

THE UNIVERSITY OF CALGARY

ASPECTS OF THE BEHAVIOURAL ECOLOGY OF
WINTERING SNOWY OWLS (NYCTEA SCANDIACA)

by

PETER CHARLES BOXALL

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES
IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE
DEGREE OF MASTER OF SCIENCE

DEPARTMENT OF BIOLOGY

CALGARY, ALBERTA

November 1979

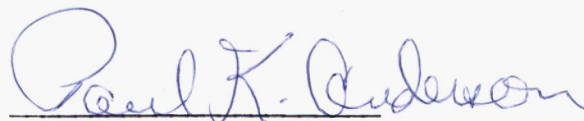
© Peter C. Boxall 1979

THE UNIVERSITY OF CALGARY
FACULTY OF GRADUATE STUDIES

The undersigned certify that they have read, and
recommend to the Faculty of Graduate Studies for acceptance
a thesis entitled "Aspects of the Behavioural Ecology of
Wintering Snowy Owls (Nyctea scandiaca)", submitted by
Peter C. Boxall in partial fulfillment of the requirements
for the degree of Master of Science.



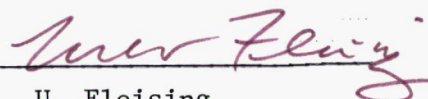
M.R. Lein, Supervisor
Department of Biology



P.K. Anderson
Department of Biology



G. Pritchard
Department of Biology



U. Fleising
Department of Anthropology

2 November, 1979
(date)

ABSTRACT

Studies of wintering populations of Snowy Owls (Nyctea scandiaca) are largely confined to periodic major movements into the eastern USA. They describe the distribution and numbers of birds involved, unusual locality records and food habits. This study investigated the population structure, movements, and behaviour of Snowy Owls wintering in southern Alberta, where the owls regularly winter.

Chapter 1 reviews the literature on Snowy Owls in winter, and outlines its role in falsely popularizing the Snowy Owl as an unpredictable winter nomad. The relationship of the Snowy Owl to the population cycles of arctic Lemmings is summarized. The study area near Calgary, Alberta, and the general methods used, are described in Chapter 2.

Chapter 3 describes the populations of Snowy Owls on the study area during two winters, 1976/77 and 1977/78, in which no massive invasion of Snowy Owls occurred anywhere in the prairie provinces. The seasonal pattern of abundance of owls showed a peak early in each winter. Possibly such peaks are related to movements of arctic fronts. The mid-winter period showed little variation in owl abundance, suggesting a stable resident population. Adult males were more numerous during the spring migration than at other times, and females predominated during mid-winter. It is proposed that juvenile Snowy Owls comprise about half of the population during non-invasion years, such as occurred in this study, whereas adult owls may predominate in years of mass movements.

Chapter 4 examines the feeding ecology of Snowy Owls on the study area. Major prey species were Microtus pennsylvanicus, Peromyscus maniculatus, and Perdix perdix. Males and females differ in diet.

Hunting behaviour of the birds is described. Hunting success of juvenile female Snowy Owls was found to be lower than for adult females.

Habitat selection by Snowy Owls is described in Chapter 5, and related to prey distribution. Owls preferred habitats with the highest availability of prey. Both adult and juvenile females defended territories. It is suggested that these territories were economically defensible and that their probable function was to protect a food supply. Juvenile female Snowy Owls defended larger territories which contained lesser amounts of profitable habitat than did those of adult females. Males did not stay on the study area as long as did females, and did not defend territories. The significance of these sexual differences in winter residency is discussed.

Territorial defence is analyzed in Chapter 6. Agonistic displays and other interactions between owls were uncommon. Advertisement of territorial status may be achieved through prolonged perching on high objects.

Chapter 7 examines the time budgets and activity cycle of territorial Snowy Owls. Owls spent about 98% of the day perched and about 2% in flight. Birds were more active in early morning and late evening than during other periods of daylight, and nocturnal hunting may be more common than formerly thought. This activity rhythm corresponded to those of major prey species. The daily energy requirements of an owl is estimated.

The relation of these findings to winter survival is discussed in Chapter 8. It is suggested that winter mortality of Snowy Owls is not unusually high, contrary to the predictions of other workers, but is probably higher for juveniles than adults. This study suggests that Snowy Owls are not unpredictable vagrants in winter, and that Alberta is a regular wintering area for large numbers of this species.

ACKNOWLEDGEMENTS

It is with pleasure that I acknowledge the support and guidance of my supervisor, M. Ross Lein. He has taught me a great deal about ornithology, field research, and ethology. His insight into the biology of raptors, and literary skill, has aided me a great deal during my studies at the University of Calgary.

M. T. Myres provided valuable criticisms of this thesis, particularly Chapter 3. I greatly appreciate his interest in my project. P. K. Anderson contributed by making a number of helpful suggestions on the small mammal work. L. O. Sinkey provided computer programs and aided me with the computer analyses of habitat data.

Charles Mamo, Glenn Webber, Bob Fisher, and Brian Free helped me a great deal in the field, and more importantly, acted as close friends during my research. Charles Mamo also provided the fine pen and ink drawings of the owls in Chapter 6. In addition, Tom Dickinson, Dan Dixon, Gord Holton, Dan Ludwig, Bill Parsons, Larry Powell, Mary Rothfels and Tim Thwaites aided me in many valuable ways. Special thanks are due to Mary Rothfels for proofing various copies of the thesis, and to Joyce Brown for helping me with the figures. My interest in owls was first aroused by Franco Phelan and Alex Palilionis at Queen's University. Without them, I would never have become a companion to owls.

Finally, I would like to thank my parents for showing a keen interest in my studies, and for providing me with much support during my education.

The research reported in this thesis was supported by the Canadian Wildlife Service (contract no. KL229-7-5410), the National Research Council through grants to M. R. Lein, and the Department of Biology, University of Calgary.

TABLE OF CONTENTS

	page
ABSTRACT	iii
ACKNOWLEDGEMENTS	v
LIST OF TABLES	xi
LIST OF FIGURES	xiii
CHAPTER 1 INTRODUCTION	1
CHAPTER 2 STUDY AREA AND GENERAL METHODS	6
1. Study Area	6
2. General Methods	11
CHAPTER 3 POPULATION STRUCTURE OF SNOWY OWLS WINTER- ING IN SOUTHERN ALBERTA, AND THE NATURE OF INVASIVE MOVEMENTS IN SNOWY OWLS	19
1. Introduction	19
2. Methods	21
3. Results	21
A. The Seasonal Pattern of Abundance	21
B. Factors Influencing Arrival	24
C. Seasonal Differences in the Occurrence of Plumage (Sex/Age) Classes	29
D. Interspecific Relations	37
4. Discussion	38
CHAPTER 4 FEEDING ECOLOGY OF SNOWY OWLS WINTERING IN SOUTHERN ALBERTA	47
1. Introduction	47
2. Methods	49

	page
3. Results	53
4. Discussion	64
A. Principle Prey Species	64
B. Sexual Differences in Feeding Ecology	66
C. Hunting Behaviour and Success	68
D. Age and Hunting Success	73
CHAPTER 5 THE USE OF SPACE BY SNOWY OWLS	75
1. Introduction	75
2. Methods	79
3. Results	84
A. The Habitat Composition of the Study Area	84
B. Analyses of Prey Abundance	86
C. Habitat Selection by Snowy Owls: Census Techniques	93
D. Analyses of Territoriality of Snowy Owls	97
i) Residency Periods	97
ii) Territories of Female Snowy Owls	100
4. Discussion	113
A. The Profitability of Habitats on the Study Area	113
B. Seasonal Differences in Habitat Selec- tion	118
C. Sexual Differences in Habitat Selection.	119

	page
D. Territoriality, Food Supply, and Profitable Foraging	121
CHAPTER 6 SPACING MECHANISMS USED BY WINTERING	
SNOWY OWLS	127
1. Introduction	127
2. Postures and Displays of Snowy Owls	128
A. General Activities	128
i) Alert Posture	128
ii) Resting Postures	131
iii) Comfort Movements	131
B. Agonistic Displays and Postures	134
i) Upright Posture	134
ii) Forward Crouch Display	137
iii) Head-Up Glide Flight-Display . . .	140
3. Territorial Interactions	143
A. Typical Observations	143
B. Responses by Recipients or Intruders .	148
C. The Effect of Sex	148
D. The Effect of Age	149
4. Territorial Advertisement	152
5. Discussion	155
CHAPTER 7 DIURNAL ACTIVITY BUDGETS OF WINTERING	
SNOWY OWLS	164
1. Introduction	164
2. Methods	165

	page
3. Results	169
A. Diurnal Time Budget	169
B. Energetics of Wintering Snowy Owls . . .	176
4. Discussion	181
CHAPTER 8 'GENERAL DISCUSSION	188
LITERATURE CITED	196

LIST OF TABLES

Table	page
1. The number of Snowy Owls in each plumage class sighted on the study area, excluding all known observations of the same individuals	30
2. A general summary of the abundance of the Snowy Owl in western and eastern North America and Alberta. The descriptions are based upon summaries given in American Birds (formerly Audubon Field-Notes)	44
3. A summary of studies on the diet of wintering Snowy Owls in North America	48
4. Prey items recovered from Snowy Owl pellets in the winter of 1976/77	54
5. Prey items recovered from Snowy Owl pellets in the winter of 1977/78	55
6. A comparison of the diets of male and female Owls based on pellet analyses	56
7. The number of attempts by Snowy Owls to capture various prey	58
8. Hunting success during winter of seven species of raptors	69
9. Distribution of habitats surveyed for Snowy Owls on study area in each winter	85
10. The abundance of small mammals in various habitat categories as determined by snap-trapping censuses, and the species composition of those animals captured in each trapping period	87
11. The numbers of rodent tracks counted crossing 100 m transects walked in various habitats	89
12. The distribution of sightings of Gray Partridge coveys by habitat category	92
13. Distribution of owl sightings by habitat category	94

Table	page
14. The distribution of sightings of non-resident owls by habitat category in the two periods of the winter of 1977/78	96
15. The distribution of sightings of non-resident Snowy Owls by habitat in the winter of 1977/78 according to plumage class category	98
16. Length of residency of male and female Snowy Owls in a specific locality. Information summarized here consists only of owls that were observed for more than two consecutive days	99
17. The habitat composition and other information for nine Snowy Owl territories	104
18. A summary of Pearson product moment correlation analyses between territory size, duration of time spent on the study area, and habitat composition for Snowy Owl territories observed in 1977/78	112
19. Measures of roadside ditches and edges of stubble-fields in Snowy Owl territories examined in 1977/78	114
20. The frequency of displays and other behaviour patterns during Snowy Owl interactions of varying intensity	147
21. The frequency of intrusions by Snowy Owls into the territories or ranges of conspecifics, and the number of responses by the resident owls	151
22. Mean perch heights of territorial and non-territorial Snowy Owls in winter	153
23. Energetic costs of activities of Snowy Owls expressed as multiples of existence metabolism	168
24. The overall time budget of wintering Snowy Owls. Each number represents the percentage of the daylight hours spent in a particular activity	177

LIST OF FIGURES

Figure	page
1. A map of the region southeast of Calgary, Alberta, showing the study area, major roads and villages. The small block of land in the northeast portion of the study area was added in the 1977/78 field season	7
2. The plumage classes of Snowy Owls. A-D. Class 1: the whitest plumages of Snowy Owls. E-H. Class 2: lightly-barred owls. I-L. Class 3: moderate to heavily-barred owls. M-P. Class 4: very heavily-barred owls	14
3. The pattern of abundance of Snowy Owls in 7-day periods in the Calgary region, throughout the winters of 1976/77 and 1977/78, and the corresponding mean temperatures. The thick horizontal bars represent the periods of relatively stable numbers in each winter (see text for further explanation). The heavy dashed line represents -10°C , and is drawn for ease of presentation. The lighter dashed line represents the average winter level of 1.63 owls/hr (see text for further explanation). The asterisk indicates the week with missing data	22
4. Positions of cold fronts in western Canada and the northern USA at 1800 hrs (MST) on each of several days. A. 21 to 24 December, 1977. B. 27 to 31 December, 1977	27
5. Seasonal abundance of Snowy Owls in each of three collective plumage class categories throughout the winters of 1976/77 and 1977/78 in southern Alberta. The horizontal bars represent the periods of relatively stable numbers of owls in each winter (see text for further explanation)	32
6. The proportion of Snowy Owls in each of three plumage class categories by 7-day periods throughout the winters of 1976/77 (A) and 1977/78 (B). Stippling represents Class 1 and 1-2 owls, vertical lines represent Class 3-4 and 4 owls, and unshaded indicates Class 2, 2-3 and 3 birds. The asterisk indicates the 7-day period with missing data.	35

Figure	page
7. Aspects of the hunting behaviour of Snowy Owls wintering in southern Alberta. A. The relationship between perch height and hunting. B. Distances at which prey were captured from hunting perches (data from both years were pooled because of small samples). C. Partitioning of hunts among habitats. A total of 51 hunting attempts (23 in 1976/77 and 28 in 1977/78) were observed	60
8. Mean numbers of rodent tracks per transect counted at various distances from the edges of stubblefields and hayfields in 1977/78. Six stubblefields and five hayfields were sampled on 25 November, and seven different stubblefields and five different hayfields were sampled on 27 November	90
9. Observation-area curves for six Snowy Owl territories observed in the Calgary region in the winter of 1977/78. Letters refer to individual designations of owls	102
10. Territories of eight Snowy Owls observed in 1977/78. The small solid circles represent one or more locations of each owl, and the large solid circles represent locations where territorial interactions were observed. Cross-hatching represents stubblefields, and stippling depicts areas outside territorial boundaries. A-D. Territories of adult females. E-H. Territories of juvenile females	106
11. Habitat utilization indices for nine Snowy Owl territories. The horizontal bars represent the means, and vertical bars the ranges. The dashed line represents the value for equal utilization. Computation of the index is explained in the text	110
12. Alert postures of Snowy Owls. A. The typical posture of an alert owl. B. The posture of an "interested" owl	129
13. Resting postures of Snowy Owls. A, B. Lateral views of resting owls. C. The posture of a sleeping owl	132

Figure	page
14. Upright postures used by Snowy Owls in agonistic interactions with conspecifics. A, B. Frontal views. C. Lateral view	135
15. The Forward Crouch Display, showing the "grading" of the display. A. Pre-flight posture. B. The posture of an owl in between the head-sways. C. The full extent of the display. Head-swaying and body-rotations occurred while the owl assumed this posture	138
16. The Head-Up Glide Flight-Display. A. Normal flight. B, C. The glide portion of the display, characterized by the upward extension of the head. D. An owl looking over its back before the glide portion of the display	141
17. The orientation of perched territorial and non-territorial Snowy Owls relative to the sun	156
18. The proportion of time spent by wintering Snowy Owls in four activities during various time periods in the winters of 1976/77 and 1977/78. The solid circles represent the means and the vertical bars standard errors. The numbers above the vertical bars represent the number of hours of observations from which each mean was calculated. The means and standard errors for each year are slightly offset for ease of presentation	170
19. Distributions of the rate of perch changes and prey-capture attempts by wintering Snowy Owls by time period. A. The number of perch-changes per hour for different time periods for each year (1976/77, n = 80; 1977/78, n = 104). B. The number of prey-capture attempts per hour (n = 36) by time attempts period (data for each winter were pooled due to small samples	174
20. Average daily energy expenditures (DEE), existence metabolism (EM), and the rate of hunting by wintering Snowy Owls in relation to mean monthly temperature during the winters of 1976/77 and 1977/78	179

CHAPTER 1

INTRODUCTION

The Snowy Owl (Nyctea scandiaca) is one of the largest members of the family Strigidae. Its circumpolar breeding range is restricted to arctic tundra areas (Portenko, 1972), and coincides with the ranges of arctic lemmings (Lemmus and Dicrostonyx spp.). Although the breeding biology of Snowy Owls is well-known (Murie, 1929; Pitelka et al., 1955a, 1955b; Sutton and Parmelee, 1956; Watson, 1957; Tullock, 1968; Parmelee, 1972; Taylor, 1974), the literature on its winter biology is largely restricted to descriptions of large-scale movements into the eastern USA (Gross, 1927, 1931, 1947; Hicks, 1932; Snyder, 1943, 1947; Stoner, 1943; Meade, 1948; and many others), unusual locality records (e.g., Bent, 1938; Bond, 1945; Behle, 1968), and food habits (e.g., Gross, 1944; Keith, 1963a). Very little is known about the behavioural ecology of Snowy Owls in their regular wintering areas.

Snowy Owls are popularly known for their massive movements into eastern North America. These movements occur approximately every four years and have been related to the periodicity of the populations of arctic lemmings (Shelford, 1945; Gross, 1947; Chitty, 1950), the major prey of Snowy Owls (Pitelka et al., 1955a; Watson, 1957). The emigrations of the owls so intrigued scientists that a Snowy Owl

investigatory committee was formed by a number of ornithologists to describe the pronounced movements of this species in North America (Snyder, 1943). The reports of this group (Snyder, 1943, 1947, 1949) suggested that the Snowy Owl was regularly present on the prairies of Canada and the north-central USA in winter, and that this represented a wintering population. Despite this, there were certain years when a major influx of Snowy Owls was reported in western North America (Snyder, 1949; Hanson, 1971). In most winters, Snowy Owls were not as abundant in eastern North America as in the west. However, the massive periodic flights, involving large numbers of Snowy Owls, occurred more often in the east (Gross, 1927). The committee attributed the differences in the presence of Snowy Owls in eastern and western North America to the possibility that movements of the birds into the eastern mid-continent resulted from peak owl populations in the eastern arctic, whereas a large influx in the west may have had its origin in either the eastern or western arctic.

Some workers studying Snowy Owl movements in eastern North America proposed that those owls which came south arrived in an emaciated condition (Gross, 1927, 1947; Thomas (1928), cited in Hicks, 1932), and that few ever returned to the arctic to breed (Gross, 1931, 1947; Bent, 1938). These workers, and others (Shelford, 1945; Burton, 1973), suggested that the winter movements were triggered by starvation which

resulted from a widespread failure of food in the arctic. Because of these comments, which are in fact unsubstantiated, the popular literature describes the Snowy Owl as an unpredictable winter nomad, whose southward movements result in death (e.g., Gillese, 1960; Angell, 1974; Walker, 1974; Weir, 1974; Downs, 1979).

This notion of the Snowy Owl has also pervaded some of the scientific literature, especially studies dealing with the regulation of avian populations (e.g., Colinvaux, 1974). David Lack, in particular, has used the example of the Snowy Owl to support his theory of population regulation (1954, 1966). Lack claimed that density-dependent mortality factors, acting outside the breeding season, were responsible for reducing the surplus numbers of birds produced during the breeding season. He claimed that food shortage was the most likely cause of this mortality. The periodic southward movements of Snowy Owls, supposedly related to food shortage in the arctic, and the hypothetical heavy mortality of these birds in winter, provided Lack with a good example for his ideas.

In contrast to the popular view, recent studies have shown that Snowy Owls are relatively common winter residents in certain regions of Ontario (Catling, 1973), Manitoba (Keith, 1960), Alberta (Bird, 1972; Sadler and Myres, 1976; Lein and Webber, 1979), and probably many other areas, even in years when major movements into the eastern USA have not

occurred (Snyder, 1949). Snowy Owls arrive on the wintering grounds in excellent health (e.g., Keith, 1960; Cohen, 1966). Extended periods of residency of individual owls in these areas (Hicks, 1932; Meade, 1948; Keith, 1960), and territorial behaviour (Keith, 1964; Quilliam, 1965) have been observed. Bird (1972) pointed out that Snowy Owls may spend more time in these southern areas than in the arctic. In addition, owls banded in winter may return to the arctic to breed (Bent, 1938; Parmelee, 1972), and subsequently to the same locality in successive winters (Bent, 1938; Oeming, 1958, 1964; Lein, pers. comm.). These studies, although incomplete, suggest that Snowy Owls are not unpredictable vagrants in winter, and indicate the need for further detailed study.

The major purpose of my study was to investigate little-known aspects of the behavioural ecology of Snowy Owls wintering in southern Alberta, an area where owls have been recorded every winter since 1960 (Sadler and Myres, 1976; Lein and Webber, 1979). Since failure to procure enough food during winter may be a major factor regulating avian populations (Lack, 1954; Fretwell, 1972), my thesis will concentrate on the use of time and space by wintering Snowy Owls, and the relation of these factors to their predatory mode of existence. From these investigations, I will appraise the ability of Snowy Owls to select profitable hunting areas, thus influencing winter survival. My findings will also pro-

vide the basis for a discussion of Lack's theory and its relation to the regulation of Snowy Owl populations. The underlying theme, throughout, was the question: Do Snowy Owls exhibit behavioural strategies designed to decrease energy expenditures and increase energy intake, so that their chances of surviving the winter, moving to the arctic breeding range, and maintaining sufficient energy reserves for breeding, are maximized?

The specific objectives of this project were:

1. To describe the sex and age structure of a Snowy Owl population on the wintering grounds, and to measure any seasonal changes in its composition.
2. To examine the feeding ecology of Snowy Owls wintering near Calgary, Alberta, particularly their food habits and hunting behaviour.
3. To determine if certain habitats are preferred by the owls on their winter range, and to determine why these habitats are preferred.
4. To study the movements of individual owls in one locality and determine if the birds defend definite hunting ranges (territories).
5. To catalogue the spacing behaviour of this species in winter.
6. To determine the activity cycle of wintering Snowy Owls, and its relation to those of its major prey.

CHAPTER 2

STUDY AREA AND GENERAL METHODS

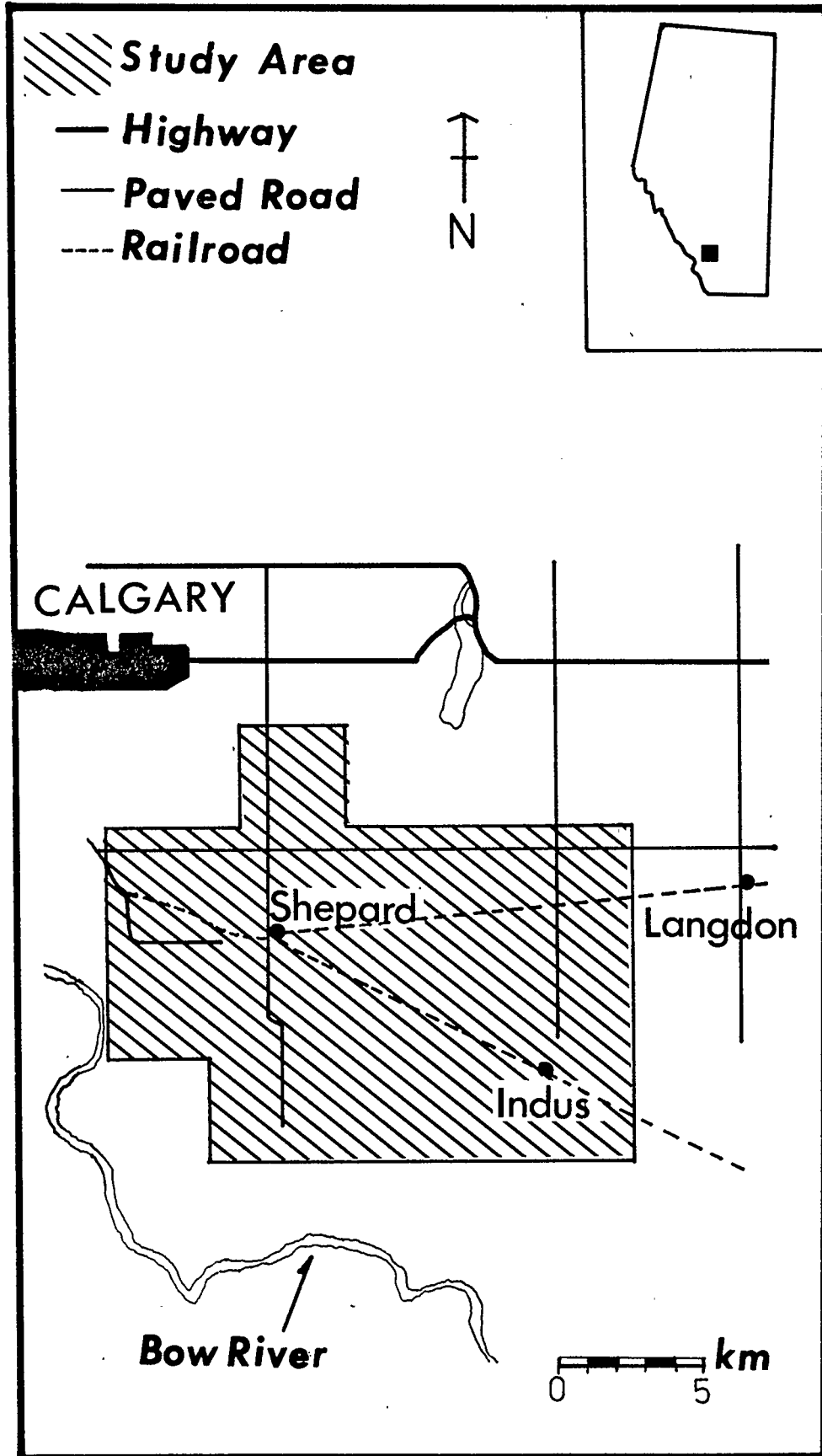
1. STUDY AREA

In December 1976, a 185 km² block of farmland southeast of the city of Calgary was chosen as the study area (Fig. 1). This area was known to have numbers of Snowy Owls in winter from a previous investigation of their distribution and abundance in the Calgary region (Lein and Webber, 1979).

The grid system of roads in the area and the low relief facilitated the location and observation of owls. High levels of human activity are centred around the western edge of the area due to its proximity to Calgary, and in the small communities of Shepard and Indus.

The predominant crop grown on the study area is barley; wheat and rye are also grown in lesser amounts. Most of the agricultural activity occurs in the fall when crops are harvested and some fields are cultivated for spring planting. Harvesting leaves a field containing stubble (the basal 10-20 cm of the stems still rooted in the ground), small piles of straw, and frequently, straw bales. A considerable number of grain seeds are left on the ground. In November 1977, I estimated the number of seeds remaining in harvested fields by randomly placing five 1 m² plots in each of three harvested barleyfields. I found that an average of 30 seeds/m² (range

FIGURE 1: A map of the region southeast of Calgary, Alberta, showing the study area, major roads and villages. The small block of land in the northeast portion of the study area was added in the 1977/78 field season.



12-40) remained in these fields.

These farming practices, as well as different crop types, grazing activity, and drainage efficiency, have resulted in a patchwork of habitats in most prairie farmland areas. The habitat in each field may vary from year to year, depending upon weather and the needs of the farmer. These changes have profound effects upon populations of birds (Owens and Myres, 1973), and no doubt on other animals.

Each year, the habitats on the entire study area were recorded between fall harvest and spring planting. Each field or other habitat block was visually inspected and classified as one of nine broadly identified habitats:

1. Stubble: fields in which cereal grains had been grown and harvested. The basal portion of the stems were left in the ground. Loose straw may or may not have been present.

2. Fallow: cultivated fields where no crop was planted during the previous season, or where crop remains had been turned-under two or more times in the fall. These fields were virtually bare soil with only vestiges of vegetation.

3. Hayfields: areas where grasses or legumes such as timothy (Phleum pratense), alfalfa (Medicago sativa), and Kentucky bluegrass (Poa pratensis) were grown. These were usually cut twice yearly to provide fodder for cattle. These fields are ploughed and reseeded only at intervals of several years.

4. Pastures: areas used to contain and feed livestock. Most of the vegetation within these fields was heavily grazed, leaving only a thin carpet of grass.

5. Sloughs: low-lying or marshy areas that fill with water in the spring but are dry for the rest of the year. Very few of the sloughs on the study area were permanently filled with water. Vegetative cover consisting of dock (Rumex spp.), sedges (Carex spp.), slough grass (Beckmannia syzigachne), and other grasses and forbs is found in these areas.

6. Residential: farmyards, small acreages, and other types of human habitation. Most farms and residences are enclosed by small planted shelterbelts.

7. Ungrazed grassland: a composite category, including a variety of areas where no agricultural or grazing activity has taken place for several years. Farms which have remained vacant for a number of years were also placed in this category. This habitat is usually characterized by heavy growth of grasses, weeds, and some shrubs or trees. Most of these areas are small and are found close to residential and industrial areas near the expanding city.

8. Industrial: factories, garages, and industrial plants lying east of Calgary. These areas are characterized by high human activity, especially truck and automobile traffic.

9. Other: a category including any areas that did not

fall into one of the above categories. This included garbage dumps and sewage treatment areas close to the western edge of the study area.

The habitat of each field was recorded directly on maps or aerial photographs of the study area. Total areas of the nine habitats were determined with the use of a computer graphics system (see Chapter 5).

Due to the low numbers of owls in 1977/78, a small block of farmland was added to the northwest portion of the study area. This area contained two owl territories, and yielded important data on wintering behaviour. In calculations of habitat area and owl distributions, this added area will only be included in analyses of 1977/78 data.

2. GENERAL METHODS

On most days in the field, I drove systematically over the entire study area at speeds of 40-50 km/h, searching areas on both sides of the road for owls. Whenever a stop was made, the surrounding region was examined with binoculars or a 20-40x telescope. Special attention was given to searching areas where birds had been seen one or two days previously. When an owl was located, a sighting number was assigned and its position was plotted onto a map of the study area. In 1976/77 sightings were plotted directly onto 1:50,000 topographic maps, using aerial photographs as a guide. In the 1977/78 season, sightings were plotted

directly onto 1:25,000 aerial photographs. I attempted to plot the location of owls to within 100 m by using an optical range finder and by referring to topographical features.

Once the owl's position was plotted, the following information was recorded: time of sighting, plumage pattern, perch height, habitat, physiognomy around the perch, distance from the owl to the nearest road, distance at which the bird was spotted, and other information about the owl's position on the perch. Similar data were also recorded for other raptors found on the study area.

In 1977/78, a more thorough and standardized census was organized in addition to surveys like those described above. This standardized census differed in that it followed a specific route, took place at the same time of day (1130-1530 MST), and a second observer always accompanied the driver. Additional information such as who spotted the owl, and the census number were recorded for owls located during these censuses. From 15 November to 15 December, and from 14-29 March, standardized censuses were driven twice weekly. A weekly schedule was followed from mid-December to mid-March. A total of 21 censuses were conducted.

The Snowy Owl exhibits the greatest sexual dimorphism in plumage of all North American owls. I attempted to determine the sex and age of each owl using plumage characteristics. Bent (1938), Keith (1960), Portenko (1972:53-56),

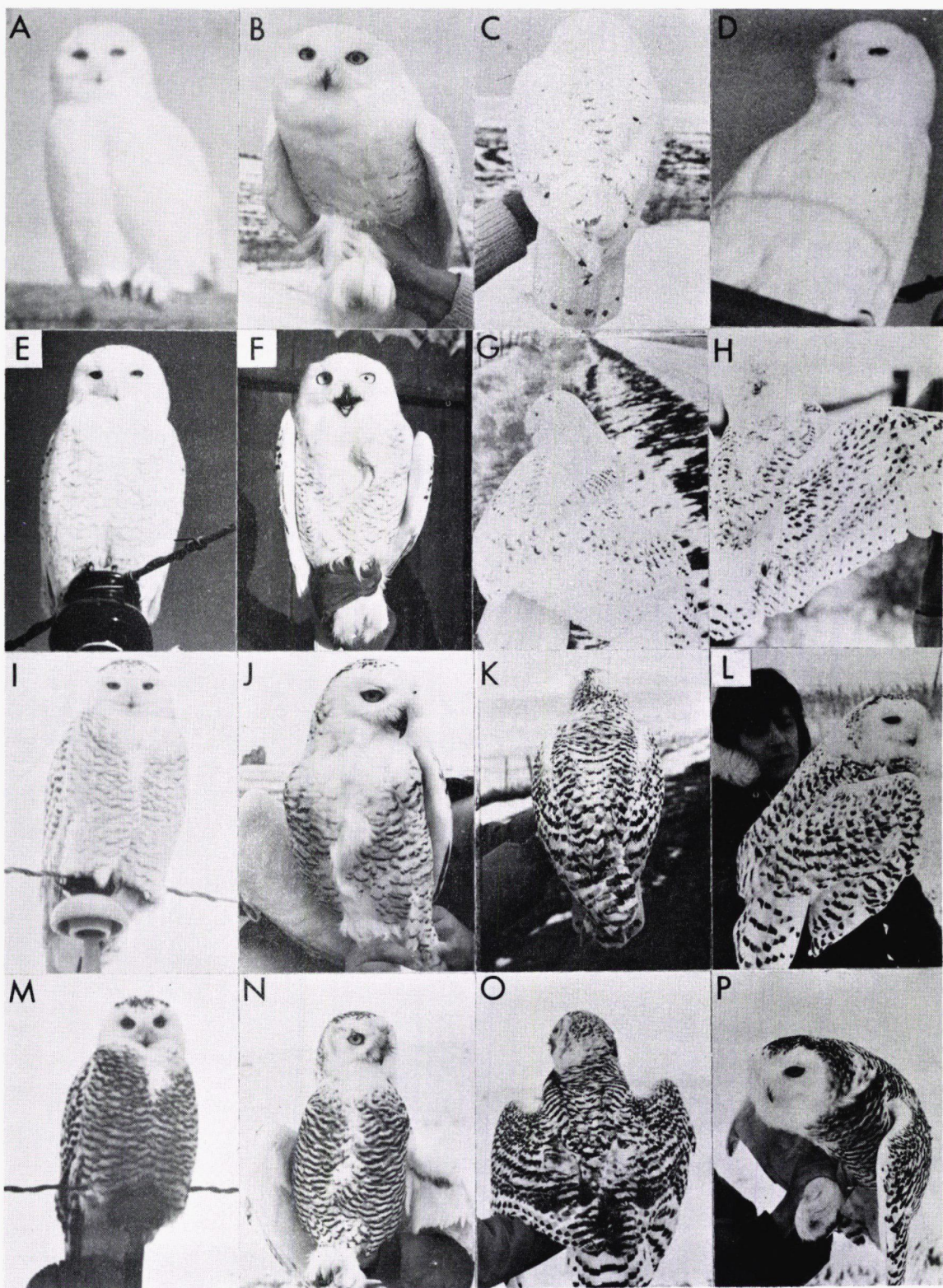
and Witherby (1943) provide descriptions of the plumage of Snowy Owls. Females possess considerable dark brown barring on all areas except the facial disc, throat, and undersides of the wings, which are usually white. Males have much less barring and are considerably lighter in appearance. Some older males are virtually free of markings. Immature birds of both sexes are more heavily barred than their mature counterparts. This results in a continuum of plumage darkness ranging from white (mature males) through intermediate barring (immature males and adult females) to very heavily marked birds (immature females). There is only one incomplete annual molt which occurs from June through September (Stresemann and Stresemann, 1966).

Plumage features thus allow field identification of sex and age classes with some degree of accuracy during winter. A system was developed to break the continuum of plumage darkness into four categories (Fig. 2). These are:

Class 1: the whitest plumages of Snowy Owls (Fig. 2A-D). Birds in this class range from pure white to mostly white with only a few dark flecks on the breast and back. The head may be faintly speckled. Barring, when present, is only pronounced on the tips of the primaries and rectrices.

Class 2: lightly-barred owls (Fig. 2E-H). Barring is noticeable over the lower breast and back, but the bars are relatively narrow, and usually appear as speckling from a distance. The barred areas are more than 50% white. Speck-

FIGURE 2: The plumage classes of Snowy Owls. A-D. Class 1: the whitest plumages of Snowy Owls. E-H. Class 2: lightly-barred owls. I-L. Class 3: moderate to heavily-barred owls. M-P. Class 4: very heavily-barred owls.



ling is noticeable on top of the head and much of the wings.

Class 3: moderate to heavily-barred birds (Fig. 2I-L). The barring is more pronounced than Class 2 birds, but the barred areas are only about 50% dark. The plumage on the breast and throat areas frequently consists of a small to moderate white region surrounded by heavily barred margins. The speckling on top of the head is pronounced but does not usually cover the entire head.

Class 4: very heavily-barred birds (Fig. 2M-P). Barring is so heavy that the brown makes up more than 50% of the barred areas. The entire breast and throat are usually heavily marked. Speckling on top of the head is extensive and may give the appearance of a "helmet" of solid dark colour.

Whenever an owl was located, its plumage was studied through a 20-40x telescope. It was assigned to one of the four classes, or placed in between two classes (e.g., Class 1-2, 2-3, 3-4). After this initial description I attempted to get as close as possible to the owl and to make more detailed notes on its plumage. When possible, I noted brown mottling on the coverts and secondaries, a characteristic of the plumage of juvenile Snowy Owls (Witherby, 1943; Portenko, 1972). These detailed descriptions were also used to identify individuals on the study area.

Since adult males are largely pure white, all birds described as Class 1 or 1-2 are probably adult males. Birds described as Class 3-4 and 4 probably represent immature

females because these owls have the darkest plumages. Photographs of owls of known sex and age (Tullock, 1968; Portenko, 1972; Lein, unpubl.), skins of owls collected by Alberta Fish and Wildlife, and owls that were trapped in the winter of 1976/77 verified these classifications. Class 2, 2-3, and 3 owls represent the overlap region in plumage darkness between mature females and immature males. Thus these owls will not be placed into a sex and age category unless: (1) the birds had been trapped and sexed and aged in the hand; (2) mottled coverts or secondaries were noted, indicating juveniles; (3) a good idea of its size was obtained relative to some known object or another Snowy Owl, indicating sex (male Snowy Owls are smaller than females, Snyder and Wiley 1976); or (4) some aspect of its behaviour, such as hooting, allowed me to classify it as a male (Watson, 1957).

I think that these methods of sexing and aging birds were quite accurate. Keith (1960) used similar methods and felt that he could identify the sex with less than 10% error. Quilliam (1965) and Weir (1973) attempted to categorize plumage darkness, but did not define their categories well enough to provide meaningful results.

One or two days per week were spent attempting to live-trap owls. For this purpose, bal-chatris traps (Berger and Mueller, 1959) or dho-gaza nets, with Starlings (Sturnus vulgaris) or Rock Doves (Columbia livia) as live bait, were used. In the first winter, four owls were captured and

colour-marked. In the second winter more effort was put into trapping, because radio-transmitters were available to place on owls for tracking purposes. Unfortunately, no owls were captured.

The movements, activity, and territorial behaviour of individual birds were recorded on the study area throughout the entire winter of both years. Usually, individual owls were watched continuously for periods of at least two hours at various times of the day. Observations were made from a car using a 20x telescope and 7x50 binoculars and recorded on a cassette tape recorder and in field notebooks. Whenever possible, photographs were taken to supplement field sketches of postures and displays.

Specific methods used in determining food habits, territories, and activity budgets will be described in the appropriate chapter.

CHAPTER 3

POPULATION STRUCTURE OF SNOWY OWLS WINTERING
IN SOUTHERN ALBERTA, AND THE NATURE OF
INVASIVE MOVEMENTS IN SNOWY OWLS

1. INTRODUCTION

Descriptions of the structure of Snowy Owl populations in winter are scarce; most accounts are of the massive periodic movements in eastern North America and Europe (references cited on p.1). Portenko (1972:118-120), summarizing the European and Asian literature, found that juvenile owls predominated in all of the southward migrations except in 1906/07 (also see Nagell and Frycklund, 1965). In North America adults predominated in the movements of the winters of 1905/06, 1926/27 (Portenko, 1972), 1964/65 (Quilliam, 1965), and 1971/72 (Weir, 1973). In other years juveniles (darkly-coloured owls) were more common (Taverner, 1928; Keith, 1960; Portenko, 1972). These descriptions of the age of Snowy Owls were based upon observations of the plumage colour of owls in the field and information supplied by taxidermists. Most of these workers did not categorize plumage colour in a detailed manner as I have done, and samples of birds collected for taxidermists are probably not representative samples of the population. Thus the validity of these early studies is doubtful.

The timing of the migration of birds of differing sex and age also affects the assessment of the structure of the population in winter. For example, Meade (1948) and Keith (1960) mention that darkly-coloured owls (juvenile females) are more prevalent at the beginning of the winter, and that white owls (adult males) are more common towards the end of the winter, and Fleming (1902) and Portenko (1972) describe winters in which juvenile females (dark-plumaged birds) were observed migrating earlier than adult males. Portenko (1972) also found that juvenile females were the first birds to appear on the breeding grounds in spring. These comments, and the fact that one can never be sure that the age of Snowy Owls has been recorded correctly by the early researchers, indicates the need for an investigation of the structure of a closely-monitored Snowy Owl population throughout a winter, and preferably for more than one winter.

In this chapter I attempt to analyze the sex and age structure of the Snowy Owl population on the study area during the winters of 1976/77 and 1977/78. The first winter was described as a "normal" winter for Snowy Owls in the Great Plains region (K. Smith, 1977), meaning that a major influx of owls was not recorded. In the winter of 1977/78, the number of Snowy Owls reported throughout North America was lower than usual (Wilds, 1978). Therefore, the data reported herein are from winters in which major southward movements did not occur into western North America.

2. METHODS

Data were obtained during the surveys and censuses described in Chapter 2. The abundance of Snowy Owls is described as the number of owls seen per hour spent searching. I chose this measure rather than numbers seen per kilometre travelled because the time spent in various activities (i.e.: observation periods, small mammal trapping, etc.) was more easily partitioned than was the distance travelled. The abundance of owls has been analyzed by seven day periods.

3. RESULTS

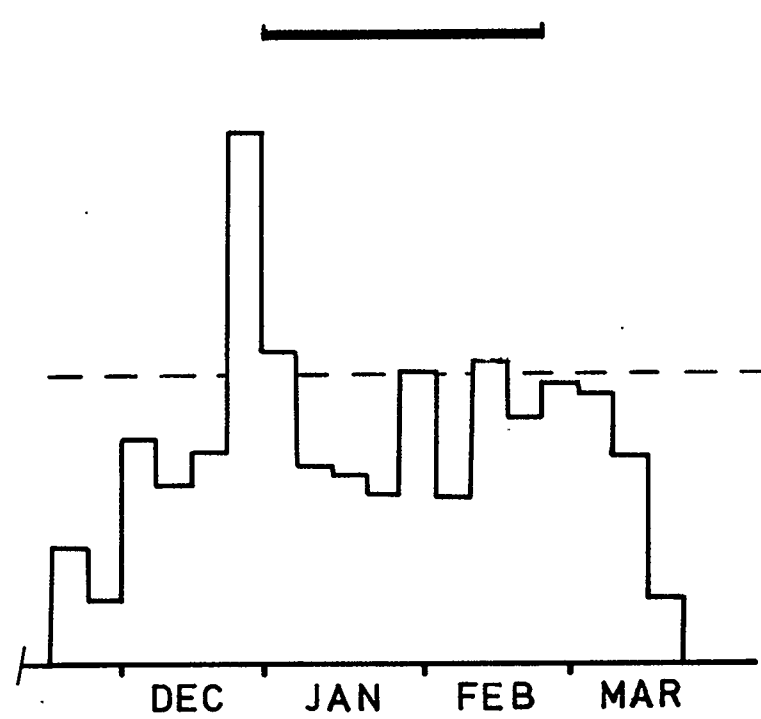
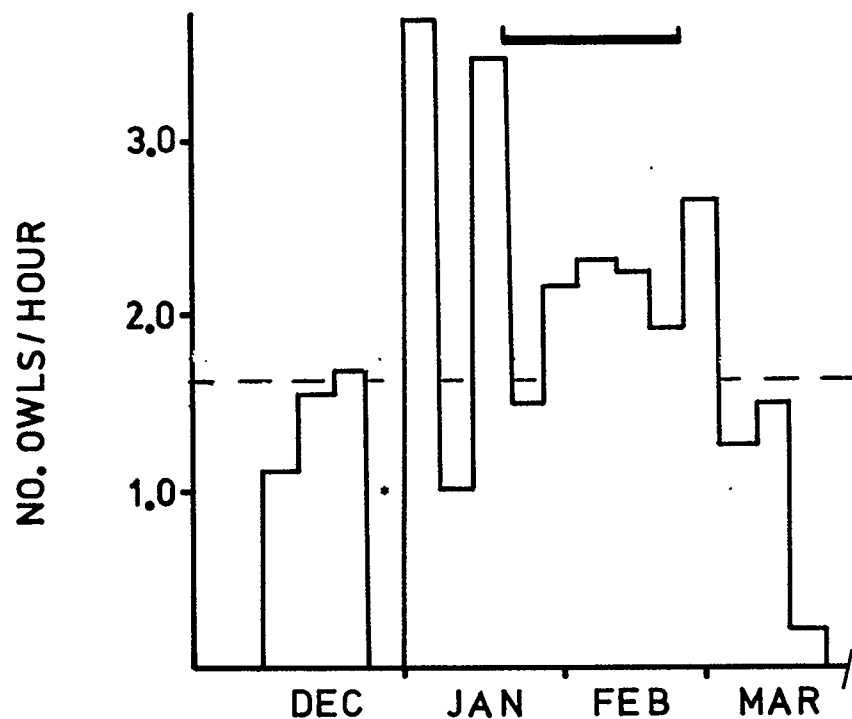
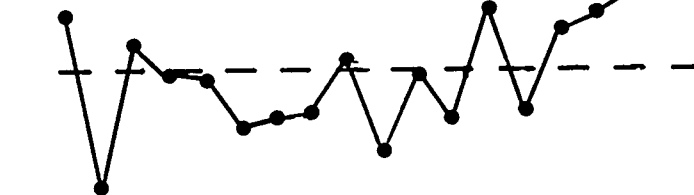
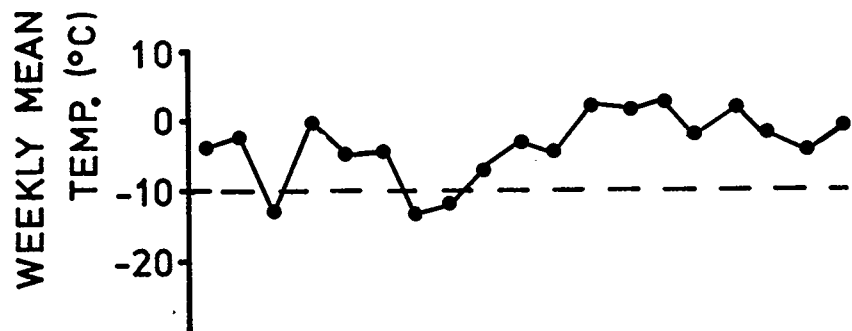
A. The Seasonal Pattern of Abundance

The first owls were seen on 19 November, 1976 and 14 November, 1977. Both birds were probably juvenile males. These dates are similar to the fall arrival dates in the Calgary region in other winters (Bird, 1972).

The pattern of the abundance of owls in each winter is shown in Figure 3. I divided each winter into three periods: (1) the fall movement, including the first main influx of birds; (2) a period where numbers are relatively stable; and (3) spring movement, beginning with the termination of territorial behaviour of the winter resident owls I had been observing on the study area.

In the first period of both winters, few birds were present in late November and the first three weeks in

FIGURE 3: The pattern of the abundance of Snowy Owls in 7-day periods in the Calgary region, throughout the winters of 1976/77 and 1977/78, and the corresponding mean temperatures. The thick horizontal bars represent the periods of relatively stable numbers in each winter (see text for further explanation). The heavy dashed line represents -10°C , and is drawn for ease of presentation. The lighter dashed line represents the average winter level of 1.63 owls/hr (see text for explanation). The asterisk indicates the week with missing data.



1976/77

1977/78

December. The main influx of owls occurred from 1-20 January in 1976/77, and from 24-31 December in 1977/78. Unfortunately no observations were made in the last week of December of 1976. Therefore the influx in January, 1977 could have started several days earlier. The main influx in January, 1977 also appeared to involve more owls, as well as occurring over a longer period of time, than did that in December 1977.

The second period, 21 January to 23 February in the first winter, and 1 January to 23 February in the second winter, was characterized by relatively stable numbers of owls. As I will discuss in Chapter 5, this represents those birds that became winter residents on the study area. In the third period numbers fell as resident owls disappeared, although new birds were observed for one or two days each. By 28 March of both winters the last owls had left, but field-work continued until mid-April to establish this.

B. Factors Influencing Arrival

Figure 3 also shows that owls were more numerous on the study area in 1976/77 than 1977/78. The mean number of owls per hour ($\pm$ S.E.) for 1976/77 was 2.00 ± 0.21 , and for 1977/78 was 1.26 ± 0.14 , for an average winter level of 1.63 owls/hr/winter. The number of owls in 1976/77 was generally above this average level, and in 1977/78 their numbers were below this level (Fig. 3). These data suggest that Snowy Owls

were more numerous in 1976/77 than in 1977/78 in southern Alberta. This agrees with the general descriptions of the abundance of Snowy Owls on the prairies during these winters (K. Smith, 1977; Wilds, 1978).

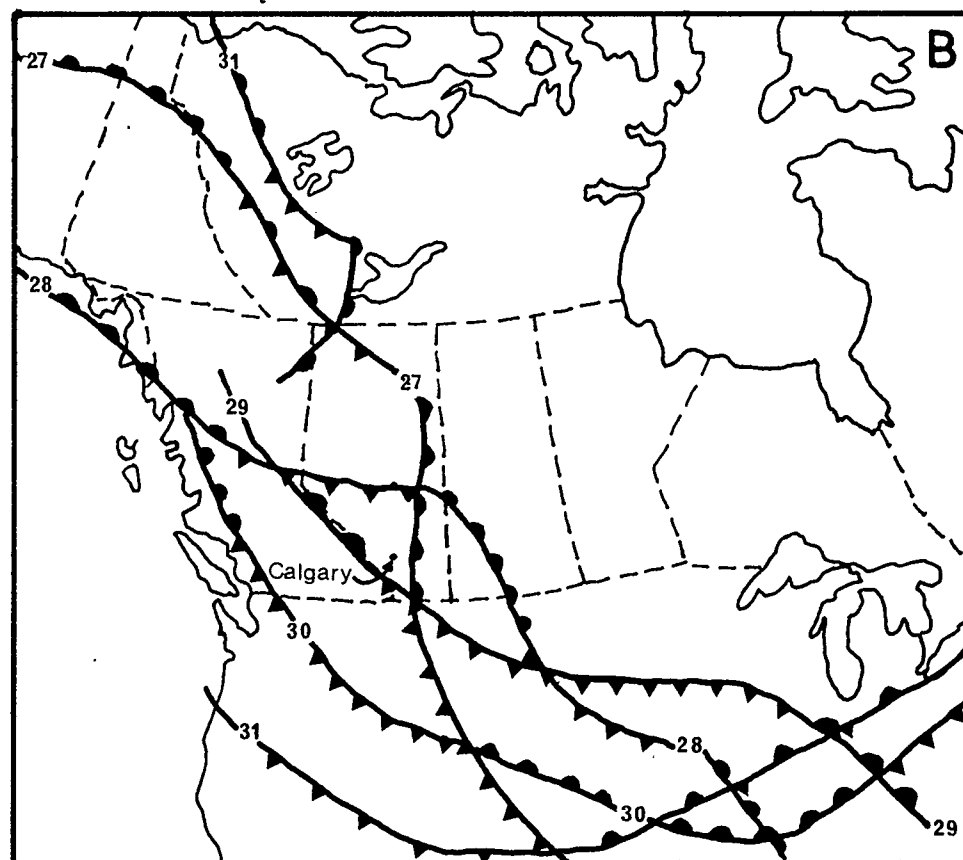
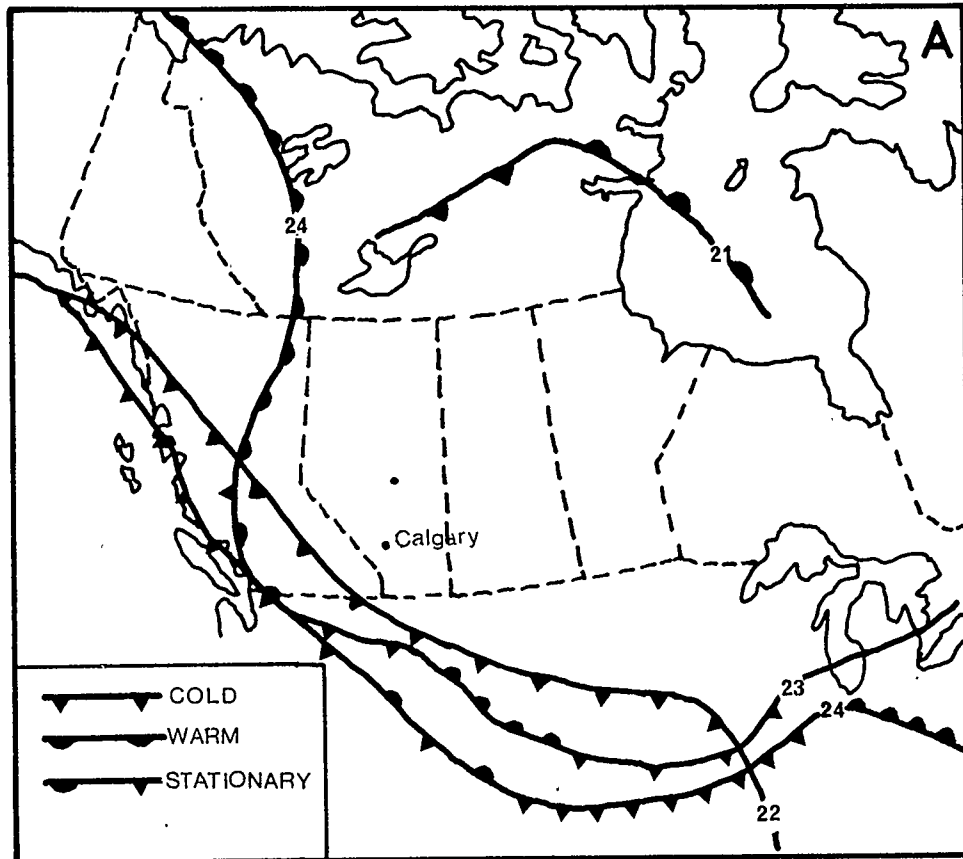
Winter weather on the prairies is influenced by two dominant air flows: one of cold air from the arctic, and the other of mild air from the Pacific Ocean (Longeley, 1972). The flow of arctic air develops from a ridge of high pressure between lows over the Gulf of Alaska and Hudson's Bay. A cold period on the prairies usually results when this ridge of high pressure moves south into Alberta.

The temperature records in Figure 3 suggest that the differences in the peak arrival times in both winters may be related to these periods of cold temperatures. The weekly mean temperature dropped below -10°C only three times in the winter of 1976/77, but was below this fairly consistently during most of the winter of 1977/78. In each winter the main influx of owls occurred during those weeks when the weekly mean temperature dropped below about -12°C for the second time. The earlier arrival of birds in 1977/78 could have been due to the fact that the first cold period in Calgary occurred earlier than in 1976/77. However, this earlier passage of a cold front did not lead to the main influx of owls significantly earlier than in 1976/77. Either the main southward movement of Snowy Owls in Alberta is normally as late as late December or early January, or

some other factor such as the timing of the passage of arctic fronts influences their arrival.

In order to see if the initial major movement of Snowy Owls in each winter correlate with movements of weather fronts, I studied weather maps prepared by the Federal Department of the Environment that were published in "The Calgary Herald". My preliminary analyses suggest that peak movements of Snowy Owls into Alberta are associated with southward movements of a high pressure arctic ridge. For example, the major influx of owls in the last week of December 1977 (Fig. 3) can be broken down into 3 days, 23, 24, and 31 December, on which the highest numbers of owls/day for that winter were recorded. Figure 4 shows the positions of areas of high and low pressure from 22 December to 31 December. On 22 December, the area of high pressure from the arctic had moved southwards, and Calgary lay just up-slope from the stationary front. On 23 December the front moved south and the ridge of high pressure lay over Calgary. Numerous owls were seen on this date (3.43 owls/hr). On 24 December the front moved further south and owls continued to be abundant (3.67 owls/hr). On 27 December the front moved north, and the abundance of owls dropped (approx. 0.8 owls/hr). However, from 28-30 December, another arctic front and associated high pressure ridge moved south, bringing large numbers of owls on 31 December and 1 January (2.5 and 2.8 owls/hr. respectively). A similar meteorolo-

FIGURE 4: Positions of cold fronts in western Canada and the northern USA at 1800 hrs (MST) on each of several days. A. 21 to 24 December, 1977. B. 27 to 31 December, 1977.



logical situation occurred during the major influxes of owls in early January 1977. This information suggests that Snowy Owls arrive in the cold air behind arctic fronts, and that Snowy Owls are seen in greatest numbers 1 or 2 days after the passage of such a front (see also Mueller and Berger, 1967).

C. Seasonal Differences in the Occurrence of Plumage
(Age/Sex) Classes

Table 1 shows the frequency of owls in each plumage class excluding all known instances of duplicate sightings. Class 1 and Class 4 owls each comprise about a quarter of all owls I located in both years. The total proportion of owls with dark plumage (Classes 3, 3-4 and 4), the majority of which represent females of both age classes, is 64% in 1976/77, and 66% in 1977/78. This suggests that females predominated in the southward movement to southern Alberta during these winters.

The proportion of juvenile owls in the total sample of birds in each winter is more difficult to assess, however. The most heavily barred owls (Classes 3-4 and 4) comprise about 40% of the birds seen in each winter. Thus about 40% of the total number of owls I observed in each year were probably juvenile females. Juvenile males are more difficult to identify. After looking at various photographs taken by Portenko (1972) and M. R. Lein (unpubl.), it would appear

TABLE 1. The number of Snowy Owls in each plumage class sighted on the study area, excluding all known observations of the same individuals.

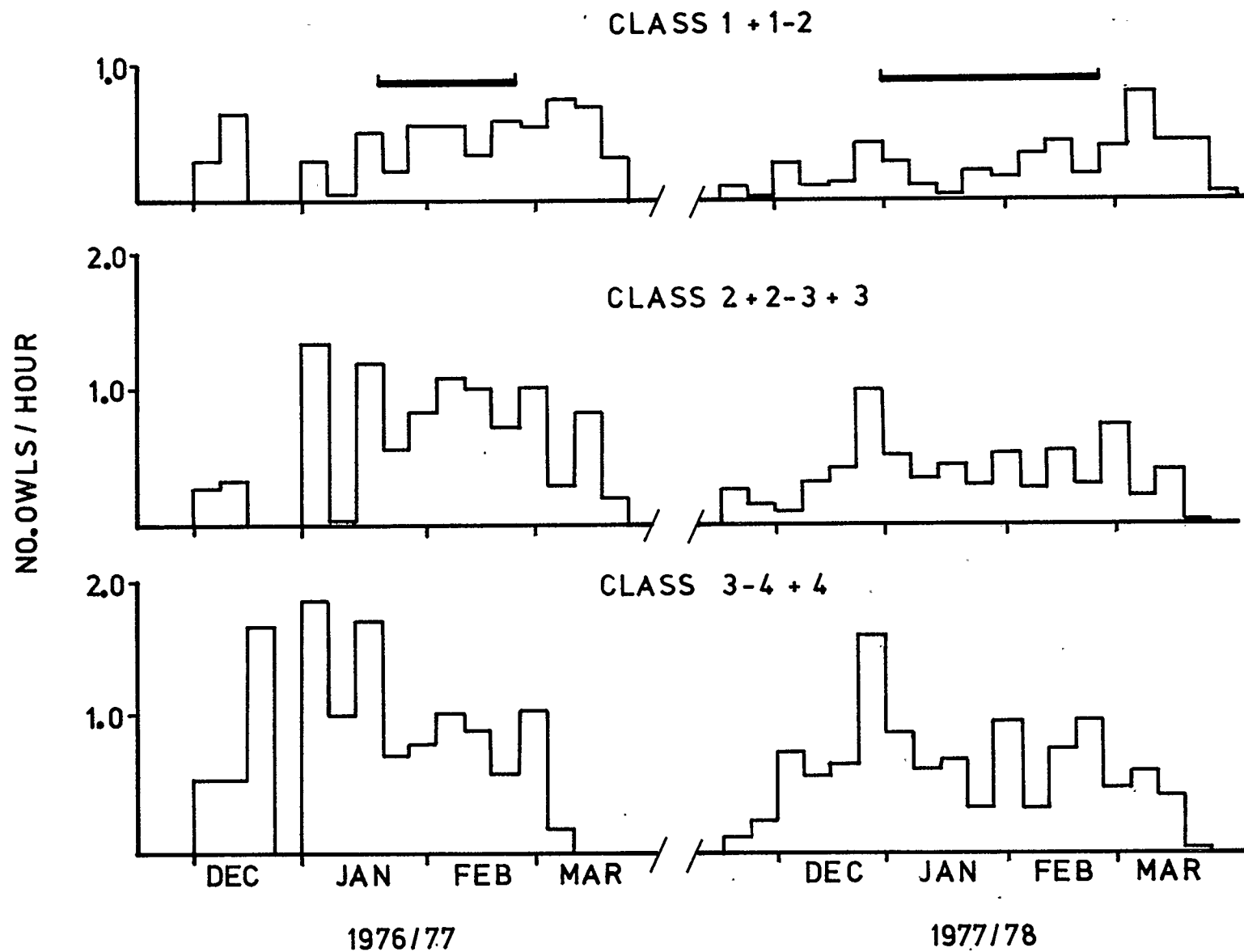
Plumage Class	Number of Owls (Percent of Total)	
	1976/77	1977/78
1	66 (25.5)	35 (20.5)
1-2	3 (1.2)	5 (2.9)
2	15 (5.8)	5 (2.9)
2-3	9 (3.5)	14 (8.2)
3	68 (26.3)	44 (25.7)
3-4	36 (14.0)	29 (17.0)
4	61 (23.7)	39 (22.8)
Total	258 (100.0)	171 (100.0)

that the majority of juvenile males are Class 2 or 2-3 birds. The few juvenile males that I was able to identify on the basis of mottled coverts confirmed this. If juvenile males comprise these plumage classes, then the proportion of juvenile owls in the winter population was about 47% in 1976/77 and 51% in 1977/78.

There are some errors involved in these sex and age classifications, as well as in the estimation of the number of birds in each plumage category. First, I probably could not identify all the individuals on the study area, so that there are some duplicate sightings in the records in Table 1. Second, the greater conspicuousness of the Class 1 owls probably inflated the number of these owls that I located relative to the darker birds, and thus tends to bias the sex ratio in favour of males. Therefore, the unequal sex ratio, favouring females, is probably representative of the population on the study area. Third, some adult females can be Class 2-3; some juvenile males can be Class 3. I am less certain about the sex and age of Class 2, 2-3 and 3 owls than I am of birds in the other plumage classes, so my estimate of the proportion of juvenile owls is tentative.

Figure 5 shows the seasonal abundance of owls in the various plumage categories for each winter. There appear to be seasonal differences in the numbers and movement patterns of putative adult males (Class 1 and 1-2) and juvenile females (Class 3-4 and 4). Juvenile females appear to be pro-

FIGURE 5: Seasonal abundance of Snowy Owls in each of three collective plumage class categories throughout the winters of 1976/77 and 1977/78 in southern Alberta. The horizontal bars represent the periods of relatively stable numbers of owls in each winter (see text for further explanation).



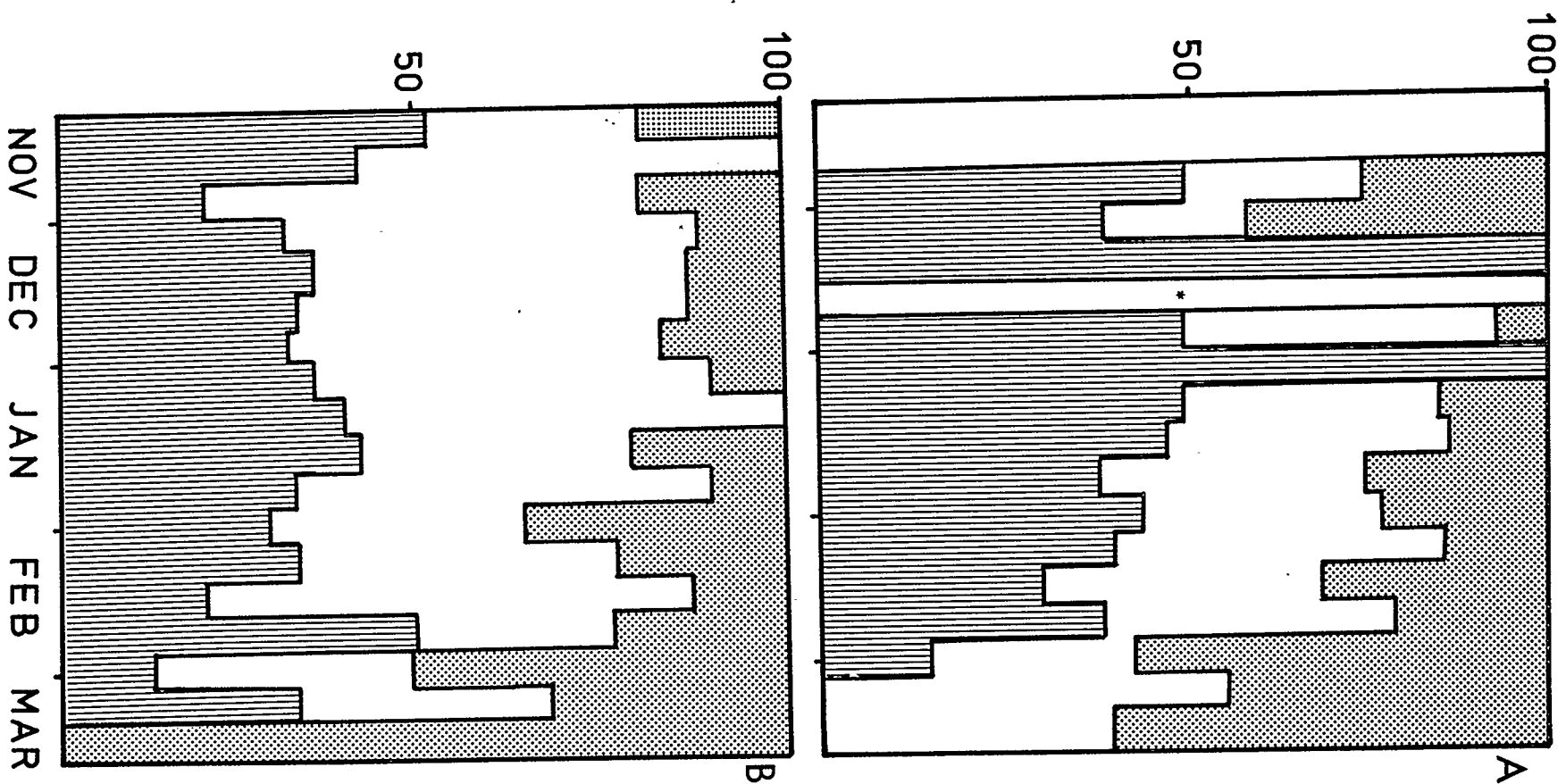
portionately numerous throughout the winter. In contrast, relatively more adult males were seen towards the end of the winter than at the beginning.

I investigated these features by comparing the absolute abundance of owls in each plumage category between the three seasonal periods in each winter using Kruskal-Wallis tests. The only significant statistic was obtained for Class 1 and 1-2 owls in 1977/78 ($p < 0.05$); for 1976/77, the statistic for this plumage category approached significance ($0.2 > p > 0.1$). Statistics for the other plumage categories in both years were not significant ($p > 0.2$). These results suggest that adult males are more concentrated or spend more time in the area during spring migration than during either the fall migration or mid-winter periods, and that the owls in the other plumage categories were not more abundant in one period compared with another.

It appeared from Figure 5 that the darkest owls (Classes 3-4 and 4), and to a lesser extent owls of Classes 2, 2-3, and 3, left the study area earlier than the adult males. In order to investigate this further, I calculated the proportion of each plumage category in the total number of owls seen in each seven day period (Fig. 6). In both winters, the Class 1 and 1-2 proportion was higher in the spring migration period than earlier in the winter. The Class 3-4 and 4 proportion declined somewhat during the spring migration period, particularly in 1976/77 when they disappeared

FIGURE 6: The proportion of Snowy Owls in each of three plumage class categories by 7-day periods throughout the winters of 1976/77 (A) and 1977/78 (B). Stippling represents Class 1 and 1-2 owls, vertical lines represent Class 3-4 and 4 owls, and unshaded indicates Class 2, 2-3, and 3 birds. The asterisk indicates the 7-day period with missing data.

PROPORTION OF OWLS



14 days earlier than the other birds. Thus these results are consistent with Portenko's (1972) statement that adult males migrate later than the other sex and age classes in the spring. On the other hand, greater mortality may be part of the reason for the decline of first-winter owls. I will return to the question of winter mortality in Chapters 4, 5 and 8.

D. Interspecific Relations

The consideration of wintering Snowy Owls in a community context is important in understanding the competitive influence of other species of raptors. Only Short-eared Owls (Asio flammeus), Great Horned Owls (Bubo virginianus), and Prairie Falcons (Falco mexicanus) were relatively abundant winter residents on the study area and could compete significantly with Snowy Owls. However, preliminary results indicate little dietary or habitat overlap between Snowy Owls and Short-eared Owls; in fact the relationship between these two species appears to be that of predator and prey (Lein and Boxall, 1979). Prairie Falcons occurred in small numbers relative to Short-eared Owls on the study area, were dominated by Snowy Owls in interspecific interactions (pers. observ.; Sadler and Myres, 1976), and probably utilized different prey species (see Chapter 4 and Enderson, 1964). The relationship between Great Horned and Snowy Owls is unclear at this time. However, I observed very few Great

Horned Owls on the study area, and this possibly indicates a low level of interspecific competition.

Therefore, preliminary data suggest that Snowy Owls wintering in southern Alberta are inhabiting a region with few serious competitors. This contrasts sharply with Snowy Owls wintering in some regions in eastern Canada where they coexist with relatively high numbers of Red-tailed Hawks (Buteo jamaicensis), Rough-legged Hawks (Buteo lagopus), American Kestrels (Falco sparverius), Great Horned Owls, and Short-eared Owls (pers. observ.; Phelan, 1976). The absence of significant competitors could explain in part the relatively high number of Snowy Owls seen during the winter in Alberta.

4. DISCUSSION

Large-scale mass movements of birds have been separated into two types: migrations and irruptions. Migrations are regular movements between definite breeding areas and wintering ranges and back again (Thomson, 1964:465). The phenomenon is thought to be an adaptation to a seasonal food shortage (Svårdson, 1957).

A typical irruption is a post-breeding movement that is poorly predictable with respect to its regularity, the proportion of the population participating and the directions taken. It is thought that few of the participants make the return journey to the previous breeding areas (Thomson,

1964:403-405). Irruptions have been considered to result from differences in a seasonal food supply between years in a given region (Lack, 1954; Svårdson, 1957). Lack (1954: 235-236) mentioned that juveniles were more common than adults in the irruptive movements of European passerines (also see Svårdson, 1955; Newton, 1970). Lack's explanation for the relative scarcity of adults in these irruptions was that the tendency to move away from the breeding areas may be greater in juveniles. Lack (1944) used this particular explanation to explain the relation of age to partial migration, in which some individuals of a species in a given breeding area are migratory while others are not, and Thomson (1964) used it to explain pre-migratory movements of birds.

In contrast to the typical passerine irruption just characterized, the periodic mass movement of boreal raptors occurs at regular rather than irregular intervals. This has been explained as being due to their vertebrate food supply (largely voles, lemmings, lagomorphs and gallinaceous birds, whose populations appear to vary in a "cyclical" manner) (Lack, 1954; Keith, 1963b; Galushin, 1974). In irruptive raptors, movement of a portion of the population, largely juveniles, occurs every year (e.g., Stewart, 1969; Mueller et al., 1977; Adamcik and Keith, 1978; Adamcik et al., 1978), but in certain years, a large portion of the population moves beyond the normal wintering areas. On such occasions

the participants are mostly adult birds (Mueller et al., 1977; Adamcik and Keith, 1978; Adamcik et al., 1978). A possible explanation for this phenomenon relates the movements to a complete failure of the food supply. Thus, during the build-up of their prey populations over several years, reproductive success is high, and many juveniles disperse because of competition with adults. This produces the movements of juveniles noted in most winters. When prey density declines most of the post-breeding population migrates. Because few young were produced under these circumstances, most of these birds are adults. The work of Hagen (1956, 1965) on various species of owls supports aspects of this view.

This explanation of the large-scale movements of raptors predicts that juvenile owls should predominate in the southward movements of Snowy Owls between major invasions, as noted by Keith (1960, 1963b) and Taverner (1928:220). My crude calculations suggested that about one half of the population of Snowy Owls seen on my study area between November and April were juveniles. In the middle of the winter, which encompasses the period of winter residence, owls with dark plumage (i.e.: Classes 3, 3-4, 4) were in a clear majority and furthermore, all of the winter residents that I observed were females (also see Chapter 5). Therefore, although juveniles comprised only about one-half and females only about two-thirds of birds seen in each winter,

all owls remaining on the study area for long periods of time were adult or immature females.

It would be instructive to investigate the structure of the Snowy Owl population during a major emigration to see if the juvenile portion falls below 50%. Preliminary observations of Snowy Owls in 1978/79 suggest that a major movement took place, and that the proportion of adult birds in the population was much higher than in 1976/77 or 1977/78.

The female-biased sex ratio I calculated is of interest because previous investigators have generally thought that the sex ratio of birds involved in the major movements was 1:1 (Watson, 1957; Portenko, 1972). Keith (1960) observed a 1:1 sex ratio in wintering owls during a non-invasion year (see James, 1958). It is difficult to compare these other studies and the present one due to geographical differences. Other evidence supporting the female-biased sex ratio for Snowy Owls in Alberta comes from the banding studies by Oeming (1955, 1958, 1964), who trapped 35 Snowy Owls in Alberta in 1954-1955, of which 26 (74%) were females.

If there is a 1:1 sex ratio in the entire arctic population, then my results suggest that males do not winter in large numbers in southern Alberta. The fact that none of the mid-winter resident owls I observed were males confirms this (see Chapter 5). Since Snowy Owls can overwinter in the arctic (Sutton, 1932; Manning et al., 1956; Parmelee et al., 1967), males could have a greater tendency

than females to remain on the breeding grounds in non-invasion years. If this is the case, Snowy Owls should be classified as partial migrants (sensu Lack, 1944). Lack believed that among partial migrants a higher proportion of adults than yearlings, and of males than females, winter in the breeding range. Lack (1954:245) thought that this disparity in migratory behaviour is due to the food supply: "for if food is scarce and there is competition for it, adults will probably survive better than juveniles, and males better than females, because adults occupy a higher place in the pecking order than juveniles, and males a higher place than females." Lack's latter statement does not fit with the reversed sexual dimorphism in size of raptors, in which females are thought to be dominant over males (see Cade, 1960; Snyder and Wiley, 1976). However, there is little direct evidence for female dominance in owls. The subject of intersexual aggression will be discussed again in Chapter 5.

The possibility of adult males migrating later than females and juveniles is intriguing because males apparently determine and defend the breeding territory (Sutton, 1932; Watson, 1957; Taylor, 1974). Evidence for the later migration of males comes from the fact that the abundance (Fig. 5) and the proportion of males in the population (Fig. 6) increases in the period of spring migration each winter. Other workers in North America have noted that males leave

later than females (Fleming, 1902, Meade, 1948; Keith, 1960). However, the only reference to spring arrival on the breeding grounds is by Portenko (1972), in which he finds that the young birds arrive first. All of these observations are puzzling. One would expect the males to leave first to secure a suitable breeding territory because owls apparently breed only in regions of high lemming abundance (Pitelka et al., 1955a; Miller et al., 1975) which are distributed unpredictably throughout the arctic (Chitty, 1950; Watson, 1956). Early departure of males would also be expected because the breeding season in the arctic is short and the breeding cycle of the Snowy Owl quite long (Parmelee, 1972). The only explanations I can provide are either that late-arriving males are either able to evict juveniles from optimal breeding areas, or that the risk of starvation through arriving too soon is to be avoided. However, there are not data available at this time to permit an evaluation of these ideas.

A few workers have noted that major movements of Snowy Owls occur in different years in the western and eastern halves of North America (Snyder, 1949; Hanson, 1971; Paxton, 1974). Table 2, derived from accounts of Snowy Owl abundance in "American Birds" (formerly "Audubon Field-Notes"), provides a general summary of these regional differences in the last 12 winters and indicates several unusual local concentrations of owls. Paxton (1974) mentions that, since

TABLE 2. A general summary of the abundance of the Snowy Owl in western and eastern North America and Alberta. The descriptions are based on summaries given in American Birds (formerly Audubon Field-Notes).

Year	West ¹	East	Alberta
1965/66	*	*	****
1966/67	****	****	****
1967/68	*	***	**
1968/69	*	**	*
1969/70	*	*	**
1970/71	*** (B.C. invasion)	**	**
1971/72	**	****	****
1972/73	**	**	***
1973/74	****	**	***
1974/75	*** (Nebraska invasion)	***	***
1975/76	***	**	***
1976/77	**	*** (Iowa invasion)	***
1977/78	**	**	**

**** = major invasion

*** = moderate numbers and localized incursions

** = few to low numbers

* = scarce

1 Western North America includes the provinces west of Ontario and the states west of Minnesota.

1900, at least 20 invasions have occurred in eastern North America, whereas only 4 have occurred in the west. The only synchronous invasions occurred in 1966/67 (Table 2). In addition, the western invasions do not appear to coincide with invasions into the eastern U.S.S.R. (Paxton, 1974).

Earlier I stated that Snowy Owls were relatively abundant every winter in Alberta. Hanson (1971) reports that the majority of Snowy Owl records in western North America (55% of records from 1946 to 1967) during Christmas Bird Counts are from Alberta. The descriptions of the abundance of birds in Alberta since 1965 (Table 2) confirms that there are consistently high numbers of wintering owls in this province.

This information suggests a more complex picture of the distribution and migration of Snowy Owls than that described in the early work of Gross and Snyder (references cited on pp. 1 and 2). As they suggest, the most likely cause of the regional variation in major invasions is geographical irregularity of peak lemming populations. However, this does not explain why some owls regularly winter in certain regions south of the arctic (e.g., Alberta).

I can propose three factors, other than the arctic food supply, that might influence the extent of the southward movement of Snowy Owls in winter: weather systems, inter- and intraspecific competition, and food supply on the winter range. Weather conditions, as described in this chapter,

are probably responsible for the timing of the southward movements, and possibly unusual local concentrations of owls. I have provided some evidence that Snowy Owls wintering in southern Alberta are not faced with many significant competitors. The remainder of this thesis deals with the food supply on the wintering grounds and behaviour associated with the procurement of food.

CHAPTER 4

FEEDING ECOLOGY OF SNOWY OWLS
WINTERING IN SOUTHERN ALBERTA

1. INTRODUCTION

Early reports by hunters and game wardens of the winter food of Snowy Owls were directed towards identifying the impact of this bird upon game species, producing a considerable bias in such reports (see Bent, 1938; Gross, 1944). Consequently, as with other raptors in the nineteenth and early twentieth centuries, many Snowy Owls were destroyed during their migrations. Gross (1944) compiled the most comprehensive list of the food items of this species and showed that it preys more frequently upon harmful animals such as rats and lagomorphs than on game species. However, his and other reports on food habits are largely anecdotal and do not indicate the quantitative composition of the winter diet.

Table 3 summarizes published accounts of the diet of wintering Snowy Owls in North America. The broad spectrum of prey utilized indicates that Snowy Owls are generalized predators in winter. This contrasts with their dietary specialization on microtines during the breeding season (Pitelka et al., 1955a; Watson, 1957).

The weights of prey items listed in Table 3 range from about 20 g for small rodents to 3600 g for the large rabbits.

TABLE 3. A summary of studies on the diet of wintering Snowy Owls in North America.

Locality	Dominant Prey	Reference
LABRADOR	microtines*, alcids, ducks, rabbits	Johnson, 1937
NEW ENGLAND	microtines*, rats, rabbits, passerines, ducks, alcids, gallinaceous birds (grouse)	Gross, 1944
ONTARIO	microtines*, rats, muskrats	Weir, 1973
	microtines*, cricetines, rats, mustelids, rabbits, passerines, ducks, small owls	Catling, 1971
	microtines*	Quilliam, 1965
	microtines*, cricetines, rabbits, muskrats, passerines	Phelan, 1976
	cricetines*, rats, rabbits, passerines, gulls, alcids	Gross, 1944
NEW YORK	microtines, mustelids, rabbits, rats, ducks, gallinaceous birds (pheasants and pigeons)	Gross, 1944
PENNSYLVANIA	microtines, rabbits, mustelids, passerines, gallinaceous birds (grouse and pheasants)	Gross, 1944
MICHIGAN	microtines*, cricetines, rats, rabbits, passerines	Allan, 1977
MANITOBA	microtines, rats, muskrats, ducks, domestic poultry	Keith, 1960
WISCONSIN	microtines, rats, muskrats, passerines, ducks	Keith, 1963a
ALBERTA	microtines, cricetines, passerines	Smith, 1976
BRITISH COLUMBIA	passerines, ducks, grebes*, alcids, gulls, shorebirds, small owls	Campbell & MacColl, 1978

*indicates the most numerous prey items found in the diet

This latter figure is 30-50% greater than the mean weight of adult Snowy Owls (Keith, 1960). Observations suggest that such large prey items are captured rather than scavenged (see Nero, 1964; Campbell and MacColl, 1978).

With the exception of a report by Smith (1976), the diet of Snowy Owls wintering in Alberta is unknown. However, as Table 3 indicates, small mammals are apparently the most important prey group for owls wintering in inland areas. This, in addition to their predation upon arctic microtines while breeding, suggests that Snowy Owls largely utilize small mammals for food in southern Alberta.

The major objective of this chapter is to describe the diet of Snowy Owls in southern Alberta. The paucity of information on foraging behaviour and its importance in the winter ecology of the Snowy Owl prompted me to study it as well. In this chapter I discuss factors influencing hunting success of Snowy Owls. These data, along with information on diet, serve as a background for subsequent discussion of the winter survival strategy of this species.

2. METHODS

Indigestible material in the diet of owls, including feathers, fur, and bones, is prevented from entering the small intestine by the small pyloric opening of the stomach, and is periodically regurgitated in compact masses called pellets. Owls have a relatively poor ability to digest bone

(Chitty, 1937; Duke et al., 1976) and the osseous remains in pellets provide the researcher with a record of the diet of the bird. Experiments comparing known diets of captive owls with subsequent pellet contents have shown that the analysis of pellets provides an accurate indication of the numbers of prey and the species composition of the diet (Glading et al., 1943; Clark, 1975).

In this study I located favourite perches of a number of resident owls. These were visited about once every two weeks during the winter in order to collect regurgitated pellets. Following the spring snowmelt, hunting ranges of resident owls were thoroughly checked for pellets. Any pellet that was found at an unlikely Snowy Owl perch, or that was not obviously of the dimensions of a Snowy Owl pellet, was omitted from the analysis. Pellets were always collected when a bird was observed to cast one. Most of the pellets collected were from owls of known sex. This allowed a comparison of the diet of males and females over the two year period.

Most pellets were intact when collected and were stored individually in small plastic bags until analyzed. In the laboratory, pellets were teased apart with forceps. Identifiable osseous material was separated from bone fragments, feathers, and hair. Bones were identified with the aid of a reference collection of skeletons of prey species. For mammalian prey, limb bones, innominates, and mandibles were

paired and an estimate of the number of individuals in a pellet was made. For avian prey, the number of metacarpal pairs was used to estimate the number of individuals in a pellet. Early in the investigation I found that the mandible pairs of small mammals consistently accounted for the maximum number of mice in a pellet. This finding is consistent with the observation of Graber (1962) and Raczynski and Ruprecht (1974) that mandibles are the best preserved elements in owl pellets.

In order to calculate prey biomass, mean weights of prey species were taken from specimens collected locally or from Banfield (1974). However, using mean weights for calculating the contribution of large species to total prey biomass may be misleading because the owls may not ingest the entire prey item. In the case of large prey, which could provide food for several days, there is a possibility that owls return to the remains of previous kills to feed (Bowles (1916) cited in Marti, 1974). Fortunately, most prey individuals in this study were small enough so that the owls ate them in entirety. In the case of Richardson's Ground Squirrels (Spermophilus richardsoni), evidence from carcass remains and observations of owls feeding indicated that owls ate all but 100-150 g of the animal. Carcasses of larger prey (e.g., White-tailed Jackrabbits, Lepus townsendii) froze rapidly. Therefore I assumed that they only provided one meal. Pitelka et al. (1955a), Watson

(1957), and Gessaman (1972) calculated the average meal size of Snowy Owls to be about 284 g. I used this figure in estimating the amount of these larger prey consumed in a single meal. Using these weights and the prey numbers in the diet, I estimated the proportion of each species in the total biomass of prey.

Snowy Owls rarely fly except while attempting to capture prey or interacting with another owl (Watson, 1957; Höhn, 1973; pers. observ.). Thus I was able to identify the purpose of most flights. The prey species involved in each attempt was usually visible to me, or was ascertained by the subsequent behaviour of the owl following the capture attempt. Therefore it was possible to determine a measure of hunting success for each prey species.

For each capture attempt I recorded the time, initial perch of the owl, habitat type in which the attempt took place, prey type, estimated distance from the perch to the prey item, and the total time that elapsed between the owl leaving the perch and the start of ingestion of the prey. If the attempt was successful, the feeding behaviour of the owl, time taken to ingest the prey, and behaviour following the capture, were also noted.

3. RESULTS

During the two field seasons a total of 100 pellets were collected (28 in 1976/77 and 72 in 1977/78). Tables 4 and 5 summarize the results of the analyses. By pooling mustelids and lagomorphs into one group, and birds other than Gray Partridges (Perdix perdix) into another, I found that there was a significant difference in the diet between the two years (chi-square test, $p < 0.01$). The greater frequency of birds, and mammals other than mice, in the diet during the second year was responsible for this difference.

The contents of pellets from male and female Snowy Owls are compared in Table 6. I pooled samples from both years because of their small sizes. Small mammals comprised about 80% of the prey captured by both sexes. However, males appear to have specialized on Peromyscus, whereas females preyed upon Microtus and Peromyscus with almost equal frequency. Partridges, jackrabbits and weasels (Mustela spp.) were found in pellets from females, but not from those of males. The larger female owls were more generalized in diet, preying upon a greater range of prey species, including prey of considerable size. These results are consistent with Schoener's (1968) theory that larger predators (females in this case) are able to prey upon a wider range of prey size than smaller predators (males).

I observed Snowy Owls in 51 hunting actions. Table 7

TABLE 4. Prey items recovered from Snowy Owl pellets in the winter of 1976/77.*

Prey	Total No. of individuals (%)	No. of pellets con- taining that prey (%)	Total Biomass (%)
<i>Peromyscus maniculatus</i>	57 (61.2)	24 (85.7)	1396.0 (35.0)
<i>Microtus pennsylvanicus</i>	28 (30.1)	14 (50.0)	1070.0 (26.6)
<i>Spermophilus richardsonii</i>	2 (2.2)	2 (7.1)	568.0 (14.2)
<i>Mustela nivalis</i>	1 (1.1)	1 (3.6)	42.2 (1.0)
<i>Lepus townsendii</i>	3 (3.2)	4 (14.3)	852.0 (21.2)
Total Mammals	91 (97.8)		3928.4 (98.0)
Small birds (Passerines)	2 (2.2)	2 (7.1)	82.2 (2.0)
Total	93 (100.0)		4010.6 (100.0)

* Sample size of 28 pellets from at least 12 different birds.

TABLE 5. Prey items recovered from Snowy Owl pellets in the winter of 1977/78.*

Prey	Total No. of individuals (%)	No. of pellets con- taining that prey (%)	Total Biomass (g) (%)
<i>Peromyscus maniculatus</i>	79 (51.0)	43 (61.4)	1935.5 (15.8)
<i>Microtus pennsylvanicus</i>	39 (25.2)	26 (37.0)	1489.8 (12.2)
<i>Spermophilus richardsoni</i>	12 (7.7)	11 (15.0)	3408.0 (27.9)
<i>Mustela frenata</i>	3 (1.9)	3 (4.3)	495.0 (4.0)
Total Mammals	133 (85.8)		6938.3 (59.9)
<i>Perdix perdix</i>	14 (9.0)	12 (17.1)	3976.0 (32.5)
<i>Asio flammeus</i>	2 (1.3)	2 (2.9)	680.0 (5.8)
Small birds (Passerines)	6 (3.9)	6 (8.6)	249.0 (2.0)
Total Birds	22 (14.2)		4905.0 (40.3)
Total	155 (100.0)		11843.3 (100.2)

*Sample size of 72 pellets from at least 13 different birds.

TABLE 6. A comparison of the diets of male and female Snowy Owls based on pellet analyses.

Prey	Male (n = 20 pellets)	Female (n = 60 pellets)
	No. of Individuals (% Total)	No. of Individuals (% Total)
Mammals		
<i>Microtus pennsylvanicus</i>	13 (24.1)	50 (34.4)
<i>Peromyscus maniculatus</i>	33 (61.1)	65 (44.8)
<i>Spermophilus richardsonii</i>	4 (7.4)	9 (6.2)
<i>Lepus townsendii</i>	0	2 (1.4)
<i>Mustela</i> spp.	0	4 (2.8)
Birds		
<i>Perdix perdix</i>	0	11 (7.6)
Passerines	4 (7.4)	4 (2.8)
Total	54 (100.0)	145 (100.0)

shows their distribution among various prey types for both years. In each year attempts to capture small mammals and birds were more common than attempts directed at other prey. This agrees with the frequency of these prey in the diets (Tables 4 and 5).

The most common foraging method (50 of 51 hunts) was "still-perch" or "sit and wait" hunting. Foraging owls typically perched on tall objects for 10-15 minutes; if no prey was located, they moved to another perch 100-200 m away. Once a prey item was sighted an owl would assume an upright posture. Several head-bobs sometimes occurred, followed by a low flight directly at the prey item. On two occasions, however, owls attempting to capture birds flew in a wide circle so that they approached from the direction of the sun. In two additional capture attempts owls appeared to utilize obstacles to prevent the detection of their approach. The following observation is an example of this:

22 December 1977. While observing a large female Snowy Owl perched on a fencepost, I noted a covey of 8 Gray Partridges feeding on a road about 400 m from the owl. The owl, upon seeing these birds, flew slowly towards them, frequently gliding about a half metre above the ground. In addition, the owl approached the covey from behind a large willow bush(Salix sp.). When the owl reached the bush, it veered up over it, and startled the partridges.

TABLE 7. The number of attempts by Snowy Owls to capture various prey.

Prey Group	No. of Hunts (% Total)			
	1976/77		1977/78	
	Number	No. Successful	Number	No. Successful
Small Mammals ^a	16 (69.9)	11 (91.7)	17 (60.7)	8 (80.0)
Birds (Passerines				
and <i>Perdix perdix</i>	3 (13.0)	0	10 (35.7)	2 (20.0)
<i>Lepus townsendii</i>	2 (8.7)	0	1 (3.6)	0
<i>Spermophilus richardsonii</i>	1 (4.3)	1 (8.3)	0	0
Unknown	1 (4.3)	0	0	0
Total	23 (100.2)	12 (100.0)	28 (100.0)	10 (100.0)

^a Includes *Microtus pennsylvanicus* and *Peromyscus maniculatus*.

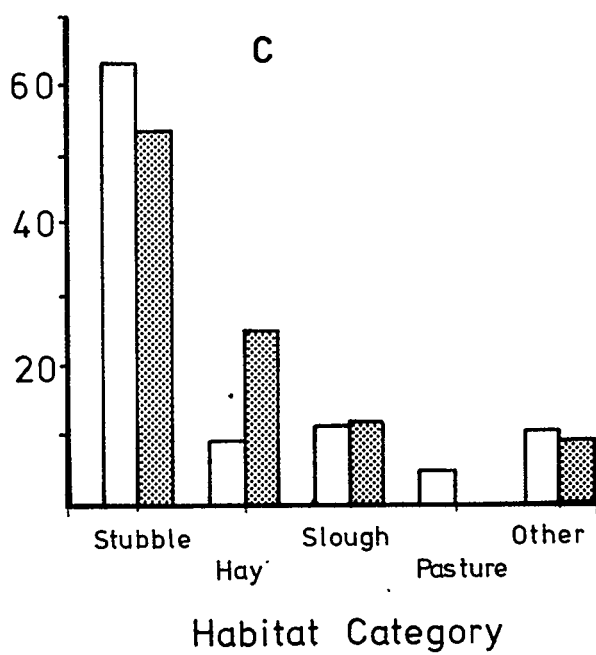
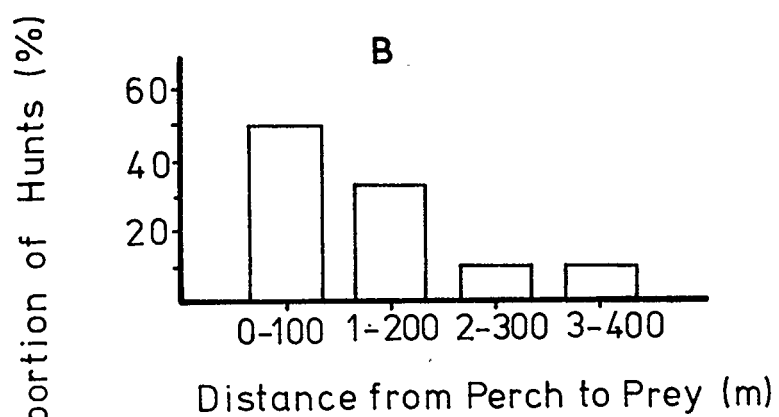
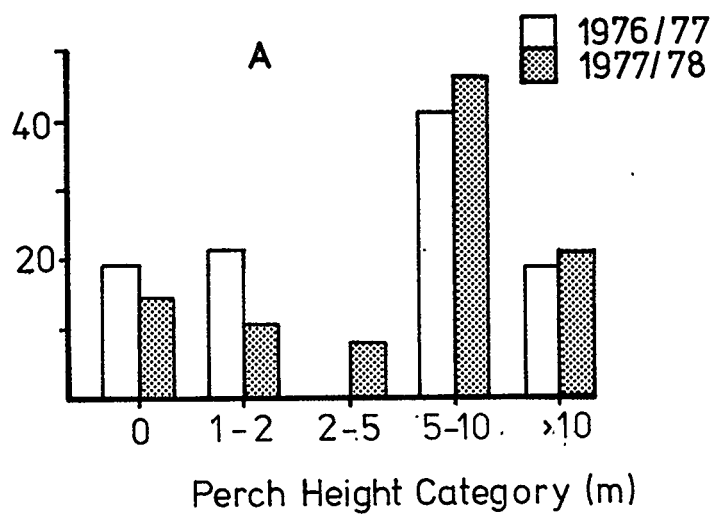
A very rapid attack flight immediately followed which was unsuccessful.

Owls seized prey with their feet and usually killed them by biting the head or by shaking them violently while holding them in their bills. Voles and mice (Microtus pennsylvanicus and Peromyscus maniculatus) were usually swallowed whole and head-first immediately after they were killed. However, this behaviour varied somewhat with the age-class of the owl and is discussed in some detail later in this chapter.

I observed Snowy Owls capturing birds on only two occasions (one Gray Partridge and one Horned Lark, Eremophila alpestris). Neither was plucked, as hawks commonly do to their avian prey (Brown, 1976). Both birds were torn into small pieces and swallowed. However, the larger flight feathers were not eaten.

Figure 7 summarizes a number of aspects of the hunting behaviour of the owls. The importance of a high perch as a vantage point for hunting owls is shown in Figure 7A. In 1976/77 and 1977/78, 68% and 58% respectively, of all hunting attempts were initiated from perches over 5 m in height (powerpoles and powerline towers). Most prey were captured within 100 m of these hunting perches (Fig. 7B). Capture attempts at greater distances were rare, and usually involved large conspicuous prey species such as jackrabbits or partridges. Finally, as Figure 7C shows, most capture attempts took place in stubblefields and hayfields (mean percent of

FIGURE 7: Aspects of the hunting behaviour of Snowy Owls wintering in southern Alberta. A. The relationship between perch height and hunting. B. Distances at which prey were captured from hunting perches (data from both years were pooled because of small samples). C. Partitioning of hunts among habitats. A total of 51 hunting attempts (23 in 1976/77 and 28 in 1977/78) were observed.



captures for both years combined are 56% and 18% respectively). Considering attempts at capturing small mammals only, 81% of all attempts in 1976/77 and 60% in 1977/78, occurred in stubblefields. Hayfields were the second most important habitat for small mammal prey (18% in 1976/77, and 24% in 1977/78). The majority of the remainder of hunts occurred in sloughs.

The overall success rate for the entire sample of capture attempts by both adult and juvenile birds was 43.1%. Enough data were gathered to compare the hunting success ratios of adult and juvenile females. Juvenile females were successful in 10 of 30 attempts (33.3%). Adult females captured prey in 10 of 15 attempts (66.6%). The difference between these success rates is significant (chi-square test, $p < 0.05$), indicating that adult females were more successful than juvenile females at capturing prey.

Direct observations of hunting owls suggested that juvenile females had some difficulty in subduing their prey. The following incidents illustrate this:

(1) 29 December 1976. I was observing an immature female owl perched on a pole. Suddenly a jack-rabbit bounded across the field about 200 m from the owl. The owl immediately took flight and struck the rabbit on the head with its feet. The force of the owl's flight carried it into the snow about 2 m past the rabbit. The owl stood

upright and the rabbit, apparently unaffected by the attack, slowly moved around the owl, sniffing the bird. This continued for about 10 seconds, when suddenly the rabbit moved into a row of dense shrubbery. The owl remained on the ground for several minutes, and then it flew a long distance away.

(2) 23 February 1978. I observed an immature female owl fly swiftly towards a ridge and capture a small mammal. The capture was made while the owl was flying and as it flew back to the perch it had just left, it dropped its prey. The owl made a quick turn, landed on the ground, and walked to where the mouse was dropped. The mouse was still alive and attempted to escape by burrowing in the snow. The owl quickly pounced on the mouse and remained on the spot for about 30 seconds. Following this, it flew to the perch with the mouse and ate it in several pieces.

In addition to having problems killing their prey, the behaviour of juvenile females following a successful capture differed from that of adults. In all cases I observed (n = 13), adult owls swallowed small mammal prey whole, immediately after catching them. In contrast to this, juveniles frequently "mouthed" prey and eventually ate them in several pieces. Observation 2 above illustrates this

behaviour. In addition, observation 2 describes a flying owl capturing prey and then dropping it while in flight. I never observed adult birds to do either of these things. These differences in behaviour resulted in different handling times (times taken between capture and the start of ingestion of prey) for the two age classes. Adults took an average of 4.3 (2-6) seconds ($n = 8$) to handle small mammals, whereas juveniles required an average of 17.9 (2-60) seconds ($n = 9$).

4. DISCUSSION

A. Principal Prey Species

Small mammals are important prey for Snowy Owls in southern Alberta. Tables 4 and 5 indicate that they contributed about 60% and 30% of total prey biomass in the two years, and that the total number of mice captured far outnumbered any other prey species. In addition, the percentage of pellets containing mice indicated that they were consistently utilized as a food source. Small mammals are also predominant in the diet of Snowy Owls on the breeding grounds (Pitelka et al., 1955a; Watson, 1957).

Gray Partridges form coveys during the winter (Jenkins, 1960; Westerskov, 1966), ranging in size from 6 to 14 birds. Partridge coveys inhabit definite ranges, spending most of their time foraging and resting in open, conspicuous areas

(Westerskov, 1966; pers. observ.). In late February, the coveys break up and pairing begins. This process is rather rapid, and once it has taken place the birds are secretive and difficult to locate (pers. observ.).

I noted a number of unsuccessful attacks against partridges in coveys. I attribute the lack of success to the fact that the partridges were in groups. Other workers have noted that raptors have more difficulty capturing birds from flocks than lone birds (Page and Whitacre, 1975; Kenward, 1978). The only successful attack on a partridge that I observed was on a single individual. These observations suggest that covey formation could be an adaptive response to predation, by allowing increased vigilance (Powell, 1974) or the confusion of an attacking predator (Kenward, 1978). Covey formation probably allows partridges to feed all day in open habitats where predators like the Snowy Owl are likely to be hunting.

The importance of partridges as prey for Snowy Owls becomes apparent when one relates the diets of the owls to the weather conditions for the two years of study. The weather during the two field seasons varied significantly (Fig. 3, and see the Annual Meteorological Summaries published by Environment Canada). Temperatures in the second year were much lower, and remained well below freezing for virtually the entire winter. Although the total snowfall in both winters was not significantly different, the consis-

tently cold temperatures in 1977/78 allowed the snow to accumulate to greater depths. The overall effect of this was to reduce the availability of small mammals to Snowy Owls (Craighead and Craighead, 1954; Clark, 1975). This is suggested by the decrease in small mammals in the diet during 1977/78 (Table 5) compared to 1976/77 (Table 4). This decrease was offset by the increase in Gray Partridges in the diet in the second winter. Therefore partridges might serve as "buffers" (sensu Errington, 1945) in southern Alberta during periods of rodent scarcity. On the breeding grounds, ptarmigan (Lagopus spp.) could serve the same ecological role (see Bent, 1938).

Ground squirrels contributed significantly to total prey biomass, but can be excluded as important prey for winter resident Snowy Owls. Ground squirrels hibernate most of the winter and do not become available to Snowy Owls until they emerge at the end of February (pers. observ.). Owls feeding on this species are more likely to be migrant owls (see Chapter 3, and Chapter 5) than winter residents. Therefore ground squirrels are probably an important food item only at the end of the winter season.

B. Sexual Differences in Feeding Ecology

Sexual dimorphism in size in birds has long been a controversial subject. One hypothesis attempting to explain its significance is differential niche utilization (Selander,

1966; Earhart and Johnson, 1970). Selander (1966) has cited evidence from various sources that females of the hawk genus Accipiter take larger prey than do the smaller males. Therefore, in Snowy Owls, one of the most dimorphic owls in North America (Snyder and Wiley, 1976), one might expect females to take larger prey more frequently than males.

The most significant difference in the prey selected by males and females was the specialization by males upon deer-mice, and the wider range of prey captured by females (Table 6). However, this result could be erroneous for several reasons. First, the sample of pellets from known male birds was small ($n = 20$). Second, larger prey species are not well represented in owl pellets (Brooks, 1929) due to their large bones and the feeding behaviour of owls.

The largest prey species taken by Snowy Owls on my study area were White-tailed Jackrabbits. This is the largest member of the genus Lepus in North America (Banfield, 1974). Only three pellets, all from female owls, contained remains of jackrabbits. Field observations of hunting females suggested that they attempted to capture jackrabbits whenever they were encountered ($n = 3$). On the other hand, males were never observed to attempt to capture jackrabbits although I observed several opportunities ($n = 4$). On 30 January 1978 I received a report of an adult female Snowy Owl killing and feeding on a rabbit. The next day I searched the area indicated by the informant and

found the frozen carcass of a large jackrabbit (weight of remains was 2630 g). The shoulders and a portion of the neck were eaten; no bones appeared to have been ingested and no jackrabbit remains were found in the eleven pellets I collected from the territorial owl in this area. This information suggests that sexual differences in the size range of prey exist and that jackrabbits are underestimated in the diet. The magnitude of the difference and the importance of jackrabbits as prey are unknown at this time.

C. Hunting Behaviour and Success

Snowy Owls were successful in 22 of 51 observed prey-capture attempts. This success rate of 43.1% is considerably higher than those observed for most other non-breeding raptors (Table 8). At first glance, one might attribute this high success to the small sample of capture attempts I observed. However, I believe that this is a good estimate of the outcome of Snowy Owl capture attempts for two reasons. First, Höhn (1973) observed a small number (12) of Snowy Owl hunts in Alberta during winter and found a success rate of 66.6%. This result is not statistically different from mine (chi-square test, $p > 0.2$).

The second reason involves what I believe is a relationship between foraging method and observable hunting success. I propose that predatory birds that spend little energy searching for prey (passive searchers) will have

TABLE 8. Hunting success during winter of seven species of raptors.

Species	Total No. of Observations	No. Successful	% Successful	Source
<i>Accipiter nisus</i>	213	23	10.8	Rudebeck, 1950
<i>Falco columbarius</i>	155	7	4.5	Rudebeck, 1951
<i>Falco columbarius</i>	343	43	12.5	Page and Whitacre, 1975
<i>Falco peregrinus</i>	260	19	7.3	Rudebeck, 1951
<i>Falco sparverius</i>	498	233	46.8	Collopy, 1973
<i>Haliaetus albicilla</i>	60	3	5.0	Rudebeck, 1951
<i>Asio flammeus</i>	577	130	22.5	Clark, 1975
<i>Nyctea scandiaca</i>	51	22	43.1	This study

higher prey-capture success rates than birds that expend a lot of energy searching for prey (active searchers). The reasons for this are related to predictions of optimal foraging theory (MacArthur and Pianka, 1966; MacArthur, 1972; Pianka, 1974). This theory predicts that active searchers should try and capture most of the prey items they encounter because the search costs per item are high relative to capture costs. In other words, attempting to capture a prey does not cost much more than continuing to search. Passive searchers, on the other hand, should attack only those prey items with small capture costs because these costs are higher than continued searching. In this case, attempting to capture something costs much more than continued searching. These theoretical predictions lead to the conclusion that active searchers should have more potential encounters with prey items than passive searchers in environments containing similar arrays of prey-types. Therefore, the observed hunting success of active-searching raptors will be lower for two reasons: (1) Passive searchers will attack only those potential prey items that are easy to capture; (2) Because of their lower prey-encounter rates, passive searchers may expend more effort to capture a prey item.

To the biologist observing these predators, numerous capture attempts by the active searcher would be recorded as unsuccessful attempts. In all probability most of these

attempts are "tests" to see if the prey is worth pursuing or if time should be spent locating other prey (see Kenward, 1978). Mech (1970) discusses this in some detail for canid predators. According to theory, tests to measure the capturability of a prey item are costly to passive searchers. Thus most observed attempts at capturing prey by passive searchers are probably true attempts at prey capture.

The success rates of various non-breeding raptors are compared in Table 8. The success rates of Snowy Owls and American Kestrels are very similar. Kestrels, like Snowy Owls, hunt mainly from a perch (Collopy, 1973; Balgooyen, 1976), and are therefore "sit and wait" or passive-searching predators (Schoener, 1971). The success rates for these two species are much higher than for the other raptors listed in Table 8. These latter species are active searchers, searching for prey while in flight. Short-eared Owls quarter open areas in a coursing flight pattern, and swoop swiftly in on small mammal prey (Clark, 1975). Rudebeck (1950, 1951) describes the hunting behaviour of the other species during migration. The fact that these species were migrating, could in part explain their low rates of success. He mentions that Merlins (Falco columbarius) and Sparrowhawks (Accipiter nisus) utilize low altitude, swift-flying techniques. They frequently follow contours in order to surprise or "ambush" avian prey. Peregrine Falcons (Falco peregrinus) search while flying at high altitudes and "stoop" at great

speed at prey. White-tailed Eagles (Haliaeetus albicilus) use techniques similar to those of the Peregrine, but not as effectively.

With the exception of the Merlin, the descriptions given above generally agree with other observations of the hunting behaviour of these species (e.g., see L. Tinbergen, 1946; Lockie, 1955; Hunt et al., 1975). For the Merlin, Page and Whitacre (1975) observed 343 hunts, 82 (24%) of which were initiated while the hawks were searching while in flight. The rest were initiated from a perch. They observed an overall success rate of 12.8% for the total sample of hunts. If we exclude the hunts made while flying, none of which were successful, the success rate rises to 17.0%.

The relationship between foraging method and success is further supported by comparisons of success rates for predators using a variety of hunting behaviours. For example, Clark (1975) found that Short-eared Owls have a higher degree of success when perch-hunting (33.3%) than while hunting in flight (18.0%). Schaller (1972) also found that single lions (Panthera leo) were more successful when "sitting and waiting" than running or driving prey. Page and Whitacre's (1975) observations on the hunting success ratios of Merlins while in flight and while perched are also supportive evidence.

The calculation of true hunting success rates are very

complex, as the age of the animal (see next section), sex, physical condition, season, and habitat can all affect the final result (see Kenward, 1978). This indicates the need for researchers to carefully select comparative data. In most cases these data are lacking and the ideas described above are tentative.

D. Age and Hunting Success

Biologists have predicted that the ability of birds to obtain food improves with age and experience (e.g., Ashmole, 1963; Lack, 1966). Several studies have confirmed this. Immature Brown Pelicans (Pelecanus occidentalis) (Orians, 1969) and Little Blue Herons (Florida caerulea) (Recher and Recher, 1969) have lower rates of success at capturing prey than do adults. Dunn (1972) found that juvenile Sandwich Terns (Sterna sandvicensis) differed from adults in foraging method and success. However, no studies on the relationship between age and hunting success in owls have been published. The hunting behaviour of owls requires just as careful co-ordination and judgment as do those of pelicans, herons and terns. Therefore, one would predict a difference in foraging success between adult and juvenile owls.

Although the sample of hunting attempts by Snowy Owls of known sex and age was small, a significant difference in hunting success was found between adult and juvenile females (p. 62). Direct observations of hunting owls also suggested

that juveniles had more difficulty than adults in subduing captured prey. These observations suggest that Snowy Owls in their first year have more difficulty in meeting their energy requirements than do older birds. However, it does not necessarily follow that juveniles have a lower intake of food per day. Several strategies may be used to compensate for reduced hunting success. For example, juveniles may spend more time foraging. Although the subject of survival strategies of juvenile Snowy Owls will be dealt with in several forms later, further observations of hunting behaviour of juvenile Snowy Owls are needed to identify the factors involved in meeting their energy requirements.

CHAPTER 5

THE USE OF SPACE BY SNOWY OWLS

1. INTRODUCTION

Early research on habitat selection focused on its significance in niche segregation (e.g., Svårdson, 1949) and speciation (e.g., Lack, 1940; Thorpe, 1945). Only recently has the importance of habitat selection been described in terms of responses to variation in the distribution and density of food (Royama, 1970; Tullock, 1970; Smith and Dawkins, 1971). The basic premise of these recent studies has been that "as long as a predator can improve its survival or reproductive success by hunting more efficiently, natural selection will favour efficient predators" (Krebs, 1978:23).

Most animals search for food which is patchy in distribution. The problem of how these clumps or patches should be exploited efficiently has been termed optimal patch choice by Pyke et al. (1977). The first investigation of this aspect of foraging behaviour (MacArthur and Pianka, 1966) showed mathematically that an efficient predator should choose only those patches with the highest prey availabilities. However, this hypothesis has not been supported by experimental studies of patch-use by animals (Krebs and Cowie, 1976; Pyke et al., 1977). Predators are usually

confronted with a number of different habitats, each offering different rates of return per unit hunting effort. On the basis of laboratory studies of learning (e.g., Mackintosh, 1969; Herrnstein and Loveland, 1975), one would expect that predators should concentrate their foraging effort on the most rewarding habitat, yet never quite abandon the less rewarding alternatives (see below). Thus the exploitation of patches by predators can be considered as probability learning, where animals only approximate the optimal rule of concentrating all effort on the most rewarding alternative (Herrnstein and Loveland, 1975). This idea has been expressed in detail for predators by Royama (1970) in what has become known as the "hunting by profitability" hypothesis.

According to Royama, predators learn which patches are the most profitable by spending time sampling all patches. Once the best areas have been located most, but not all, foraging time is allocated to these areas. The predator will continually sample less profitable areas in order to monitor changes in profitability. Experimental studies by Smith and Dawkins (1971), Smith and Sweatman (1974), and Zach and Falls (1976) have shown that birds allocate the greatest amount of time to an area of the highest food abundance, and less time to areas with lower food abundance. However, there was not a simple ranking of hunting effort among patches in direct proportion to prey densities, and the birds occasionally foraged in suboptimal areas. These

results support Royama's model of hunting by profitability.

For migratory birds, profitable foraging areas must be rapidly located on the winter range in order to maximize survival. Many migratory birds maintain a feeding territory in winter in areas where food is predictably abundant (Craighead and Craighead, 1954; Zahavi, 1971; Lederer, 1977). Presumably the selection of the territory is based upon previous foraging success in that area. This means that animals must remember where they have foraged successfully. In fact, the learning component in territorial behaviour might be so important that the maintenance of exclusive feeding areas could be based on knowledge of the depression of food in that area (see Charnov et al., 1976). This could improve an individual's foraging efficiency through the avoidance of recently depleted resources. To my knowledge, only two studies (Gill and Wolf, 1977; Kamil, 1978) provide evidence that birds remember where they have foraged in the wild.

The question of whether territorial birds should defend only the highest quality habitats, or an array of profitable and unprofitable habitats, can be analyzed by considering Brown's (1964) principle of economic defendability. This principle implies that a feeding territory represents a balance between the amount of food contained in a defended area and the costs of harvesting and retaining exclusive use of it. The simplest way to apply Brown's principle is to

assume that the available food energy in each territory is constant, and that territory size or its habitat composition is regulated to maintain this energy level. Studies utilizing this approach have found an inverse relationship between territory size and food density (Stenger, 1958; Simon, 1975; Gass et al., 1976), which is consistent with Brown's model. Therefore the territories defended by birds probably will not contain only the most profitable habitats, but a number of different habitats of different profitabilities (Pyke et al., 1977).

Against this theoretical background I will describe the habitat selection and territoriality of Snowy Owls. These subjects have twofold importance to the biology of this species. First, the size and stability of Snowy Owl populations on the wintering grounds could be related to the availability of prey which, in turn, is probably the result of habitat characteristics. Second, the ability of Snowy Owls to forage efficiently in winter could be one of the most important factors regulating Snowy Owl populations.

The patchwork of types of vegetation on the study area provides Snowy Owls with a range of choices of habitats. As Lein and Webber (1979) have shown, Snowy Owls prefer certain habitats over others. It was unknown, however, whether this finding was the result of the selection of areas with high food availability. In the present study, prey were sampled in most habitats to permit an index of the profitability of

these habitats to Snowy Owls. These data, along with the distribution of habitats on the study area and observations of habitat use by Snowy Owls, should permit an appraisal of the ability of this species to recognize and forage in optimal areas.

2. METHODS

In order to determine the habitat composition of the study area, the habitat maps described in Chapter 2 were transcribed onto current 1:25,000 mosaic aerial photographs of the study area. These photographs were prepared for computer analyses of habitat composition by placing them on the digitizing surface of a G.T.O. electronic coordinate digitizer, and determining the coordinates of habitat boundaries in relation to a common origin. Each field on the study area was given a number designation and classified as one of the nine habitat categories for each of the two years. These data were recorded on magnetic disk and transferred directly to a D.E.C. PDP 11/40 electronic computer. Using programs developed by Larry O. Sinkey, Faculty of Environmental Design, University of Calgary, the total area of each field and each habitat on the study area was obtained.

Habitat selection by the owls was investigated using two methods, instantaneous or scan sampling, and focal animal sampling (Altmann, 1974). The first method involved recording the habitats in which owls were situated when

first sighted during censuses and surveys. When an owl was perched on the boundary between two habitats, a value of 0.5 owl was assigned to each of the two habitat categories. Selection was then investigated by counting the number of owls sighted in each habitat and comparing this distribution of sightings with a theoretical one based on the availability of habitats (Lein and Webber, 1979).

Although these data include sightings of the same individual on different days, only one observation per individual on a single day was used. Therefore, these data consist of independent observations of habitat usage. In some analyses observations of residents (known wintering individuals) were excluded in order to compare their habitat preferences with those of non-residents (owls remaining in one locality for less than three days).

The second method consisted of recording the positions and movements of resident owls during observation periods. The entire array of positions for each known individual was then analyzed using a technique developed by Odum and Kuenzler (1955). This involved forming a minimum convex polygon by connecting the outermost positions of a bird, such that all of the locations of that individual are included inside the area. The area of this polygon, called the maximum utilized area, was then determined using a compensating polar planimeter. In order to determine if the minimum sample of owl locations needed to accurately

represent the size of the utilized area had been obtained, observation-area curves were drawn for each owl observed in detail. This involved plotting series of four consecutive positions, joining the outermost points as described above, and calculating the areas of each resulting polygon. The number of observations were then graphed against their corresponding areas. As Odum and Kuenzler (1955) have shown, as the number of positions increases, the area increases asymptotically until further locations result in no observed increase in area. Only those owls whose observation-area curves approached an asymptote where further locations resulted in less than 1% increase in area were chosen for detailed analysis. The habitat composition of each utilized area was also calculated using the planimeter.

The profitability of habitats is dependent upon the availability of prey. Although the density of rodents is correlated with their availability to raptors, other factors such as vegetation and weather also play a role in determining availability (Craighead and Craighead, 1954). In this study most of the effort in examining habitat profitabilities was placed in estimating the abundance of small mammals and partridges. Rodent abundance was determined by trapping surveys. In addition, tracking censuses were conducted in various habitats to measure the availability of small mammals to visual predators.

Preliminary rodent-trapping surveys were carried out in

1976/77. The results of these were used to design a more comprehensive program in 1977/78. This trapping program involved the use of parallel trap-lines, each consisting of five stations placed 25 m apart. Every station had five snap-traps (Victor Mouse Traps) placed 5 m from a central point and roughly equi-distant from each other. Therefore, each trap-line consisted of 25 traps, and covered a linear distance of 105 m. Two trap-lines were placed in each field to be sampled and one was used in habitats such as sloughs, road allowances or ditches. The first line was set parallel to, and 10 m from the edge of the field, and the second line was set 25 m from the first towards the centre of the field. This method was chosen to yield information on the distribution of rodents in relation to edges of fields.

The paucity of large pastures and ungrazed grasslands made trapping difficult in these habitats, and farmyards were impossible to sample because of human disturbance. Therefore I decided to trap in the remaining five habitats: stubble-field, fallow, hayfield, slough, and roadside ditch or fence-row. Most of these were sampled outside, but adjacent to, the study area in order to minimize disturbance of prey.

During each trapping session, three replicates were run in each habitat. Traps were set for 48 hours and checked twice daily. Trapping sessions were repeated at five-week intervals, weather permitting.

In order to provide an independent check on the indices of rodent abundance provided by trapping, tracking censuses were made in the major habitats following light snowfalls. These consisted of walking 100 m transects 10 m from the edge of fields. The number of rodent tracks crossing the transect were counted. In addition, several tracking censuses were conducted to determine the distribution of tracks from the edge towards the centre of fields. The procedure was similar to that described above except that five transects were walked in each field. The first transect was 10 m from the edge, and each subsequent one was 25 m further from the edge of the field.

All sightings of other prey species were recorded to provide measures of their habitat use. Particular attention was given to Gray Partridges because of their importance in the diet of Snowy Owls (Table 5). When possible, observations were made of their feeding behaviour and several were collected to investigate stomach contents. This information provided a good idea of habitat use of Gray Partridges.

In most analyses in this chapter statistical tests used to indicate differences between observed and expected frequencies are chi-square goodness of fit tests. In cases where expected frequencies are less than five, several classes were combined to make these values large enough. In cases where the sample size was so small that more than two classes had to be combined, log-likelihood ratio tests

(G-tests) were performed. The methods and rationale behind these procedures can be found in Zar (1974).

3 RESULTS

A. The Habitat Composition of the Study Area

The percentage distributions of the habitats surveyed for owls on the study area for both years are shown in Table 9. These figures represent the habitat composition of about 96% of the study area. The remaining 4% included refuse dumps and a sewage treatment plant which were not inspected for owls, and roads and railways, which were not categorized as habitats. The figures for each habitat category between years are very similar. The slight increase in the percentage of fallow in 1977/78 was largely due to the cultivation of some pastures and several small sloughs. Other minor variations can be attributed to the addition of a small area to the northern part of the study area in 1977/78, or to climatically-influenced differences in harvesting between the years.

The major habitat categories are stubblefields and fallow, which together comprise about 70% of the study area in each year. Hayfields and pastures together make up about 20% of the study area and sloughs about 4%. The other habitats are very minor categories.

B. Analyses of Prey Abundance

Four trapping sessions were conducted during the fall and winter of 1977/78. With the exception of a session scheduled for February which was missed because of inclement weather, these were held at about 5-week intervals starting on 20 October. The results of these sessions are shown in Table 10 as the number of Microtus and Peromyscus captured per trap per day.

Trapping success was much lower than anticipated. Despite this, total trapping success differed significantly between habitats (Kruskal-Wallis one-way analysis of variance test, $p < 0.01$). Roadside ditches, fence rows and sloughs supported the highest abundance of rodents. The second ranking habitat in terms of rodent abundance was stubble. Hayfields ranked third and fallow apparently supported the fewest rodents.

Overall capture rates declined as the winter progressed and rose again in the spring. Although shrews (Sorex vagrans and S. cinereus) were trapped throughout the winter (probably as the result of their continuous activity rhythm and very high metabolic rate (Banfield, 1974)), their remains were not found in Snowy Owl pellets (Tables 4 and 5). It appears that shrews were available prey, but were not utilized by the owls.

The pattern of rodent abundance in different habitats is supported by the results from the tracking censuses.

TABLE 10. The abundance of small mammals in various habitat categories as determined by snap-trapping censuses and the species composition of those animals captured in each trapping period.

Habitat	No. of <i>Microtus</i> and <i>Peromyscus</i> captured /trap/day				
	October	November	January	April	Total
Roadside Ditch and Fence Row	0.075	0.005	0.000	0.061	0.14
Slough	0.039	0.014	0.000	*	0.053
Stubble	0.013	0.002	0.000	0.015	0.030
Hayfield	0.010	0.005	0.000	0.007	0.022
Fallow	0.000	0.000	0.000	0.015	0.015
Totals	0.137	0.026	0.000	0.098	

Species	Total No. of each species captured (%)				
	October	November	January	April	Total
<i>Peromyscus maniculatus</i>	21 (56.8)	6 (40.0)	0 (0.0)	11 (39.3)	38
<i>Microtus pennsylvanicus</i>	12 (32.4)	2 (13.3)	0 (0.0)	13 (46.4)	27
<i>Sorex</i> spp.	4 (10.8)	7 (46.7)	4 (100.0)	4 (14.3)	19
Totals	37 (100.0)	15 (100.0)	4 (100.0)	28 (100.0)	

* Sloughs were all flooded in April and therefore none were sampled.

Table 11 shows that roadside ditches and fence rows ranked first in terms of the number of tracks counted. The number of tracks counted in these habitats in Table 11 are probably an underestimate because the tall, dense vegetation prevented a uniform snow-cover. For this reason, transects were impossible to walk in sloughs where the vegetation was particularly high. More tracks were found in stubblefields than in hayfields; no tracks were found in fallow.

The most interesting aspect of these analyses is the distribution of tracks within fields (Fig. 8). More tracks were found close to the edges of stubblefields. The number of tracks declined steeply as transects were walked further from the periphery of the field. This trend is much more apparent for stubblefields than hayfields. This suggests that rodents are concentrated around the perimeters of stubblefields and, to a lesser extent, the edges of hayfields.

Table 12 gives sightings of Gray Partridge coveys by habitat. In the few cases where coveys were observed on the boundary between two habitats, one half of an observation was placed in each habitat. In each winter, coveys were observed more frequently than expected in stubblefields and farmyards (residential) and were rarely seen in fallow. Selection of farmyards could be the result of good cover in the shelterbelts surrounding most farms, or the high availability of food (spilled grain and animal feed) in those areas. Utilization of the other habitats showed some

TABLE 11. The numbers of rodent tracks counted crossing 100 m transects walked in various habitats.

Dates	No. of Rodent Tracks							
	Stubblefields		Fallow		Hayfields		Roadside Ditch and Fence Row	
	Mean $\pm$ SE	n	Mean $\pm$ SE	n	Mean $\pm$ SE	n	Mean $\pm$ SE	n
November 19	3.2 $\pm$ 1.6	5	0.0	5	—		—	
November 24	5.3 $\pm$ 2.4	7	0.0	6	2.3 $\pm$ 0.6	3	10.1 $\pm$ 4.3	9
November 25	3.9 $\pm$ 1.3	7	0.0	4	2.6 $\pm$ 1.1	5	—	
November 27	3.5 $\pm$ 2.0	6	0.0	2	2.6 $\pm$ 1.1	5	6.0 $\pm$ 2.8	2

FIGURE 8: Mean numbers of rodent tracks per transect counted at various distances from the edges of stubblefields and hayfields in 1977/78. Six stubblefields and five hayfields were sampled on 25 November, and seven different stubblefields and five different hayfields were sampled on 27 November.

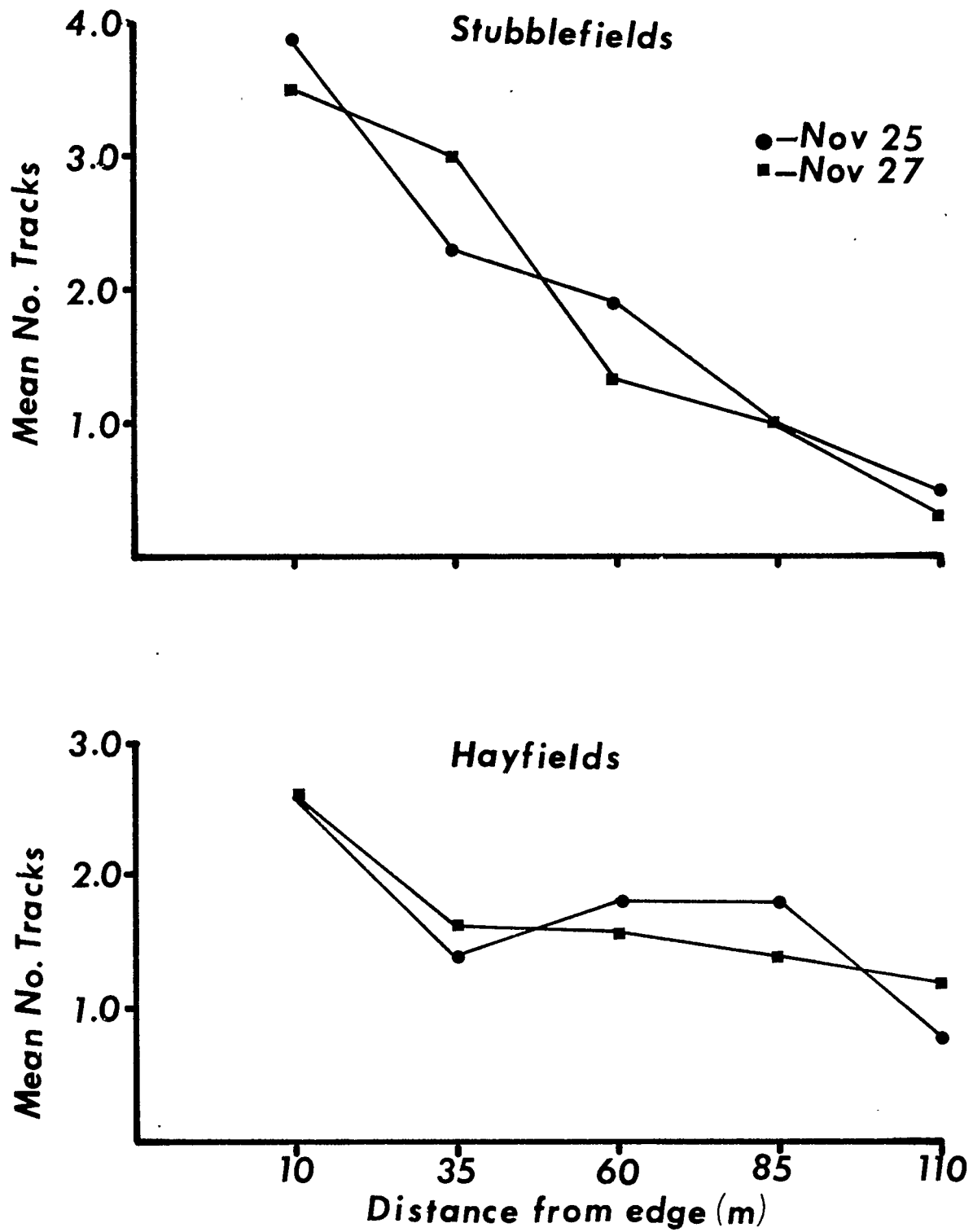


TABLE 12. The distribution of sightings of Gray Partridge coveys by habitat category.

	No. of Sightings of Partridge Coveys (Expected No.) ¹						Total	p(G)
	Stubble	Fallow	Hayfield	Pasture	Slough ²	Residential		
1976/77	19.5 (14.7)	4.0 (12.6)	2.0 (4.7)	9.5 (3.2)	1.0 (2.5)	3.0 (0.9)	39	0.1 < p > 0.05
1977/78	22.0 (17.8)	3.5 (16.8)	9.0 (5.9)	0.5 (3.4)	5.0 (2.5)	8.0 (1.1)	48	p < 0.01

1 Expected values based on the distribution of habitats surveyed on the study area.

2 Ungrazed Grassland is included in this habitat category.

differences between years. Pastures were preferred in 1976/77 and sloughs and hayfields were preferred in 1977/78. These differences are difficult to explain, but are probably the result of annual variations in snow cover. When the observed frequencies were compared to expected frequencies (based on the distribution of habitats on the study area) using G-tests, the difference between them in 1976/77 is almost significant, while in 1977/78 they are highly significantly different (Table 12).

Casual observations of partridges indicated that barley and wheat seeds in the stubblefields were heavily utilized as food. The crop contents of three road-killed birds confirmed this. In addition, owl pellets consisting of partridge remains frequently contained these seeds, presumably from the crops of their avian prey. Westerskov (1966), investigating the winter diet of partridges near Edmonton, Alberta, found similar results. These observations and the habitat distributions of sightings indicate that stubblefields are the most important habitats for partridges in winter.

C. Habitat Selection by Snowy Owls: Census Techniques

The numbers of owls sighted in each habitat in each year are shown in Table 13, along with the expected numbers of owl sightings based on the percentage area of each habitat surveyed on the study area. The observed and expected

TABLE 13. Distribution of owl sightings by habitat category.

Owl Category (year)	No. of Owls Sighted (Expected No.) ¹						Total	p(X ²)
	Stubble	Fallow	Hayfield	Pasture	Slough + Ung. ²	Residential + Industrial		
All sightings (1976/77)	176.0 (131.6)	62.0 (113.7)	41.0 (41.2)	38.5 (28.9)	28.0 (20.3)	3.5 (13.3)	349	p < 0.001
Non-residents (1976/77)	134.5 (98.0)	50.5 (84.8)	38.0 (30.7)	26.5 (21.6)	8.0 (15.1)	2.5 (9.9)	260	p < 0.001
All sightings (1977/78)	165.5 (137.6)	90.0 (129.8)	63.5 (45.8)	25.5 (26.0)	26.5 (18.6)	1.0 (14.1)	372	p < 0.001
Non-residents (1977/78)	87.5 (73.3)	59.0 (69.1)	28.5 (24.4)	14.0 (13.9)	9.0 (9.9)	0.0 (7.5)	198	p < 0.05

1 Expected values based on the distribution of habitats survey on the study area.

2 Ung. is Ungrazed Grassland.

distributions are statistically different as shown by chi-square goodness of fit tests (see Table 13). Owls showed preferences for stubblefields, sloughs and ungrazed grassland in both years, and tended to avoid fallow and areas with high human activity. Sightings of owls in pastures in 1976/77, and in hayfields in 1977/78, were greater than expected by chance. These habitat preferences are still evident when sightings of known resident birds are excluded from the analysis (Table 13).

In order to determine seasonal differences in habitat selection, sightings of non-resident owls in 1977/78 were divided into those sighted before, and those sighted after, 11 December. This date represents the first observed territorial behaviour in 1977/78. Sightings in 1976/77 were not analyzed in this manner because I did not know when territorial behaviour started. Numerous owls in the second winter were resident on the study area for several weeks or more following 10 December. Before this date all owls were probably migrants, remaining on the study area for only one day, or at most two days. Table 14 shows the observed and expected distributions of owl sightings by habitat in these time intervals. The observed distribution of sightings prior to 11 December was not significantly different from the expected distribution, suggesting that the migrating owls were not selecting any particular habitat. As Table 14 indicates, the habitat preferences exhibited by

TABLE 14. The distribution of sightings of non-resident owls by habitat category in the two periods of the winter in 1977/78.

	No. of Owls Sighted (Expected No.) ¹					Total	p(G)
	Stubble	Fallow	Hayfield	Pasture	All Others ²		
13 November to 10 December	14.5 (17.8)	23.0 (16.6)	4.5 (5.9)	4.0 (3.4)	2.0 (4.4)	48	0.25 < p > 0.1
11 December to 28 March	73.0 (55.5)	36.0 (51.8)	24.0 (18.5)	10.0 (10.7)	7.0 (13.7)	150	p < 0.005

1 Expected values based on the distribution of habitats surveyed on the study area.

2 This category includes Slough, Ungrazed Grassland, Residential, and Industrial.

These habitats were combined due to 0 cells in the Residential and Industrial categories.

owls following 10 December were essentially the same as those shown in Table 13.

Table 15 shows the habitat distributions of non-resident owls throughout the entire winter of 1977/78, partitioned into the various plumage class groups described in Chapter 2. The observed habitat distributions of immature females (Classes 3-4 and 4), and owls of plumage class 2, 2-3 or 3, were significantly different from the expected distributions. Class 3-4 and 4 birds avoided fallow and preferred hayfields and the "other" category (sloughs and ungrazed grassland). Class 2, 2-3 and 3 owls also avoided fallow and selected stubblefields. Adult males (Classes 1 and 1-2) showed no significant habitat preference. This could be due to the small sample of adult males relative to the other classes. However, I believe that this difference is genuine, as will be discussed below.

D. Analyses of Territoriality of Snowy Owls

i) Residency Periods

There was a sexual difference in the length of time an owl remained on the study area. Of the owls that I could recognize individually ($n = 22$), females, both adults and juveniles, remained in an area much longer than males (Table 16). A Mann-Whitney U test indicates that this difference is highly significant ($p < 0.001$).

TABLE 15. The distribution of sightings of non-resident Snowy Owls by habitat category in the winter of 1977/78, according to plumage class group.

Plumage Class Group	No. of Owls Sighted (Expected No.) ¹					Total	p(G)
	Stubble	Fallow	Hayfield	Pasture	Other		
Class 1 and 1-2	23 (20.4)	17 (19.0)	8.5 (6.8)	4.0 (3.9)	2.5 (2.9)	55	p > 0.50
Class 2, 2-3, and 3	67 (44.4)	24.5 (41.4)	15 (14.8)	8.5 (8.5)	5.0 (6.2)	120	p < 0.001
Class 3-4 and 4	60 (59.2)	36 (55.2)	34 (19.7)	10 (11.4)	20 (14.4)	160	p < 0.001

1 Expected values based on the distribution of habitats surveyed on the study area.

TABLE 16. Length of residency of male and female Snowy Owls in a specific locality. Information summarized here consists only of owls that were observed for more than two consecutive days. Data from both winters is combined.

	Females	Males
Mean number of days	44.8 $\pm$ 5.99	6.57 $\pm$ 1.96
$\pm$ S.E.		
Range	3-80	3-17
No. of Owls	15	7

Other sexual differences in spacing behaviour were noted. Although most males moved through the study area in one or two days, some appeared to be "semi-resident", remaining on a small range for up to 17 days. While they inhabited these areas, I observed them hunting and in agonistic encounters with other non-resident owls. Females, on the other hand, tended either to move through the study area, or to become resident in an area for up to 80 days, defending a territory. Although the ranges of males were not studied in detail, I noted that the sizes of the territories of females were considerably larger than the ranges of semi-resident males.

ii) Territories of Female Snowy Owls

Hinde's (1956) definition of territorial behaviour, which is used in this study, encompasses three components: (1) restriction of movements to a more or less clearly defined area; (2) defence of that area; and (3) self-advertisement within the area. Observations of resident female Snowy Owls suggested that mutually exclusive ranges were maintained. Common boundaries and overlap between these ranges were rare. I also observed that these areas were defended through the use of postural displays and physical interaction (see Chapter 6). These observations strongly suggest that these ranges were territories.

In 1977/78 the study area contained at least 13 ter-

ritorial female owls. I was able to observe six of these birds in some detail. Data on these owls were supplemented by observations on the other seven owls in 1977/78, and on three owls in 1976/77. The observation-area curves for the six owls in 1977/78 are shown in Figure 9. The three owls in 1976/77 had similarly-shaped curves. Each curve reached an asymptote as described on page 81, and therefore I conclude that sufficient observations were made to accurately define the territories of these birds. The territories of the six focal owls and two others in 1977/78, are depicted in Figure 10.

The size, habitat composition, and other information for each territory are shown in Table 17. Several points merit comment. First, territory size appears to differ between years (1976/77 mean = 154.6 ha, 1977/78 mean = 266.0 ha). This difference is not quite significant (Mann-Whitney U test, $p = 0.19$).

Second, territory size appears to be larger for juveniles than adults. In 1977/78 the mean territory size for four adults was 195 ± 30 ha, and for two juveniles 408 ± 30 ha. Unfortunately the sample sizes are too small for a statistical comparison. However, the areas utilized by four other juveniles and one adult owl that were observed in this year confirm the inverse relationship between age and territory size. Although the observation-area curves for these birds did not reach the 1% plateau, the territories

FIGURE 9: Observation-area curves for six Snowy Owl territories observed in the Calgary region in the winter of 1977/78. Letters refer to individual designations of owls.

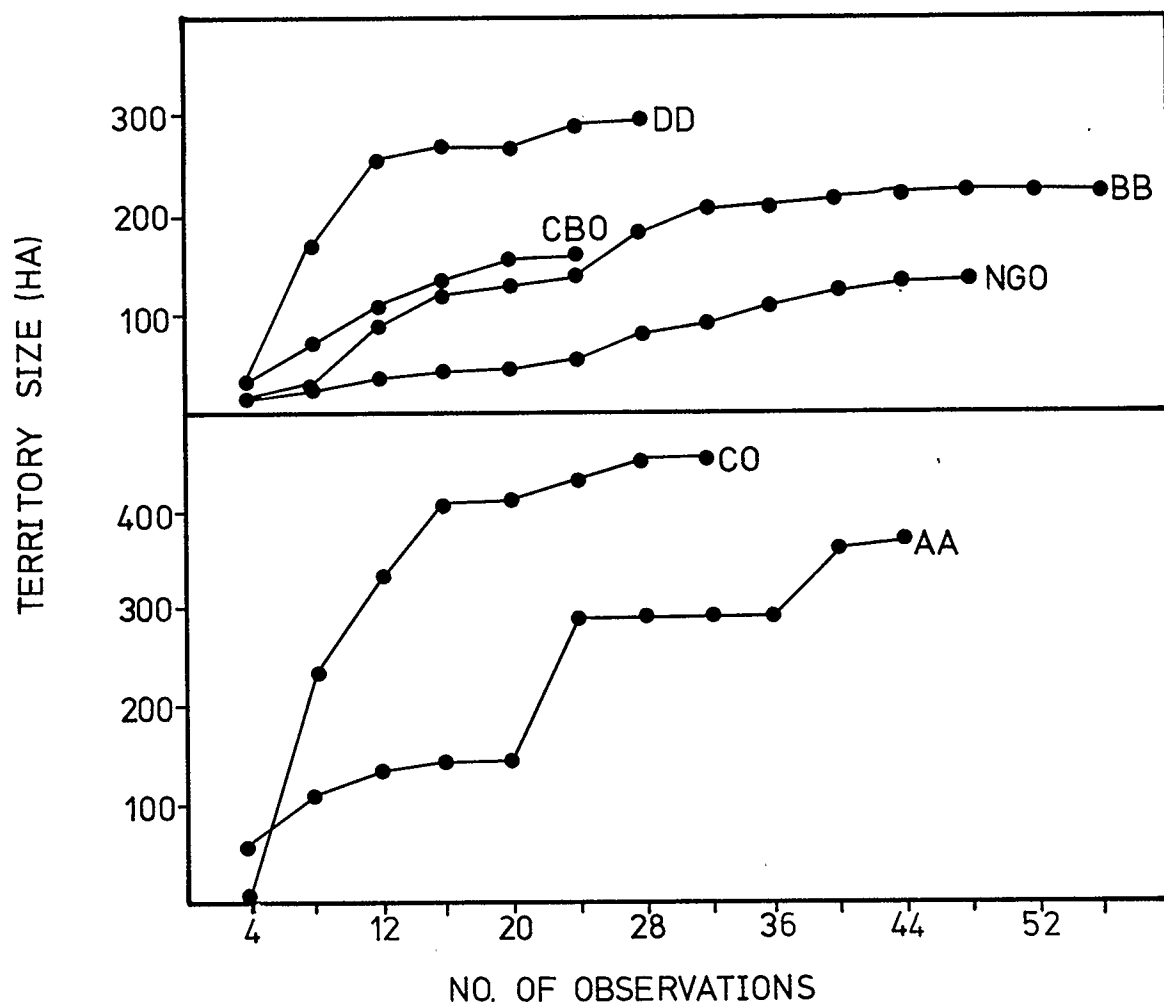


TABLE 17. The habitat composition and other information for nine Snowy Owl territories.

Bird	Age ¹	Year	Area of Territory (ha)	Habitat Composition of Territory (%)							
				Stubble	Fallow	Hay	Pasture	Ungrazed Grassland	Slough	Farmyard	Other ²
YRT	A	1976/77	162	54.6	26.2	-	0.9	-	12.3	1.9	4.1
MOF	J	1976/77	150	33.4	34.2	5.3	11.4	7.6	6.1	-	2.0
LPM	J	1976/77	152	25.3	45.8	-	-	18.1	9.9	0.7	0.2
DD	A	1977/78	283	52.2	16.4	16.3	2.0	-	10.9	0.8	1.4
BB	A	1977/78	220	63.0	6.2	11.0	7.7	-	5.9	2.9	3.3
CBO	A	1977/78	151	43.9	39.5	12.3	-	-	2.8	1.2	0.3
NGO	(A)	1977/78	127	55.5	26.1	13.2	1.8	-	-	1.2	2.2
AA	J	1977/78	365	29.4	16.5	17.6	22.4	2.8	7.8	0.8	2.7
CO	J	1977/78	450	8.9	63.1	-	21.0	3.3	1.7	1.1	0.9

1 A - adult J - juvenile (A) - probably adult

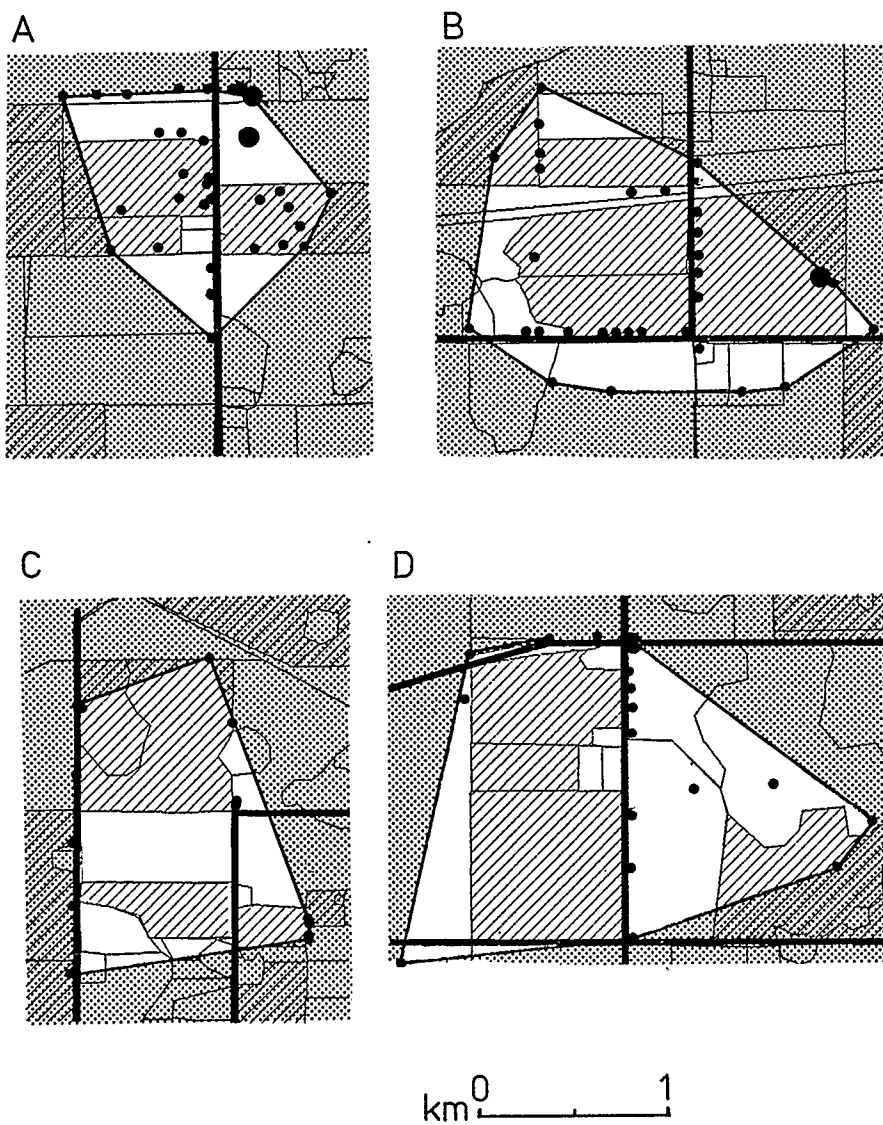
2 This category includes roads and railroad right of ways.

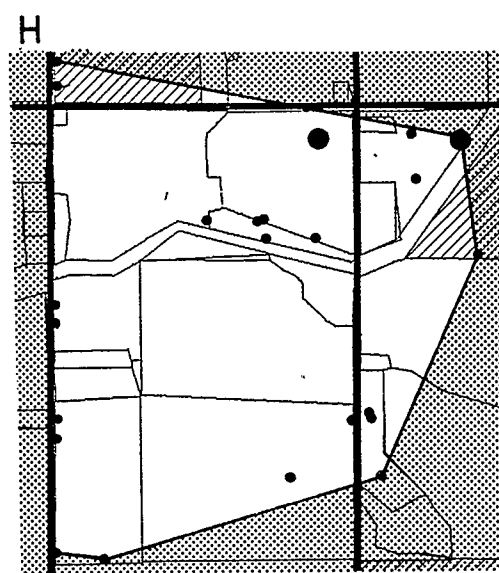
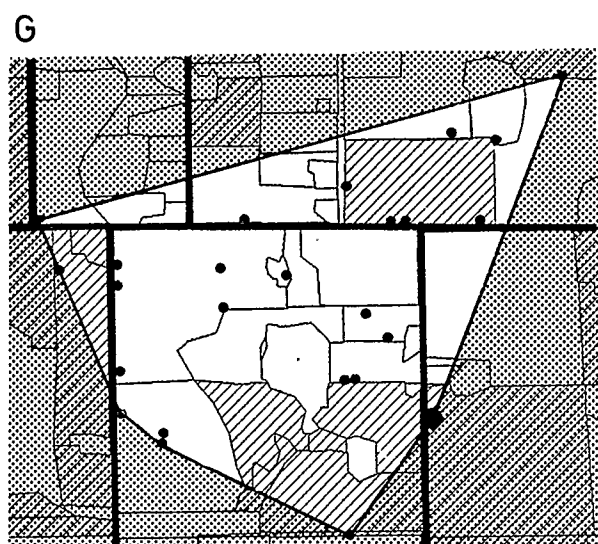
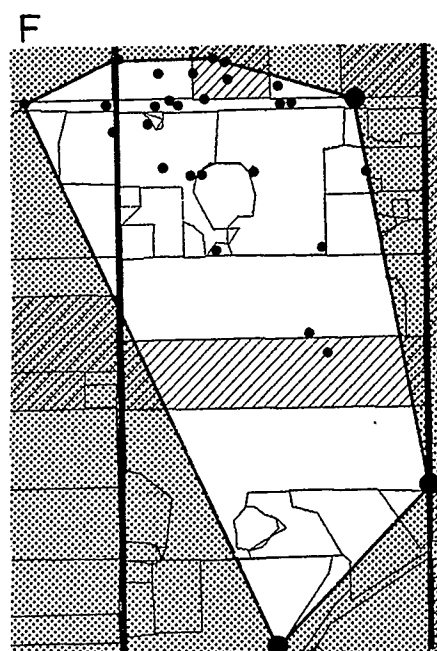
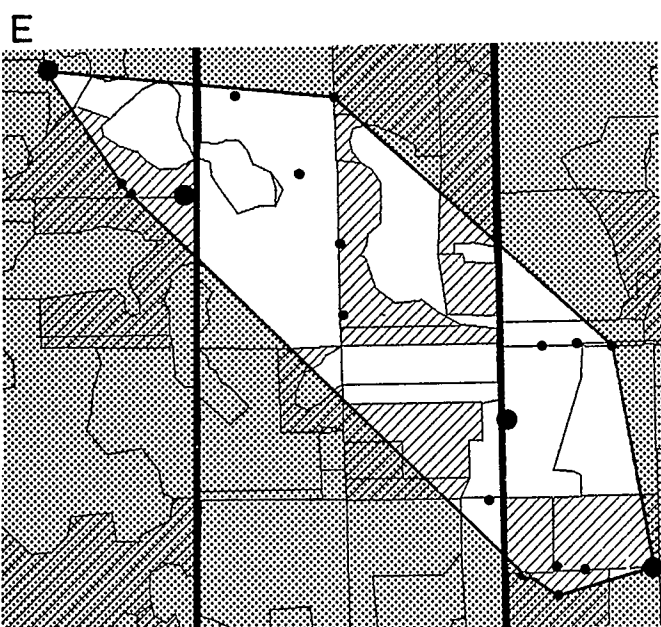
of two of these juveniles are plotted in Figures 10E and 10F. The areas of the polygons enclosing the positions of these birds are 378 ha and 373 ha respectively. The territories of the other two juveniles were even larger than these. Since the observation-area curves for these individuals show that the number of sightings were insufficient, these areas are under-estimates of their true territory sizes. These two territories are larger than those of the adult owls, and are comparable to those of the juveniles in Table 17. These results strongly suggest that the territories of juvenile female Snowy Owls are larger than the territories of the older females.

Third, a comparison of the distribution of habitats in each territory (Table 17) with the distribution of habitats on the study area (Table 9), suggests that most of these territories were not representative samples of the study area. The birds were defending areas composed of certain habitats above and below their proportional availabilities.

The utilization of habitats by territorial owls was further examined by determining the number of locations for each territorial owl that fell into each of the habitat categories found in its territory. An expected number of sightings for each habitat was calculated, based on the percentage distribution of habitats in each territory. Indices of habitat utilization were then determined by dividing the observed number of sightings in each habitat

FIGURE 10: Territories of eight Snowy Owls observed in 1977/78. The small solid circles represent one or more locations of each owl, and the large solid circles represent locations where territorial interactions were observed. Cross-hatching represents stubblefields, and stippling depicts areas outside territorial boundaries. A-D. Adult Snowy Owls. E-H. Juvenile Snowy Owls.





by the expected number. A value of 1.0 indicates no preference; above 1.0 indicates preference, and below 1.0 indicates avoidance. The mean and range of these indices for each habitat category on the nine territories are plotted in Figure 11. The mean index for each habitat, except for the "others" category, is significantly different from a theoretical mean index of 1.0 (one-tailed t-test, all $p < 0.05$). These results show that despite variability in the distribution of habitats in territories, territorial Snowy Owls preferred stubble and hayfields, and avoided fallow.

I attempted to correlate the proportion of each habitat in the territory and the duration of residency on the study area with territory area. Table 18 shows a summary of these correlation analyses. The only variables showing a significant correlation with territory size are the proportions of stubble and pasture. Pasture shows a positive correlation with territory size, due primarily to its importance in the territories of juvenile owls (see Table 17). More important is the negative correlation between the percentage of stubble and territory area. This indicates that smaller territories contained a greater proportion of stubble than did larger territories. Since adult owls defended smaller areas than juveniles, it would follow that adult Snowy Owls defended more stubble per unit territory area than did juveniles.

FIGURE 11: Habitat utilization indices for nine Snowy Owl territories. The horizontal bars represent the means, and vertical bars the ranges. The dashed line represents the value for equal utilization. Computation of the index is explained in the text.

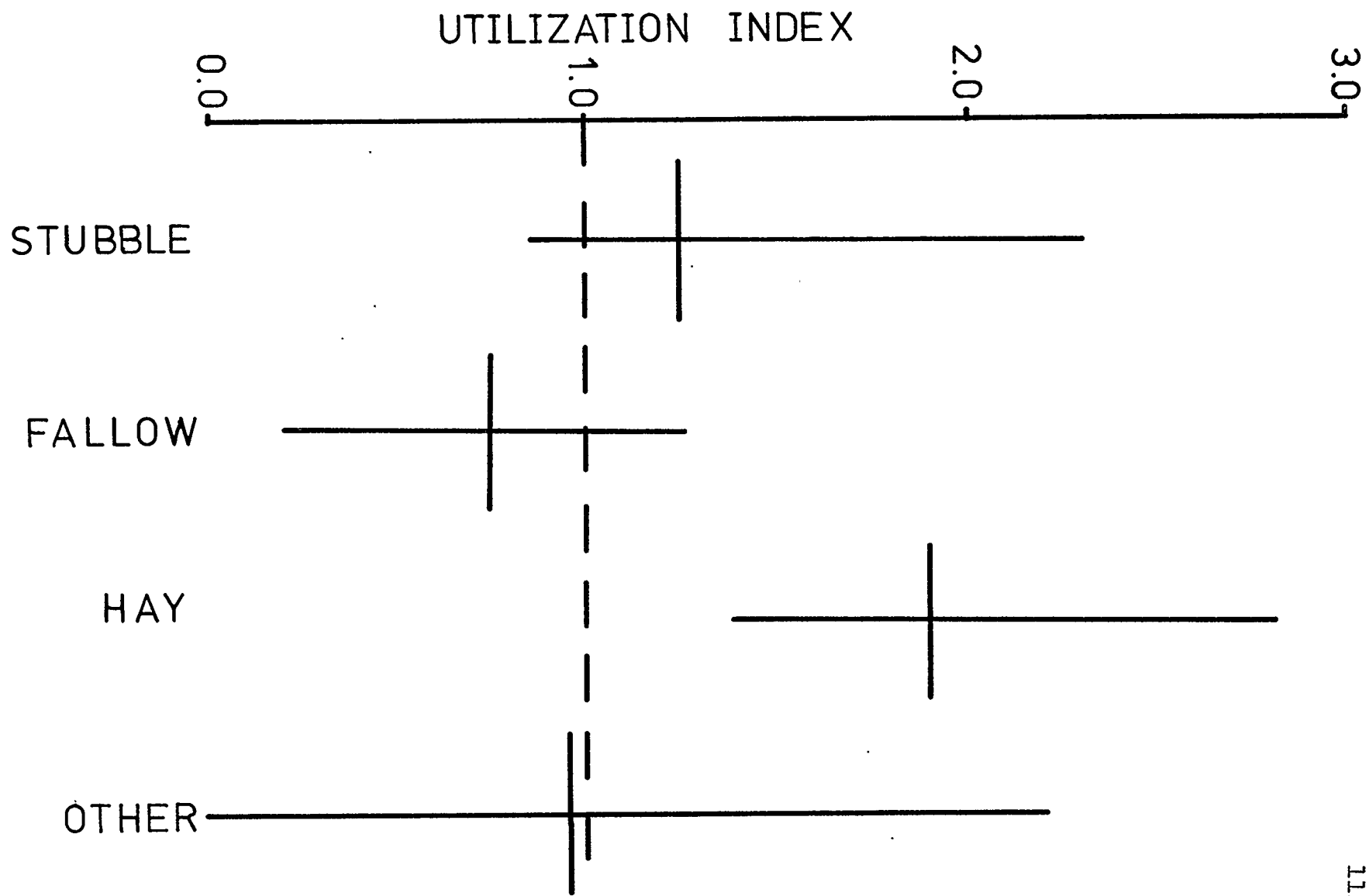


TABLE 18. A summary of Pearson product moment correlation analyses between territory size, duration of time spent on the study area, and habitat composition for Snowy Owl territories, studied in 1977/78.

	Residency		Proportion of Total Territory Area									
			Stubble		Fallow		Hay		Pasture		Slough	
	r ¹	p ²	r	p	r	p	r	p	r	p	r	p
Territory Size	0.45	0.35	-0.83	0.05	0.39	0.44	-0.45	0.36	0.88	0.03	0.29	0.58

1 These values represent correlation coefficients

2 These values represent the probability associated with each correlation coefficient and were determined by randomization (Edgington, 1969).

Rodents tended to be concentrated near the uncut edges of stubblefields, and in roadside ditches and road allowances (see Fig. 8 and Tables 10 and 11). Therefore, one would expect optimal Snowy Owl territories to contain a large proportion of these areas. I measured the total length of roadside ditches and road allowances (LRD), and the length of edges of stubblefields bordering such areas (LSRD) in each territory. While I did not inspect the territories closely enough to determine if all the edges of stubblefields not bordering roads were suitable to support rodents, I did measure the total length of all edges of stubblefields (LES). These data (Table 19) show that LRD was greater in the territories of juveniles, but the proportion of this next to stubblefields (LSRD/LRD) was much higher in the territories of adults. Thus adult owls defended areas in which the location of stubblefields were important. Adults appear to have selected territories in which stubble borders on roadside ditches. They have achieved this by choosing areas where roads cross or meet at T-intersections (see Fig. 10B, C, D).

4. DISCUSSION

A. The Profitability of Habitats on the Study Area

The results of the trapping and tracking surveys indicated that rodents were concentrated in uncultivated areas

TABLE 19. Measures of roadside ditches and edges of stubblefields in Snowy Owl territories examined in 1977/78.

Age	Owl	LRD ¹	LES ²	LSRD ³	$\frac{\text{LSRD}}{\text{LRD}}$	$\frac{\text{LSRD}}{\text{TA}^4}$
Adult	NGO	1.39	4.04	0.76	0.55	0.59
	CBO	1.14	1.96	0.78	0.68	0.52
	BB	3.06	6.10	2.21	0.72	1.00
	DD	2.58	4.81	1.74	0.67	0.62
Juvenile	AA	4.85	5.18	1.43	0.29	0.39
	CO	3.40	2.66	0.75	0.22	0.17

1. Total length of roadside ditch (km)
2. Total length of the edge of stubblefields in territory (km)
3. Total length of roadside ditch bordering stubblefields (km)
4. Territory area (km²)

offering abundant cover. These particular habitats are usually arranged in long thin strips bordering fields (fencerows and roadside ditches), or in small patches surrounded by grazed or cultivated fields (sloughs). The major reason for these concentrations of small mammals is probably extensive cultivation, which has reduced the natural habitat of these animals. Fencerows, roadside ditches and sloughs are among the few areas where vegetation resembling natural habitat exists. Therefore, they represent refugia for small mammals (Ogilvie and Furman, 1959).

These habitats contained the densest vegetative cover, probably due to the lack of extensive cultivation. Southern and Lowe (1968), Sparrowe (1972), and Wakeley (1978) have shown that high density of vegetation decreases prey vulnerability to raptors. Sparrowe (1972) has shown that the duration of time a hawk was exposed to a prey item controlled whether an attempt was made to capture that prey. His results indicate that vegetative cover controls the time a predator is exposed to food, and thus limits the success of visual predators hunting in habitats with dense vegetation. Therefore, although prey were concentrated in sloughs, roadside ditches, and fencerows, they were not readily available to predators like Snowy Owls. For this reason, these habitats are probably not very profitable to Snowy Owls.

The other major habitats on the study area can be ranked in descending order on the basis of rodent abundance

as follows: stubble, hayfields, pasture, and fallow. Because of the lack of vegetative cover and food, fallow can be excluded as profitable habitat for mice and partridges, and thus for owls. This is reflected in the poor trapping success (Table 10), the total absence of rodent tracks (Table 11) and other sign (pers. observ.), and the scarcity of partridge sightings (Table 12) in these areas. Owls showed positive choice of pastures in 1976/77 (Table 13), as did partridges (Table 12). The low snowfall in 1976/77 could have enabled partridges to forage in pastures, and the owls may have responded positively to this use of habitat by potential prey. However, partridges were not recovered from pellets collected in 1976/77 (Table 4). I have no explanation for the slight preference of pastures by owls in 1976/77.

Trapping and tracking of rodents, and sighting of Gray Partridges showed that while some prey were found in hayfields, they were more abundant in stubblefields, roadside ditches, and sloughs. In addition, the vegetative cover in hayfields was more uniform and dense than in stubblefields. I believe that these observations, in addition to the scarcity of hayfields in the study area, suggest that they are of secondary importance to hunting Snowy Owls.

Stubblefields are probably the most profitable habitats for Snowy Owls. Overall trapping and tracking success was higher in stubble than in any other cultivated habitat,

indicating that rodents were more abundant there. In addition, the vegetation in stubblefields is less dense than in hayfields, and thus rodents are probably more easily detected by visual predators. I believe that the profitability of stubble is due particularly to the concentration of prey around the edges of the fields. In most cases, roadside ditches or fencerows border stubblefields. Although the cover offered by fencerows and roadside ditches supports numerous prey, it may offer little food to Peromyscus, which is largely granivorous. The abundant seeds left in the stubble following harvesting could entice these animals to move out of ditches and fence rows. One would expect these movements to involve Peromyscus more than Microtus, because voles are mainly herbivorous (Thompson, 1965; Zimmerman, 1965). The fact that Peromyscus maniculatus is the most abundant prey species in the diet of Snowy Owls on the study area (Tables 4 and 5), and that most hunts were observed in stubblefields (Fig. 7C), supports this hypothesis.

Snowy Owls were seen more often than expected by chance in stubblefields, hayfields, sloughs, and ungrazed grassland (Table 13). Fallow, pasture, residential, and industrial areas supported fewer owls than expected by chance. This suggests, on the basis of the previous discussion on habitat profitability, that most owls were selecting the most profitable habitats on the study area. Lein and Webber (1979)

also observed a preference for stubblefields by wintering Snowy Owls, but did not know if this habitat was preferred for hunting. The fact that most of the attempts at prey capture which I observed occurred in stubble and hayfields (Fig. 7C), further suggests that owls were selecting profitable hunting areas. This particular explanation of habitat selection is tentative, but the hypothesis may be examined more rigorously by investigating the behaviour of individual birds.

B. Seasonal Differences in Habitat Selection

The data show a seasonal difference in habitat selection. Early in the winter Snowy Owls were found in each habitat category in proportion to its occurrence within the study area (Table 14). As soon as territorial behaviour became widespread, a marked shift in habitat utilization occurred. This change in habitat utilization also involved non-territorial owls (Tables 13 and 14), and thus the shift in habitat preferences cannot be due to the effects of territorial owls on non-territorial owls. I propose two hypotheses to explain these observations: (1) Snowy Owls are not foraging in the early stages of migration, but are merely resting in habitats where they are recorded; (2) Snowy Owls have not learned, early in the winter, which of the available habitats are most profitable.

Since other raptors feed during migration (Hofslund,

1973; Mueller and Berger, 1967}), and because I have observed non-resident owls foraging and casting pellets in November, I believe that the second hypothesis is more likely to be correct. If this is the case, then some Snowy Owls must be restricting their movements to the prairies in winter, learning which habitats are profitable. Alternatively, some owls might be returning to the prairies each winter (see Bent, 1938; Oeming, 1958, 1964), and they may retain their familiarity with the array of habitats available.

C. Sexual Differences in Habitat Selection

Some workers have recently proposed that there is geographic separation between the sexes of some raptors in winter (Mills, 1975; Platt, 1976). Strong evidence comes from the studies of American Kestrels by Mills (1975, 1976) and Koplín (1973). Using broad habitat classifications (i.e.: agricultural land, desert, forest) these authors have discovered distinctly different sex ratios in most areas. In addition, other winter surveys of American Kestrels have revealed that males winter predominantly in the northern part of the winter range of the species (Roest, 1957; Johnson and Enderson, 1972).

The sexual differences in spacing patterns of wintering Snowy Owls discovered in this study can be summarized as follows: (1) adult males did not prefer any particular

habitat category on the study area, whereas the other owls appeared to show distinct preferences and avoidances of certain habitats (Table 15); and (2) males did not remain in one locality and become territorial, as did females. In addition, in both years there were fewer adult males seen on the study area in December and January (Figs. 5 and 6) than later in the winter. I believe these results suggest the possibility of geographical separation between the sexes in wintering Snowy Owls.

In this study, only one broad habitat category, agricultural land, was examined for owls. If an approach similar to that of Mills (1976) was used, in which a number of geographical areas are surveyed, evidence that males winter in open areas other than the agricultural lands of southern Alberta might be revealed. Keith (1964) observed two territorial males in marshland in Wisconsin, and Mitchell (1947) reported that a male maintained a territory "all winter" in Peel County, Ontario. Geographic separation between the sexes of Snowy Owls could also be related to a tendency of males to remain in the arctic in order to maintain or secure a breeding territory in an area where lemmings are abundant. Tullock (1969) describes an adult male over-wintering in its breeding area in the Shetland Isles. This particular hypothesis has been used to explain male-biased sex ratios of Gyrfalcons (Falco rusticolus) in the arctic in winter (Platt, 1976).

I can suggest only one explanation for the sexual differences in spacing behaviour, and the possible geographic separation between male and female Snowy Owls in winter. Females are larger than males in most raptor species (Snyder and Wiley, 1976), suggesting that some aspect of female dominance, acting in concert with intersexual competition for food, may result in winter habitat separation (see Amadon, 1959; Cade, 1960; Selander, 1966; Mills, 1976). Evidence for female dominance comes from Cade's (1955) discovery that female American Kestrels are more aggressive than males (but see Nelson, 1977). However, in the four aggressive interactions between male and female Snowy Owls that I observed, neither sex was consistently dominant. Unfortunately, sufficiently detailed data on female dominance in winter are not available for Snowy Owls, and female dominance resulting in sexual differences in spacing behaviour can not be reliably tested for any raptor species.

D. Territoriality, Food Supply, and Profitable Foraging

It is now generally accepted that feeding territories function to provide an individual with an adequate supply of food (Brown, 1964; Schoener, 1968; Brown and Orians, 1970). However, according to the principle of economic defendability (Brown, 1964), such territorial behaviour will only be manifested when the costs of defending a food supply are exceeded by the resultant gains. Recent studies

of feeding territories have shown that territories: (1) apparently contain adequate food to support each territorial individual (Gass et al., 1976; Kodric-Brown and Brown, 1978); and (2) are only defended when the costs of defence and other activities can be recovered from the resources within the territory (Gill and Wolf, 1975; Carpenter and MacMillen, 1976). All of these studies have utilized nec-tivorous birds for which precise measures of food density and availability are possible. For the most part, these measures are difficult to obtain for carnivorous birds.

I have shown that stubblefields, and to a lesser extent hayfields, are probably the most profitable habitats on my study area for Snowy Owls. Territories contained high proportions of stubble (Table 17) and territorial owls utilized stubble and hayfields more often than expected by chance on the basis of their availability in the territories (Fig. 11). These observations, in addition to the analyses of prey abundance (Tables 10, 11, 12), suggest that the amount of stubble and hayfields in territories is directly related to the amount of food in territories.

In investigating the food-value of territories to Snowy Owls, I used the approach suggested by Kodric-Brown and Brown (1978) which assumes that the territories of the owls were beneficial to their inhabitants. Theoretically, if the territories were uneconomical, the birds should abandon them and either become non-territorial or move to another area

where resources are economical to defend. This approach yields two predictions specific to this study. First, smaller territories should contain more stubble and hayfield per unit territory area. In other words, the density of food in territories (which is related to the proportion of stubble and hayfield) is negatively correlated with territory size. Second, given that the concentration of rodents near the edges of stubblefields is a real phenomenon, smaller territories should contain more edges of stubblefields per unit area than larger territories.

The negative correlation between territory size and proportion of stubble (Table 18) meets this first prediction. The proportion of each territory that was hayfield was also negatively correlated to territory size, but this was not statistically significant. This could be the result of the low availability of hayfields relative to stubble on the study area. Investigating the second prediction is more difficult. The length of the edges of stubblefield per unit territory area is negatively correlated with territory size ($r_s = -0.66$, $p < 0.1$), but this, as described above, is probably an inaccurate measure of the uncultivated edges of stubblefields. The length of edges of stubblefields bordering roadside ditches per unit territory area is negatively correlated with territory size ($r_s = -0.49$), but the result is also insignificant. These negative correlations are consistent with the second prediction. However, the sample of

territories is too small to reliably investigate the validity of these trends.

The above results tentatively suggest that the density of resources in Snowy Owl territories is inversely related to territory size. Similar results have been obtained for Rufous Hummingbirds (Selasphorus rufus) (Gass et al., 1976; Kodric-Brown and Brown, 1978), Ovenbirds (Seiurus aurocapillus) (Stenger, 1958), Winter Wrens (Troglodytes troglodytes) (Cody and Cody, 1972), and Townsend's Solitaires (Myadestes townsendii) (Lederer, 1977). It appears that the size of feeding territories of these birds is regulated to provide an individual with an adequate supply of food. It is unfortunate that only a few territories could be analyzed in this study. However, I feel that the similarity of the relationships between territory size and food supply in all these species is real, and that these territorial systems are subject to the same economic constraints. Thus the winter territories of Snowy Owls probably provide another example of Brown's principle of economic defendability.

The effect of age on various characteristics of territoriality is very apparent in my results. Kodric-Brown and Brown (1978) and Gass (1978) have indicated that immature Rufous Hummingbirds also differ from adults in territorial behaviour. Both studies mention that immatures had sub-optimal territories and frequently intruded into more

profitable territories to steal food. In my study, younger owls had larger territories with a lower proportion of profitable areas within them. The reasons for this are difficult to explain. The younger birds may either have been forced out of profitable territories by adults, or they may not have learned how to assess the profitability of a territory. The observations of lower hunting success by juvenile females (Chapter 4) suggests that they are generally not as experienced as the older birds. This could also be true of the selection of territories. However, as I will show in the next chapter, territorial intrusions by juveniles were probably more frequent than those by adults, suggesting that juveniles recognized areas more profitable than their own. This indicates that lack of experience by juveniles, as well as behavioural interactions between juveniles and adults, are probably responsible for age differences in territoriality.

If the crude measures of prey availability in the various habitats are indicative of their true availabilities, then I conclude that habitat selection by Snowy Owls is a mechanism for maximizing net energy intake. Observations and analyses of habitat usage and feeding ecology (Chapter 4) suggest that these birds forage predominantly in profitable habitats and defend economical territories. These conclusions might seem commonplace in light of the rich literature on territoriality and foraging behaviour of birds, but this

appears to be the first attempt to describe this behaviour in detail in owls.

CHAPTER 6

SPACING MECHANISMS USED BY WINTERING SNOWY OWLS

1. INTRODUCTION

Spacing of animals can be achieved through fighting or through some sort of aggressive display. Fighting, however, involves a risk of injury to both combatants. This is particularly true for raptors which possess powerful talons and beaks. Death as a result of territorial disputes has been reported in some raptor species (e.g., Goshawks, Brüll, 1972). Therefore, the ritualized displays or other forms of behaviour used in interactions are generally thought to have evolved to establish dominance without resorting to physical combat (Marler and Hamilton, 1966:178).

Male Snowy Owls vocalize and posture while on breeding territories (Sutton, 1932; Watson, 1957; Taylor, 1974). Although combat between breeding and non-breeding owls has been recorded, fighting between breeding males has not been reported (Pitelka *et al.*, 1955b; Watson, 1957). Therefore, it is thought that these vocalizations and postures are ritualized behaviours which are used to defend breeding territories. Our knowledge of the defence of winter territories by Snowy Owls is limited to a few descriptions of aggressive interactions (Keith, 1964; Quilliam, 1965; Weir, 1973). Threat displays by owls on the wintering grounds

have not been reported.

This chapter outlines the agonistic behaviour of wintering Snowy Owls, describes how winter territories are advertised and defended, reports how frequently interactions of various types occur, and outlines some hypotheses about the aggressive nature and plumage variability of Snowy Owls.

2. POSTURES AND DISPLAYS OF SNOWY OWLS

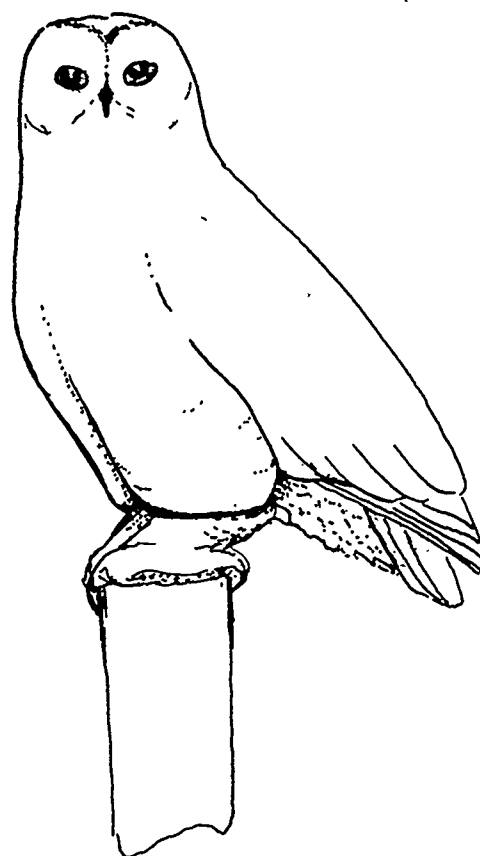
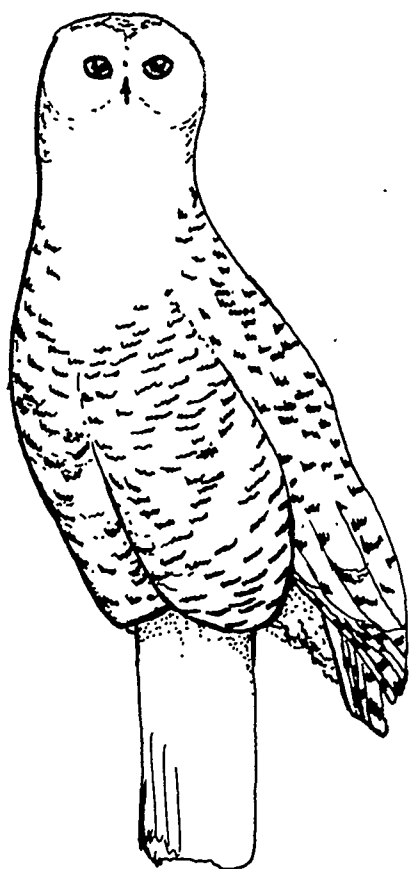
A. General Activities

i) Alert Posture

In the alert posture owls held their heads upward and extended their legs, with the body axis oriented about 60° above horizontal (Fig. 12A). In some cases the feathers were held closely to the body. When an owl became particularly interested in some object, the neck was extended, the wings were held tightly to the body, and the feathers of the neck and back were sleeked (Fig. 12B). The owl did not usually orient toward or away from the object of interest unless it was about to take flight.

The alert posture was assumed by owls actively searching for prey, being mobbed by other birds, or disturbed by automobile traffic. The extreme form of this posture was sometimes accompanied by circular or vertical bobbing movements of the head (see Fig. 2 in Råber, 1950). These

FIGURE 12: Alert postures of Snowy Owls. A. The typical posture of an alert owl. B. The posture of an "interested" owl.

**A****B**

movements may serve to increase parallax in order to facilitate the determination of the distance of some object (Daanje, 1950).

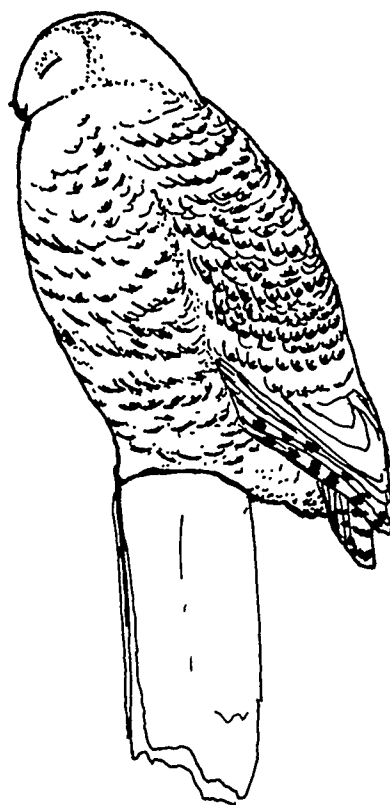
ii) Resting Postures

I have found that Snowy Owls spend much of the daylight hours dozing or sitting quietly, slowly scanning their surroundings (see next chapter). In these cases the head was held close to the body, plumage was not sleeked, and the legs were not extended (see Fig. 13A-C). Sometimes the head was held at a slight angle, and the eyelids covered the eyes (Fig. 13A, C). In these cases I assumed the bird was sleeping.

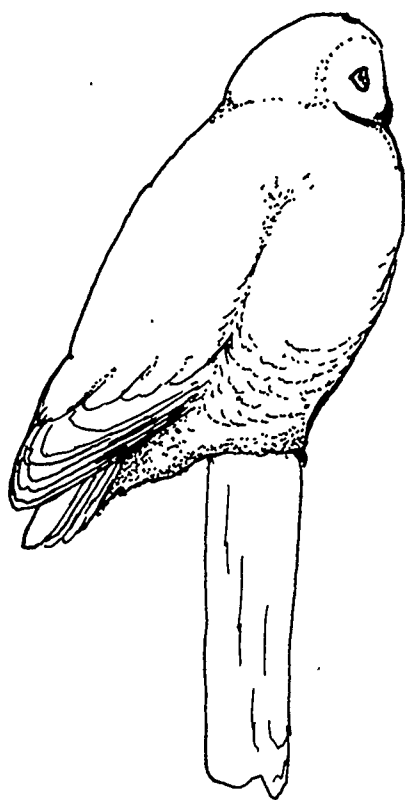
iii) Comfort Movements

Snowy Owls preen sporadically throughout the day. The feathers of the breast and belly were preened more frequently than those of other regions. Feathers were occasionally swallowed. Other common maintenance behaviours included head-scratches and wing-stretches. These were identical to descriptions of the same behaviours in Short-eared Owls (see Clark, 1975). Bill-wiping was observed on one occasion after an owl had eaten a partridge. Face-washing (described by Rusk, 1969) was observed on two occasions after pellets had been regurgitated.

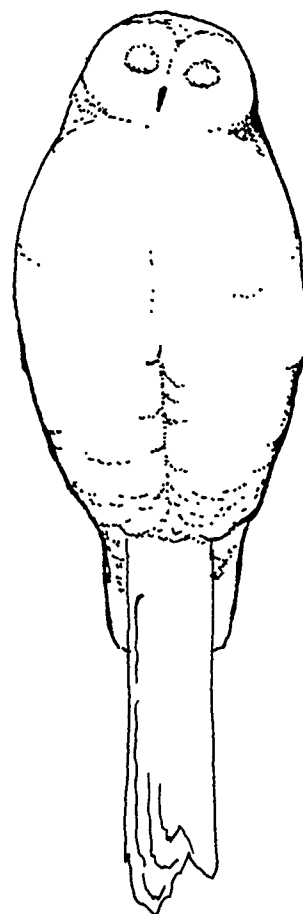
FIGURE 13: Resting postures of Snowy Owls. A, B. Lateral views of resting owls. C. The posture of a sleeping owl.



A



B



C

B. Agonistic Displays and Postures

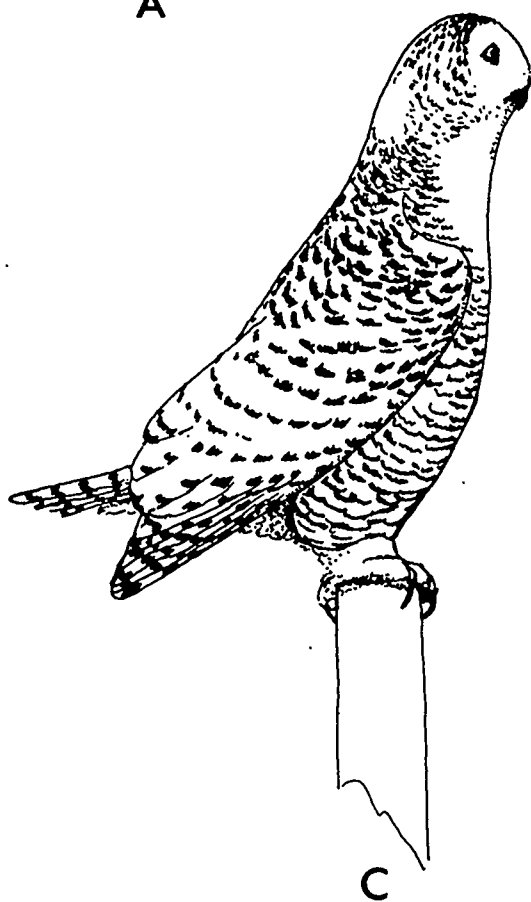
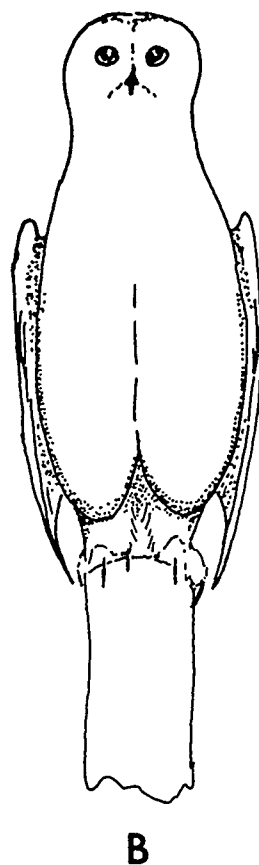
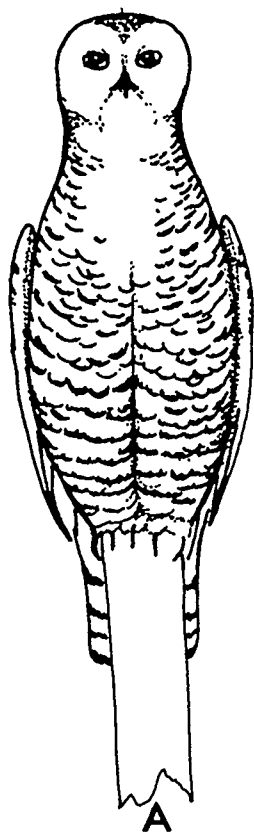
In this section, the term "display" will be used to describe behaviour patterns that seem to have become specialized in form to serve a signal function (Moynihan, 1962). I will follow ethological convention by capitalizing the name (e.g., Forward Crouch). The word "aggressive" will refer to behaviour directed towards another individual which could lead to physical injury, whereas agonistic behaviour will include threat and submissive behaviour patterns as well as aggressive actions (Hinde, 1970). The number of observations of each of these postures is shown in Table 20.

i) Upright Posture

This was the most common agonistic posture used by territorial owls. It was characterized by an extreme extension of the head to a vertical position above the body, sleeked plumage, and wings held slightly outwards from the body (Fig. 14). The tail was raised slightly in about half of the occurrences of this display. This posture is probably a more intense version of the alert posture, but the head was not usually moved, and owls sometimes remained in this posture for up to 10 minutes.

The Upright Posture was usually given before and after physical interactions (see below), and always at the initial approach of another owl. In all cases that I observed, the posturing owl was facing its opponent.

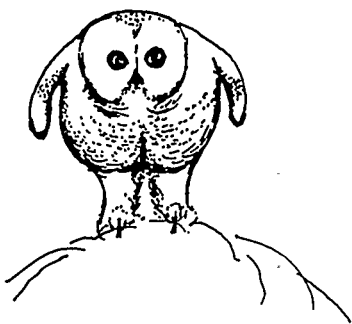
FIGURE 14: Upright Postures used by Snowy Owls in agonistic interactions with conspecifics. A, B. Frontal views. C. Lateral view.



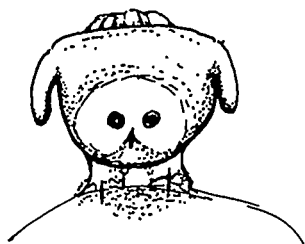
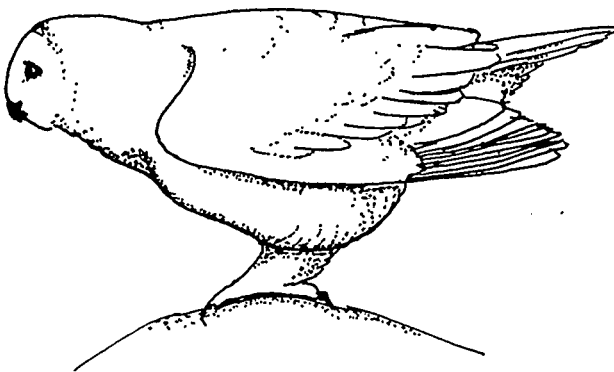
ii) Forward Crouch Display

This display was used by birds perched on the ground on small mounds, or occasionally on fenceposts. Owls would assume the Upright Posture, then slowly crouch, keeping the legs straight, until the axis of the body was parallel to the ground (Fig. 15). The neck and head were extended slightly below the horizontal plane. The erected feathers on the back of the bird were particularly prominent. While crouched in this position, the bird would sway its head from side to side in a very exaggerated manner (Fig. 15C). On two occasions I also observed that owls turned their bodies about 30° from one side to the other while swaying their heads. Displaying owls held their wings out slightly, and opened their beaks. I never heard vocalizations accompanying this display. Head-swaying typically continued for about 15-20 seconds, followed by a slight relaxation of the neck, and a marked lifting of the tail (Fig. 15B). At this point the displaying bird peered intently at its opponent for 20-30 seconds. Then it crouched low, extending its neck again, and continued to sway its head. Recipients of Forward Crouch displays turned their backs toward displaying owls in four of eight of the displays I observed. At this point, the displayer assumed the Upright Posture and usually continued watching its opponent. I observed territorial owls to use this display only when the recipient was at a territorial boundary.

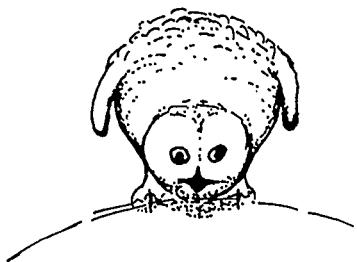
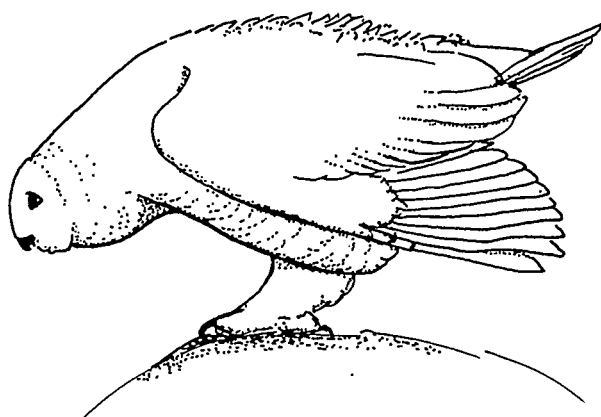
FIGURE 15: The Forward Crouch Display, showing the "grading" of the display. A. Pre-flight posture. B. The posture of an owl in between the head-sways. C. The full extent of the display. Head-swaying and body-rotations occurred while the owl assumed this posture.



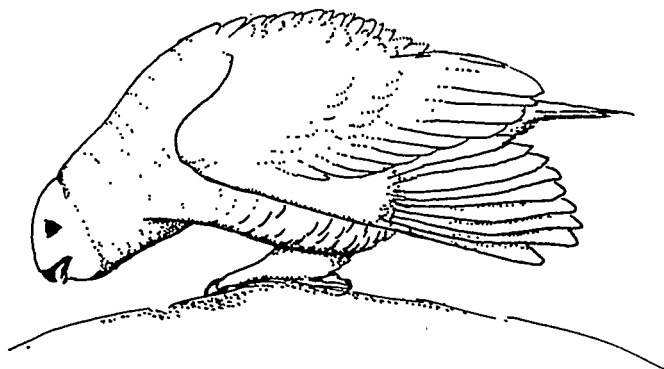
A



B



C



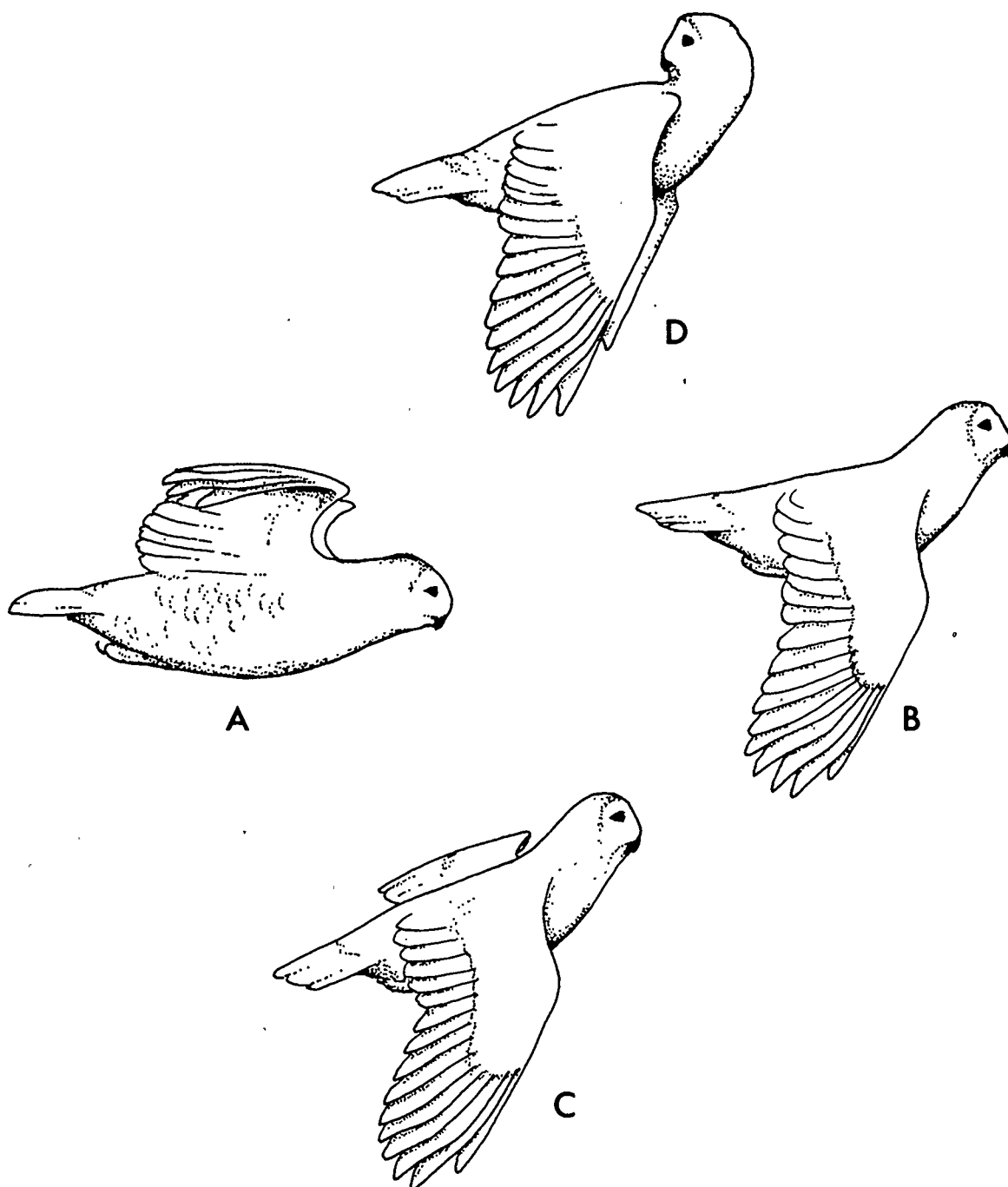
The Upright Posture and Forward Crouch were the only agonistic postures used by perched birds. My description of the Forward Crouch is very similar to the threat posture of breeding males described by Watson (1957) and Pitelka et al. (1955b). A threat posture somewhat similar to the Upright Posture has been described by Scherzinger (1974).

The sleeked plumage, position of the wings, and the straight legs of the Upright Posture may be derived from intention movements of flight. Components of the Forward Crouch are particularly similar to movements preparatory to flight in Snowy Owls, as a comparison of Figures 15A and 15C suggest. The lowered head, extended neck, and slightly outstretched wings are very similar in these two postures. Because flight is an integral part of attack behaviour in Snowy Owls (Keith, 1964; Hume, 1975), an intention to fly towards a conspecific could have evolved into a signal which warns a recipient of the tendency to attack (Daanje, 1950).

iii) Head-Up Glide Flight-Display

This flight-display involves extension of the neck and orientation of the body axis about 30° above horizontal while gliding (see Fig. 16). These adjustments resulted in a slight rise in altitude. This position was held briefly, then the owl resumed its slow wing-beats and lost altitude. This was repeated a number of times. The gliding and shifting of the body plane resulted in an undulating flight

FIGURE 16: The Head-Up Glide Flight-Display. A. Normal flight. B, C. The glide portion of the display, characterized by the upward extension of the head. D. An owl looking over its back before the glide portion of the display.



pattern of an amplitude of about five metres. Owls commonly used this modified flight pattern during interactions, or when flying from one part of their territory to another.

This display has not been described by other workers. Taylor (1974) describes an aerial courtship display in which an undulating flight pattern occurred. However, the head was not extended and the wing-beats were considerably exaggerated.

3. TERRITORIAL INTERACTIONS

I observed 27 territorial interactions in which the postures described above, or other more aggressive behaviours, occurred. Most interactions ($n = 24$) involved a single territorial resident and a transient or migrant bird. Interactions between territorial residents were rare ($n = 3$).

A. Typical Observations

1) Example of an interaction involving displays only. 13 February 1978. I noted a territorial owl, NGO, perched on a 12 m powerpole in the middle of its territory. Suddenly it assumed the Upright Posture and, after several seconds, flew towards another owl. This intruder was an immature female, sitting on a fencepost in the resting posture about 600 m away. NGO gave three Head-Up Glides as it approached, then landed on a fence-

post about 300 m away from the intruder. Immediately NGO oriented towards the other bird and performed a Forward Crouch, including very exaggerated head-swings and body-rotations. Following this display, NGO looked towards the intruder while in the Upright Posture, and then continued with more Forward Crouches. After about four minutes NGO flew to a small mound about 200 m from its opponent, and performed Forward Crouches until the other bird oriented its back towards NGO, but remained in the resting position. At this point, NGO stopped displaying, but remained alert.

2) Example of a perch-supplant. 17 December 1977. An immature female, VB, was perched on a fencepost within its territory. The bird gradually assumed the Upright Posture and looked intently at some object in the distance. I scanned the region where the owl was staring, and noted an immature female about 1.6 km away, perched on a powerpole commonly used as a perch by VB. VB leaned forward, assuming a Forward Crouch posture similar to Figure 15B. After staying in this position for about a minute, VB flew towards the other bird with very deep wing-beats. When VB was within 300 m the other bird flew rapidly out of the area. VB subsequently perched on the vacant pole, assumed the

Upright Posture, and watched the retreat of the intruder.

3) Example of an interaction involving a chase and physical combat. 14 December 1977. While trying to locate VB within its territory, I noted another owl, also an immature female, perched on a powerpole. Immediately this new bird took flight and flew towards another flying owl which I later identified as VB. Both owls flew very rapidly towards each other, and clashed together feet to feet, while holding their bodies perpendicular to the ground (see Hume, 1975). Following this, the new owl fell several metres downwards, but recovered and flew towards the boundary of VB's territory. VB gave chase, and after about 30 m eventually caught up to the other owl. Then VB grabbed the other owl's tail in its bill, disrupting the flight of the intruder, and struck the back of the owl with her feet. The intruder fell towards the ground uttering several shrill squeals, but pulled up about 5 m from the ground, and flew very quickly away. Meanwhile VB had given several Head-Up Glides, and perched on a small mound where it watched the other bird retreat. The loser perched 1.6 km away on a powerpole, oriented its back towards VB, and started preening.

These three cases are examples of interactions where the responses by one individual to another affect the subsequent behaviour of both. Using this definition of an interaction, the encounters I observed can be placed into one of four categories in decreasing order of aggressive intensity: fighting, chasing, supplanting, and posturing. Table 20 shows the distribution of the 27 interactions among these categories and the frequency of various agonistic components involved in each category. Upright Postures were associated with every interaction except one chase and one interaction involving only displays. Chases by the territorial owl followed three of eight Forward Crouch display sequences. Fighting was not observed following these displays. Head-Up Glides were used commonly in the more aggressive interactions, probably because of the use of flight in chases and fights. Physical combat was rare, only occurring in 5 (18.5%) of the 27 interactions. On the other hand, interactions involving only displays or chases were the most common types of interactions; each comprised one-third of all the interactions observed. Finally, 8 instances of one owl displacing another from a perch were observed. Three of these displacements were followed by chases, and one was followed by physical combat.

TABLE 20. The frequency of displays and other behaviour patterns during Snowy Owl interactions of varying intensity.

Behaviour Pattern	Occurrences of Behaviour Patterns During Interactions (% occurrence) ¹				Total Number of Occurrences
	Display Interactions (n = 9)	Supplanting Interactions (n = 4)	Chase (n = 9)	Fight (n = 5)	
Upright Posture	8 (88.9)	4 (100.0)	8 (88.9)	5 (100.0)	25
Forward Crouch	5 (55.6)	—	3 (33.3)	—	8
Head-Up Glide	4 (44.4)	—	6 (66.6)	3 (60.0)	13
Perch-supplanting	—	4 (100.0)	3 (33.3)	1 (20.0)	8
Chasing	—	—	9 (100.0)	3 (33.3)	12
Physical Combat	—	—	—	5 (100.0)	5

1. The percentage occurrence of that behaviour in the total number of interactions in each category.

B. Responses by Recipients or Intruders

Unfortunately I did not record in detail the responses of recipients of agonistic behaviour. However, I did notice some interesting things. First, following interactions in which the intruder remained in the locality, they turned their backs toward the displayer ($n = 9$). Observations 1 and 3 above illustrate this. This behaviour was particularly apparent when the owl was the recipient of Forward Crouch displays (5 of 8 cases). In the three instances in which owls did not orient away from the aggressor, they were chased. I also noted three cases in which two owls were perched on adjacent poles. These were not classified as interactions. However, in each case one owl was facing away from, and the other facing towards, the other bird.

Second, in four of the five interactions involving physical combat, the loser flew rapidly away from the other owl, at an altitude of about 45 m. Snowy Owls rarely flew at as great an altitude as this in other circumstances.

Finally, in most of the interactions ($n = 18$), recipients left the locality and were never seen again. Thus, interactions did not seem to be prolonged, and territorial contests were settled quite quickly.

C. The Effect of Sex

Seven of 23 interactions in which the sex of both participants could be determined were between males and fe-

males. Three of these encounters involved agonistic displays by females towards males. The other four involved one chase in which a female drove a male out of her territory, and three fights in which males were victorious twice. (Victory was established when the opposing bird was driven from the territory, and the victor remained in the area several days following the encounter). Thus there was no evidence of one sex dominating the other.

D. The Effect of Age

Nine of ten interactions between juvenile and adult females were initiated by the juvenile. Juveniles even induced attacks in three encounters in which the adult bird was a territorial resident, as the following observation illustrates:

13 January 1978. I located BB, an adult female, perched on a powerpole about 500 m away from a juvenile female perched on a large hill. BB was in the alert posture and was not facing the other owl. BB did not appear to be concerned about the presence of the other owl in her territory, and only glanced occasionally in that direction. After several minutes, the intruder flew behind the hill out of sight. BB appeared to notice this, and several minutes later flew to the hilltop and assumed the Upright Posture. After about 10

seconds I noted the other owl flying directly toward BB. BB waited until the intruder was about five metres away, and then jumped in the air. Both birds met feet to feet, and the intruder was knocked backwards. Following this, the intruder flew rapidly away at an altitude of about 40 m. BB slowly followed and perched on a powerpole where she watched the other owl retreat.

Table 21 summarizes intrusions by Snowy Owls into the territories of conspecifics. Eight of ten intrusions into the territories of ten adult Snowy Owls were by juvenile females. In contrast to this, in 18 intrusions into the territories of juvenile females, nine were by other juveniles and eight were by adult owls. The difference between the frequency of intrusions by adult and juvenile owls into the territories of juveniles versus those of adults is significantly different (chi-square two sample test, $p < 0.05$).

Table 21 also demonstrates that aggressive responses by territory-holders toward invaders were more common by territorial juvenile females (17 of 17 intrusions) than responses by territorial adults. I observed five cases where a territorial adult failed to display to or attack a juvenile invader.

TABLE 21. The frequency of intrusions by Snowy Owls into the territories or ranges of conspecifics, and the number of responses by the resident owl.

Resident Individual(s)	Number of Intrusions (Number of Agonistic Responses by Territory Residents)		
	Adults	Juveniles	Unknowns
Adults			
Males (3 owls)		3 (2)	
Females			
CBO		1	
BB		1	
DD		1	
YRT			1
NGO		1 (1)	1
Unnamed		1	
Adult Total	0 (0)	8 (3)	2 (0)
Juveniles			
Females			
LPM	1 (1)		
MOF		2 (2)	
AA	1 (1)		
CC			1 (1)
FTO	1 (1)	1 (1)	
VB	1 (1)	3 (3)	
CO	1 (1)	1 (1)	
NNGO	2 (2)	1 (1)	
Unnamed	1 (1)	1 (1)	
Juvenile Total	8 (8)	9 (9)	1 (1)

4. TERRITORIAL ADVERTISEMENT

In most birds territorial advertisement is in the form of vocalizations (e.g., Krebs, 1977). Although auditory communication by male Snowy Owls is important in advertising breeding territories (Sutton, 1932; Taylor, 1974), Snowy Owls have been described as silent on the winter range (e.g., Witherby, 1943; Karalus and Eckert, 1973). Observations describing territorial behaviour in winter (Keith, 1964; Quilliam, 1965; this study) suggest that this is probably true. This raises the question of how territorial status is advertised in this species on the winter range.

I propose two methods by which Snowy Owls can make themselves more prominent or conspicuous on territories and perhaps prevent intrusions: (1) by perching on tall objects; and (2) by orienting while perched such that the lighter portions of their plumage are directed into the sun.

In order to investigate whether territorial birds perched on tall objects more often than non-territorial birds, mean perch heights were calculated for both groups (Table 22). I divided owl sightings into five two-hour time periods to account for temporal variations in perch height (see Chapter 7). Only owl sightings in 1977/78 were analyzed because I had more information on the territorial status of birds than in 1976/77. Over the entire daylight period, territorial owls perched higher than non-territorial

TABLE 22. Mean perch heights of territorial and non-territorial Snowy Owls in winter.

Time period	Territorial		Non-territorial	
	Mean Perch Height ± S.E. (m)	Number of Observations	Mean Perch Height ± S.E. (m)	Number of Observations
0800 - 1000	6.28 ± 0.85	72	4.20 ± 1.01	37
1000 - 1200	6.50 ± 1.02	48	5.12 ± 0.97	50
1200 - 1400	7.30 ± 0.91	72	5.83 ± 1.00	65
1400 - 1600	7.02 ± 0.82	66	6.63 ± 1.02	55
1600 - 1800	10.20 ± 1.30	25	5.90 ± 2.60	11

owls (randomization test, $p = 0.014$; Edgington, 1969).

The difference in perch height between the two groups is probably not due to the availability of high perches (powerpoles and transmission towers), as these were abundant everywhere. Similarly, an explanation of this result in terms of the selection of hunting perches is unlikely, since I observed non-territorial owls capturing prey from high perches. Therefore territorial status is probably the most important factor affecting the height at which owls perched throughout the day.

Territorial owls tended to use high perches under almost all circumstances. On three occasions, during strong winds (>40 km/h) and very cold temperatures, I observed territorial owls perching on 25 m powerline towers or 12 m powerpoles, probably in response to non-territorial owls I observed near them. In addition, I noted on numerous occasions that neighbouring territorial owls perched on high objects simultaneously. These cases were not identified as territorial interactions, but they could have prevented aggressive encounters. This could explain the lack of disputes I observed between territorial owls on the study area.

I investigated the orientation of perched owls by recording the directions in which territorial and non-territorial birds faced on a circular scale relative to the sun. The circle representing the owl was divided into four

equal quadrants, one facing the sun, two perpendicular, and one away.

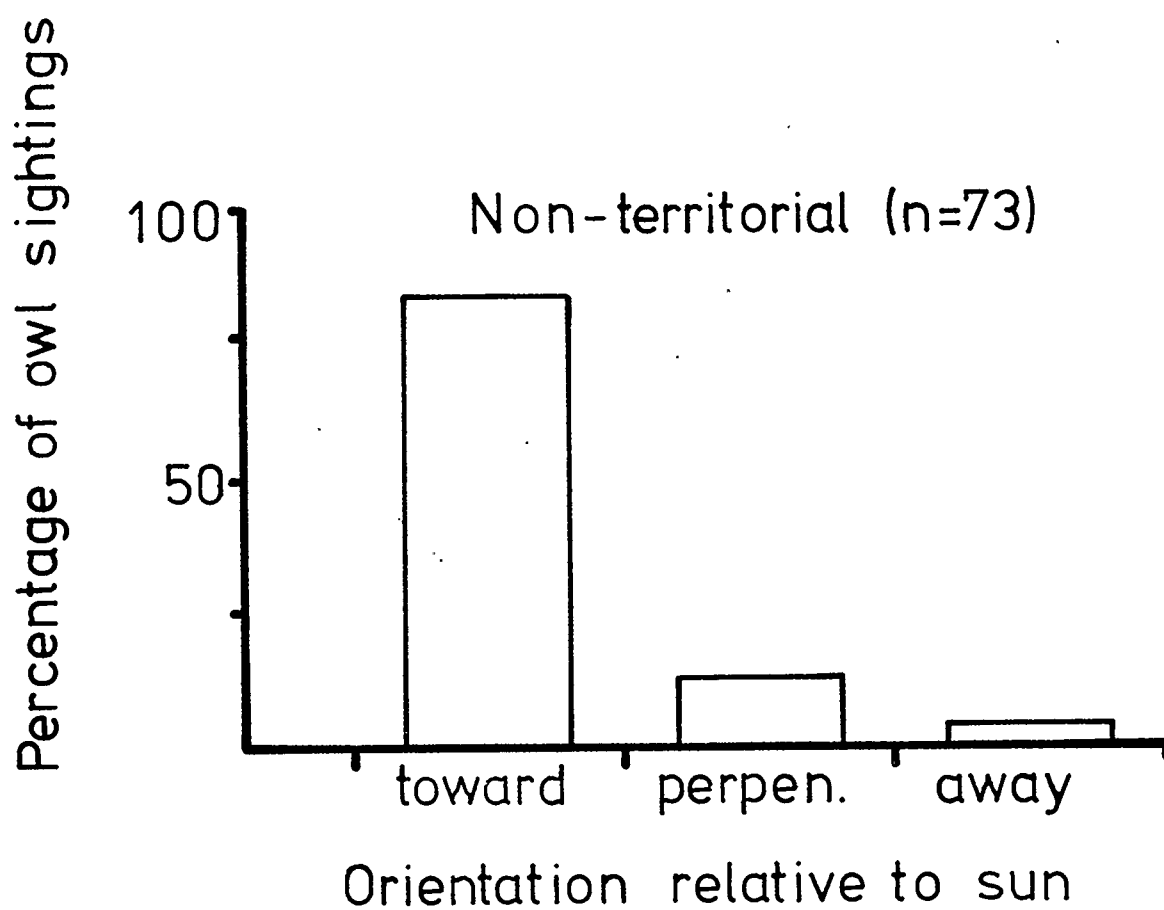
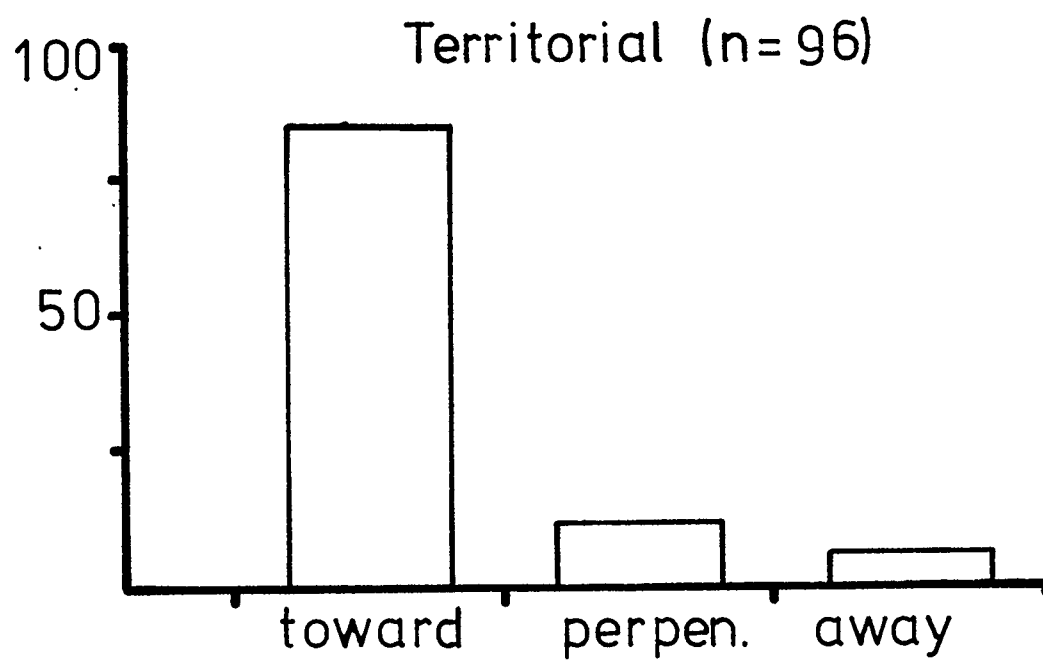
Figure 17 shows frequency histograms of the directions territorial and non-territorial owls faced relative to the sun on calm sunny days. Most territorial owls (84.4%) and non-territorial owls (83.6%) were observed facing the sun. These distributions of directional preferences of perched owls are significantly different from ones of equal preference (chi-square tests, $p < 0.001$). Orienting towards the sun occurred regardless of perch height and time of day. In fact, during observations of individual owls, I found that perched owls rotated 180 degrees during the day, always facing the sun.

5. DISCUSSION

Numerous workers have suggested that territorial individuals are seldom defeated while on their territories (e.g., Lorenz, 1938; N. Tinbergen, 1939; Nice, 1943). Territorial individuals also provide "keep-out" signals (Krebs, 1977) in order to prevent interactions which carry a risk of injury and which waste time and energy. These signals warn recipients that the territory is occupied and that there is a high probability the territory-holder would win any encounter.

In over 700 hours in the field, I observed only 27 agonistic interactions between Snowy Owls. Thus, it is

FIGURE 17: The orientation of perched territorial and non-territorial Snowy Owls relative to the sun.



reasonable to assume that territorial interactions between Snowy Owls are uncommon. I suggest that this is a result of efficient advertisement of territorial status. Since Snowy Owls are not vocal in winter, the "keep-out" signals used by territorial owls are probably visual ones. I suggested two possible mechanisms above: (1) perch height as a sign of dominance, and (2) using the sun to emphasize conspicuousness. These behaviours are what one would expect from a rather sedentary bird of open country. Territorial owls perched higher than non-territorial owls did throughout the day (Table 22), suggesting that high perches are probably selected by a dominant owl to enhance its conspicuousness and to give it a better view of the territory. Since hunting is usually done from a high perch (Fig. 7), the owls could be searching for prey as well as advertising territorial status.

Orientation towards the sun, however, was practised by both territorial and non-territorial owls (Fig. 17). This makes an explanation of this phenomenon in the context of territorial behaviour difficult. However, non-territorial owls were usually solitary and acted aggressively towards other owls near them (Chapter 5). For non-territorial owls, orientation towards the sun might be used to maintain individual distance, a phenomenon describing the tendency of individuals to avoid close contact with each other (Brown, 1975).

Another possibility is that orientation towards the sun could be used to gather radiant solar energy, thus facilitating thermoregulation. However, two lines of evidence argue against this explanation. First, the thermal conductance of Snowy Owl plumage is so low (Gessaman, 1972) that there is little possibility of radiant heat penetrating the skin. Second, light-coloured plumage, such as the white ventral surfaces of most Snowy Owls, absorbs less solar radiation than dark-coloured plumage (Hamilton and Heppner, 1967; Lustick, 1969). Thus Snowy Owls should orient the dark-coloured portions of their plumage toward the sun when cold-stressed and the lighter portions when heat-stressed. Since the thermo-neutral zone of Snowy Owls is from about 2.5-18.5°C (Gessaman, 1972), and most of the temperatures encountered in this study were below this (Fig. 3), Snowy Owls were cold-stressed and should not have faced the sun as frequently as I observed in order to gather solar energy.

Most of the displays of Snowy Owls, particularly the Upright Posture and the Head-Up Glide, appear to accentuate the ventral portion of an owl's body. The extension of the head could serve to increase the size of the white region on the facial disc and breast of Snowy Owls, by exposing white feathers on the throat (see Fig. 14). The Forward Crouch display appears to emphasize the facial disc by the exaggerated movements of the head. In addition, aggressive owls always oriented directly toward the opponent, whereas

non-aggressive owls, or losers of encounters, oriented the fronts of their bodies away from the opponent. Thus there is a possibility that certain regions of an owl's body, particularly the breast, throat and facial disc, are more important than others in communicating aggressive tendencies related to spacing behaviour.

However, there is much to be explained about the plumage variability of Snowy Owls. Specifically, why is there a large degree of sexual dimorphism in plumage colouration; why are males the lighter-coloured sex; and why are juveniles darker than adults? As I will discuss below, I believe that this plumage variability is related to the recognition of sex.

Hamilton (1961) has hypothesized that since courtship behaviour in birds involves a combination of sexual and aggressive behaviours (Hinde, 1953, 1970), sexual dimorphism in plumage may facilitate sex-recognition and reduce hostility between members of a potential breeding pair. Hamilton claimed that this would permit more rapid breeding in environments with a short breeding season. One should expect Snowy Owls to exhibit strategies which reduce the time spent preparing for breeding because the arctic breeding season is shorter than the breeding seasons of owls of more southern latitudes. Since Snowy Owls probably show the largest degree of sexual dimorphism in plumage of North American owls, Hamilton's hypothesis could explain this

greater degree of plumage dimorphism in this species. The darker colour of females could reflect selection for crypticity while providing nest-related parental care. If white plumage is important in agonistic behaviour, then one would expect the most territorial class of Snowy Owls to be the lightest, particularly on the ventral surface of their bodies. Thus the lighter colour of male Snowy Owls could relate to the fact that they are territorial while breeding (Sutton, 1932; Pitelka et al., 1955b; Watson, 1957), and that they defend territories in winter in some regions (e.g., Mitchell, 1947; Keith, 1964).

Four points emerge from the analysis of intrusions into territories (Table 21): (1) juvenile owls intruded into the territories of both adults and juveniles; (2) adults only invaded the territories of juveniles; (3) territorial juvenile owls interacted with every invader, regardless of its sex or age; and (4) adults rarely interacted with juvenile intruders unless they were attacked. The important questions raised by these observations are: why are invading juvenile owls tolerated within the territories of adult owls; and why are the territories of juveniles invaded by adults whereas the territories of other adults are not? The fact that I observed more intrusions and more aggressive encounters by juveniles suggest that they are more aggressive than adults, an observation noted for other species of birds (Brown, 1963; Harrington and Groves, 1977; Balda and

Balda, 1978; Groves, 1978). However, as I will discuss below, I believe that this aggressiveness of juveniles and relative non-aggressiveness of adults may be related to prior experience in territorial defence in winter.

Prior experience in territorial defence undoubtedly plays a role in determining the efficiency of territorial defence, and could explain some of my observations. My analyses in Table 21 show that the territories of juveniles experienced a number of intrusions by both adult and juvenile owls. I never observed adult owls invading the territories of adult females. In these cases, one might hypothesize that territorial adults, which probably have had at least one winter's experience of interactions with conspecifics, are probably conveying messages warning of aggressive tendencies. As mentioned above, these could include perch height or the use of visual displays. Adult owls are aware of these signals and refrain from entering defended areas. However, inexperienced juveniles could be misinterpreting the behavioural messages used by adult owls, and invade their territories. Groves (1978) also uses this explanation in analysing age differences in aggression in shorebird flocks.

Admittedly the ideas presented above are speculative and other interpretations are probably possible. The complex sensory apparatus of owls would make the study of strigiform communication an interesting prospect. Snowy

Owls are very observable and lend themselves to an investigation of communication. Future studies of territorial advertisement in Snowy Owls could include the use of mounted dummy owls in various postures. I performed some preliminary experiments with a mounted adult female in the alert posture, by placing it on the ground and on fenceposts in five territories. I got no response to the model. Watson (1957), using a one-dimensional model, also obtained no response on the part of breeding territorial males. This suggests that species recognition in Snowy Owls is more complex than in other birds, as numerous experiments utilizing similar techniques with passerines have been successful (e.g., Lack, 1939).

CHAPTER 7

DIURNAL ACTIVITY BUDGETS
OF WINTERING SNOWY OWLS

1. INTRODUCTION

The popular concept of wintering Snowy Owls is that they are diurnal birds of prey (e.g., Peterson, 1947). However, there is little evidence to support this notion. Their general conspicuousness and the continuous daylight in the arctic during their breeding season are probably responsible for this view. Keith (1964) was apparently the first to note that wintering Snowy Owls become more conspicuous just before sunset. He attributed this to their propensity to perch on high objects, which were used for hunting, at this time. Since his observation, anecdotal reports have indicated that these owls show crepuscular peaks of activity (Weir, 1973; Young, 1972; Höhn, 1973). Nagell and Frycklund (1965:55) have provided the most complete description of the winter activity of this species. They mention that "the owl studied was particularly active in the afternoons and evenings, but operated also in the early morning. Many of the reported observations point to quite regular night activity in contrast to the conception generally held. At daytime, from about 10 AM to 3 PM, the activity was low, and the owl sat generally motionless on

a stone. Between 3 and 4 PM the bird began to hunt flying around its territory."

These brief reports represent the extent of our knowledge on the winter activity of Snowy Owls. This chapter investigates temporal patterns in the behaviour of Snowy Owls. Only observations of territorial owls will be analyzed because the behaviour of migrant and resident individuals has been shown to differ in other species (Rappole and Warner, 1976).

2. METHODS

From early December to late February of both winters, I observed individual owls for periods ranging from one to six hours. These observation periods were made only during the daylight hours, which, in winter, is from about 0800 to 1800 (MST) in the Calgary region. The behaviour of the birds was divided into five categories and the duration of each activity was measured with a stopwatch. Over the two winters, 138 hours of time budget data were collected on territorial owls. Due to small samples in some hourly periods, these observations will be analyzed by dividing the interval 0800-1800 into five two-hour periods. In calculations of monthly time budgets, raw data were corrected for unequal samples in these time periods.

The behavioural categories were:

- (1) Alert. This category represents perched birds

that were in the alert posture (see Fig. 12), scanning their surroundings. Alert birds were usually quite active and were assumed to be searching for prey.

(2) Resting. Resting represents perched birds that were sleeping or dozing (Fig. 13).

(3) Preening. This category contains all forms of comfort movements, including birds actively manipulating feathers with their bills, scratching with feet, rousing and stretching.

(4) Flight.

(5) Other. All activities not corresponding to any of the above were lumped in this category. These included feeding and intraspecific and interspecific interactions.

It was sometimes difficult to determine whether an owl was alert or resting. Therefore, during every observation period I attempted to quantify these behavioural categories by counting the number of times an owl turned its head in one minute. These counts were made every five minutes while observing birds, and also at times when the activity of an owl was in question. After preliminary observations of hunting and resting owls, I chose a value of 6 head turns per minute as the lower limit for an alert owl. Cases in which an owl was peering intently at a prey item or some other object were considered in the alert category.

Hourly records of wind speed and temperature were gathered while observations were in progress in order to

test for effects of these weather variables on activity.

The energy budget and daily energy expenditure (DEE) of Snowy Owls was estimated using the following equation:

$$\text{DEE} = (\text{Aa} \times \text{Ca}) + (\text{Ar} \times \text{Cr}) + (\text{Ap} \times \text{Cp}) + (\text{Af} \times \text{Cf}) + (\text{Ao} \times \text{Co}) \quad (1)$$

The variables Aa, Ar, Ap, Af and Ao represent the amount of time spent alert, resting, preening, flying, and in other activities respectively. The variables Ca, Cr, Cp, Cf and Co represent the energetic costs per unit time of each of these behaviours.

Table 23 shows the estimated costs of activities based on multiples of existence metabolism. The existence metabolism of Snowy Owls in kcal/day was found using the following equation from Gessaman (1972):

$$\text{EM} = 191.68 - 5.69\text{Ta}, \quad (2)$$

where Ta is ambient temperature. The energetic costs in Table 23 agree with estimates of similar activities of other species (see King, 1974; Tarboton, 1978). The rationale in using existence metabolism for calculating energy budgets can be found in King (1974:70-79).

For all energy calculations I used monthly mean temperatures (grand mean of the daily means in each month)

TABLE 23. Energetic costs of activities of Snowy Owls expressed as multiples of existence metabolism (EM).

Activity	Cost
Alert ^a	1.3
Rest ^a	1.0
Preening ^a	1.7
Flight ^b	14.0
Other	1.7

^aTaken from King (1974).

^bThis multiple is derived from Tucker's (1974) equation 12, using 1.802 kg as the mean mass of male and female Snowy Owls (Snyder & Wiley, 1976).

taken from Environment Canada weather bulletins from the Calgary International Airport, located about 20 km from the study area. Accurate weather data could not be collected on the study area because of the size of the area and the time involved. I compared a number of my own temperature readings with those from the airport, and there was a difference of only two to three degrees. Since I will be using monthly mean temperatures, the difference between the airport and study area readings is probably not significant.

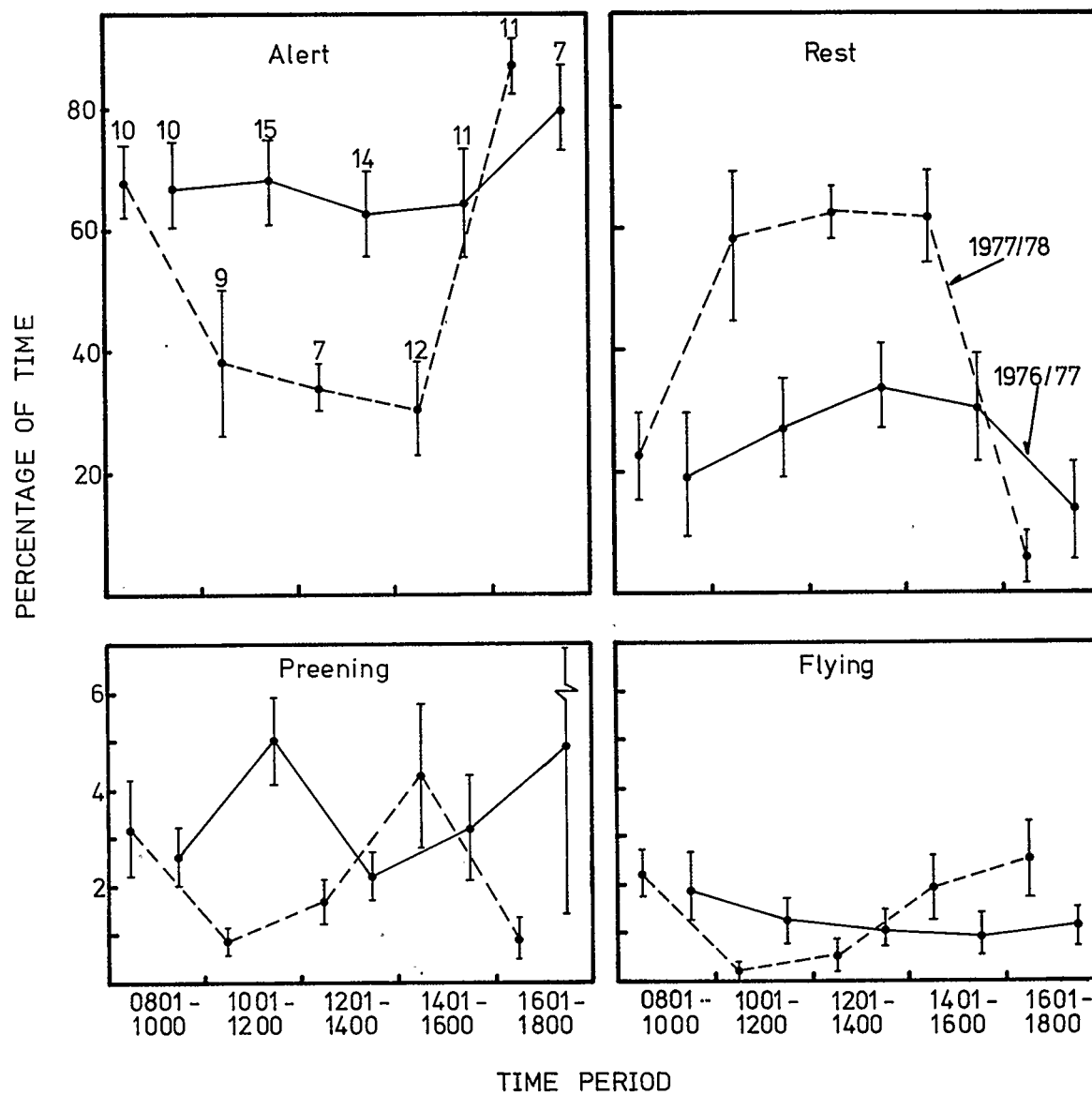
Unfortunately activity data are available only for the period from 0800-1800. This left 58.4% of the 24 hour day unsampled. Therefore, when calculating the total number of hours spent per day in the various activities, I assumed that the diurnal time budget was representative of the 24 hr time budget. As will be shown later, this assumption is probably incorrect, and therefore the calculated daily energy expenditure will only be an estimate of the true value for wintering Snowy Owls.

3. RESULTS

A. Diurnal Time Budget

Diurnal differences in activity were detected by calculating the mean percentage of time spent in each activity for each of the five time periods (Fig. 18). In 1977/78 the distributions show that the owls spent more time alert

FIGURE 18: The proportion of time spent by wintering Snowy Owls in four activities during various time periods in the winters of 1976/77 and 1977/78. The solid circles represent the mean and the vertical bars standard errors. The numbers above the vertical bars represent the number of hours of observations from which each mean was calculated. The means and standard errors for each year are slightly offset for ease of presentation.



in the early morning (0800-1000) and the evening (1600-1800) than at other times. The mean percentage of time flying is also high in the early morning and from 1400-1800. These activity maxima are separated by a period of inactivity (resting) from 1000 to 1600. I performed a single factor ANOVA on the actual hourly samples of the four behavioural categories for each year. The only significant results were found for the alert, resting, and flying categories in 1977/78 (all F statistics significant at the 0.05 level). The amount of time spent in these behaviours in the three time periods in the middle of the day (1000-1600) were not significantly different from each other, but were significantly different from the early morning and evening time periods (Student-Neuman-Keuls multiple range tests, $p = 0.05$).

This bimodal activity pattern is not as apparent in 1976/77 (Fig. 18). This could be due to the fact that temperatures were higher in 1976/77 than 1977/78 (see Fig. 3). The mean percentage of time spent alert is higher in the evening than at other times, and more time was spent resting during 1000-1600 than during the other time periods. Although the mean percentages of time in any behavioural category are not significantly different (single factor ANOVA, all $p > 0.05$), they show a trend similar to the bimodal pattern in 1977/78.

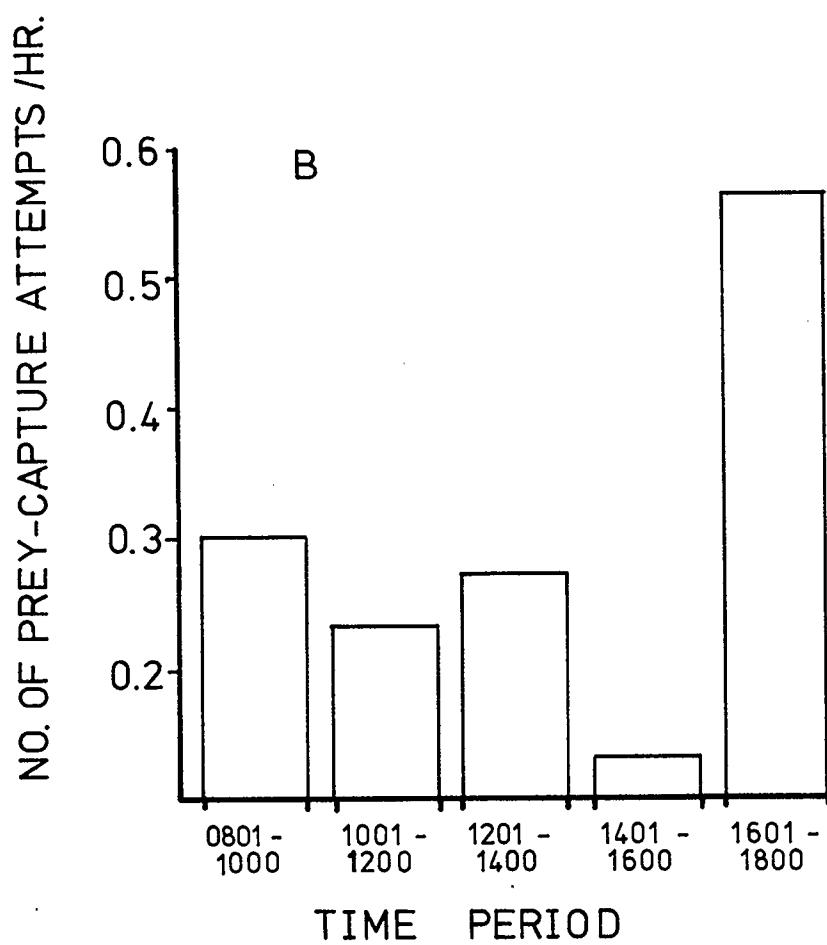
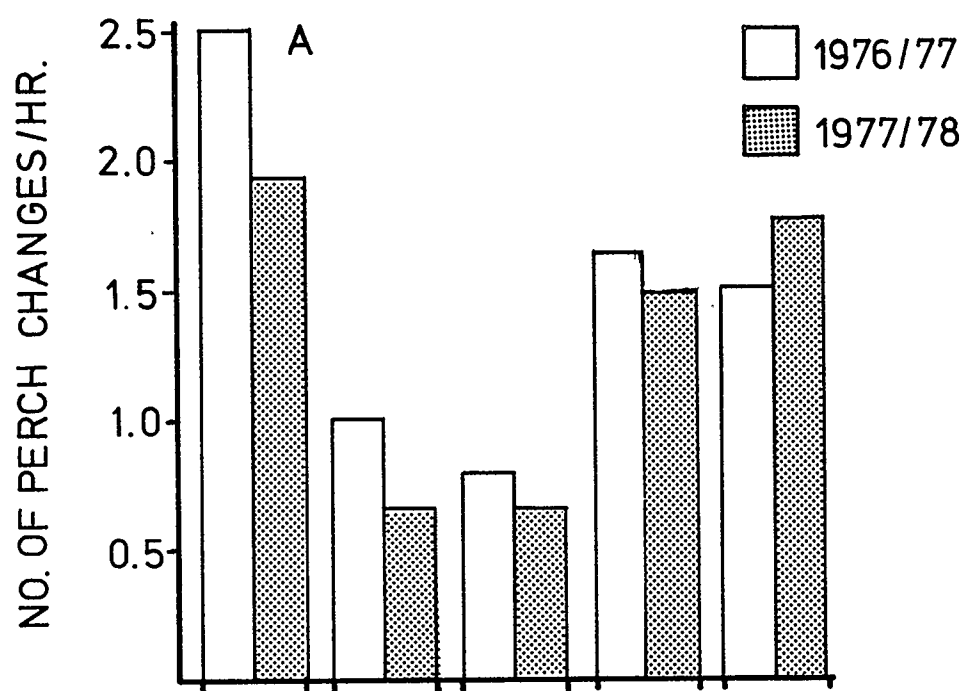
The distribution of time spent preening throughout the

day also seems to show a bimodal pattern (Fig. 18). However, in this case the two peaks differ between both years. It is difficult to interpret these results. The amount of time preening is probably dictated by higher priority behaviour patterns (Gibson, 1977) such as active and rest.

The results depicted in Figure 18 suggest that resident Snowy Owls are alert and probably hunting more often around sunrise and sunset. Other evidence supports this conclusion. Perch-changes, which are indicative of hunting behaviour (see Chapter 4), occurred more often in the early morning and late afternoon than mid-day in both years (Fig. 19A). Figure 19B shows that hunting tended to occur more frequently in the early morning and particularly in the late afternoon than at other times. The distributions in Figure 19 are statistically different from rectangular ones in which the rate of perch-changes or attempts to capture prey are the same in each time period (chi-square tests, $p < 0.05$). Finally, Table 22 shows that mean perch height was higher in the evening than in the other time periods. This correlates well with the distribution of attempts to capture prey, (Fig. 19B) as high perches were used more often than low perches for hunting (Fig. 7A).

I attempted to determine the effects of weather on activity. In order to do this, I analyzed activity data in each time period separately in order to decrease the variability caused by the diurnal activity rhythm. No signifi-

FIGURE 19: Distributions of the rate of perch changes and prey-capture attempts by wintering Snowy Owls by time period. A. The number of perch-changes per hour for different time periods for each year (1976/77, $n = 80$; 1977/78, $n = 104$). B. The number of prey-capture attempts per hour ($n = 36$) by time (data for each winter were pooled due to small samples).



cant correlations were found between temperature or wind speed and the amount of time spent in any of the measured activities in any time period. However, I suspect that sample sizes are not large enough, and temperature and wind speed readings not accurate enough, to investigate subtle relationships between hourly activity of wintering Snowy Owls and weather conditions. The effects of weather on activity will be considered in a more general manner below.

By combining activity data for each year and correcting for unequal samples in the bi-hourly periods, I obtained an estimate of the percentage of time an owl spent in each activity during daylight (Table 24). The most interesting result is that resident owls spent about 98% of the daylight hours perched. In addition, owls were alert more often than resting. This latter result is more pronounced in 1976/77 than 1977/78. More time was also spent in flight and in other behaviours in the second year than in the first.

B. Energetics of Wintering Snowy Owls

Using the overall time budget (Table 24), equations 1 and 2, and the grand mean of the daily mean temperatures in each winter, estimates of the average diurnal energy costs were made for both winters. These are 122.1 kcal and 140.9 kcal for 1976/77 and 1977/78 respectively. Assuming that the time budget data in Table 24 are representative of the

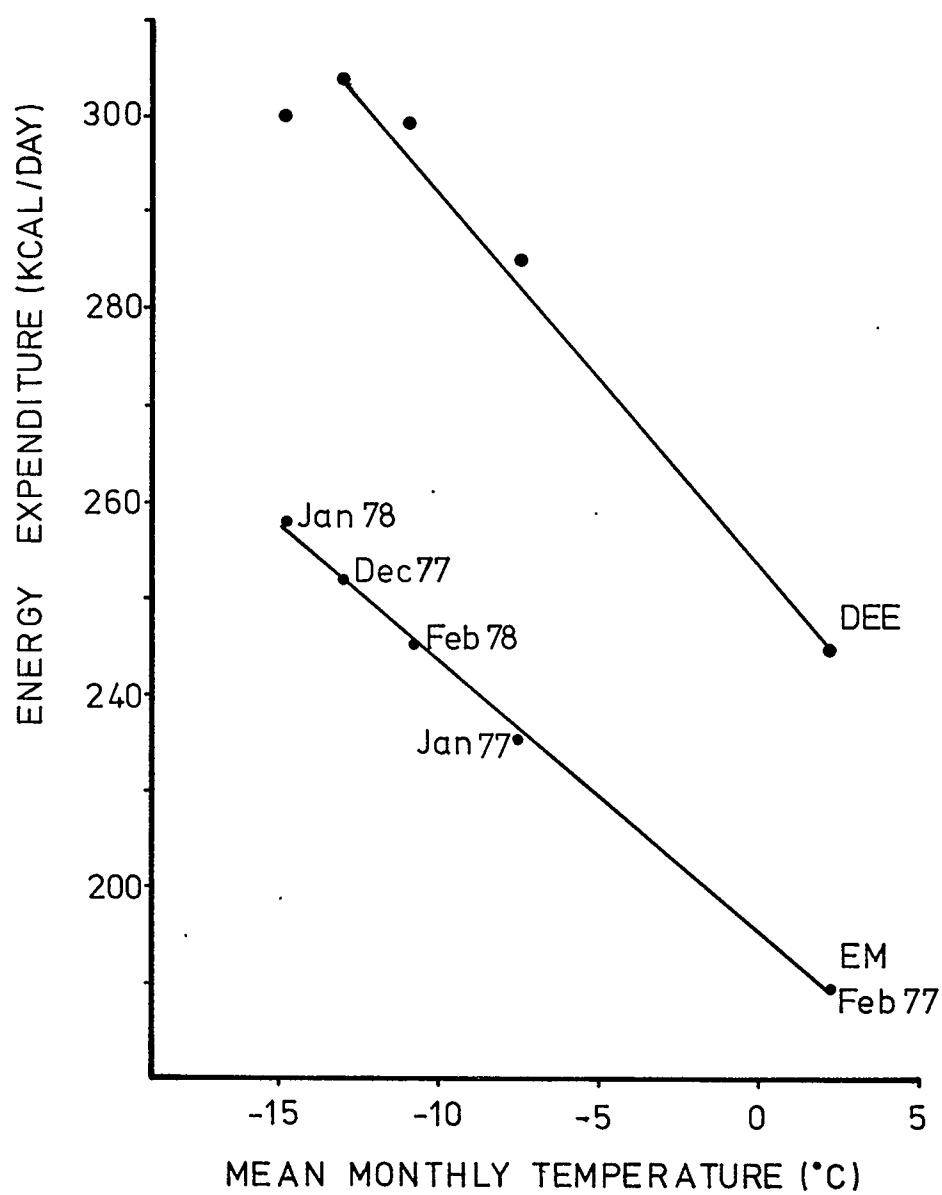
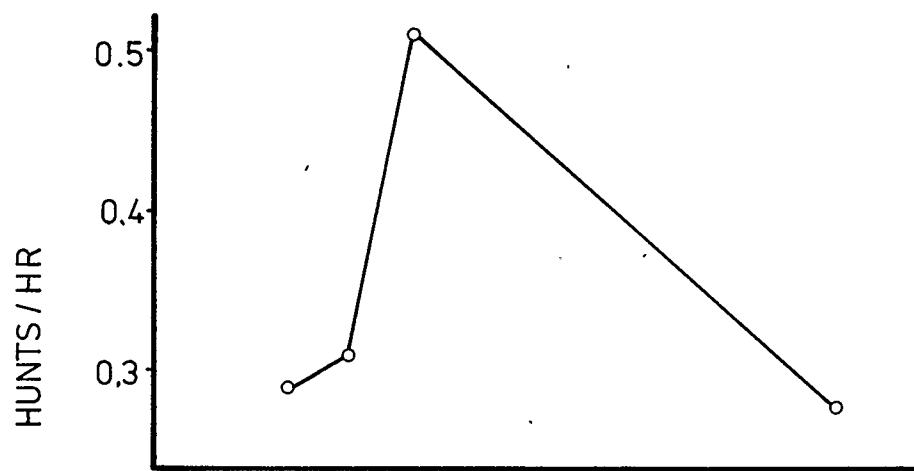
TABLE 24. The overall diurnal time budget of wintering Snowy Owls.

Year	% Daylight Hours Spent in Activity					No. of Hours of Observations
	Alert	Rest	Preening	Flight	Other	
1976/77	65.6	25.8	4.8	1.2	2.6	58
1977/78	55.0	39.6	2.1	1.5	1.8	69
Both years	59.9	33.2	3.3	1.3	2.2	127

entire 24 hr period, these values become 292.8 kcal/day for 1976/77, and 337.9 kcal/day for 1977/78. These values are expressed more meaningfully as the biomass of prey required per day. Using the mean weights of small mammal prey on the study area, their energetic values (1.40 kcal/g for Microtus (Golley, 1961) and 1.61 kcal/g for Peromyscus (Kaufman and Kaufman, 1975)), and the assimilation efficiency of Snowy Owls (77%, Gessaman, 1972), I estimate that Snowy Owls needed to ingest 182 g of Peromyscus (about 7 individuals) or 209 g of Microtus (about 5.5 individuals) per day in 1976/77. In 1977/78, due to the colder temperatures, the food requirements rose to about 209 g of Peromyscus (about 8.5 individuals) or 245 g of Microtus (about 6.5 animals) per day. These figures agree with other estimates of food requirements of adult Snowy Owls. Watson (1957), after observing captive and wild owls at various temperatures, concluded that free-living Snowy Owls needed 150-250 g of lemmings (Lemmus spp.) per day. Gessaman (1972) found that at 5°C an adult female required about 248 g of lemmings per day, and at -15°C this rose to about 300 g.

In order to compare this theoretical food intake with observed intake, I compared daily energy expenditures and the rate of attempts to capture prey on a monthly basis. Monthly time budgets were translated into energetic costs in the same manner as described above, and plotted against monthly mean temperatures (Figure 20). The mean number of

FIGURE 20: Average daily energy expenditures (DEE), existence metabolism (EM), and the rate of hunting by wintering Snowy Owls in relation to mean monthly temperature during the winters of 1976/77 and 1977/78.



attempts to capture prey per hour per month are also plotted. There is no correlation between diurnal energy expenditure (or temperature) and attempted prey captures on a monthly basis ($r = 0.07$, $p > 0.1$). In addition, there is apparently no behavioural response (i.e., time budgeting) to changes in temperature, as indicated by the parallel EM and DEE lines in Figure 20. Most birds respond to cold by decreasing their activity (see Raveling et al., 1972; Kessel, 1976). If this were the case for Snowy Owls we would expect the EM and DEE lines to converge near the Y-axis.

4. DISCUSSION

Aschoff (1964, 1967) has argued that the proximate factors (Zeitgebers) to which behavioural periodicities are entrained usually differ from the ultimate causes which give a rhythm its adaptive value. In most birds, the timing of foraging and roosting behaviour has been related to light intensity, as well as to temperature (Aschoff, 1964; Morton, 1967; Kessel, 1976). These Zeitgebers are also responsible for activity maxima of the prey species of some birds (e.g., insectivorous birds; Verner, 1965; Gibson, 1977). Thus the cycles of both predator and prey are entrained to the same cues. This has an obvious adaptive value for the predator.

Most studies of the activity cycles of owls have shown that their activity is coupled to the light-dark cycle

(Glass, 1969; Erkinaro, 1972, 1973). Erkinaro's work, in particular, has shown that most owls of the boreal region have two major activity periods per day, and that within these periods there are short "bursts" of activity. This activity pattern closely follows that of their major prey species (Erkinaro, 1973).

The analysis of the activity patterns of Snowy Owls in this study is preliminary, but some parallels can be drawn between the activity patterns of these owls and their prey. In Chapter 4 I showed that the prey of Snowy Owls on the study area consisted primarily of Peromyscus maniculatus, Microtus pennsylvanicus, and Gray Partridges. Peromyscus are essentially nocturnal, although some diurnal activity occurs during winter (Hamilton, 1937). Their winter activity pattern consists of a major period of activity early in the evening, starting at sunset and lasting one to two hours, and another late in the night, around 0300 (Falls, 1968). Microtus, on the other hand, tend to show bursts of activity throughout the 24 hour period. However, these activity peaks are of greater amplitude near sunrise and sunset (Hamilton, 1937). Westerskov (1966) has found that Gray Partridges forage throughout the day in winter, but most intensively in the late afternoon.

The activity cycle of wintering Snowy Owls in southern Alberta probably follows those of its main prey species. The pronounced activity of Snowy Owls at sunset and the few

hours before coincides with activity maxima of all three prey species. Other raptors utilizing these prey species also show an activity pattern similar to that of Snowy Owls (Craighead and Craighead, 1954).

Some modifying influences upon hunting activity of birds of prey include gorging and fasting. It has frequently been shown that captive owls, including Snowy Owls, often eat more than their daily needs at a single meal (Räber, 1950). This is usually followed by one or more days of fasting (Watson, 1957). The extent to which this occurs in the wild is unknown. Birds of prey have been found to gorge themselves in the field (Craighead and Craighead, 1954; L. H. Brown, 1976). However, they still maintain considerable interest in prospective prey items and sometimes kill more than their needs, even when satiated (L. H. Brown, 1976; Nunn et al., 1976; Räber, 1950). This phenomenon has been found with other predators in the wild (Kruuk, 1972).

In this study, capturing prey during mid-day apparently had little effect on the evening activity period. The following observation illustrates this:

8 February, 1977. From 1300-1304 a female Snowy Owl captured and ate three small mammals. The owl then proceeded to perch on the ground and rest, dozing for long periods. At about 1515, the owl became very active, and flew to the top of a large

powerpole. From this perch at 1545 another small mammal was captured and ingested. Following this hunting action the owl flew to another powerpole and made two more unsuccessful attempts to capture prey at 1630.

In contrast to this, I found that a few owls were not hunting during early morning observation periods and spent most of their time "loafing". This possibly was the result of successful hunting before the observation periods began.

The activity cycle of wintering Snowy Owls in southern Alberta is very similar to the diurnal portion of their activity cycle during the breeding season. Shields (1969) found that the owls were very active from 0600 to 0800 and particularly from 1600 to 1800 in early summer near Barrow, Alaska. These intervals were separated by periods of relatively low activity. This activity cycle was apparently correlated to the activity periods of lemmings. The significance of this apparent similarity is unclear. Either seasonal variation in the activity rhythm of Snowy Owls does not occur, or it affects only nocturnal activity during winter. The latter hypothesis seems more likely due to the fact that most animals exhibit seasonal changes in their activity periods due to the seasonal variation in daylength (e.g., Erkinaro, 1973).

As mentioned throughout this chapter, and also by Nagell and Frycklund (1965), there are suggestions that

Snowy Owls are active and doing some hunting during the night. Evidence for this comes primarily from my calculations of daily energetic expenditures of owls on a monthly basis (Fig. 20). My estimates of the amount of energy needed by owls was not correlated with the rate of attempts to capture prey during the daylight hours (Fig. 20). Although this discrepancy could be the result of my crude estimations, I think the most likely explanation is that the birds were hunting during night. In addition, the most numerous prey species in the diet, Peromyscus maniculatus (Tables 4 and 5), is largely nocturnal (Falls, 1968). Of the successful hunting attempts in which I could determine the prey species, very few appeared to be Peromyscus. Thus the majority of hunting attempts on these animals probably occur after 1800.

Shields (1969) showed that breeding Snowy Owls are active about two hours before midnight and also from about 0400 to 0600. These activity periods were not as pronounced as the period from 1600 to 1800. Later on in the year, when the days became shorter, Shields found that the owls were most active at sunset and during the following darkness. I believe that this description is probably true for the owls wintering on my study area. Other evidence for nocturnal activity comes from the fact that some Snowy Owls winter in the arctic (Manning et al., 1956; Parmelee et al., 1967), and from the few nocturnal observations of owls I was able

to gather. I did spend some time attempting to observe birds after dark with an image-intensifying telescope. Although owls were impossible to locate in the dark after they had flown, I noticed several times that birds which were hunting and perched on high objects at 1800 remained so for up to one and one-half hours after dark. In addition, during several excursions to the study area from 1900 to 2000 a few owls were located perched on tall objects. On similar trips to the study area from midnight to 0200, I never located birds. This could be due to the fact that they were perched on low objects while roosting in the middle of the night.

I failed to find strong correlations between time spent in certain behaviours and temperature or wind conditions. Also, there were no apparent behavioural adjustments of time budgets to temperature on a monthly scale (Fig. 20). This latter result could be due to the level of analysis. However, Gessaman (1972) found that: (1) the thermal conductance of Snowy Owls is the lowest recorded for any other animal except the Adelie Penguin (Pygoscelis adeliae); (2) overall insulation of Snowy Owl plumage is equivalent to the highest insulation reported for arctic mammals; and (3) Snowy Owls have a lower standard metabolic rate than other avian species of comparable body weight. These results suggest that Snowy Owls did not need to make extensive behavioural adjustments to the ranges of temperatures

they encountered during this study. Gessaman (1972) suggested that these owls possess a thermoneutral zone (a range of temperatures where neither physical nor chemical mechanisms for controlling heat production need be employed), between 2.5°C and 18.5°C. Temperatures consistently below 2.5°C were encountered only in the winter of 1977/78. The owls decreased their activity slightly during this year (see Table 24), especially in the middle of the day (Fig. 18).

CHAPTER 8

GENERAL DISCUSSION

David Lack (1954, 1966) has argued for the importance of food shortage in winter in regulating the sizes of avian populations. He stated that the existence of food shortage has led to the evolution of various types of behaviour in birds which increase their chances of surviving a winter. I have examined these ideas in Snowy Owls by investigating the question: "Is winter survival of Snowy Owls related to foraging efficiency?" The purpose of this chapter is to summarize the results of this study and discuss them in terms of this question.

The Snowy Owl possesses several mechanisms to increase its feeding efficiency and decrease its energy expenditure in winter. First, Snowy Owls hunted in profitable areas, maximizing their chances of capturing prey. Most owls were observed in the habitats which contained the highest availabilities of prey, and most attempts to capture prey took place in these habitats, indicating that these areas were in fact used for hunting.

Second, female owls (and probably males in other geographical areas as well) defended a territory, the size of which was related to the food supply it contained. Thus the probable function of these territories was to ensure

an adequate supply of food for the winter. However, my knowledge of the territorial system of the Snowy Owl was not adequate to determine whether these birds defended more or less food than they needed to survive the winter. The fact that some owls remained on their territories for virtually the entire winter suggests that at least some territories contained an adequate amount of food.

Third, energy conservation was apparent in the hunting methods used by the owls, and in the manner in which territories were defended. I demonstrated that perching occupied most of a territorial owl's time budget. Prolonged perching, which requires little energy expenditure, reflects the "sit and wait" hunting tactics of Snowy Owls. Territorial owls make themselves more conspicuous and obtain better views of their territories by perching for long periods on tall objects. This advertisement of territorial status, and the use of displays, may explain the fact that I observed few physical interactions in defence of territories.

These results provide indirect evidence that food supply is an important factor in the winter biology of Snowy Owls. Shortage of food has been implicated as an important cause of post-fledging mortality in birds (Lack, 1954). It has generally been accepted that mortality rates of birds are high during the period of immaturity, but subsequently are age-independent, so that a constant fraction of adults die

annually (Nice, 1937; Deevey, 1947; Lack, 1954). A high mortality rate among first-year birds has been documented for some owls (Honer, 1963; Stewart, 1969; Southern, 1970; Adamcik and Keith, 1978; Hirons et al., 1979), hawks (Olsson, 1958; cited in Southern, 1970; Mueller et al., 1977), and many other birds (see Lack, 1954). High mortality occurs in the nest due to predation, starvation, or inclement weather (Welty, 1975). However, a large portion of fledged birds also succumb (e.g., Lack, 1946). In birds of prey this mortality is due primarily to starvation (Brown, 1976), presumably because of the inability of immatures to procure food on their own. For example, Barn Owls (Tyto alba) and Great Grey Owls (Strix nebulosa), which prey predominantly upon microtines, exhibit massive movements much like the Snowy Owl. In certain years, these movements are associated with a mass mortality of young owls due to starvation (Honer, 1963; Höglund and Lansgren, 1968; Stefansson, 1979). These movements have been called starvation emigrations (Adamcik and Keith, 1978).

In this study, I demonstrated that juvenile female Snowy Owls were not as successful at capturing prey as were adult females, and that they also took longer than adults to prepare prey for ingestion. These results suggest that inexperienced juveniles were relatively inefficient at hunting. When comparing the quality of the territories of the two age-groups, juveniles had larger territories

containing lesser amounts of profitable habitat. Juveniles probably spent more time in interactions with conspecifics than did adults. These findings suggest that Snowy Owls in their first year could be subjected to a higher mortality rate due to food stress than are adults, which is consistent with the theory of mortality rates of most bird species (Lack, 1954).

However, as mentioned in Chapter 1, there is little direct evidence of high mortality due to natural causes in Snowy Owls wintering south of the breeding grounds. It could be that many immatures die within the breeding range as they become independent from their parents, or that they perish during post-breeding movements and their carcasses are not discovered. In this thesis I hypothesized that juveniles may be more common in the usual southward movements to the winter range than in the massive emigrations, suggesting that these younger birds have a greater tendency than adults to move away from the arctic in winter. The strategy of moving south to a milder climate where prey availability is probably greater, may increase the chances of juvenile Snowy Owls surviving the winter.

The work of Chitty (1950) and Gross (1947) has shown that the massive movements of Snowy Owls are related to two factors: (1) the high population density of owls due to a good food supply; and (2) the abrupt absence of their major prey, the lemmings. However, whether the stimulus involved

in releasing the invasive movements is food shortage or overpopulation, is a question that has been long debated (Lack, 1954; Svårdson, 1957). Lack believed that overpopulation was the proximate factor triggering mass movements, while food shortage was an ultimate factor explaining the movements.

In Great Horned Owls, for example, breeding stops early in the decline of their prey base, and thus there are few owls available to compete for the dwindling food supply (Adamcik et al., 1978). In Barn Owls, on the other hand, high reproduction, encompassing several large clutches per pair per year, occurs while food is abundant and the decline of their prey base is so rapid that numerous owls are present and are competing for food. This shortage of food and intense intraspecific competition, apparently triggers the starvation emigrations I described earlier (Honer, 1963). In Snowy Owls, the microtine prey base undergoes 3-5 year cycles, but the short arctic breeding season will not allow second clutches in years of abundant food. Therefore, the owls vary the size of their single clutch to meet the increasing or decreasing food supply (e.g., Hagen, 1956). However, nesting success (proportion of young fledged) of Snowy Owls is relatively low, even in years when prey are numerous (Murie, 1929; Sutton, 1932; Pitelka et al., 1955a; Sutton and Parmelee, 1956; but see Watson, 1957). This perhaps suggests that following a good

breeding season, there are not unusually high numbers of Snowy Owls present as there might be with other species of owls. Thus, overpopulation might not be a major factor causing the massive periodic movements of Snowy Owls in winter.

In addition, a widespread shortage of major prey may not affect Snowy Owls as much as other species of owls. The large size of Snowy Owls may allow them to prey on a wider range of prey species than can smaller owls (Schoener, 1969; Lein and Boxall, 1979). Thus the birds can switch more readily to alternate prey when microtines are scarce. The fact that Snowy Owls are generalized feeders in winter (as opposed to the breeding season) supports this view. This ability of Snowy Owls to become generalized feeders in certain situations, as well as the short arctic breeding season and low nesting success, suggest that the starvation emigrations characteristic of some strigiform species are not as common as originally thought in Snowy Owls.

The problem in answering questions pertaining to the cause of periodic mass movements of Snowy Owls lies with understanding the extent of the "normal" post-breeding movements, or movements of owls occurring in between major ones. If most owls winter outside the arctic, then the mass movements of owls may be amplifications of usual post-breeding movements, and would be influenced by food supply on the winter range as well as the breeding range. If most

Snowy Owls winter in the arctic, then a shortage of food following breeding is an important factor causing their invasions. Although my study suggests that a large population of Snowy Owls winters in southern Alberta, we know too little about Snowy Owls in other regions to investigate these ideas thoroughly.

In summary, my results indicate that the Snowy Owl population wintering in southern Alberta is a relatively stable one within years. Most of the birds are probably not vagrants, and some may return to southern Alberta in successive winters (Oeming 1958, 1964). This suggests that the prairie provinces probably are a regular wintering area for some Snowy Owls, as predicted by Snyder (1947, 1949). The behaviour and ecology of the owls wintering in southern Alberta is related to the increase of foraging efficiency through territoriality, energy conservation, and the selection of optimal hunting habitat. As Lack (1954) predicted for birds in general, juvenile Snowy Owls appeared to have had more difficulty than adults in hunting and obtaining territories. Although this may result in higher mortality rates for juveniles than adults, no direct evidence of this was obtained.

This study has raised a number of questions that may be fertile ground for further study. First, the possibility of geographical separation between the sexes of Snowy Owls in winter should be investigated. This type of study would

probably necessitate surveys of those Snowy Owls wintering in the arctic and in other areas. Second, the winter biology of juvenile Snowy Owls should be examined more closely, concentrating perhaps on the adaptive significance of plumage variability. Finally, a long-term investigation of the distribution and abundance of Snowy Owls wintering in the prairie provinces over a number of winters is clearly needed. These studies will provide us with more knowledge about irruptive phenomena in owls, and more importantly, predictions about the effects of human disturbances on the biology of these birds.

LITERATURE CITED

- Adamcik, R. S. and L. B. Keith. 1978. Regional movements and mortality of Great Horned Owls in relation to Snowshoe Hare fluctuations. *Can. Field-Natur.* 92:228-234.
- Adamcik, R. S., Todd, A. W., and L. B. Keith. 1978. Demographic and dietary responses of Great Horned Owls during a Snowshoe Hare cycle. *Can. Field-Natur.* 92:156-166.
- Allan, T. A. 1977. Winter food of the Snowy Owl in northwestern lower Michigan. *Jack-Pine Warbler* 55:42.
- Altmann, J. 1974. Observational study of behavior: sampling methods. *Behaviour* 49:227-267.
- Amadon, D. 1959. The significance of sexual differences in size among birds. *Proc. Amer. Phil. Soc.* 103: 531-536.
- Angell, T. 1974. *Owls*. Univ. of Wash. Press, Seattle.
- Aschoff, J. 1964. Survival value of diurnal rhythms. *Symp. Zool. Soc. Lon.* 13:79-98.
- Aschoff, J. 1967. Circadian rhythms in birds. *Proc. XIV Int. Ornithol. Congr.*, pp. 95-111.
- Ashmole, N. P. 1963. The regulation of numbers of tropical oceanic birds. *Ibis* 103:458-473.
- Balda, R. P. and J. H. Balda. 1978. The care of young Pinon Jays (Gymnorhinus cyanocephalus) and their integration into the flock. *J. Ornithol.* 119:146-171.
- Balgooyen, T. G. 1976. Behaviour and ecology of the American Kestrel (Falco sparverius) in the Sierra Nevada of California. *Univ. Calif. Publ. Zool.* 103:1-85.
- Banfield, A. W. F. 1974. *The Mammals of Canada*. Univ. of Toronto Press, Toronto.
- Behle, W. H. 1968. Records of the Snowy Owl for Utah. *Wilson Bull.* 80:231-232.
- Bent, A. C. 1938. Life histories of North American birds of prey. Part 2. *U. S. Nat. Mus. Bull. No.* 170.
- Berger, D. D. and H. C. Mueller. 1959. The bal-chatri: a trap for birds of prey. *Bird-Banding* 30:18-26.

- Bird, C. D. 1972. The Snowy Owl in the Calgary area, 1964-1972. *Calgary Field Natur.* 3:106-107.
- Bond, R. M. 1945. A record of the Snowy Owl in southern California. *Condor* 47:217.
- Brooks, A. 1929. On pellets of hawks and owls. *Condor* 31:222-223.
- Brown, J. L. 1963. Aggressiveness, dominance and social organization in the Stellar Jay. *Condor* 65:460-484.
- Brown, J. L. 1964. The evolution of diversity in avian territorial systems. *Wilson Bull.* 76:160-169.
- Brown, J. L. 1975. *The Evolution of Behavior*. Norton and Co., Inc., New York.
- Brown J. L. and G. H. Orians. 1970. Spacing patterns in mobile animals. *Ann. Rev. Ecol. Syst.* 1:239-262.
- Brown, L. H. 1976. *Birds of Prey*. Hamlyn Publ. Group, Ltd., London.
- Brüll, H. 1972. Goshawks and falcons. In B. Grzimek, ed. *Grzimek's Animal Life Encyclopedia*. Van Nostrand Reinhold Co., New York. P. 339.
- Burton, J. A. (ed.). 1973. *Owls of the World*. E. P. Dutton and Co. Inc., New York.
- Cade, T. J. 1955. Experiments on winter territoriality of the American Kestrel, (Falco sparverius). *Wilson Bull.* 67:5-17.
- Cade, T. J. 1960. Ecology of the Peregrine and Gyrfalcon populations in Alaska. *Univ. Calif. Publ. Zool.* 63:151-290.
- Campbell, R. W. and M. D. MacColl. 1978. Winter foods of Snowy Owls in southwestern British Columbia. *J. Wildl. Mgmt.* 42:190-192.
- Carpenter, F. L. and R. E. MacMillen. 1976. Energetic cost of feeding territories in a Hawaiian Honeycreeper. *Oecologia* 26:213-223.

- Catling, P. M. 1973. Food of Snowy Owls wintering in southern Ontario, with particular reference to the Snowy Owl hazard to aircraft. Ontario Field Biol. 27:41-45.
- Charnov, E. L., Orians, G. H., and K. Hyatt. 1976. The ecological implications of resource depression. Amer. Natur. 110:247-259.
- Chitty, D. 1937. A laboratory study of pellet formation in the Short-eared Owl (Asio flammeus). Proc. Zool. Soc. Lon. 108A:267-287.
- Chitty, H. 1950. Canadian arctic wild life enquiry, 1943-49; with a summary of results since 1933. J. Anim. Ecol. 19:180-193.
- Clark, R. J. 1975. A field study of the Short-eared Owl, Asio flammeus (Pontoppidan), in North America. Wildl. Monogr. No. 47.
- Cody, M. L. and C. B. J. Cody. 1972. Territory size, clutch size, and food in populations of wrens. Condor 74:473-477.
- Cohen, R. 1966. Banding notes on the Snowy Owl. Kingbird 16:73-77.
- Colinvaux, P. A. 1974. Introduction to Ecology. Wiley and Sons Inc., New York.
- Collopy, M. W. 1973. Predatory efficiency of American Kestrels wintering in northeastern California. Raptor Res. 7:25-31.
- Craighead, J. J. and F. C. Craighead. 1954. Hawks, Owls and Wildlife. Wildl. Mgmt, Inst., Washington, D.C.
- Daanje, A. 1950. On the locomotory movements in birds and the intention movements derived from them. Behaviour 3:49-98.
- Deevey, E. S. 1947. Life tables for natural populations of animals. Quart. Rev. Biol. 22:283-314.
- Downs, A. 1979. Over the editors's desk. B. C. Outdoors, 35:4.

- Dunn, E. K. 1972. Effect of age on the fishing ability of Sandwich Terns Sterna sandvicensis. Ibis 114:360-366.
- Duke, G. E., Evanson, O. A. and A. Jegers. 1976. Meal to pellet intervals in 14 species of captive raptors. Comp. Biochem, Physiol. 53A:1-6.
- Earhart, C. M. and N. K. Johnson. 1970. Size dimorphism and food habits of North American owls. Condor 72:251-264.
- Edgington, E. S. 1969. Statistical Inference: the Distribution-free Approach. McGraw-Hill Book Co., New York.
- Enderson, J. H. 1964. A study of the Prairie Falcon in the central Rocky Mountain region. Auk 81:332-352.
- Erkinaro, E. 1972. Precision of the circadian clock in Tengmalm's Owl, Aegolius funereus (L.), during various seasons. Aquilo Ser. Zool. 13:48-52.
- Erkinaro, E. 1973. Structure of the diel activity period in Tengmalm's Owl, Aegolius funereus, and the Short-eared Owl, Asio flammeus, and its seasonal changes. Aquilo Ser. Zool. 14:59-67.
- Errington, P. L. 1945. Some contributions of a 15-year local study of the Northern Bobwhite to a knowledge of population phenomena. Ecol. Monogr. 15:1-34.
- Falls, J. B. 1968. Activity. In J. A. King, ed. Biology of Peromyscus (Rodentia). Amer. Soc. Mammal, Stillwater, Okla. Pp. 543-570.
- Fleming, J. H. 1902. Further notes on the Snowy Owl in Ontario. Auk 19:400.
- Fretwell, S. D. 1972. Populations in a Seasonal Environment. Princeton Univ. Press, Princeton.
- Galushin, V. M. 1974. Synchronous fluctuations in populations of some raptors and their prey. Ibis 116:127-134.
- Gass, C. L. 1978. Rufous Hummingbird feeding territoriality in a suboptimal habitat. Can. J. Zool. 56:1535-1539.

- Gass, C. L., Angeher, G. and J. Centa. 1976. Regulation of food supply by feeding territoriality in the Rufous Hummingbird. *Can. J. Zool.* 54:2046-2054.
- Gessaman, J. A. 1972. Bioenergetics of the Snowy Owl (Nyctea scandiaca). *Arctic Alpine Res.* 4:223-238.
- Gibson, F. 1978. Ecological aspects of the time budget of the American Avocet. *Amer. Midl. Natur.* 99: 65-82.
- Gill, F. B. and L. L. Wolf. 1975. Economics of feeding territoriality in the Golden-winged Sunbird. *Ecology* 56:333-345.
- Gill, F. B. and L. L. Wolf. 1977. Nonrandom foraging by sunbirds in a patchy environment. *Ecology* 58: 1284-1296.
- Gillese, J. P. 1960. White raider from the north. *Weekend Magazine* 10:27.
- Glading, B., Tillotson, D. F. and D. Selleck. 1943. Raptor pellets as indicators of food habits. *Calif. Fish Game* 29:92-121.
- Glass, M. L. 1969. Some remarks on the evening departure during winter of the Long-eared Owl (Asio otus). *Dansk. Ornithol. Foren. Tidsskr.* 65:173-179.
- Golley, F. B. 1961. Energy values of ecological materials. *Ecology* 42:581-584.
- Graber, R. R. 1962. Food and oxygen consumption in three species of owls (Strigidae). *Condor* 64:473-487.
- Gross, A. O. 1927. The Snowy Owl migration of 1926-27. *Auk* 44:479-493.
- Gross, A. O. 1931. Snowy Owl migration 1930-31. *Auk* 48:501-511.
- Gross, A. O. 1944. Food of the Snowy Owl. *Auk* 61:1-18.
- Gross, A. O. 1947. Cyclic invasions of the Snowy Owl and the migration of 1945-1946. *Auk* 64:584-601.

- Groves, S. 1978. Age-related differences in Ruddy Turnstone foraging and aggressive behavior. *Auk* 95: 95-103.
- Hagen, Y. 1956. The irruption of Hawk Owls (Surnia ulula L.) in Fennoscandia 1950-1951. *Sterna* 24:1-22.
- Hagen, Y. 1965. The food, population fluctuations, and ecology of the Long-eared Owl (Asio otus) in Norway. Norwegian State Game Res. Inst. Papers, Ser. 2. No. 23.
- Hamilton, T. H. 1961. On the functions and causes of sexual dimorphism in breeding plumage characters of North American species of warblers and orioles. *Amer. Natur.* 95:121-123.
- Hamilton, W. J. 1937. Activity and home range of the field mouse Microtus pennsylvanicus pennsylvanicus (Ord.). *Ecology* 18:255-263.
- Hamilton, W. J. III. and F. Heppner. 1967. Radiant solar energy and the functions of black homeotherm pigmentation: an hypothesis. *Science* 155:196-197.
- Hanson, W. C. 1971. The 1966-67 Snowy Owl incursion in south-eastern Washington and the Pacific northwest. *Condor* 73:114-116.
- Harrington, B. A. and S. Groves. 1977. Aggression in foraging migrant Semipalmated Sandpipers. *Wilson Bull.* 89:336-338.
- Herrnstein, R. J. and D. M. Loveland. 1975. Maximising and matching on concurrent ratio schedules. *J. Exp. Anal. Behav.* 24:107-116.
- Hicks, L. E. 1932. The Snowy Owl invasion of Ohio in 1930-1931. *Wilson Bull.* 44:221-226.
- Hinde, R. A. 1953. The conflict between drives in the courtship and copulation of the Chaffinch. *Behaviour* 5:1-31.
- Hinde, R. A. 1956. The biological significance of the territories of birds. *Ibis* 98:340-369.
- Hinde, R. A. 1970. *Animal Behaviour*. Second edn. McGraw-Hill Book Co., New York.

- Hirons, G., Hardy, A., and P. Stanley. 1979. Starvation in young Tawny Owls. *Bird Study* 26:59-63.
- Hofslund, P. B. 1973. Do hawks feed during migration? *Raptor Res.* 7:13-14.
- Höglund, N. H., and E. Lansgren. 1968. The Great Gray Owl and its prey in Sweden. *Viltrevy* 5:363-421.
- Höhn, E. O. 1973. Winter hunting of Snowy Owls in farmland. *Can. Field-Natur.* 87:468-469.
- Honer, M. R. 1963. Observations on the Barn Owl (Tyto alba guttata) in the Netherlands in relation to its ecology and population fluctuations. *Ardea* 51:158-195.
- Hume, R. A. 1975. Talon-grappling by Snowy Owls. *Bird Study* 22:260.
- Hunt, W. G., Rogers, R. R. and D. J. Slowe. 1975. Migratory and foraging behavior of Peregrine Falcons on the Texas coast. *Can. Field-Natur.* 89:111-123.
- James, D. 1958. The changing seasons. *Amer. Birds* 12:256-260.
- Jenkins, D. 1960. Social behaviour of the partridge, Perdix perdix. *Ibis* 103:156-189.
- Johnson, D. H. and J. H. Enderson. 1972. Roadside raptor census in Colorado-winter 1971-72. *Wilson Bull.* 84:489-490.
- Johnson, R. A. 1937. The food of the Snowy Owl (Nyctea nyctea) during a migration to the Gulf of St. Lawrence. *Can. Field-Natur.* 51:136-137.
- Kamil, A. C. 1978. Systematic foraging by a nectar-feeding bird, the Amakihi (Loxops virens). *J. Comp. Physiol. Psychol.* 92:388-396.
- Karalus, K. E. and A. W. Eckert. 1973. The Owls of North America. Doubleday and Co., Inc., Garden City, New York.
- Kaufman, D. W. and G. A. Kaufman. 1975. Caloric density of old-field mice during post-natal growth. *Acta Theriol.* 20:83-95.

- Keith, L. B. 1960. Observations on Snowy Owls at Delta, Manitoba. *Can. Field-Natur.* 74:106-112.
- Keith, L. B. 1963a. A note on Snowy Owl food habits. *Wilson Bull.* 75:276-277.
- Keith, L. B. 1963b. *Wildlife's Ten Year Cycle*. Univ. of Wisc. Press, Madison.
- Keith, L. B. 1964. Territoriality among wintering Snowy Owls. *Can. Field-Natur.* 78:17-24.
- Kenward, R. E. 1978. Hawks and doves: Factors affecting success and selection in Goshawk attacks on Wood-pigeon. *J. Anim. Ecol.* 47:449-460.
- Kessel, B. 1976. Winter activity patterns of Black-capped Chickadees in interior Alaska. *Wilson Bull.* 88: 36-61.
- King, J. R. 1974. Seasonal allocation of time and energy resources in birds. In R. A. Paynter, ed. *Avian Energetics*. Publ. Nutt. Orn. Club No. 15. Pp. 4-85.
- Kodric-Brown, A. and J. H. Brown. 1978. Influence of economics, interspecific competition, and sexual dimorphism on territoriality of migrant Rufous Hummingbirds. *Ecology* 59:285-296.
- Koplin, J. R. 1973. Differential habitat use by sexes of American Kestrels wintering in northern California. *Raptor Res.* 7:39-42.
- Krebs, J. R. 1977. Song and territory in the Great Tit, Parus major. In B. Stonehouse and C. M. Perrins, eds. *Evolutionary Ecology*. MacMillan Ltd., London. Pp. 47-62.
- Krebs, J. R. 1978. Optimal foraging: Decision rules for predators. In J. R. Krebs and N. B. Davies eds. *Behavioural Ecology*. Sinauer Ass. Inc., Sunderland, Massachusetts. Pp. 23-63.
- Krebs, J. R. and R. J. Cowie. 1976. Foraging strategies in birds. *Ardea* 64:98-116.
- Kruuk, H. 1972. Surplus killing in carnivores. *J. Zool.* 166:233-244.

- Lack, D. 1939. The behaviour of the Robin. Part II. A partial analysis of aggressive and recognitional behaviour. Proc. Zool. Soc. Lond. 109A:169-219.
- Lack, D. 1940. Habitat selection and speciation in birds. Brit. Birds 34:80-84.
- Lack, D. 1944. The problem of partial migration. Brit. Birds 37:122-130, 143-150.
- Lack, D. 1946. Do juvenile birds survive less well than adults? Brit. Birds 39:258-264.
- Lack, D. 1954. The Natural Regulation of Animal Numbers. Oxford Univ. Press, London.
- Lack, D. 1966. Population Studies of Birds. Oxford Univ. Press, London.
- Lederer, R. J. 1977. Winter feeding territories in the Townsend's Solitaire. Bird-Banding 48:11-18.
- Lein, M. R. and C. A. Webber. 1979. Habitat selection by wintering Snowy Owls (Nyctea scandiaca). Can. Field-Natur. 93:176-178.
- Lein, M. R. and P. C. Boxall. 1979. Interactions between Snowy and Short-eared Owls in winter. Can. Field-Natur. 93:411-414.
- Lockie, J. D. 1955. The breeding habits and food of Short-eared Owls after a vole plague. Bird Study 2:53-69.
- Longeley, R. W. 1972. The climate of the prairie provinces. Environment Canada Climatological Studies No. 13.
- Lorenz, K. 1938. A contribution to the comparative sociology of colonial-nesting birds. Proc. VIII Int. Ornithol. Congr., pp. 207-218.
- Lustick, S. 1969. Bird energetics: effects of artificial radiation. Science 163:387-390.
- MacArthur, R. H. 1972. Geographical Ecology. Harper and Row Publ., Inc., New York.
- MacArthur, R. H. and E. R. Pianka. 1966. On optimal use of a patchy environment. Amer. Natur. 100:603-609.

- Mackintosh, N. J. 1969. Comparative studies of reversal and probability learning: rats, birds and fish. In R. M. Gilbert and N. S. Sutherland, eds. *Animal Discrimination Learning*. Academic Press, Inc., London. Pp. 137-162.
- Manning, T. H., Höhn, E. O. and A. M. MacPherson. 1956. The birds of Banks Island. *Natl. Mus. Canada Bull.* No. 143.
- Marler, P. and W. J. Hamilton III. 1966. *Mechanisms of Animal Behavior*. John Wiley and Sons Inc., New York.
- Marti, C. D. 1974. Feeding ecology of four sympatric owls. *Condor* 76:45-61.
- Meade, G. M. 1948. The 1945-46 Snowy Owl incursion in New York State. *Bird-Banding* 19:51-59.
- Mech, L. D. 1970. *The Wolf*. Nat. Hist. Press, New York.
- Miller, F. L., Russell, R. M. and A. Gunn. 1975. Distribution and numbers of Snowy Owls on Melville, Eglinton and Bynam Martin Islands, N. W. T. Canada. *Raptor Res.* 9:60-64.
- Mills, G. S. 1975. A winter population study of the American Kestrel in central Ohio. *Wilson Bull.* 241-247.
- Mills, G. S. 1976. American Kestrel sex ratios and habitat separation. *Auk* 93:740-748.
- Mitchell, M. H. 1947. Snowy Owls in Peel Co., Ontario. *Can. Field-Natur.* 61:68-69.
- Morton, M. L. 1967. Diurnal feeding patterns in White-crowned Sparrows, Zonotrichia leucophrys gambelli. *Condor* 69:491-512.
- Moynihan, M. 1962. Display patterns of tropical American "nine-primaried" songbirds. I. Chlorospingus. *Auk* 79:310-344.
- Mueller, H. C. and D. D. Berger. 1967. Fall migrations of Sharp-shinned Hawks. *Wilson Bull.* 79:397-415.
- Mueller, H. C., Berger, D. D. and G. Allez. 1977. The periodic invasions of Goshawks. *Auk* 94:652-663.

- Murie, O. J. 1929. Nesting of the Snowy Owl. Condor 31:3-12.
- Nagell, B. and I. Frycklund. 1965. Invasionen av fjälluggla (Nyctea scandiaca) i södra Skandinavien vintrarna -1963 samt något om artens beteende på övervintringslokalerna. Vår Fågelvärld 24:26-55.
- Nelson, R. W. 1977. Behavioral ecology of coastal Peregrines (Falco peregrinus pealei). Ph.D. thesis. University of Calgary.
- Nero, R. W. 1964. Snowy Owl captures duck. Blue Jay 22:54-55.
- Newton, I. 1970. Irruptions of crossbills in Europe. In A. Watson, ed. Animal Populations in Relation to their Food Resources. Blackwell Publ., Oxford. Pp. 337-357.
- Nice, M. M. 1937. Studies on the life history of the Song Sparrow. I. A population study of the Song Sparrow. Trans. Linn. Soc. N. Y. 4:1-247.
- Nice, M. M. 1943. Studies in the life history of the Song Sparrow. II. The behavior of the Song Sparrow and other passerines. Trans. Linn. Soc. N. Y. 6:1-328.
- Nunn, G. L., Klem, D., Kimmel, T. and T. Merriman. 1976. Surplus killing and caching by American Kestrels (Falco sparverius). Anim. Behav. 24:759-763.
- Odum, E. P. and E. J. Kuenzler. 1955. Measurement of territory and home range size in birds. Auk 72:128-137.
- Oeming, A. F. 1955. A preliminary study of the Great Gray Owl (Scotiaptex nebulosa nebulosa) (Forster) in Alberta with observations on some other species of owls. M.Sc. thesis. Univ. of Alberta.
- Oeming, A. F. 1958. Recoveries of Alberta banded Snowy Owls. Can. Field-Natur. 72:171-172.
- Oeming, A. F. 1964. Banding recovery of a Great Gray Owl. Blue Jay 22:10.

- Ogilvie, R. T. and T. Furman. 1959. Effect of vegetational cover of fence rows on small mammal populations. *Ecology* 40:140-141.
- Orians, G. H. 1969. Age and hunting success in the Brown Pelican (Pelecanus occidentalis). *Anim. Behav.* 17:316-319.
- Owens, R. A. and M. T. Myres. 1973. Effects of agriculture upon populations of native passerine birds of an Alberta fescue grassland. *Can. J. Zool.* 51:697-713.
- Page, G. and D. F. Whitacre. 1975. Raptor predation on wintering shorebirds. *Condor* 77:73-83.
- Parmelee, D. F. 1972. Canada's incredible arctic owls. *Beaver* 303:30-41.
- Parmelee, D. F., Stephens, H. A., and R. H. Schmidt. 1967. The birds of southeastern Victoria Island and adjacent small islands. *Natl. Mus. Canada Bull.* 222.
- Paxton, R. O. 1974. The changing seasons. *Amer. Birds* 28:604-609.
- Peterson, R. T. 1947. A Field Guide to the Birds. Houghton Mifflin Co., Boston.
- Phelan, F. J. S. 1976. The response of avian predators to population cycles of small mammals (especially Microtus) on Amherst and Wolfe Islands, near Kingston, Ontario, Canada. M.Sc. thesis. Queen's University.
- Pitelka, F. A., Tomich, P. Q. and G. W. Treichel. 1955a. Ecological relations of jaegers and owls as lemming predators near Barrow, Alaska. *Ecol. Monogr.* 25:85-117.
- Pitelka, F. A., Tomich, P. Q. and G. W. Treichel. 1955b. Breeding behavior of jaegers and owls near Barrow, Alaska. *Condor* 57:3-18.
- Pianka, E. R. 1974. Evolutionary Ecology. Harper and Row Publ, Inc., New York.
- Platt, J. B. 1976. Gyrfalcon nest site selection and winter activity in the western Canadian arctic. *Can. Field-Natur.* 90:338-345.

- Portenko, L. A. 1972. Die Schnee-Eule. Neue Brehm-Bucherei. No. 454. A. Ziemsen Verlag, Wittenberg.
- Powell, G. V. N. 1974. Experimental analysis of the social value of flocking by Starlings in relation to predation and foraging. *Anim. Behav.* 22:501-505.
- Pyke, G. H., Pulliam, H. R. and E. L. Charnov. 1977. Optimal foraging: a selective review of theory and tests. *Quart. Rev. Biol.* 52:137-154.
- Quilliam, H. R. 1965. Winter study of Snowy Owls on Wolf Island, Ontario *Field Biol.* 19:1-8.
- Räber, H. 1950. Das Verhalten gefangenen Waldohreulen (Asio otus otus) und Waldkauze (Strix aluco aluco) zur Beute. *Behaviour* 2:1-95.
- Raczynski, J. and A. L. Ruprecht. 1974. The effect of digestion on the osteological composition of owl pellets. *Acta Ornithol.* 14:1-14.
- Rappole, J. M. and D. W. Warner. 1976. Relationships between behavior, physiology, and weather in avian transients at a migration stopover site. *Oecologia* 26:193-212.
- Raveling, D. G., Crews, W. E. and W. D. Klimstra. 1972. Activity patterns of Canada Geese during winter. *Wilson Bull.* 84:278-295.
- Recher, H. F. and J. A. Recher. 1969. Comparative foraging efficiency of adult and immature Little Blue Herons (Florida caerulea). *Anim. Behav.* 17:320-322.
- Roest, A. J. 1957. Notes on the American Sparrow Hawk. *Auk* 74:1-19.
- Royama, T. 1970. Factors governing the hunting behaviour and selection of food by the Great Tit (Parus major). *J. Anim. Ecol.* 39:619-668.
- Rudebeck, G. 1950. The choice of prey and modes of hunting of predatory birds with special reference to their selective effect. *Oikos* 2:65-88.

- Rudebeck, G. 1951. The choice of prey and modes of hunting of predatory birds with special reference to their selective effect. *Oikos* 3:200-231.
- Rusk, M. S. 1969. Snowy Owl face-cleaning. *Kingbird* 19:15-16.
- Sadler, T. S. and M. T. Myres. 1976. Alberta birds, 1961-1970, with particular reference to migration. *Prov. Mus. Alberta, Nat. Hist., Occ. Paper No. 1.*
- Schaller, G. B. 1972. *The Serengeti Lion.* Univ. of Chicago Press, Chicago.
- Scherzinger, von W. 1974. Zur Ethologie und Jugendentwicklung der Schnee-Eule (Nyctea scandiaca) nach Beobachtungen in Gefangenschaft. *J. Ornithol.* 115: 8-49.
- Schoener, T. W. 1968. Sizes of feeding territories among birds. *Ecology* 49:123-141.
- Schoener, T. W. 1969. Models of optimal size for solitary predators. *Amer. Natur.* 103:277-313.
- Schoener, T. W. 1971. Theory of feeding strategies. *Ann. Rev. Ecol. Syst.* 2:369-404.
- Selander, R. K. 1966. Sexual size dimorphism and differential niche utilization in birds. *Condor* 68:113-151.
- Shelford, V. E. 1945. The relation of Snowy Owl migration to the abundance of the collared lemming. *Auk* 62:592-596.
- Shields, M. 1969. Activity cycles of Snowy Owls at Barrow Alaska. *Murrelet* 50:14-16.
- Simon, C. A. 1975. The influence of food abundance of territory size in the iguanid lizard, Scleropus jarrovi. *Ecology* 56:993-998.
- Smith, H. C. 1976. Comparison of food items found in pellets of seven species of owls. *Edmonton Natur.* 4:36-38.

- Smith, J. N. M. and R. Dawkins. 1971. The hunting behaviour of individual Great Tits in relation to spatial variations in their food density. *Anim. Behav.* 19:695-706.
- Smith, J. N. M. and H. P. A. Sweatman. 1974. Food-searching behavior of titmice in patchy environments. *Ecology* 55:1216-1232.
- Smith, K. 1977. The changing seasons. *Amer. Birds* 31: 292-303.
- Snyder, L. L. 1943. The Snowy Owl migration of 1941-42. *Wilson Bull.* 55:8-10.
- Snyder, L. L. 1947. The Snowy Owl migration of 1945-46. *Wilson Bull.* 59:74-78.
- Snyder, L. L. 1949. The Snowy Owl migration of 1946-47. *Wilson Bull.* 61:99-102.
- Snyder, N. F. R. and J. W. Wiley. 1976. Sexual size dimorphism in hawks and owls of North America. *Ornithol. Monogr.* No. 20.
- Southern, H. N. 1970. The natural control of a population of Tawny Owls (Strix aluco). *J. Zool.* 162:197-285.
- Southern H. N. and V. P. W. Lowe. 1968. The pattern of distribution of prey and predation in Tawny Owl territories. *J. Anim. Ecol.* 37:75-97.
- Sparrowe, R. D. 1972. Prey-catching behavior in the Sparrow Hawk. *J. Wildl. Mgmt.* 36:297-308.
- Stefansson, O. 1979. Lappugglan Strix nebulosa i Norrbotten 1975-78. *Vår Fågelvärld* 38:11-22.
- Stenger, J. 1958. Food habits and available food of ovenbirds in relation to territory size. *Auk* 75: 335-346.
- Stewart, P. A. 1969. Movements, population fluctuations, and mortality among Great Horned Owls. *Wilson Bull.* 81:155-162.
- Stoner, D. 1943. The 1941-42 Snowy Owl incursion in New York State. *Bird-Banding* 14:116-127.

- Stresemann, E. and V. Stresemann. 1966. Die Mauser der Vogel. J. Ornithol. 107:1-445.
- Sutton, G. M. 1932. The birds of Southampton Island. Mem. Carnegie Mus. Vol. 12 Part 2., pp. 3-267.
- Sutton, G. M. and D. F. Parmelee. 1956. Breeding of the Snowy Owl in southeastern Baffin Island. Condor 58:273-282.
- Svårdson, G. 1949. Competition and habitat selection in birds. Oikos 1:156-174.
- Svårdson, G. 1955. Crossbills in Sweden in 1953. Brit. Birds 48:425-428.
- Svårdson, G. 1957. The "invasion" type of bird migration. Brit. Birds 50:314-343.
- Tarboton, W. R. 1978. Hunting and the energy budget of the Black-shouldered Kite. Condor 80:88-91.
- Taverner, P. A. 1928. Birds of western Canada. Natl. Mus. Can. Bull. No. 41.
- Taylor, P. S. 1974. Breeding behavior of the Snowy Owl. Living Bird 12:137-154.
- Thompson, D. Q. 1965. Food preferences of the Meadow Vole (Microtus pennsylvanicus) in relation to habitat affinities. Amer. Midl. Natur. 74:76-86.
- Thomson, A. Landsborough. (ed.). 1964. A New Dictionary of Birds. McGraw-Hill Book Co., New York.
- Thorpe, W. H. 1945. The evolutionary significance of habitat selection. J. Anim. Ecol. 14:67-70.
- Tinbergen, L. 1946. De Sperwer als roofvijand van Zangvogels. Ardea 34:1-213.
- Tinbergen, N. 1939. The behaviour of the Snow Bunting in spring. Trans. Linn. Soc. N. Y. 5:1-94.
- Tucker, V. A. 1974. Energetics of natural avian flight. In R. A. Paynter, ed. Avian Energetics. Publ. Nutt. Orn. Club. No. 15. Pp. 298-333.

- Tullock, G. 1970. The coal tit as a careful shopper. Amer. Natur. 105:77-80.
- Tullock, R. J. 1968. Snowy Owls breeding in Shetland in 1967. Brit. Birds 61:119-132.
- Tullock, R. J. 1969. Snowy Owls breeding in Shetland. Scottish Birds 5:244-257.
- Verner, J. 1965. Time budget of the male Long-billed Marsh Wren during the breeding season. Condor 67:125-139.
- Wakeley, J. S. 1978. Factors affecting the use of hunting sites by Ferruginous Hawks. Condor 80:316-326.
- Walker, L. W. 1974. The Book of Owls. Alfred A. Knopf Inc., New York.
- Watson, A. 1956. Ecological notes on the lemmings Lemmus and Dicrostonyx in Baffin Island. J. Anim. Ecol. 25:289-302.
- Watson, A. 1957. The behaviour, breeding and food ecology of the Snowy Owl. Ibis 99:419-462.
- Weir, R. D. 1973. Snowy Owl invasion on Wolfe Island, winter 1971-72. Ontario Field Biol. 27:3-17.
- Weir, R. D. 1974. Snowy Owl. Can. Wildl. Serv., Hinterland Who's Who.
- Welty, J. C. 1975. The Life of Birds. Second edn. W. B. Saunders Co., Toronto.
- Westerskov, K. 1966. Winter food and feeding habits of the Partridge (Perdix perdix) in the Canadian prairies. Can. J. Zool. 44:303-322.
- Wilds, C. P. 1978. The changing seasons. Amer. Birds 32:313-320.
- Witherby, H. F. (ed.). 1943. The Handbook of British Birds. H. F. and G. Witherby Ltd., London.

- Young, C. M. 1972. The Snowy Owl migration of 1971-72 in the Sudbury region of Ontario. Amer. Birds 27:11-12.
- Zach, R. and J. B. Falls. 1976. Ovenbird (Aves: Parulidae) hunting behavior in a patchy environment: an experimental study. Can. J. Zool. 54:1863-1879.
- Zahavi, A. 1971. The social behaviour of the White Wag-tail, Motacilla alba alba wintering in Israel. Ibis 113:203-211.
- Zar, J. H. 1974. Biostatistical Analysis. Prentice-Hall, Inc., Engelwood Cliffs, N. J.
- Zimmerman, E. G. 1965. A comparison of habitat and food of two species of Microtus. J. Mammal. 46:605-612.