristics of the predator and prey and the density and quality of alternative foods for the predator (Leopold, 1933; Holling, 1959). Because each of these variables exerts an influence on the others, the overall effect of any one may depend on changes in another (Holling, 1959).

5.1.1. Predator Density

The survival time of a colonizing population is theoretically dependent on its size (MacArthur and Wilson, 1967) and to be successful, an introduced species should have a high rate of population increase (Andrewartha, 1971; Gliwicz, 1982). Therefore, successful colonization is closely dependent on an island's ecology (Jones and Whitehead, 1969). On isolated islands, mammalian populations are limited in growth by survival and reproductive potential, whereas on partially or temporarily isolated islands, the rate of immigration also acts to determine successful colonization. Although loosely interwoven populations are more stable in terms of rates of fluctuations and extinctions (Emlen, 1984), individuals in closed populations are affected by common (local) environmental and behavioural factors (e.g. local food availability, social spacing mechanisms) and once established, their populations may also achieve stability. Through ecological release (MacArthur and Wilson, 1967; Ricklefs, 1976) or density compensation (Williamson, 1981) island populations often occur at densities higher than those of neighboring mainland populations (Krebs, Keller and Tamarin, 1969; Watson, 1971; Gliwicz, 1982).

Red foxes are believed to have colonized Baccalieu Island ca. 1959, but may have been there 50 years before. Although pack ice occurs in the vicinity from February to April and theoretically, foxes could reach the island as often as two out of every five years; on average, an ice bridge would be available for fox crossings only three weeks/year of ice occurrence (Davidson, 1985; pers. obs.). Furthermore, dispersal among foxes occurs principally in the fall from

September to December (Sheldon, 1950; Lloyd, 1975; Storm et al., 1976). Given these limitations, the fox population on Baccalieu Island is probably a relatively closed system, highly dependent on local ecological conditions. Although closed populations are usually highly unstable, the lack of food on Baccalieu Island during late winter and spring (when ice is present) may force some individuals to emmigrate and because "dispersal may reduce the impact of stochastic disturbances on population variation" (Vance, 1980), a relatively stable population may exist (Watson, 1971; Emlen, 1984). Territoriality among foxes may further dampen population fluctuations (Williamson, 1981; Schantz, 1984) and limit population growth (Dasmann, 1964; Schantz, 1984; cf. Emlen, 1984).

5.1.2. Prey Density

Many studies have shown that fox predation can exert both short- and long-term effects on gull populations (Kruuk, 1964; Kadlek, 1971; Patton and Southern, 1977; Southern et al., 1985). These findings, however, cannot be extended to include the potential effects of predation on all seabird species. First, most gulls are ground nesters and therefore, eggs and young are highly visible and accessible to terrestrial predators. As well, adult gulls and terns are vulnerable to nocturnal predation (Kruuk, 1964; Nisbett, 1975). Second, although gulls are known to mob predators, mobbing may prove ineffective against a large terrestrial predator such as the fox. The last and most important point is that gulls commonly breed in small colonies (Salomonsen, 1979), and therefore the ratio between predator and prey could easily be offset disturbing colony stability.

Predation also effects mortality and productivity in large seabird colonies, but, the overall impact may be comparatively small (Murie, 1959; Morse, 1980; Gaston, et al., 1985). Stonehouse (1962) contended that on Ascension Island the success of terns despite heavy and consistent predation by cats was in part, the result of large numbers of nesting birds (cf. Williams, 1984). Similarly on Baccalieu Island, the massive breeding population of storm-petrels and their reproductive potential appear to outweigh the predatory pressure imposed by the resident foxes. However, considering the potential destructiveness of canids (Errington, 1948), under conditions favouring predator population growth, even the largest of seabird colonies may experience intense predatory pressures.

5.1.3. Predator Characteristics

Rats (*Rattus spp.*), feral cats (*Felis catus*), arctic and red foxes have commonly been implicated in seabird population declines, in part, a result of their more frequent introduction and small burrowing species (e.g. auklets, petrels) have experienced greatest depredations. However, the rat and cat have been implicated as greater threats to seabird colonies (Fisher and Lockley, 1954; Moors and Atkinson, 1984). Compared to foxes, both are more fecund with respect to multiple litters per year (Nowak and Paradiso, 1984) and exhibit greater social tolerance increasing their potential density. As well, rats and cats are typically not native to the local fauna and rats are often capable of entering small burrows. All of these factors increase a predators' chances for successful colonization and the extent of potential damage.

The red fox has the most extensive worldwide distribution among the canids (Stains, 1975; Zimen, 1980), and its success is partly related to an ability to adapt to a variety of habitats and circumstances (Ables, 1975; Lloyd, 1980). Most studies have shown that the major foods taken by foxes are small rodents, hares, rabbits, wild fruits, berries and insects (Korshgen, 1959) and in Newfoundland, hares and landbirds are important (Dodds, 1955; see also Mercer, Hearn and Finlay, 1979). In comparison, prey diversity is restricted on islands (Ricklefs, 1969) and seabirds often constitute an important part of fox diet (Murie, 1959). On islands lacking alternative prey, Murie (1959) found that seabirds made-up as much as 100% of scat by occurrence, similar to findings (~ 94%) on Baccalieu Island.

5.1.4. Prey Characteristics

Seabird colonies are highly conspicuous and the large numbers of potential prey are likely to attract predators (Wittenberger, 1981). Similarly within colonies, predators are more likely to destroy nests in areas of high nesting density, since the probability of detecting additional nests is greatly increased (Tinbergen, Impekoven and Franck, 1967; Murdoch and Oaten, 1975). Cliff nesters are relatively safe from terrestrial predators and seabirds with direct (social) anti-predator defenses (i.e. mobbing) may secure greater protection by nesting in central portions of a colony. In contrast, predation pressure determines areas that are successful for burrow- and ground-nesting seabirds with no social anti-predator defense. The spacing, cover and accessibility of nests play important roles in the anti-predator strategies of burrow-nesting seabirds (Tinbergen et al., 1967; Schranck, 1972; Buckley and Buckley, 1980).

Foxes commonly dug storm-petrel nests in the grass and fern habitats where high nest density and relatively soft soil probably increased predation success. Burrows situated in wooded and heath habitats however, may have gained partial protection from the larger root systems and bedrock, and possibly lower nest densities. On the other hand, direct predation on adult storm-petrels during colony arrival and feeding shifts was highest in the wooded habitat and may have resulted from obstacles limiting successful escape (cf. Kruuk, 1972). This speculation is partially confirmed by the observation that wings and whole storm-petrels were frequently found entangled among tree branches and on the ground with no signs of predation (pers. obs.; W. Montevecchi, pers. comm.). Furthermore, nocturnal activity among storm-petrels makes them temporarily susceptible to higher levels of fox predation.

5.1.5. Availability of Alternative Foods

Most seabirds leave their nesting grounds after the breeding season, and local mammalian predators have to rely on alternative food sources. Alternative foods influence predation partly by determining the numbers of predators and by their overall importance in the predators' diet (Moors and Atkinson, 1984). In some situations where alternative foods are scarce, the predator population may be limited and may stabilize at low levels or in extreme cases, die out. If however, alternative foods are plentiful, then the number of predators may be maintained at levels beyond which can be supported by the resident seabird populations. Alternative foods however, may also act to buffer the impact of fox predation on seabird populations (Norman, 1971).

Stonehouse (1955) contended that the non-synchronized breeding habits or continuing presence of breeding seabirds (some tropical seabirds may also nest three times in two years) on Ascension Island (for dates see Ashmole, 1963) allowed the predator population to increase such that two of the seabird species were exterminated. Afterwards however, predator numbers declined and both predator and prey populations appeared to thrive successfully. In temperate or subarctic regions, by comparison, seabird breeding seasons are much shorter, and seabird absence during non-nesting periods may limit the growth and survival of predator populations. This is the case on Baccalieu Island, where the lack of alternative foods may limit the resident fox population by decreasing fecundity and/or juvenile survival during the first winter.

5.1.6. Caching Behaviour

In order to reproduce, an animal must accummulate sufficient nutritional reserves and therefore, caching food may assure survival and enhance reproductive success (Morse, 1980). Food abundance and hunger state may increase the hoarding response, hence, energy maximization and predator efficiency. Tinbergen (1965) found that eggs stored by red foxes during periods of prey abundance were recovered as long as two months later. It has also been suggested that the arctic fox migrates south in November and does not return to its larders until March (Freuchen, 1915; Braestrup, 1941). Although the actual timing of larder use on Baccalieu Island is unknown, few items, if any, remain in larders prior to the arrival of seabirds the following year (pers. obs.). Therefore, on islands lacking alternative prey, cached foods may not only supplement diet, but help to assure survival. Storm-petrels made-up over 50% by weight of fresh winter scat, further suggesting that lardered foods are important for foxes during periods of low prey availability (although the winter diet of foxes may also consist of scavenged or scatter hoarded storm-petrels).

Scatter hoarding is common among Red foxes (Murie, 1936; Scott, 1943; Tinbergen, 1965; Henry, 1976; Macdonald, 1976) and the "random" spacing of cached foods is believed to reduce the probability of inter- and intraspecific theft by decreasing the average number (Tinbergen, 1965) or variance (Henry, 1976), of losses. However, a number of investigations have also mentioned the occurrence of multiple carcasses (Errington, 1935, 1937, 1967) or food remains (Sargeant, 1972; Sargeant et al., 1984; Hewson, 1985) at red fox denning sites. Furthermore, examination of prey remains in both red (Sargeant, 1972, 1978) and arctic fox (Stephenson 1970; Savage and Cooper, 1982) dens, suggests a heavy reliance by den residents on nearby, abundant, and vulnerable prey as primary sources of food. Therefore, it is possible that the potential for larder hoarding exists among both arctic and red foxes as an extension of provisioning food for young (i.e. during the denning period) and is dependent on or may occur under conditions of a super-abundance of prey, a colder climate which would decrease the rate of putrefaction (Macdonald, 1976) and/or decreased inter-specific competition. Although intraspecific theft does occasionally occur (Tinbergen, 1965; Henry, 1976; pers. obs.), the maintenance of well-delineated territories among foxes (Ables, 1969; Sargeant, 1972; Preston, 1975; Storm and Montgomery, 1975) would hold theft between unrelated individuals to a minimum (Henry, 1976) and cache use by relatives would still benefit the caching individual (Henry, 1976) by increasing its inclusive fitness (Hamilton, 1964). Moreover, because larders are commonly located at denning sites, which are central to resident fox activity, intraspecific theft would seem unlikely.

5.2. MANAGEMENT CONSIDERATIONS

5.2.1. Intercompensations ?

Mammalian predation is difficult to analyze because both functional and numerical response are complicated by buffering, territoriality and learning (Keith, 1974), and few studies have successfully demonstrated that predators limit their prey. Therefore, it is important not to confuse the fact of predation with the effect of predation (Errington, 1948; Ables, 1975). Errington (1948) believed that intercompensations among prey were responsible for reducing the estimated potential effects of predation. Ricklefs (1969) found that in the absence of terrestrial predation nest losses among Procellariiformes occurred as a result of "internal factors" (e.g. hatching failure, crowded conditions). Competition for food supplies (Nettleship, 1972; Furness and Birkhead, 1984) and avian predation (Kruuk, 1964; Kadlek and Drury; Hatch, 1970; cf. Morris and Hunter, 1976) may also be important during the breeding season. Mortality resulting from non-mammalian predation is evidenced by the large numbers of corpses found at some breeding colonies (e.g. Great Island; pers. obs.), where no mammals are present. In addition, Witt (1980) found that 61% of avian prey taken by foxes consisted of scavenged food. The opportunistic nature of foxes suggests that a proportion of fox diet may actually consist of surplus or scavenged prey.

Predation by gulls (Great Black-backed, *Larus marinus*; Glaucous, *Larus hyperboreus*; Glaucous-winged *Larus glaucescens* and Herring Gulls *Larus argentatus*) is frequently an important source of seabird egg and chick mortality and among smaller species (e.g. petrels, auklets), adult mortality (Fisher and Lockley, 1954; Evans and Nettleship, 1985). On two Aleutian Islands where storm-petrels and auklets were abundant, Trapp (1979) found that Glaucous-winged Gull (*Larus glaucescens*) droppings contained as much as 61% storm-petrel and 85% auklet remains, respectively. Similarly, Herring Gulls nesting on Gull Island and Great Island, Newfoundland, have been found to prey heavily on storm-petrel[illegible]aycock and Threlfall, 1975; Pierotti, 1979), particularly when alternative sources of food were unavailable (Haycock, 1973). Why then is predation on the storm-petrels by gulls infrequent or limited on Baccalieu Island?

The presence of red foxes on Baccalieu Island is believed to deter ground nesting by avian predators. This contention is based on a minimum of 5 factors: (1) Herring Gulls nest extensively on Puffin Island located < 200 m from Baccalieu Island where very few pairs nest, (2) gulls on Baccalieu are preyed on by foxes (based on predation rates and the population size of gulls on Puffin Island, impact may be as high as 14% of the breeding population) (3) gulls will colonize islands after the disappearance of foxes (Bailey and Faust, 1980; see also Buckley and Buckley, 1980), (4) on islands with gulls, nocturnal seabirds may be fewer in number or nest away from gull concentrations (Bailey and Faust, 1981), (5) gulls are opportunistic omnivores and if they were to colonize Baccalieu Island, they would be likely to prey extensively on storm-petrels. Common Ravens ($\geq$ 100 individuals) thrive on Baccalieu island, but being cliff-nesters, they apparently escape heavy nest and adult predation by foxes.

It is an interesting question to consider how large a gull population would equal the predatory pressure imposed by foxes? Assuming that storm-petrels are taken by gulls from May - August at a rate of 1 adult storm-petrel every 4 days, a moderately small gull population of 500 pairs could exert equivalent predatory impact (31,000 indiv/yr) to that of the resident foxes on Baccalieu Island. Although highly speculative, the predatory impact of foxes may in part, compensate for losses that would otherwise result from avian predation.

5.2.2. Future Needs

Seabirds are highly vulnerable to alterations in breeding environment, and it is highly desireable to be able to predict changes in local populations. Although the present thesis provides information regarding the role of the red fox on Baccalieu Island, long-term investigations are needed to accurately define the foxes' relationship to the breeding seabirds on the island. Therefore, the following recommendations are proposed:

(1) The continued censusing of all breeding seabird populations at a minimum interval of once every 5 years.

(2) Randomly chosen, fixed plots should be set-up in habitats where Leach's Storm-Petrels experience intense fox predation (i.e. grass, wooded habitats). By concurrently examining random control plots, intervention effects may be isolated from changes associated with fox predation.

(3) An intensive tagging program be directed at the fox population to accurately determine population size and structure.

(4) The continued mark/recapture of foxes at a minimum interval of once every 5 years. This would provide information on changes in population size, survival rates and possibly rates of emigration and immigration.

(5) Provide incentives for lighthouse-keepers to accurately record ice conditions and its occurrence between the mainland and the island and any sightings of ice use or dispersal by foxes.

(6) As a management concern, special consideration should be given, and care taken, to prevent the possible introduction or accidental occurrence of alternative prey species (e.g. rats from coast guard cutters) to Baccalieu Island.

5.2.3. Summary

Baccalieu Island supports one of the largest known Leach's Storm-Petrel colonies in the world. The predatory behaviour of resident foxes conforms to the patterns found in other studies on red fox diet; that availability largely governs prey choice. Although Leach's Storm-Petrels suffer high levels of fox depredation, (1) the population's reproductive potential appears to outweigh the effects of predation and (2) its massive size acts as a buffer, limiting the extent of damage experienced by the smaller seabird populations. The lack of alternative foods for foxes during non-nesting periods appears to severely limit the predator population. The presence of foxes may also deter ground-nesting avian predators from establishing colonies on the island and thereby limit avian predation. Although introduced predators are known to inflict severe pressures on small seabird colonies, the present findings suggest that colony size and the lack of alternative foods for predators may weaken predatory impact. Because the red fox is native to Newfoundland and has reached Baccalieu Island via a natural occurrence, its presence and role as a predator should be considered an acceptable part of the ecosystem.

Figure 5-1: Endpiece: Red fox scavenging along the seabird cliffs of Baccalieu Island during the winter.

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APPENDIX A

Summary of avian species sighted
during April - May 1984 and
February - March 1985

List of avian species sighted through (A) April 26 - May 20 1984 and (B) February 6 - March 7 1985.

SPECIES	DATE NOTED	
Anatidae		
Common Eider (*Somateria mollissima*)	A	B
Oldsquaw (*Clangula hyemalis*)	A	B
Accipitridae		
Bald Eagle (*Haliaeetus leucocephalus*)	A	B
Falconidae		
Gyrfalcon (*Falco rusticolus*)	A	
Merlin (*Falco columbarius*)	A	
Laridae		
Great Black-backed Gull (*Larus marinus*)	A	
Glaucous Gull (*Larus hyperboreus*)	A	B
Iceland Gull (*Larus glaucoides*)		B
Alcidae		
Black Guillemot (*Cepphus grylle*)	A	B
Strigidae		
Snowy Owl (*Nyctea scandiaca*)	A	
Picidae		
Black-backed Three-toed Woodpecker (*Picoides arcticus*)		B
Alaudidae		
Horned Lark (*Eremophila alpestris*)	A	

Corvidae		
American Crow (*Corvus brachyrhynchos*)	A	
Common Raven (*Corvus corax*)	A	B
Paridae		
Black-capped Chickadee (*Parus atricapillus*)	A	B
Boreal Chickadee (*Parus hudsonicus*)	A	B
Muscicapidae		
American Robin (*Turdus migratorius*)	A	
Sturnidae		
European Starling (*Sturnus vulgaris*)	A	B
Emberizidae		
Yellow-rumped Warbler (*Dendroica coronata*)	A	
Fox Sparrow (*Passerella iliaca*)	A	
White-throated Sparrow (*Zonotrichia albicollis*)	A	
Savannah Sparrow (*Passerculus sandwichensis*)	A	
Common Grackle (*Quiscalus quiscula*)	A	
Fringillidae		
Pine Grosbeak (*Pinicola enucleator*)	A	B
Evening Grosbeak (*Hesperiphona vespertina*)	A	
White-winged Crossbill (*Loxia leucoptera*)		B
Purple Finch (*Carpodacus purpureus*)	A	
Northern Junco (*Junco hyemalis*)	A	
Snow Bunting (*Plectrophenax nivalis*)	A	B

For complete checklist; See Wells and Montevecchi (1984)

APPENDIX B

Summary of Baccalieu Island contour analysis

To estimate the relative increase in surface area for Baccalieu Island resulting from slope, topographical analysis of island contour was performed on a 1:50,000 map of Baccalieu Island (Can. Dept. Energy, Mines and Resources). Fifteen transects were drawn perpendicular to the island at relatively equal intervals, however, intervals were sometimes unevenly spaced in an effort to examine areas which would best describe island contour (H. Butler, pers. comm.). Cross-sections of the island were plotted (see next page) and scaled relative to the planar distance, and then measured using a Numonics digitizer. The ratio between these values (Y/X) provided an estimate of the proportional increase in surface area at each segment resulting from island contour and the mean of these values was used as an estimate of overall increase in area, due to slope.

PROFILE	Y/X
A	1.43
B	1.70
C	1.62
D	1.63
E	1.56
F	1.33
G	1.31
H	1.83
I	1.62
J	1.46
K	1.36
L	1.67
M	1.68
N	1.72
O	2.00
MEAN ± S.D.	1.59 ± 0.19

Cross-Sectional Profiles of Baccalieu Island