National Library
of Canada

Bibliothèque nationale
du Canada

Canadian Theses Service

Services des thèses canadiennes

Ottawa, Canada
K1A 0N4

CANADIAN THESES

THÈSES CANADIENNES

NOTICE

The quality of this microfiche is heavily dependent upon the quality of the original thesis submitted for microfilming. Every effort has been made to ensure the highest quality of reproduction possible.

If pages are missing, contact the university which granted the degree.

Some pages may have indistinct print especially if the original pages were typed with a poor typewriter ribbon or if the university sent us an inferior photocopy.

Previously copyrighted materials (journal articles, published tests, etc.) are not filmed.

Reproduction in full or in part of this film is governed by the Canadian Copyright Act, R.S.C. 1970, c. C-30.

AVIS

La qualité de cette microfiche dépend grandement de la qualité de la thèse soumise au microfilmage. Nous avons tout fait pour assurer une qualité supérieure de reproduction.

S'il manque des pages, veuillez communiquer avec l'université qui a conféré le grade.

La qualité d'impression de certaines pages peut laisser à désirer, surtout si les pages originales ont été dactylographiées à l'aide d'un ruban usé ou si l'université nous a fait parvenir une photocopie de qualité inférieure.

Les documents qui font déjà l'objet d'un droit d'auteur (articles de revue, examens publiés, etc.) ne sont pas microfilmés.

La reproduction, même partielle, de ce microfilm est soumise à la Loi canadienne sur le droit d'auteur, SRC 1970, c. C-30.

THIS DISSERTATION
HAS BEEN MICROFILMED
EXACTLY AS RECEIVED

LA THÈSE A ÉTÉ
MICROFILMÉE TELLE QUE
NOUS L'AVONS REÇUE

Canadä

NL-339 (r.86/06)

THE UNIVERSITY OF ALBERTA

ASPECTS OF THE ECOLOGY, FOOD HABITS AND FORAGING CHARACTERISTICS OF GYRFALCONS IN THE CENTRAL CANADIAN ARCTIC

by

KIM GORDON POOLE

A THESIS
SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH
IN PARTIAL FULFILMENT OF THE REQUIREMENT FOR THE DEGREE
OF MASTER OF SCIENCE

DEPARTMENT OF ZOOLOGY

EDMONTON, ALBERTA

SPRING 1987

ISBN 0-315-37788-7

THE UNIVERSITY OF ALBERTA

RELEASE FORM

NAME OF AUTHOR: KIM GORDON POOLE

TITLE OF THESIS: ASPECTS OF THE ECOLOGY, FOOD HABITS AND FORAGING CHARACTERISTICS OF GYRFALCONS IN THE CENTRAL CANADIAN ARCTIC

DEGREE FOR WHICH THESIS WAS PRESENTED: MASTER OF SCIENCE

YEAR THIS DEGREE GRANTED: SPRING 1987

Permission is hereby granted to THE UNIVERSITY OF ALBERTA LIBRARY to reproduce single copies of this thesis and to lend or sell such copies for private, scholarly or scientific research purposes only.

The author reserves other publication rights, and neither the thesis nor extensive extracts from it may be printed or otherwise reproduced without the author's written permission.

(SIGNED) Kim G. Poole

PERMANENT ADDRESS:

4814 Matonabee St.
Yellowknife, N.W.T.
X1A 2H4

DATED 27 Jan. 1987

THE UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled Aspects of the Ecology, Food Habits and Foraging Characteristics of Gyrfalcons in the Central Canadian Arctic submitted by Kim G. Poole in partial fulfilment of the requirements for the degree of Master of Science.

....

Supervisor

....

....

....

W. G. Evans..

....

Date....Jan 27/87.........

Abstract

A population of breeding gyrfalcons (Falco rusticolus), studied from 1982 to 1986 on a 2,000 km^2 study area in the central arctic of the Northwest Territories, occupied 14 to 18 territories each year. The mean internest distance was 10.6 km, giving a density that approaches the highest recorded. There was a tendency for regularity in spacing of territories. Most (85%) nests were in abandoned stick nests of ravens (Corvus corax) or golden eagles (Aquila chrysaetos). Mean size of clutch (±SD) was 3.80±0.52, of brood was 2.53±0.89, and mean productivity was 1.50±1.43 fledged young. Reproductive success declined with increased severity of spring weather.

Three prey species (rock ptarmigan (Lagopus mutus), arctic ground squirrel (Spermophilus parryii) and arctic hare (Lepus arcticus)) accounted for 96.5% of the total prey biomass identified. Gyrfalcons responded functionally to the varying availability of prey. Ptarmigan and hares were taken in May and June of all years (98.2% biomass). About 1 July, when nestling gyrfalcons were growing rapidly, juvenile ground squirrels emerged and vulnerability of ptarmigan appeared to decline. Squirrels were used extensively in July and August of 1984 and 1985, but in 1986 there was a nearly complete failure of squirrel production, and ptarmigan continued to be the dominant prey species throughout the summer. Spring counts suggested densities of breeding ptarmigan were relatively constant during the study. Mean weight of prey taken by male gyrfalcons (250 g) was significantly less than prey captured by females (330 g). As predicted by optimal foraging theory, larger prey items, on average, were brought to the nest as foraging time away from the nest increased.

Brood size was manipulated at two gyrfalcon nests in 1986. The parent birds responded to altered brood size by compensatory changes in total prey biomass fed to the nestlings, suggesting that food was not limiting brood size. Conditions of food abundance were also observed at nests of unmanipulated broods, indicating that food was not limiting during the nestling period. I suggest that spacing of pairs was set during courtship and prelaying when food was most likely to be limiting. Courtship and prelaying coincided with the yearly low in prey availability and a period when the male was doing most of the hunting for himself and the female. The observation that most pairs did not initiate laying until after the spring arrival of migrating ptarmigan is consistent with this conclusion.

Acknowledgements

The majority of funding and logistical support for this research came from the Department of Renewable Resources, Government of the N.W.T., and the Boreal Institute for Northern Studies through their Northern Science Training Grant and Grant-in-Aid for Northern Research. Additional support was provided by the Canadian Wildlife Service, the Arctic Institute of North America, the Science Advisory Board of the N.W.T. (summer student program), the Polar Continental Shelf Project, the Canadian Broadcasting Corporation in Yellowknife, and the Max and Marjorie Ward Scholarship. This study was carried out while I was on Education Leave from the Government of the N.W.T., and I thank the Departments of Education and Renewable Resources for their support.

Assistance from Renewable Resources staff in Cambridge Bay was invaluable; the project could not have continued without them. Thanks go to the Regional Biologists K. Jingfors (1984) and Dr. A. Gunn (1985-86), and to M. Aneroluk, G. Arlooktoo, R. Binne, L. Jones, and D. Kaomoyok. Field assistance was provided primarily by C. Adjun, Dr. R.G. Bromley, T. Kinley, K. Lambert, N. MacLean, B. Powers, P. Rivard and D. Stern, and I thank them and others for their interest and companionship. Special thanks go to Bobby Kingnektak who was my friend and assistant for most of the project. Bobby introduced me to the Kilgavik area and its wildlife, and taught me to travel safely and comfortably. Doris Kaotaluk, Bobby's wife, cheerfully assisted at camp; her tea and hot meals were especially welcome after long, cold days "in the saddle".

Work on gyrfalcons at Kilgavik was begun in 1982 and 1983 by Dr. R.G. (Bob) Bromley, and I am grateful for the use of his data. I owe special thanks to Bob for assistance and encouragement throughout all

phases of this research. Identification of insects collected at Kilgavik was provided by Dr. G.F. Bennett (Memorial University) and Dr. R.E. Lewis (Iowa State University). Fellow graduate student G. Court and Dr. W.B. McGillivray (Alberta Provincial Musuem) helped identify species of birds from prey remains. Staff of the Canadian Wildlife Service in Edmonton - R. Fyfe and U. Banasch, and Wainwright - P. Trefry, H. Trefry, and H. Armbruster, provided ideas and advice on many aspects of the project.

I sincerely thank Dr. D.A. Boag, my supervisor, whose support, encouragement, criticisms and speedy reviews greatly facilitated the planning of field work and thesis preparation. I also thank the members of my supervisory committee, Drs. W.G. Evans, S.J. Hannon, J.R. Spence, W.M. Tonn (all University of Alberta), and Dr. R.G. Bromley (N.W.T. Renewable Resources), for comments and criticisms throughout the research period.

I thank fellow graduate students at the University of Alberta for assistance on statistical procedures and use of the computer facilities. G. Court provided a welcome sounding board for stimulating discussions on all aspects of raptor ecology. Reviews of drafts of this thesis were provided by Dr. D.A. Boag, Dr. R.G. Bromley, Dr. C.C. Shank, and L. Wakelyn, and I am grateful for their helpful suggestions.

Lastly, I would like to acknowledge my parents, who from the beginning encouraged my interest in the outdoors. Special appreciations go to Louise, my wife, for her patience and encouragement throughout the fieldwork and preparation of this thesis, and for understanding why I spent as much time as I did with the gyrfalcons of Kilgavik.

Table of Contents

List of Tables

List of Figures

I. INTRODUCTION

> "...the Jerfalcon...is well calculated, from the whiteness of its plumage, for traversing a snowy waste, without alarming the birds on which it preys."
>
> Sir John Richardson, Point Lake, N.W.T., June 1821

The gyrfalcon (Falco rusticolus) is the largest of the falcons, a predator superbly adapted for life in arctic regions. It has for centuries been held in high esteem by falconers, resulting in many early recordings of observational accounts of the species (summarized in Dement'ev 1960, Cade 1968). As interest shifted in the past 50 years from the falconer's fascination to a more scientific approach, workers have examined some aspects of its ecology, primarily those involving distribution and food habits (e.g., Kishchinskii 1957, Cade 1960, Bengtson 1971, Roseneau 1972, Pulliainen 1975, Langvatn and Moksnes 1979, Barichello 1983, Burnham and Mattox 1984, Nielsen 1986). Interest in captive propagation increased our understanding of the breeding biology of the species (Platt 1977, Wrege and Cade 1977). More recently, research during winter and early spring has provided descriptions of the behaviour of wild gyrfalcons during courtship and the establishment of territories (Platt 1976, 1977, Woodin 1980, Nielsen 1986).

Despite the gyrfalcon's Holarctic distribution and the number of studies undertaken, surprisingly little is known about its basic biology. For example, it was only within the past 10 years that the incubation period for gyrfalcons was determined to be about 35 days, not 28 or 29 days as believed previously (Platt 1977, Cade 1982). The difficulty of obtaining even such basic information is understandable given the distribution and population density of the species. The vast majority of the breeding range of gyrfalcons lies north of 60°N in remote arctic and subarctic environments, making research logistically difficult and expensive. Even in undisturbed populations the distance between nest sites in high density areas is rarely less than 10 km (Cade 1982). Thus, many studies have dealt with few nesting pairs for short periods of time, often only during the period from late incubation to fledging of young. Consequently, much remains to be learned about the ecology of gyrfalcons throughout their range.

The gyrfalcon breeds across the Northwest Territories (N.W.T.), in suitable arctic and alpine tundra habitat (Cade 1982). Interest in gyrfalcons in the N.W.T. increased early in the 1980s as a result of attempts to develop a commercial harvest for the Inuit to supply wild-captured birds to meet world demands (see Bromley 1983 for a review). Studies by the Department of Renewable Resources, Government of the N.W.T., begun in 1982, attempted to gather baseline-information on distribution and abundance of the species. These efforts consisted primarily of annual surveys by helicopter of nesting populations in selected areas of the N.W.T. (Bromley 1983, Bromley and McLean 1986). In reviews of the current literature it was apparent that many aspects of the ecology of the species in the N.W.T. were poorly understood, and that in order to control and justify harvest levels there was a need for an understanding of the biological factors affecting the productivity of the population. The relationship between predator and prey, and the foraging attributes of the species, so important in determining density and productivity of all breeding raptors (Newton ~~1979~~), was one subject for which little information was available.

Between 1984 and 1986, I was able to study a poorly known population of gyrfalcons nesting on the Kilgavik study area in the central Canadian arctic. Kilgavik is a local Inuit word meaning falcon. The problems inherent in studying a species breeding at a naturally low density were partially offset by proximity of logistical support at Cambridge Bay, 140 km from the centre of the study area, and the relative ease of travel within the study area itself. The study concentrated initially on documenting the natural history of the population (Poole and Bromley 1985). I continued these preliminary studies, but changed the emphasis. The primary objectives became an assessment of the food habits and foraging strategies of nesting gyrfalcons, and their response to natural changes in prey availability and to artificial changes in prey demand through brood manipulation. I examined how fluctuations in the availability of prey throughout the gyrfalcon's lengthy breeding season affected the productivity of the population, and how the pairs coped with these fluctuations in the prey base. Manipulation of brood size in a two nests in the final year of research enabled a preliminary examination of the effect of brood size on foraging characteristics in gyrfalcons. The results are presented in three chapters addressing the following: 1) Natural history of the gyrfalcon in the central Canadian arctic, 2) Food habits and foraging characteristics of gyrfalcons at Kilgavik, Northwest Territories, and 3) Foraging responses by gyrfalcons to manipulations of brood size.

Literature Cited

Barichello, N. 1983. Selection of nest sites by gyrfalcons (Falco rusticolus). Unpubl. M.Sc. thesis, Univ. of B.C., Vancouver.

Bengtson, S.-A. 1971. Hunting methods and choice of prey of gyrfalcons Falco rusticolus at Myvatn in northeast Iceland. Ibis 113:468-476.

Bromley, R.G. 1983. 1982 raptor survey. N.W.T. Dept. Ren. Res. File Rep. No. 35, Yellowknife.

Bromley, R.G., and B.D. McLean. 1986. Raptor surveys in the Kitikmeot and Baffin Regions, Northwest Territories, 1983 and 1984. N.W.T. Dept. Ren. Res. File Rep. No. 65, Yellowknife.

Burnham, W.A., and W.G. Mattox. 1984. Biology of the peregrine and gyrfalcon in Greenland. Meddel. om Grønland, Bioscience 14:1-25.

Cade, T.J. 1960. Ecology of the peregrine and gyrfalcon populations in Alaska. Univ. Calif. Publ. Zool. 63:151-290.

Cade, T.J. 1968. The gyrfalcon and falconry. Living Bird 7:237-240.

Cade, T.J. 1982. The Falcons of the World. Cornell Univ. Press, Ithaca, N.Y.

Dement'ev, G.P. 1960. The Gyrfalcon (Trans. from Russian). Franch'sche Verlangshandlung, Stuttgart.

Kishchinskii, A.A. 1957. On the biology of the gyrfalcon (Falco gyrfalco gyrfalco) in the Kola Peninsula. Ornithologiia (U.S.S.R.) 1:1-31.

Langvatn, R., and A. Moksnes. 1979. On the breeding ecology of the gyrfalcon Falco rusticolus in central Norway. Fauna Norv. Ser. C, Cinclus 2:27-39.

Newton, I. 1979. Population Ecology of Raptors. Buteo Books, Vermillion, S. Dakota.

Nielsen, Ó.K. 1986. Population ecology of the gyrfalcon in Iceland, with comparative notes on the merlin and the raven. Unpubl. Ph.D. thesis, Cornell Univ., Ithaca, N.Y.

Platt, J.B. 1976. Gyrfalcon nest site selection and winter activity in the western Canadian arctic. Can. Field-Nat. 90:338-345.

Platt, J.B. 1977. The breeding behavior of wild and captive gyrfalcons in relation to their environment and human disturbance. Unpubl. Ph.D. thesis, Cornell Univ., Ithaca, N.Y.

Poole, K.G., and R.G. Bromley. 1985. Aspects of the ecology of the gyrfalcon in the central arctic, Northwest Territories, 1983 and 1984. N.W.T. Dept. Ren. Res. File Rep. No. 52, Yellowknife.

Pulliainen, E. 1975. Choice of prey by a pair of gyrfalcons *Falco rusticolus* during the nestling period in Forest-Lapland. Ornis Fenn. 52:19-22.

Roseneau, D.G. 1972. Summer distribution, numbers, and food habits of the gyrfalcon (*Falco rusticolus* L.) on the Seward Peninsula, Alaska. Unpubl. M.Sc. thesis, Univ. Alaska, College, Alaska.

Woodin, N. 1980. Observations on gyrfalcons (*Falco rusticolus*) breeding near Lake Myvatn, Iceland, 1967. Raptor Research 14:97-124.

Wrege, P.H., and T.J. Cade. 1977. Courtship behavior of large falcons in captivity. Raptor Research 11:1-27.

II. NATURAL HISTORY OF THE GYRFALCON IN THE CENTRAL CANADIAN ARCTIC

Introduction

Aspects of the natural history of gyrfalcons (*Falco rusticolus*) have been described for populations in many locations over the vast range of the species. Gyrfalcons have been studied in the Palearctic from the U.S.S.R. (Kishchinskii 1957, Dement'ev 1960), through Scandinavia (Hagen 1952, Pulliainen 1975, Langvatn and Moksnes 1979) to Iceland (Bengtson 1971, Nielsen 1986). Major efforts have been made to examine the distribution and some aspects of the biology of the species in Greenland (Jenkins 1974, Burnham and Mattox 1984), and in North America, including Alaska (Cade 1960, Roseneau 1972), the Yukon (Platt 1976, 1977, Mossop 1980, Barichello 1983) and portions of the Northwest Territories (N.W.T.) (Bromley 1983, Poole and Bromley 1985, Bromley and McLean 1986).

The N.W.T. contains enormous expanses of potentially excellent gyrfalcon habitat (Cade 1982), yet only in recent years have basic distributional studies been undertaken (Bromley 1983, Bromley and McLean 1986). Prior to 1980 studies were local in nature, of short duration, or were ancillary to other research objectives. Some information is available from the Thelon River area of central N.W.T. (Kuyt 1980), the western arctic along the Anderson River (R. Fyfe pers. comm.), Ellesmere Island (Muir 1975) and Wager Bay, northwest of Hudson Bay (Calef and Heard 1979). Yet little is known thus far about the basic ecology of the species in the N.W.T.

From 1984 to 1986 I examined a high density population of gyrfalcons at the Kilgavik study area in the central Canadian arctic.

Research on the study area was initiated in 1982 (Bromley 1983). Relative ease of access enabled a number of sites to be monitored regularly throughout the breeding season. The study was situated many hundreds of kilometres from previous sites of gyrfalcon research, in an area within which the ecological relationships differed from those at other major study sites in North America and Iceland.

Many facets of the ecology of the species were examined from prelaying to fledging during three breeding seasons, including distribution and density of breeding birds, food habits, nest site selection, breeding biology and behaviour, causes of egg and nestling mortality, and productivity. Information was also gathered on sympatric nesting raptors at Kilgavik, including the golden eagle (Aquila chrysaetos), tundra peregrine falcon (Falco peregrinus tundrius) and rough-legged hawk (Buteo lagopus), as well as the common raven (Corvus corax), which can be considered a functional raptor (White and Cade 1971). The aim of this first chapter is to describe the natural history of the gyrfalcon in a previously unstudied region. This will provide a framework within which to interpret the ecological questions examined in the subsequent chapters of this thesis.

Study Area

The study area encompasses approximately 2,000 km^2 of rugged tundra on the N.W.T. mainland east of Bathurst Inlet, centred at about 68°10'N and 106°15'W (Fig. 2.1). The area lies within 20 km of the coast along the southeast side of Melville Sound and Elu Inlet, and includes some islands in these water bodies. The boundaries of the study area were determined mainly by geological features; in all directions except

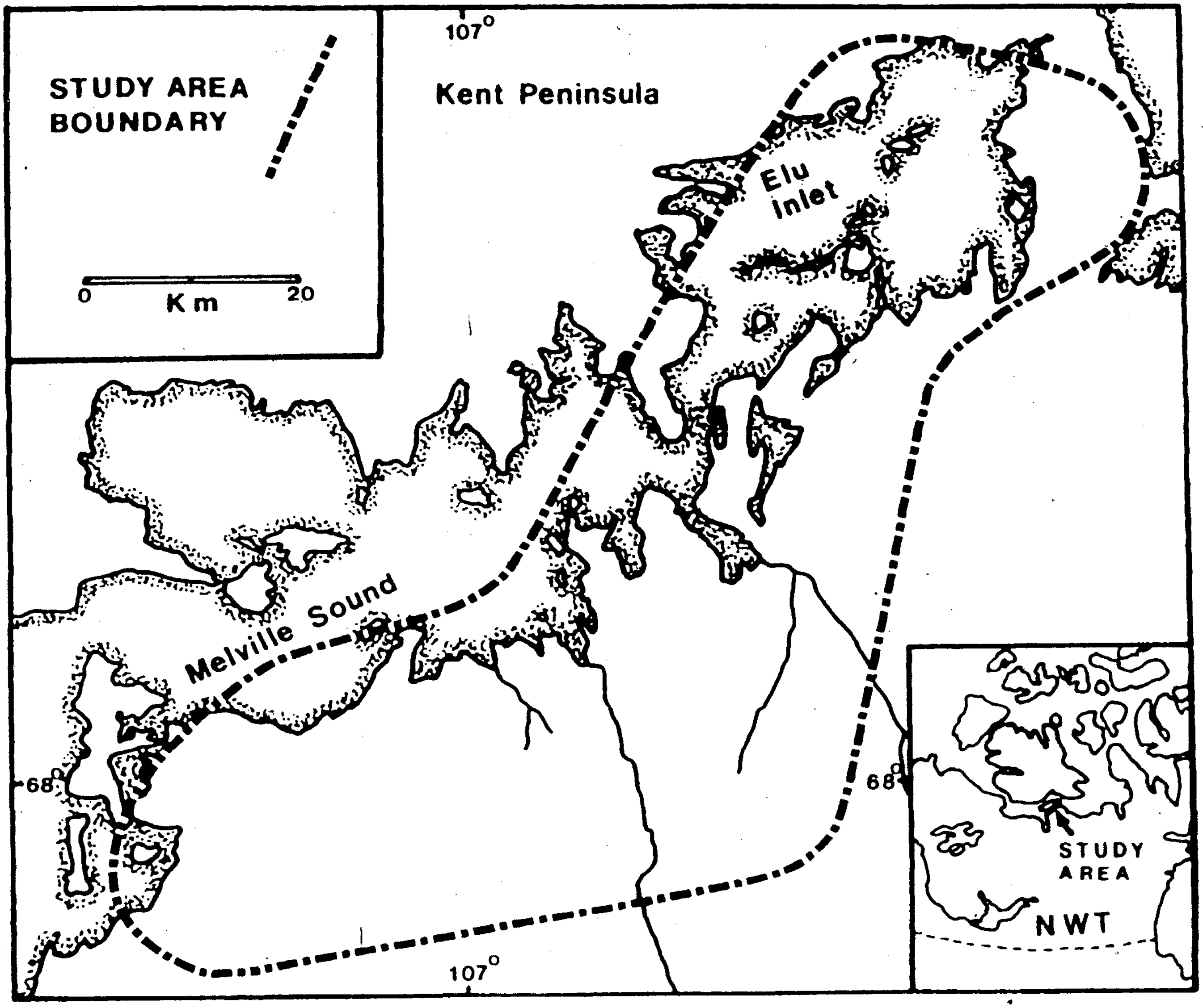

Figure 2.1 Kilgavik study area, N.W.T.

southwest towards Bathurst Inlet, rock formations that could support cliff-nesting raptors diminish and the tundra topography becomes rolling or flat.

Granitic intrusions and diabase dykes and sills form the main geological features of the area (Fraser 1964). The diabase formations, lines of cliffs or circular blocks of rock rising above the surrounding terrain, provide nesting ledges facing in most directions. Elevations range from sea level to 375 m, with the highest elevations attained in the southwestern section of the study area.

The flora consists of wide-ranging, low-arctic tundra species (Porsild and Cody 1980). *Carex* spp., cotton-grass (*Eriophorum* spp.), lichens and mosses predominate in moist areas. Willows (*Salix* spp.), birch (*Betula* sp.), Labrador tea (*Ledum palustre*), crowberry (*Empetrum nigrum*) and bell heather (*Cassiope tetragona*) are the dominant vascular plants. Fifty-three species of birds and 17 species of mammals were recorded on the study area (see Appendix 1). There are no permanent human inhabitants, although local Inuit sporadically hunt, fish and trap in the region during the winter.

The climate is cold and dry, with January and July mean daily maximum temperatures of -30° and 10°C, respectively; precipitation varies from 100 to 150 mm annually (Maxwell 1980). The land is snow-covered for about 260 days of the year with snow-melt usually beginning in mid- to late May. Sea ice usually persists until the second or third week of July. Weather data from Cambridge Bay, 140 km northeast of the centre of the study area, were used to examine the effects of late winter-early spring conditions on the chronology of the gyrfalcon annual cycle. While the Kilgavik region experiences on average slightly warmer conditions than Cambridge Bay, weather systems appear to affect both areas similarly.

Methods

Surveys for raptors at Kilgavik were initiated in July 1982 by personnel of the Department of Renewable Resources, Government of the N.W.T., as part of a program to determine densities of breeding raptors, primarily gyrfalcons, at various locations across the N.W.T. (Bromley 1983, unpubl. data). Intensive studies of gyrfalcons at Kilgavik began in the spring of 1983 (Poole and Bromley 1985). Because the researchers were unfamiliar with the area and no spring surveys were undertaken in 1982, I do not include these data in all analyses. I conducted research at Kilgavik in May and the first 2 weeks of July and August of 1984, and from early May to early to mid-August, 1985 and 1986. A week was spent on the study area in late March and early April 1986 to observe winter territory occupancy and prey abundance.

The terminology relating to nesting activity is as follows:

Territory - an area containing one or more nest sites within the range of a pair of actual or potential breeders (Postupalsky 1974).

Nest site - the actual site of the nest. More than one nest site may be present within one territory, being used in different years. Nest sites within 3 km of each other are considered alternatives, unless evidence indicates separate territories.

Occupied territory or nest site - a territory or nest site where a single bird or a pair of birds is present at some time during the breeding season, although eggs may not be present. The presence of eggs may be inferred by a bird in incubation posture on the nest.

Productive territory - a territory within which a minimum of one chick is raised to an advanced stage of development (at least 25 days of age) and is known or assumed to have fledged.

Production - the total number of young fledged or raised to an advanced stage of development from all productive territories.

Productivity - expressed as the mean number of known or assumed fledged young per occupied territory.

Snowmobile surveys were conducted each spring until snow-melt prevented such travel, usually in early to mid-June. Previously located raptor nest sites were surveyed, and all cliffs capable of supporting raptors were systematically examined to locate new sites. Most sites were surveyed at least twice in the spring and often more frequently; thus the probability of missing birds that were actually on territory during prelaying and early incubation was negligible. No new territories were discovered during July helicopter surveys in areas that had been examined by snowmobile, lending support to the conclusion that the spring surveys were thorough. Arrival dates of all migrants were noted, as well as other indices of spring phenology, such as the date when 50% of the land was clear of snow cover. Prey densities, primarily breeding rock ptarmigan (<u>Lagopus mutus</u>), were assessed, and will be discussed in Chapter 3. Use of 'ptarmigan' in this report refers to <u>L. mutus</u> unless specified otherwise.

To determine the chronology of the gyrfalcon breeding cycle the following assumptions were made: the laying interval was 48 hours (P. Trefry pers. comm.); incubation began with the penultimate egg (Platt 1977); clutch size was three unless there was evidence of four eggs or young; the incubation period was 35 days (Cade and Weaver 1976); and the fledging period was 47 days (Jenkins 1974, this chapter). Hatch date was observed (three sites in 1985, four sites in 1986) or calculated by back-dating from the estimated age of nestlings. The growth of 20 known-age chicks was measured throughout the nestling period, greatly increasing the accuracy of age estimation.

After the termination of snowmobile travel, access to sites was made by foot, by helicopter (Bell 206B Jet Ranger), and by boat along the coast following the breakup of the sea ice in July. From 12 to 16 hours of helicopter flying time were used each July to systematically survey the study area, visit all gyrfalcon sites, and band nestlings. Young gyrfalcons were fitted with a standard U.S. Fish and Wildlife Service lock-on band on the right tarsus. A blue anodized band was riveted around the left tarsus. Weight and a series of morphometric measurements (length of wing chord, seventh primary, one of the central rectrices, and total tarsus) were taken from each nestling. Notes were taken on the nature of the nest substrate (ledge, old or new stick nest; identity of builder), nest aspect, percent overhang above nest, and nest and cliff height from bottom (details in Barichello 1983).

Four adults were captured in the spring using standard trapping techniques (R. Bromley pers. comm.). The adults were handled in the same manner as the nestlings, but with the numbered band placed on the left tarsus and a larger blue band, marked with a three digit alpha-numeric code, fitted to the right tarsus.

Nest sites were observed for periods of from 1 to 10 hours throughout the field seasons to document feeding habits (Chapter 3) and nesting behaviour. Observation distances ranged from 200 to 400 m; 7x binoculars and 20x spotting scopes were used. Gyrfalcons appeared to habituate rapidly to the presence of observers at these distances. Observation time totaled 170 hours in 1984, 398 hours in 1985 and 233 hours in 1986.

Time-lapse cameras have been used successfully by other researchers to obtain data on the biology of gyrfalcons (Jenkins 1978, N. Barichello pers. comm.) and peregrines (Enderson et al. 1973, Court 1986). To record activities at the nest, I also used time-lapse 8 mm movie cameras (Temple 1972), which were set up at three gyrfalcon nest sites in 1985 and four in 1986. The units exposed one frame every 3 minutes, providing a sampled documentation of behaviour at the nest. Each roll of film provided 1 week of coverage. A frame interval of 6 or 9 minutes was selected in instances where access to the site was not possible on a weekly basis, such as during spring thaw. The films were analyzed in an 8 mm film editor (MKM Industries, Inc. Model 824). Of over 118,000 exposed frames, 3.1% were unusable because of darkness or inclement weather. Unit malfunction caused the loss of 2 weeks of film, and exposure problems prevented midday analysis of some rolls of film from one site in 1985, eliminating 37% of the frames exposed at that site.

To determine the density of nesting pairs, I calculated the average distance between each nest site of occupied territories (mean internest distance; Ratcliffe 1980), such that no distance was measured twice (i.e., 15 distances from 16 sites). As a second method, I used the mean internest distance as the radius for a circle of territorial influence, drawn around the outermost nesting pairs, to provide a hypothetical boundary to the study population (Ratcliffe 1980). Although the latter method enabled density to be expressed as pairs per unit area, it may not have been appropriate in this case because of the naturally great internest distances in gyrfalcon populations, and the large amount of water incorporated in areas situated along coast lines. Both calculations will be provided for completeness.

The GMASD test (geometric mean, arithmetic mean square distance, Brown 1975) was used to evaluate the spatial distribution of gyrfalcon territories each year. Three territories located on islands in Elu Inlet were excluded from calculations. The GMASD test is the geometric mean of all internest distances divided by the arithmetic mean of these distances. GMASD values below 0.65 indicated random distribution; values above 0.65 denoted regular spacing increasing to perfect regularity at a value of 1.0 (Nilsson et al. 1982).

Weather parameters (mean temperature, number of days of snow and total precipitation) from 21 April to 30 May were examined in relation to laying dates, brood size and production of gyrfalcons. These dates cover the period during which weather may have the greatest impact on a breeding pair, from about 2 weeks prior to laying to two thirds through incubation.

Differences among data sets were considered significant when $P \leq 0.05$, unless stated otherwise.

Results

Density

Twenty-one gyrfalcon territories were located during the course of the study, with 14 to 18 occupied each year. The mean internest distance (±SD) between occupied nest sites at Kilgavik ranged from 9.5±5.4 km in 1983 to 11.4±4.3 km in 1985. Actual nearest neighbour distances ranged from 1.0 to 20.0 km. The average mean internest distance from 1983 to 1986, 10.6 km, was used to calculate a study area size of 4,450 km^2 by Ratcliffe's (1980) method. Approximately 1,350 km^2 of ocean were included in the above estimate; its removal reduced the study area to 3,100 km^2. Using this conservative value as the area encompassing the population studied, I calculated a density, for all territories located during the study, of one per 150 km^2, and an annual average of one occupied territory per 190 km^2. Eliminating tracts of land and ocean far (>10 km) from any gyrfalcon nest sites resulted in a study area of 2,000 km^2, and densities of one territory per 95 km^2 for all territories and an annual average of one occupied territory per 125 km^2.

The GMASD values indicated a degree of regularity in territory spacing in the contiguous portion of the study area in most years (1984, GMASD value 0.87; 1985, 0.76; 1986, 0.74), but random spacing in 1983 (0.49). A value of 0.74 was obtained when all territories occupied from 1983 to 1986 were considered.

Nest Sites

Thirty-four different nest sites were used for 59 nesting attempts during the study. Most sites were nests built by ravens (62%) or golden eagles (23%). Two sites (6%) were stick nests of uncertain origin and three sites (9%) were ledges with no stick substrate. During a complete survey of the study area in 1984 (Poole and Bromley 1985), 19 nests built by ravens and 31 built by golden eagles were located, thus selection by gyrfalcons for raven nests was evident (X^2=14.6, $P<0.01$). Some of the nest sites were occupied alternately by gyrfalcons and ravens or golden eagles. Mean brood size of gyrfalcons in nests built by golden eagles was similar to that in nests built by ravens (1.94 versus 2.03, Mann-Whitney Test U=386.0, P=0.77). In several instances freshly built raven nests were usurped by gyrfalcons, forcing the ravens to rebuild elsewhere. I saw no evidence of gyrfalcons taking over nest sites currently occupied by golden eagles.

The mean cliff and nest height of all nesting attempts was 24.5±9.8 m and 12.9±6.5 m, respectively, and ranged from a nest at a height of 4 m on a 16 m cliff, to one 30 m from the base of a 45 m cliff. Mean overhang was 81%, with most nest sites (68%) covered by a complete overhang and only five sites (15%) with less than 50% overhang. Nest sites used by gyrfalcons faced in all directions, with no one direction preferred (X^2=5.06, df=7, P>0.5). The number of nests with a southerly versus northerly aspect was similar, 12 and 13, respectively. Mean brood size (in this case the mean number of young fledged, including sites that failed) differed, with 1.59 young produced on southerly- and 2.35 young on northerly-oriented sites; the difference approached significance (Mann-Whitney Test U=500.0, P=0.08).

Nine sites were located on cliffs adjacent to the ocean, hence nest sites ranged in altitude from near sea level to about 215 m above sea level. Protection from mammalian predators was generally good, with only 10 sites accessible to humans without full climbing gear, and only a few sites likely accessible to mammalian predators such as foxes (Vulpes vulpes and Alopex lagopus) and wolverines (Gulo gulo).

The average number of known alternative nest sites within each territory was 1.7±0.9 and ranged from one to three. Gyrfalcons usually switched nest sites each year, but in some territories the same nest was used year after year. Most alternative sites were located within 1 km of one another on the same cliff or occasionally on adjacent cliffs. The greatest distances between alternatives were 4.8 and 3.2 km, with the alternatives located along linear features, in these cases a valley and a line of cliffs along a lake, respectively. The sites 4.8 km apart were considered alternatives because both sites were never occupied in the same year, and the peculiarities in plumage colour of the pair using the site each year were identical.

Winter Occupancy

All 21 territories were visited during a survey from 28 March to 3 April, 1986. Eight territories had evidence of use (fresh excrement or prey remains and pellets). Gyrfalcons were observed at six of these territories. Lone males were seen at four sites and pairs were observed at two. Probably some birds were missed because of their skittish nature at this time. Of the eight sites occupied in early April, seven were occupied later in the spring (May) and eggs were produced at six sites.

Based on accumulation of excrement relative to snow layering at and below winter roosts (Cade 1960, Platt 1977, Barichello 1983), some gyrfalcons had been present since at least early February, but there was no evidence for continuous occupancy throughout the winter. From similar evidence, ravens had been present at Kilgavik since at least early March, and the first golden eagle was sighted on 2 April.

Spring Phenology

Late winter-early spring weather varied greatly from 1983 to 1986 (Table 2.1). Weather at this time ranged from a cold spring in 1983 which broke eight 40-year daily minimum temperature records for May, to

Table 2.1. Mean temperature, number of days of snow and total precipitation for late April and May, Cambridge Bay, N.W.T., 1983 to 1986.[a]

		1983	1984	1985	1986	40 year mean
21-30 April	T[b]	-19.4	-15.1	-18.5	-17.3	-17.2
	P[c]	2(4)	0(Tr)	2(4)	1(16)	
1-10 May	T	-20.3	-7.5	-10.1	-12.5	-13.3
	P	2(8)	0(Tr)	3(68)	2(13)	
11-20 May	T	-17.2	-6.9	-1.4	-8.8	-10.8
	P	2(6)	0(Tr)	5(32)	1(12)	
21-30 May	T	-8.5	-5.0	-1.6	-7.2	-6.0
	P	3(40)	0(Tr)	5(20)	6(201)	

---

[a] Data from Atmospheric Environment Service, Environment Canada (unpubl.).

[b] Mean temperature (°C).

[c] No. days with precipitation (amount of precipitation in mm).

a warm, dry spring in 1984, with temperatures many degrees above normal. The weather in the spring of 1985 was mild but wet. In 1986 normal temperatures but fierce storms were encountered. The weather in May 1986 was particularly bad, as three major storms, with winds of up to 70 kph and driving rain, freezing rain and snow pellets, battered the area for a total of 9 days. The poor weather in 1986 continued well into June; 50% snow-melt was attained on 2 June in 1983, 15 May in 1984 and 19 May 1985, but because of snow accumulation during storms, not until 18 June in 1986. Although there was a significant difference among years in arrival dates of migrants (Kruskal-Wallis 1-way ANOVA, $X^2=14.9$, $P<0.01$), only 1983, with its extremely low temperatures, was significantly later than the subsequent 3 years (Duncan Multiple Range Test, $P<0.05$).

The Incubation and Nestling Period

There was a significant difference between years in the initiation dates of laying in gyrfalcons during the course of the study (Kruskal-Wallis Test $H=13.0$, $P<0.01$). Median date of clutch initiation was earlier in 1984 and 1986 (Fig. 2.2). No relationship was found between median laying date and weather parameters examined from 21 April to 30 May each year. The spread in laying dates ranged from 6 days in 1985 to 30 days in 1983, with the mean of yearly median laying dates being 8 May. Summing all years, most pairs started laying by 15 May. Hatch dates ranged from 1 to 30 June (mean 15 June), with most young fledged, after a nestling period of about 7 weeks, by late July to early August.

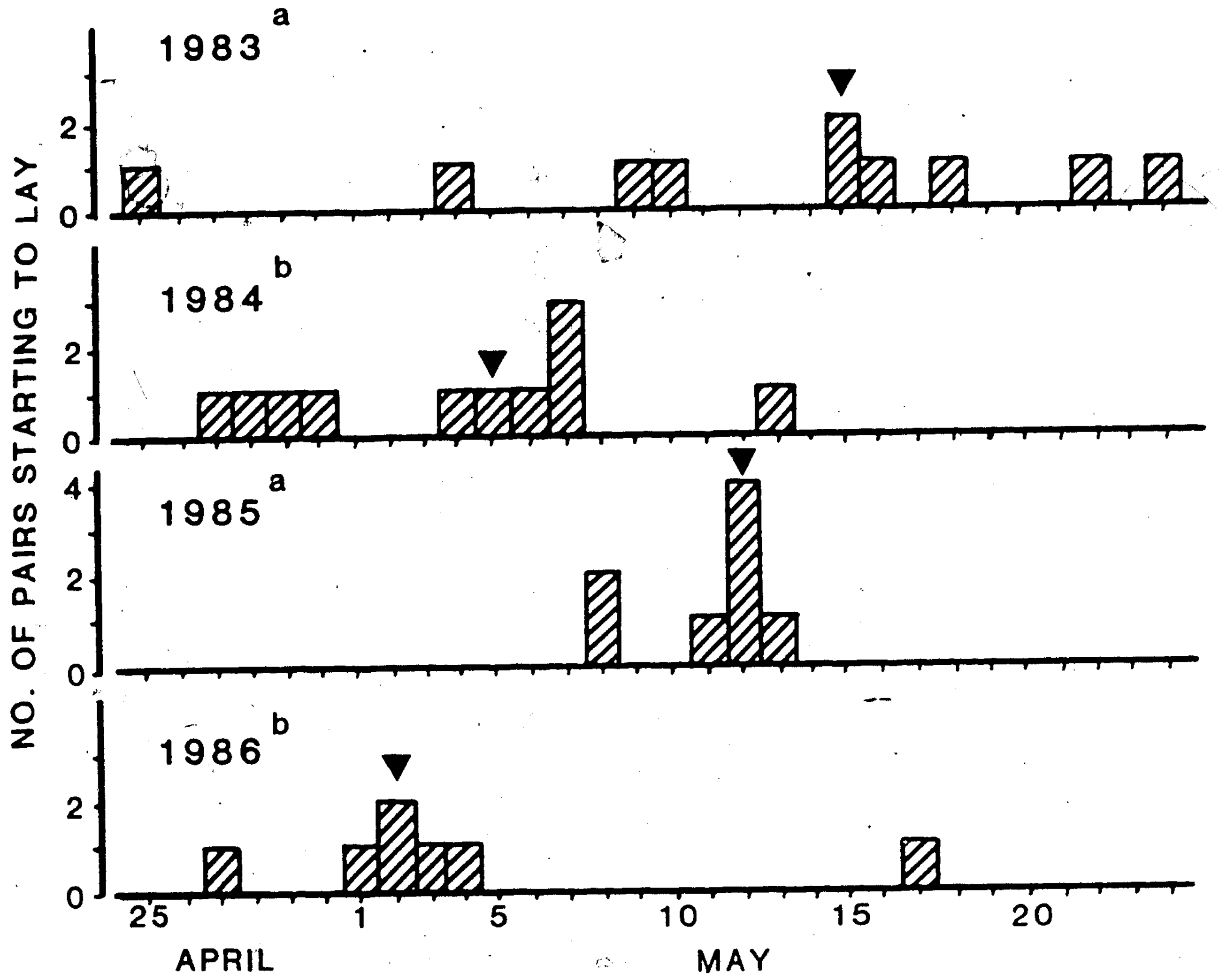

Figure 2.2 Dates of initiation of laying by gyrfalcons at Kilgavik, N.W.T., 1983 to 1986. Triangles indicate median date. Years superscripted with unlike letters differed based on Duncan Multiple Range Test ($P<0.05$).

A mean clutch size of 3.80±0.52 (SD) eggs was obtained for 20 nests over the course of the study (Table 2.2). A clutch of four was by far the most common, found in 85% of nests. Two clutches of three and one of two eggs were also observed. The two-egg clutch may not have been the full compliment. Not included in the above calculations was a renest with a clutch of three (Poole 1987).

Because of within-pair differences between sexes in colour of plumage, it was relatively easy to identify from time-lapse films the sex of the adult incubating or brooding at the nest, even with poor exposure. The colour phase of adults observed each year from 1982 to 1986 approached a 1:1 ratio (63 grey:65 white). Thirty-one (55%) of the 56 pairs observed were composed of adults of different colour. Half (28) of all pairs, including five of the seven nestings under time-lapse monitoring, were grey male:white female pairs. Only 5% of all pairs were white male:grey female pairs, contradicting the generalization made by Cade (1960) that male gyrfalcons tend to be paler than females.

Male participation in incubation varied among pairs. Analysis of time-lapse film from site 112 in 1985 (the only site where cameras were in place prior to hatch) during the last half of incubation showed that the male participated in 26% of the incubation. Summing direct observations from all sites, the male incubated 24% of the time in 1985 (n=119 hours, 3 sites) and 17% in 1986 (n=41 hours, 4 sites).

Of seven sites that were monitored regularly at hatch, six broods hatched within 48 hours, and the seventh in 72 hours. Evidence of greater asynchrony in hatching, based on differences in weight and plumage development, was observed at several sites where there appeared to be a spread of up to 6 days in the estimated age of siblings.

Table 2.2. Breeding success of gyrfalcons on the Kilgavik study area, 1982 to 1986.

	1982	1983	1984	1985	1986	Mean[a]
No. of occupied territories	11	18	15	14	17	16
No. of pairs laying(%)	10(91)	15(83)	12(80)	9(64)	13(76)	12.3(77)
Mean clutch size (no. of nests)	--	3.3(4)	4.0(6)	3.8(5)	4.0(5)	3.80(20)
No. of pairs producing young(%)	9(82)	12(67)	11(73)	9(64)	9(53)	10.3(64)
No. of pairs fledging young(%)	9(82)	11(61)	11(73)	9(64)	7(41)	9.5(59)
Production	--	25	31	20	20	24
No. of young banded	0	22	29	20	20	
Mean brood size, successful pairs	--	2.27	2.82	2.22	2.86	2.53[b]
Productivity	--	1.39	2.07	1.43	1.18	1.50[c]

[a] The 1982 data was not used because the survey was likely incomplete as the researchers were unfamiliar with the area, and no spring surveys were done.

[b] 1-way ANOVA F=1.40 df=3,34 P=0.26

[c] 1-way ANOVA F=1.14 df=3,60 P=0.36

The spread in estimated age of siblings could, however, have been exaggerated somewhat by the slightly retarded growth observed in many last-hatched chicks (Figs. 2.3, 2.4). The rate of weight gain during the linear period of growth (6 to 26 days in males, 6 to 27 days in females) was similar for last-hatched nestlings compared with other chicks (Analysis of Covariance: males F=2.57, P=0.11; females F=0.40, P=0.40), suggesting that weight gain was delayed slightly but not reduced. There was no significant difference in the highest weight attained between last-hatched and other nestlings (t-test: males t=-1.38, P=0.2; females t=0.35, P>0.5).

Nearly continuous brooding (>80% of time-lapse frames each day) took place at most sites until the chicks were 10 to 13 days old, although at one site in 1985 it persisted until the chicks were 19 days old. In 1986, all brooding terminated when the chicks were between 16 and 21 days old; in 1985 some brooding at two sites persisted until 31 and 32 days.

Participation by males in brooding, as analyzed from time-lapse films, ranged from 5 to 25% (mean 13%, n=1142 hours). No relationship between the time spent brooding and such variables as brood size or weather was apparent which might explain the differences in division of brooding by sex among sites. In one pair the male brooded 5.0% of the time in 1985 and 4.8% in 1986, suggesting within-pair consistency in division of brooding.

Fledging dates were obtained for 11 nestlings of known age. Males fledged at 45 to 47 days of age (mean 46.0 days, n=7), and females left the nest 47 to 50 days after hatch (mean 48.3 days, n=4).

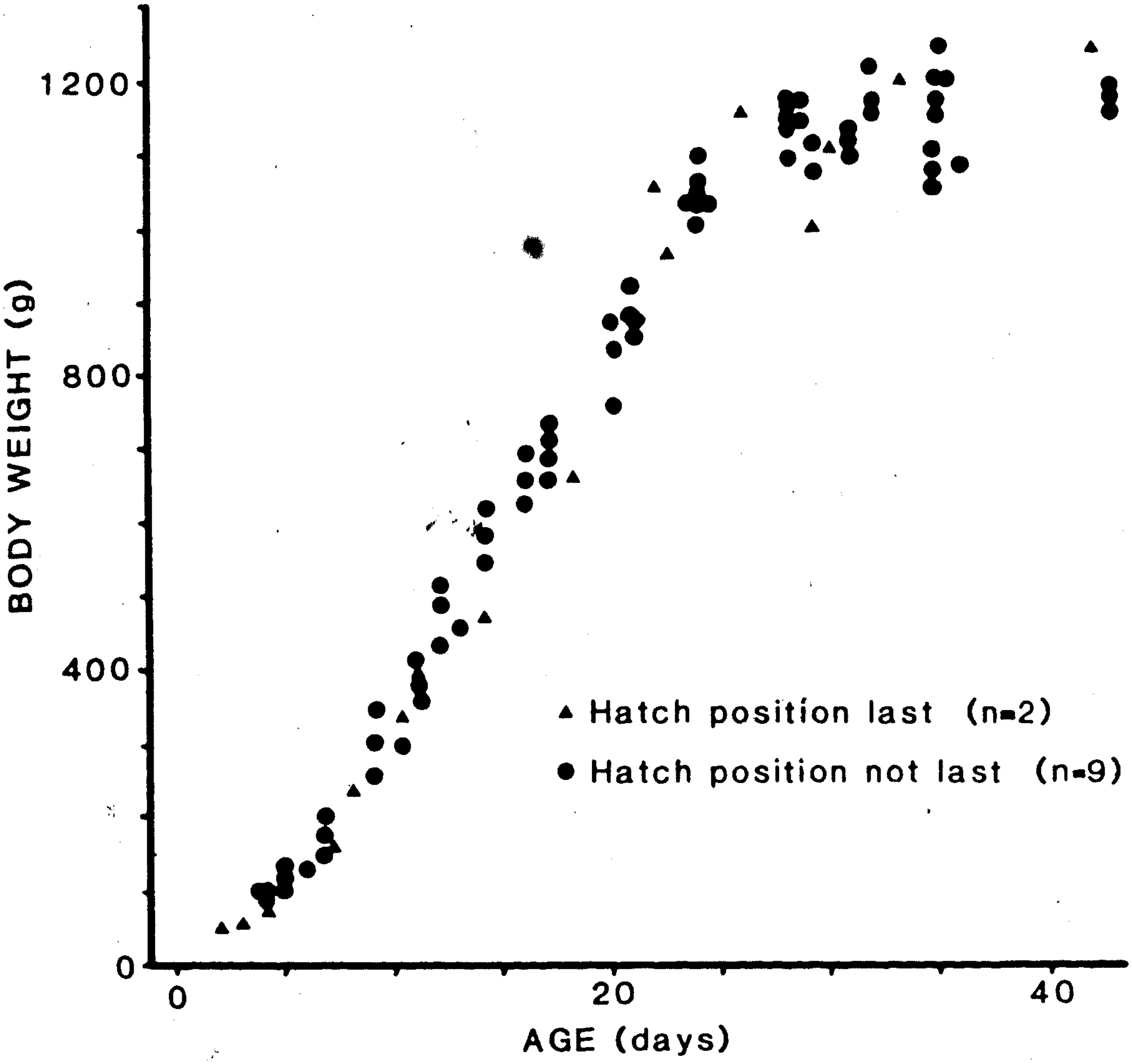

Figure 2.3 Relationship between age and weight in male nestling gyrfalcons of different hatch positions.

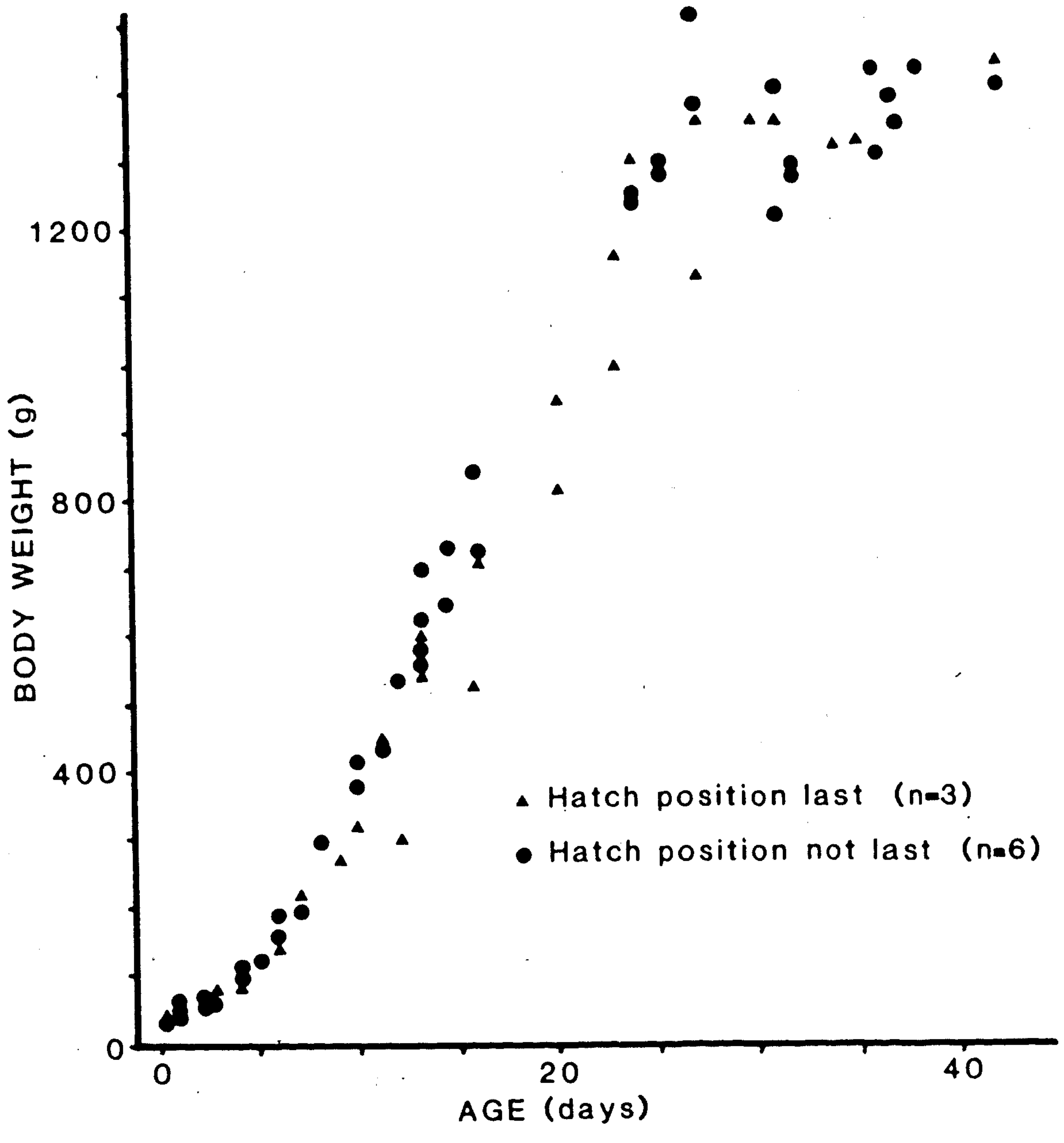

Figure 2.4 Relationship between age and weight in female nestling gyrfalcons of different hatch positions.

The sex ratio of nestlings banded each year from 1984 to 1986 varied from predominantly females (1984; 11 males:18 females) to predominantly males (1985; 14:6) to a near even sex ratio (1986; 9:11). The ratio in 1985 approached significance (X^2=3.2, P=0.074). However, the combined 3-year ratio (n=69) was even (34:35, P>0.9).

Although annual mean brood size and productivity varied between years, the differences were not significant (P>0.25, Table 2.2). The mean brood size from 1983 to 1986 was 2.53±0.89 young, while productivity averaged 1.50±1.43 young. No correlation was found between laying date and brood size on a within year basis (P=0.26-0.49). When laying dates from all years were combined, the relationship approached significance (P=0.06), but the correlation remained weak (r=-0.27). Annual mean brood size also did not correlate with either April-May or June weather variables. In 1986, the year with the lowest productivity, the highest mean brood size was attained. Despite differences in spring weather and prey availability (Chapter 3), total production for the study area varied from year to year only 23% on either side of the mean, ranging from 20 to 31 young produced annually.

Spring weather did appear to have an influence on production of young. Production was negatively correlated with the number of days that snow fell (r=-0.93, P=0.04) and with total precipitation (r=-0.86, P=0.07) from 21 April to 30 May. Mean temperature alone had little influence on overall reproductive performance (r=0.02, P=0.49).

Failure to lay had a major influence on productivity; 15 of 64 pairs (23%) occupying sites from 1983 to 1986 did not initiate a clutch. Pairs that failed at some point in the breeding cycle were seldom seen on subsequent visits to the territory.

Using the terminology of Mearns and Newton (1984), territories were considered as either 'regular' or 'irregular' depending on their history of occupancy. Regular territories (n=9) were those used three or more times in the 5 years of the study, irregular territories (n=12) were occupied 1 or 2 years. Only six (29%) of the 21 territories were occupied every year and of these only four (19%) were always productive. The regular territories accounted for 74% of total production; however, there was no significant difference in productivity between territories used regularly and irregularly (Mann-Whitney Test U=506.5, P=0.136).

Egg/Nestling Mortality

Summing data from 1983 to 1986 (Table 2.2), if we assume 3.8 eggs was the mean clutch size for all pairs laying eggs (49 pairs), then about 186 eggs would have been laid. Since total production over the 4 years was 96 fledglings, a 48% reduction was experienced.

The exact causes of mortality were difficult to pinpoint. Eleven nests experienced total clutch or brood loss; however, only one clutch loss and two brood losses were actually observed. All three of these losses occurred in 1986, and two were a direct result of severe spring weather. The clutch loss observed was a consequence of freezing rain and snow virtually covering the nest. Late and excessive melt water saturated one nest with young chicks (they likely died from exposure), and the collapse of one nest built upon snow caused the second case of brood loss. Nine addled eggs were found, and one egg disappeared during incubation in a nest that was ultimately successful. Loss of six nestlings was detected, with disappearance of two chicks from each of two nests occurring at approximately 1 week and 20 days of age. Only two dead young were observed. One nestling may have starved after falling off the nest. The other nestling appeared to have succumbed to an infestation of the parasitic fly Protocalliphora avium at about 10 days of age (G. Bennett and G. Wobeser pers. comm.).

Post-fledging

Young falcons remained within 200 to 300 m of the nest for the first 7 to 10 days post-fledging, but by 2 weeks travelled up to 1 km away. They would, however, return to the nest area on a regular basis, especially when prey was being supplied by one of the adults. By 20 days post-fledging, young in some territories had moved away from the general vicinity of the nest, possibly to areas with more abundant prey.

There has been only one band returned to date from the 91 young banded at Kilgavik. A juvenile male was captured in mid-September in Cambridge Bay, 145 km northeast of its nest site, approximately 6 weeks post-fledging.

Discussion

Density and Nest Sites

The appropriateness of using Ratcliffe's (1980) method to delineate study area size at Kilgavik is questionable. Large tracts of land and ocean up to 20 km from the nearest gyrfalcon territory were included because of the curvilinear nature of the distribution of territories. Elimination of these tracts resulted in a more realistic size of study area (2,000 km^2). Territory distribution is primarily coastal in nature and perhaps use of the mean internest distance is most appropriate for discussions of population density (Ratcliffe 1980).

Regardless of which method is used, the density of gyrfalcons breeding at Kilgavik (one pair per 125 km^2) approaches the highest known in the world. Regional densities are generally much lower (Cade 1982), such as on the Yukon North Slope at one occupied territory per 975 km^2 (Platt 1977), and on the Seward Peninsula, Alaska, at one pair per 916 km^2 (Roseneau 1972). Mid-summer densities across the mid-arctic latitudes of the N.W.T ranged from one pair per 233 km^2 to one pair per 1,456 km^2 (Bromley 1983, Bromley and McLean 1986), and Barichello (1983) observed densities at about one pair per 175 km^2 (mean internest distance 12.5 km) for a gyrfalcon population in the Ogilvie Mountains of the central Yukon. In northeastern Iceland, reportedly the area with the highest regional population density (Cade 1982), Nielsen (1986) observed one pair per 113 km^2. However, in Iceland, an average of only 22 pairs was successful each year (one per 236 km^2) compared to 9.5 pairs at Kilgavik (one per 210 km^2).

Gyrfalcons share the study area with many raptors that build stick nests. During an extensive helicopter survey of the study area in 1984, 19 raven, 31 golden eagle and 76 rough-legged hawk nests were observed in addition to the 15 sites occupied by gyrfalcons (Poole and Bromley 1985). Approximately 30 peregrine falcon territories have also been documented; however, peregrines at Kilgavik typically use "vegetated shelves" (Ratcliffe 1980), not suitable for gyrfalcons. With the abundance of stick nests and numerous ledges available throughout the study area, it is unlikely that the availability of nest sites is limiting the density of breeding gyrfalcons at Kilgavik. The regularity in spacing of territories observed in most years supports this conclusion. Newton (1979) suggested that pairs of raptors may be evenly spaced where nest sites are freely available, and that the distance between nest sites is correlated with food supply.

Gyrfalcon use of stick nests built by ravens has been widely reported (e.g., Kishchinskii 1957, Cade 1960, Bromley 1983, Nielsen 1986). At Kilgavik ravens were present at least as early as mid-winter, possibly year-round, and began nest construction in April. Interspecific interactions were common in spring between gyrfalcons and ravens, probably representing competition for nest sites. The observation made at Kilgavik of gyrfalcons taking over nests newly built by ravens, has also been reported in Iceland (Nielsen 1986). At Kilgavik, the two species did have some degree of tolerance for one another, as exhibited by young of each species successfully fledging from nests as close as 65 m apart on the same cliff face. In this case encounters were minimized by each species leaving and returning to its nest by opposite directions.

Use of stick nests built by rough-legged hawks has been documented in many gyrfalcon populations (Hagen 1952, Swartz et al. 1975, Platt 1977, Langvatn and Moksnes 1979). However, at Kilgavik, no use of hawk nests was observed in 59 gyrfalcon nestings over 5 years. This difference may reflect the fact that the sites used by rough-legged hawks at Kilgavik tended to be on smaller cliff faces and were often easily accessible to man or predators (Poole and Bromley 1985). Rough-legged hawk sites generally had poor protection from the elements, and often were still snow covered at the time gyrfalcons had completed laying. Use of rough-legged hawk nests by gyrfalcons in other areas may be related to narrower nesting requirements by rough-legged hawks (White and Cade 1971), a paucity of "better" sites with greater protection and less accessibility, or less strict nesting requirements of gyrfalcons in regions of less harsh climate.

Nests built by golden eagles at Kilgavik tended to have little overhang, and correspondingly little protection from the elements, but reproductive success was similar to that found in better protected raven nests. Gyrfalcons use nests of golden eagles in other regions where they nest sympatrically (Barichello 1983, Bromley 1983). Ledges with no stick substrate have also been used to varying degrees (Kuyt 1980, Barichello 1983, Bromley 1983, Nielsen 1986).

Barichello (1983) found that southerly-oriented nests fledged fewer young than those oriented north, similar to the situation at Kilgavik. Apart from the availability of sites, the use and relative nesting success at sites facing a particular direction is influenced by many factors. As pointed out by Manniche (1910 cited i[illegible]de 1960), in regions above the Arctic Circle north-facing sites would receive solar radiation and heat during the coolest period of the day and avoid receiving direct sunlight during the heat of the afternoon. Signs of overheating by nestlings were observed at west-facing sites during periods of sunshine and little wind. The direction of strong prevailing winds and resultant accumulations of snow must also be assessed.

Winter Occupancy

Few details exist on winter occupancy by gyrfalcons of nesting territories (Platt 1977, Nielsen 1986). Winter occupancy imparts an advantage in ownership of a nesting territory (Nielsen 1986), but depends upon a reliable prey base during a time when prey is often scarce and light levels sufficient for hunting are of short duration.

Resident arctic hare (Lepus arcticus), small scattered groups of rock ptarmigan and possibly microtine rodents could provide an adequate winter prey base at Kilgavik. As the study area is located above the Arctic Circle, light intensity and duration around the winter solstice may restrict hunting opportunity and prohibit residency in the dead of winter.

In agreement with other studies (Platt 1977, Nielsen 1986), only adult gyrfalcons were observed at Kilgavik in late winter. Juveniles, the least experienced cohort at hunting, likely move south to treeline where densities of prey are greater, although evidence for this occurrence in the central N.W.T. is circumstantial at best. More males than females were observed in late winter, possibly because males are more involved in territorial establishment and defense (Platt 1977) and therefore return earlier.

The Breeding Season

Gyrfalcons at Kilgavik tended to lay their eggs towards the later part of the range of dates for the species (Cade 1982). Laying by Yukon gyrfalcons was completed by mid-April in the central part of that territory (Barichello 1983) and by late April on the North Slope (Platt 1977). In Iceland about 80% of all pairs initiated laying during the first 3 weeks of April (Nielsen 1986). Most nests in the Baffin region of the eastern arctic were initiated in the second and third weeks of May (Bromley and McLean 1986). At a nest studied by Muir (1975) on Ellesmere Island in the high arctic (ca. 76°N), gyrfalcons initiated laying around 20 May, similar to some of the late nesters observed in this study. Undoubtedly, weather and early spring food supply influenced the timing of the breeding season in each area, as the gradient of laying dates was not related solely to latitude.

There was significant variation in the dates of laying between years on the study area (Fig. 2.2), possibly influenced by the timing of influx of large numbers of migrating ptarmigan (Chapter 3). The degree of influence was difficult to quantify. I suspect interactions between availability of prey and spring weather conditions (see Productivity and Spring Weather) may have influenced laying dates.

Few studies report on the role of the male in incubation. The range in male participation observed at Kilgavik, 17 to 25%, was higher than the 6% observed by Bente (1981) in the Alaska Range in east central Alaska. The reason for this disparity was not evident but may relate to food supply (Chapter 3). The male generally relieved the female when he brought food to the nest, incubating while she ate and rested.

Participation by males in brooding varied widely among sites at Kilgavik, but averaged 13% for all sites. Other studies reported male brooding at 1% (Bente 1981) and 6% (Jenkins 1974). Jenkin's results, based upon analysis of time-lapse photography, are the most comparable to this study. As the male gyrfalcon provides most if not all of the food to the female and nestlings for at least the first 10 days post-hatch (Cade 1982, Chapter 3), the differences observed between regions may relate to the degree of food-stress. Under periods of food-stress the male may have to spend most of its time foraging with little or no inclination to brood. However, the consistency in male participation in brooding in one pair observed at Kilgavik in 2 years of different numbers of nestlings and availability of prey, suggested that brooding responsibilities may be generally pre-set between members of a given pair.

At Kilgavik nearly continuous brooding was observed of young up to 19 days old at some sites, and recorded for short durations (<20% of frames each day) when nestlings were up to 32 days of age. Most late brooding was observed in 1985, when cool wet weather persisted throughout the mid-nestling period. Cade (1960, 1982) and Platt (1977) stated that brooding in gyrfalcons ceased when the young were about 10 days old. Jenkins (1978) found brooding dropped off when the chicks were around 15 days old and ceased at 19 days. Bente (1981) reported that brooding/shading continued until 27 days. No significant relationship was found at Kilgavik on a within-year basis between brooding and weather variables as has been reported for other raptors (Enderson et al. 1973, Newton 1978), although differences in the persistence of brooding between regions may have been due to differences in climate. The tendency for gyrfalcon sites to have a complete overhang and good protection from the elements may mitigate the impact of inclement weather on nestling thermoregulation.

The mean brood size of all successful pairs (2.54, Table 2.2) lay within the range reported (2.20 - 3.05) for North America by Platt (1977:Table 15). Recent studies have reported a mean brood size of 2.14 young in the central Yukon (Barichello 1983, n=51 nests), and 2.78 in northeastern Iceland (Nielsen 1986, n=91 nests).

The paucity of band returns make it unclear where adult and juvenile gyrfalcons from the Kilgavik area go when the onset of colder weather occurs and the availability of prey decreases. Although conjecture, it is likely that the adults are almost year-round residents on the study area, except for a brief period in mid-winter when they may move south to treeline, perhaps following the major ptarmigan migration. Those juveniles that survive the initial months after dispersing may ultimately move to treeline as well, although evidence from the one band return to date did not suggest initial dispersal towards the south. However, a pattern of initial dispersal in all directions from the natal site is well documented in raptors (Newton 1979).

Egg/Nestling Mortality

The réduction from number of eggs produced to number of young fledged is difficult to obtain from most studies, because of the difficulty in detecting total clutch or brood losses. The reduction estimated from the Kilgavik data (48%) was higher than the 36% estimated from Icelandic data (Nielsen 1986). I calculated a "loss" of 38% from mean clutch and brood sizes reported by Cade (1960), however, this underestimates the true loss by not accounting for sites experiencing total reproductive failure.

The causes of egg and nestling mortality were varied. A number of addled eggs were observed but many more likely went undetected. Addled eggs included both infertile eggs and eggs containing embryos that died at various stages of development. Pesticide (organochlorine) concentrations from addled eggs collected in 1983 were low (R. Bromley unpubl. data), an expected result as both predator and major prey are generally resident in the arctic.

The observation that Protocalliphora avium larval infestation was probably the proximate cause of death of a nestling may lend support to the claim by Kishchinskii (1957) that parasites are partly responsible for gyrfalcons using alternative nests to enable cleansing of heavily infested sites. Dipterous larvae infestations were observed at several sites over the course of the study and were often present or heaviest on the youngest member of the brood. The stress from this parasite load may have increased energy drains on these young and contributed to the slightly retarded growth of last-hatched nestlings observed at many sites (Figs. 2.3, 2.4). Flesh fly infestations have been reported to result in death of nestling birds (Gold and Dahlsten 1983, Garrison et al. 1986). Varying degrees of infestation with fleas (_Ceratophyllus vagabundus vagabundus_, R. Lewis pers. comm.) were also observed at nest sites occupied by gyrfalcons, golden eagles and rough-legged hawks.

Loss of a brood in 1986 through nest collapse was noteworthy, because the stick nest had been built by ravens that spring, but usurped by the gyrfalcon pair probably only weeks before laying. The nest, however, was built on a snow ledge rather than a rock ledge. When the snow melted, the nest fell, killing the 10 day old nestlings. One other nest built by ravens on a snow ledge in 1986 collapsed with melt; these ravens renested 100 m away. To my knowledge there are no reports in the literature of freshly-built raven nests collapsing in this manner early in the breeding season of their construction. Both Roseneau (1972) and Platt (1977) reported loss of 6% of their sites through deterioration with age. Cade (1960) also reported collapse of two stick nests with young gyrfalcons, but the young survived in both cases.

Productivity and Spring Weather

There was no significant difference in productivity between territories regularly and irregularly used at Kilgavik. This suggests that the contribution of irregularly used territories was diminished not by reduced breeding success, but by reduced occupancy, such that irregularly used territories may have been occupied only in 'good' years. The reasons why some territories and not others were occupied every year possibly relates to both the physical characteristics of the site and the access from it to a good prey base. I presume that each year surplus birds were present that could occupy vacant territories when conditions were amenable. However, in 3 years of field work I saw a gyrfalcon more than 2 km from an occupied nest site only once. Thus, whether 'floaters' are common or even exist is conjecture.

In discussions of productivity of raptor populations it is important to document those pairs that failed early in the breeding season, including non-breeding territorial pairs (Newton 1979). Only the inclusion of these pairs gives a meaningful representation of the productivity of a population (i.e., the mean number of young for all pairs that were present at the start of the breeding season). Bromley and McLean (1986) found that summer surveys overestimated the productivity of gyrfalcons in the N.W.T. by 50% in those areas where spring surveys had also been carried out. Unfortunately, gyrfalcons breed early in cold remote regions, and few researchers have been on hand to document prelaying territorial occupancy.

Productivity at Kilgavik averaged 1.50 young per pair, similar to figures obtained from Iceland (1.25 young, Nielsen 1986), Baffin Island (1.6 young, Bromley and McLean 1986), and the Yukon (1.73 young, Barichello 1983). The reasons for yearly differences in productivity at Kilgavik cannot be related primarily to the number of rock ptarmigan present, as densities of breeding ptarmigan did not vary a great deal from 1983 to 1986 (Chapter 3). Delayed arrival of large numbers of migrating ptarmigan may have caused some pairs to forgo breeding in some years; however, spring weather conditions may have had more of an influence, both directly on the gyrfalcons and indirectly by affecting the prey (Swartz et al. 1975, Nielsen 1986).

The climate encountered at Kilgavik is more severe than that found in most other areas where intensive studies on gyrfalcons have been conducted. This harsh climate probably contributes to later laying, more specific nesting requirements (i.e., no use of exposed rough-legged hawk nests), and brooding continuing later into the nestling period. However, despite the harsh climate, the relatively rich prey base seasonally available at Kilgavik (Chapter 3) enables the gyrfalcons to achieve fairly high population density and productivity, and to allow the males to participate in more than just food provision.

The influence of spring weather on breeding performance of raptors has been noted previously (Cavé 1968, Newton 1979, Newton and Marquiss 1986) and has been suggested for gyrfalcons (Swartz et al. 1975, Nielsen 1986). The importance of high female body weight to initiation of laying has also been determined (Newton 1979, Newton et al. 1983). Cold weather and precipitation increase the energy needs of the female and at the same time may reduce hunting efficiency and hence feeding rate, both factors that would influence the amount of weight gain and therefore the ability to lay or incubate (Cavé 1968). Poor condition of the female resulting from these factors may also lead to production of eggs of lower quality, and hence lower fledging success (Hochachka 1985). At Kilgavik, poor spring weather may also have retarded the migration of ptarmigan into the region, delaying increases in prey availability.

Thus, weather likely influences gyrfalcon breeding success directly through increased energy demands and decreased hunting success, and indirectly by lowering the early availability of both migratory and resident prey. In a species that initiates laying and incubation during or after the arrival of large numbers of its main prey (Chapter 3), short periods of poor spring weather may be sufficient to tip the energy balance towards a lowered reproductive season.

Literature Cited

Barichello, N. 1983. Selection of nest sites by gyrfalcons (Falco rusticolus). Unpubl. M.Sc. thesis, Univ. of B.C., Vancouver.

Bengtson, S.-A. 1971. Hunting methods and choice of prey of gyrfalcons Falco rusticolus at Myvatn in northeast Iceland. Ibis 113:468-476.

Bente, P.J. 1981. Nesting behavior and hunting activity of the gyrfalcon Falco rusticolus, in south central Alaska. Unpubl. M.Sc. thesis, Univ. of Alaska, Fairbanks.

Bromley, R.G. 1983. 1982 raptor survey. N.W.T. Dept. Ren. Res. File Rep. No. 35, Yellowknife.

Bromley, R.G., and B.D. McLean. 1986. Raptor surveys in the Kitikmeot and Baffin Regions, Northwest Territories, 1983 and 1984. N.W.T. Dept. Ren. Res. File Rep. No. 65, Yellowknife.

Brown, D. 1975. A test of randomness of nest spacing. Wildfowl 26:102-103.

Burnham, W.A., and W.G. Mattox. 1984. Biology of the peregrine and gyrfalcon in Greenland. Meddel. om Grønland, Bioscience 14:1-25.

Cade, T.J. 1960. Ecology of the peregrine and gyrfalcon populations in Alaska. Univ. Calif. Publ. Zool. 63:151-290.

Cade, T.J. 1982. The Falcons of the World. Cornell Univ. Press, Ithaca, N.Y.

Cade, T.J., and J.D. Weaver. 1976. Gyrfalcon X peregrine hybrids produced by artificial insemination. J. North American Falconers' Assoc. 15:42-47.

Calef, G.W., and D.C. Heard. 1979. Reproductive success of peregrine falcons and other raptors at Wager Bay and Melville Peninsula, Northwest Territories. Auk 96:662-674.

Cavé, A.J. 1968. The breeding of the kestrel Falco tinnunculus L., in the reclaimed area Oostelijk Flevoland. Netherlands J. Zool. 18:313-407.

Court, G.S. 1986. Some aspects of the reproductive biology of tundra peregrine falcons. Unpubl. M.Sc. thesis, Univ. of Alberta, Edmonton.

Dement'ev, G.P. 1960. The Gyrfalcon (Trans. from Russian). Franch'sche Verlangshandlung, Stuttgart.

Enderson, J.H., S.A. Temple and L.G. Swartz. 1973. Time-lapse photographic records of nesting peregrine falcons. Living Bird 11:113-128.

Fraser, J.A. 1964. Geological notes on northeastern District of Mackenzie, Northwest Territories. Geol. Surv. Can., Ottawa. Pap. 63-40. Map 45-1963.

Garrison B.A., C. Vouchilas and D.F. Stauffer. 1986. Nestling great crested flycatcher parasitized by larval fly (*Protocalliphora hirudo*). Wilson Bull. 98:321.

Godfrey, W.E. 1986. The Birds of Canada, revised edition. Nat. Mus. Nat. Sci., Nat. Mus. Can., Ottawa.

Gold, C.S., and D.L. Dahlsten. 1983. Effects of parasitic flies (*Protocalliphora* spp.) on nestlings of mountain and chestnut-backed chickadees. Wilson Bull. 95:560-572.

Hagen, Y. 1952. The gyrfalcon (*Falco rusticolus*) in Dovre, Norway. Skrifter utgitt av de[illegible] Norske Videnskap-Akademi. I. Mat.-Naturv. Klasse, [illegible]-37.

Hall, E.R. 1981. The Mammals [illegible]rth America. Vols. I & II. Second ed. John Wiley & Sons, [illegible]

Hochachka, W.M. 1985. The effect of food availability on black-billed magpie reproduction. Unpubl. M.Sc. thesis, Univ. of Alberta, Edmonton.

Jenkins, M.A. 1974. Behavior of the gyrfalcon (*Falco rusticolus*) from hatching to fledging: a time-lapse photographic study. Unpubl. M.Sc. thesis, Brigham Young Univ., Provo.

Jenkins, M.A. 1978. Gyrfalcon nesting behavior from hatching to fledging. Auk 95:122-127.

Kishchinskii, A.A. 1957. On the biology of the gyrfalcon (*Falco gyrfalco gyrfalco*) in the Kola Peninsula. Ornithologiia (U.S.S.R.) 1:1-31.

Kuyt, E. 1980. Distribution and breeding biology of raptors in the Thelon River area, Northwest Territories, 1957-1969. Can. Field-Nat. 94:121-130.

Langvatn, R., and A. Moksnes. 1979. On the breeding ecology of the gyrfalcon *Falco rusticolus* in central Norway. Fauna Norv. Ser. C, Cinclus 2:27-39.

Manniche, A.L.V. 1910. The terrestrial mammals and birds of north-east Greenland. Meddel. om Grønland 45:1-200.

Maxwell, J.B. 1980. The Climate of the Canadian Arctic Islands and Adjacent Waters. Vol. 1. Climatological Studies No. 30. Envir. Can. Hull, Quebec.

Mearns, R., and I. Newton. 1984. Turnover and dispersal in a peregrine Falco peregrinus population. Ibis 126:347-355.

Mossop, D. 1980. The Yukon Territory gyrfalcon harvest experiment (1974-79). Final draft. Yukon Wildl. Branch, Whitehorse.

Muir, R.D. 1975. A study of the breeding biology of arctic gyrfalcons. Can. Wildl. Serv., Ottawa. unpubl. rep.

Newton, I. 1978. Feeding and development of sparrowhawk Accipiter nisus nestlings. J. Zool., Lond. 184:465-487.

Newton, I. 1979. Population Ecology of Raptors. Buteo Books Vermillion, S. Dakota.

Newton, I., and M. Marquiss. 1986. Population regulation in sparrowhawks. J. Anim. Ecol. 55:463-480.

Newton, I., M. Marquiss and A. Village. 1983. Weights, breeding and survival in European sparrowhawks. Auk 100:344-354.

Nielsen, O.K. 1986. Population ecology of the gyrfalcon in Iceland, with comparative notes on the merlin and the raven. Unpubl. Ph.D. thesis, Cornell Univ., Ithaca, N.Y.

Nilsson, I.N., S.G. Nilsson and M. Sylven. 1982. Diet choice, resource depression, and the regular nest spacing of birds of prey. Biol. J. Linnean Soc. 18:1-9.

Platt, J.B. 1976. Gyrfalcon nest site selection and winter activity in the western Canadian arctic. Can. Field-Nat. 90:338-345.

Platt, J.B. 1977. The breeding behavior of wild and captive gyrfalcons in relation to their environment and human disturbance. Unpubl. Ph.D. thesis, Cornell Univ., Ithaca, N.Y.

Poole, K.G. 1987. A replacement clutch in wild gyrfalcons, Central Arctic, Northwest Territories. Can. Field-Nat. in press.

Poole, K.G., and R.G. Bromley. 1985. Aspects of the ecology of the gyrfalcon in the central arctic, Northwest Territories, 1983 and 1984. N.W.T. Dept. Ren. Res. File Rep. No. 52, Yellowknife.

Porsild, A.E., and W.J. Cody. 1980. Vascular plants of continental Northwest Territories, Canada. Nat. Mus. Nat. Sci., Ottawa.

Postupalsky, S. 1974. Raptor reproductive success: some problems with methods, criteria, and terminology. Pp 21-31 In: Hamerstrom, F.N., Jr., B.E. Harrell and R.R. Olendorff, (eds.). Management of Raptors. Raptor Res. Rep. No. 2.

Pulliainen, E. 1975. Choice of prey by a pair of gyrfalcons Falco rusticolus during the nestling period in Forest-Lapland. Ornis Fenn. 52:19-22.

Ratcliffe, D. 1980. The Peregrine Falcon. Buteo Books, Vermillion, S. Dakota.

Roseneau, D.G. 1972. Summer distribution, numbers, and food habits of the gyrfalcon (Falco rusticolus L.) on the Seward Peninsula, Alaska. Unpubl. M.Sc. thesis, Univ. Alaska, College, Alaska.

Swartz, L.G., W. Walker II, D.G. Roseneau and A.M. Springer. 1975. Populations of gyrfalcons on the Seward Peninsula, Alaska, 1968-1972. Pp 71-75. In: Proc. of Conf. on Raptor Conserv. Techniques, Part 6. Raptor Research Rep. No. 3.

Temple, S.A. 1972. A portable time-lapse camera for recording wildlife activity. J. Wildl. Manage. 36:944-947.

White, C.M., and T.J. Cade. 1971. Cliff-nesting raptors and ravens along the Colville River in arctic Alaska. Living Bird 10:107-150.

III. FOOD HABITS AND FORAGING CHARACTERISTICS OF GYRFALCONS AT KILGAVIK, NORTHWEST TERRITORIES

Introduction

"My overall conclusion is that....almost every aspect of the natural population ecology of a given species can be explained in terms of food" (Newton 1979:290). Since Newton was referring to raptorial birds, an adequate food supply would seem of paramount importance for successful breeding of the gyrfalcon (Falco rusticolus), which inhabits arctic and subarctic regions of the Northern Hemisphere. Ptarmigan (Lagopus spp.) form the dominant food item in the diet of gyrfalcons in most regions throughout its vast distribution (e.g., Kishchinskii 1957, Cade 1960, Langvatn and Moksnes 1979, Nielsen 1986). Other prey items are of at least seasonal importance in some areas (e.g., seabirds and gulls, Dement'ev 1960; ducks, Bengtson 1971; rodents, Bente 1981; and arctic hare (Lepus arcticus), Muir and Bird 1984).

Numerous studies have documented a numerical response (Solomon 1949) in gyrfalcons, that is, an annual variation in density of breeding pairs that parallel changing densities of prey (Cade 1960, Bengtson 1971, Roseneau 1972, Barichello 1983, Nielsen 1986). Few have examined whether the rates of consumption of particular prey change relative to changes in prey availability during the breeding season (functional response: Solomon 1949), and whether these changes have an effect on the reproductive success of the birds. Given Newton's (1979) insistence upon the importance of food, a thorough understanding of the population ecology of gyrfalcons in any region would seem to require an understanding of any functional response manifested.

Between 1984 and 1986, I was able to examine these relationships during prelaying to fledging in a gyrfalcon population in the central Canadian arctic where, because spring weather conditions vary greatly from year to year, availability and use of prey also vary. In this location gyrfalcons must cope not only with fluctuations in the nature of the food base over their lengthy breeding season, but also with year to year changes in relative availability of particular prey. The primary objectives of the study were to examine food habits relative to the available prey base and to relate food habits to reproductive success. Lengthy periods of observation of nesting birds also enabled me to examine some aspects of optimal foraging theory (Krebs et al. 1983). In addition, evidence was collected that provided a basis for postulating the relative importance of the various factors affecting density of breeding pairs, timing of laying, and productivity in this gyrfalcon population.

Methods

Research was conducted on the Kilgavik study area, approximately 2,000 km^2 of rugged tundra east of Bathurst Inlet in the central Canadian arctic (68°10'N, 106°15'W). Intensive studies were initiated there by R. Bromley in early May, 1983 (Poole and Bromley 1985). I conducted field work at Kilgavik for 2 months during 1984 and from early May to early August of 1985 and 1986. In addition, a week was spent on the study area in late winter 1986. Terminology pertaining to nesting activities of gyrfalcons, and a general description of the vegetation, climate and geology of the area are reported in Chapter 2.

The availability and vulnerability of potential gyrfalcon prey species were assessed by a variety of methods. I based availability on the relative or absolute abundance of a prey species, and vulnerability on the physical and biological conditions that cause one species to be preyed upon more heavily than another (Craighead and Craighead 1956). Relative vulnerability was assessed mainly by changes in behaviour and plumage. Ptarmigan, the major prey species, were observed during snowmobile travel in May, and their numbers recorded to document the timing of migration into the study area. The chronology of breeding and moult, and changes in behaviour in ptarmigan were followed closely. The rock ptarmigan (*L. mutus*) was virtually the only grouse species present; only two willow ptarmigan (*L. lagopus*) were observed during my research. Thus, in this report "ptarmigan" denotes *L. mutus* unless specified otherwise.

Six 1x2 km plots were censused to determine densities of breeding ptarmigan once males were displaying on territory. Five plots were chosen in a random fashion in 1983 and a sixth was located, non-randomly, near the base camp in 1984 (Poole and Bromley 1985). The physiography of the plots varied considerably, from plots which contained rolling landscape with 30% exposed rock and 70% dry to medium-moist tundra, to a rugged area with 85% rock and 15% moist tundra. Most vegetated areas contained tussock meadows, consisting primarily of sedge (*Carex* spp.), various grasses and cotton-grass (*Eriophorum* spp.). Willows (*Salix* spp.) were interspersed throughout most of the vegetated areas.

The plots were surveyed during the morning in two traverses by three observers spaced at approximately 167 m intervals and walked parallel to the long axis of the plot. Four observers were used on some plots in 1983, which dropped the spacing interval to 125 m. The number and sex of ptarmigan observed were noted. Once territorial, male ptarmigan are easy to detect because of their flight-song and ground displays (MacDonald 1970) and conspicuous white colour on a rapidly darkening background.

Because of difficulties with travel during snow-melt, not all plots were censused each year. Most plots were censused annually once or twice. To determine relative changes in numbers, the population counts from all plots censused each year were compared to the counts on the same plots in 1983, which were given the value 1.0. The mean number of male ptarmigan observed was used in the case of multiple censuses of one plot. Two plots were censused five times each in May 1984 to examine the precision of the census technique.

Twenty-five ptarmigan were collected as non-selectively as possible (e.g., shooting from flocks) in late May from 1984 to 1986 to estimate the sex and age composition of the population (see Weeden and Watson 1967, Parker et al. 1985 for means of determining sex and age). The information obtained from the censuses was used along with the age ratios to examine fluctuations in numbers of breeding ptarmigan. The proportion of yearling ptarmigan in spring populations usually track fluctuations in the density of breeding birds (Weeden and Theberge 1972).

Difficulties were encountered in quantifying numbers of arctic ground squirrels (Spermophilus parryii). Distribution tended to be diffuse, with squirrels found throughout the study area in most dry habitats. Their presence above ground varied with the weather, and live-trapping for a mark-recapture estimate proved to be too time-consuming. Thus, only a subjective assessment of numbers could be made.

To compare passerine densities with other arctic regions, transects were established in the manner of Burnham and Mattox (1984). A 1 km transect was walked, with all passerines counted within 15 m on either side of the two observers. Five transects were censused in 1985 and 1986.

Microtines were trapped (Victor snap-traps) from the latter half of June to 15 July on plots established in various habitats near base camp, located at a different site each year. Two lines of 10 traps, baited with peanut butter, were set on 10x40 m grids. Grids were moved every 5 days. Trapping effort varied from 180 trap-days in 1984 to 600 trap-days in 1986.

Relative densities of other potential prey for gyrfalcons, such as arctic hare, waterfowl (Anatidae) and shorebirds (Charadriidae and Scolopacidae), were roughly assessed by sightings made during several thousands of kilometres of snowmobiling and several hundreds of kilometres of foot travel over the course of each season.

Three methods were used to detail food habits and examine feeding behaviour of gyrfalcons at Kilgavik. Prey remains and pellets were collected from the nest, from the base of the nesting cliff, and at accessible perches and plucking sites on each visit to a nest site. Items excessively dried or weathered, or otherwise obviously aged, were discarded. Collections were concentrated at three sites in 1985 and four sites in 1986. At these seven main sites collections were made usually every 3 to 7 days, with the number of visits over the season at each site, ranging from 6 to 17 (mean 11.7 visits per site). Collections were made irregularly at other gyrfalcon sites.

Each collection was dried in the laboratory, sorted by species, and the minimum number of individuals was determined by counting the most frequently occurring bone or body part representing one individual. For ptarmigan this bone was usually the sternum (Langvatn 1977, Nielsen 1986). Individual ground squirrels were usually detected by counting piles of viscera (stomach, large and small intestine) or pelts found on the nest. Pellets were examined macroscopically, and often provided evidence of smaller prey items, such as passerine birds and microtines. Some microtines were identified to species from dentition using a dissection microscope.

From collections of ptarmigan in 1986 I measured the length of the humeri with calipers (to the nearest 0.1 mm) and found that male ptarmigan, on average, had significantly longer humeri than females (males 59.1±1.57[SD] mm, n=13; females 57.3±1.47 mm, n=10; 1-tailed t-test t=2.80, P<0.01), although a great deal of overlap existed (range of males: 55.5-61.4 mm; females: 55.0-58.9 mm). All right humeri (to avoid duplication of individuals) collected in prey remains were also measured, to determine if a trend in differential use of one sex over the other during the season could be detected.

Time-lapse 8 mm movie cameras (Temple 1972), placed at seven gyrfalcon nests during the study (three sites in 1985 and four in 1986, Chapter 2), were used to provide documentation of feeding frequency and duration, and some aspects of feeding behaviour. The timing of direct feedings and food deliveries were calculated from time-lapse data. Prey items were fed directly to the young by one of the adults and either consumed entirely or partially eaten and cached, or were presented in the form of food delivery (Jenkins 1974), when a prey item was dropped off and the nestlings fed themselves. I use "feeding rate" (number of feeding events per day) to encompass both forms of feeding. The number of feeding events observed on film for any hourly segment and for each day over the nestling period was corrected for the proportion of time lost because of darkness or weather. Over 118,000 frames were examined in an 8 mm film editor (MKM Industries, Inc. Model 824). Time-lapse data were coded and analyzed by computer.

Direct observation was the final method used to document food habits and feeding behaviour. Observation periods of from 1 to 10 hours at distances of 200 to 400 m were conducted, using 7x binoculars and 20x spotting scopes. Approximately 27% of the 801 observation hours were during the prelaying and incubation period. Direct observations were compared with prey remains and pellet collections to give prey totals for any one period. Observations added few large prey items to the total, but did detect some smaller prey items, such as passerine birds, that were not evident in prey remains or pellet analyses. Identification of prey species from analysis of time-lapse film proved difficult. In only 16.3% of 1230 feedings recorded on time-lapse films were prey identified to species. Extensive caching by gyrfalcons prevented treating each identification as a separate prey individual; a large prey item could be retrieved and fed to young nestlings up to three times.

Biomass of prey was calculated using mean weights obtained from limited collections (K. Poole unpubl. data) and from weights given in Banfield (1974) for mammals and Dunning (1984) for birds. Biomass is more meaningful than number of individuals when dealing with prey of varying size, as at Kilgavik, and when assessing the relative role of a species in the total prey base (Kishchinskii 1957, Steenhof 1983). For completeness, however, both numbers of individuals of a species and calculated biomass were included in discussions of prey use.

Differences between data sets were considered significant when $P \leq 0.05$, unless stated otherwise.

Results

Prey Availability

Few prey species were available to gyrfalcons in mid- to late winter. During 800 km of snowmobile travel over the study area in late March and early April, 1986, I observed only two ptarmigan and no more than 25 sets of tracks. Tracks and droppings would have been readily detected in the loose snow covering the area at that time. One arctic hare was also observed. Microtines were the only other potential prey present, but were only vulnerable during periods of activity above the snow.

Ptarmigan migrated into the Kilgavik area in early May each year, generally from the southwest. Large flocks (up to 50 birds) were present on 10 May 1983 when observations were started that year (Poole and Bromley 1985). By the same date in 1984 ptarmigan had already dispersed onto territories. By contrast, only 30 ptarmigan and little evidence of the birds were observed from 2 to 6 May 1985, but large flocks (some with more than 200 birds) were observed from 7 to 10 May. In 1986 we saw moderate numbers (7 to 24 per day) of ptarmigan from 1 to 4 May and large flocks (up to 80 birds) were observed from 5 to 7 May.

In 1983 most ptarmigan were dispersed and territorial by 25 May, whereas this event began before 10 May in 1984 and on 20 May in 1985. In 1986, good weather in early spring led ptarmigan to begin displaying on 9 May; however, a major 4-day storm began 10 May, causing the birds to reflock. This pattern was repeated twice more that month, when major storms began 22 and 27 May. The ptarmigan did not become permanently dispersed and territorial until early June.

Densities of territorial male ptarmigan on the census plots increased about 40% from 1983 to 1985 and fell slightly in 1986 (Table 3.1, Fig. 3.1). Multiple censuses of a given plot produced little variation in numbers counted. In multiple surveys of plots B and F in 1984, a range of 7 to 9 and 0 to 2 male ptarmigan per plot was obtained, respectively, indicating that one or two censuses of a plot were adequate to estimate, to within two birds, the number of territorial males present. The yearling:adult ratio observed in the annual ptarmigan collections remained constant at about 1:1 (1984 12 yearlings:13 adults, 1985 13:12, 1986 13:12).

Timing of spring moult and accompanying behavioural changes varied greatly between male and female rock ptarmigan at Kilgavik. In 1985, female ptarmigan started moulting head and neck feathers about 20 May, and by 10 June, about the time of laying in an average spring, most females were in the summer plumage and were very cryptic in both their colour and behaviour. Males, on the other hand remained in their white winter plumage well into June, displaying even after the females were on eggs. By mid-June flecks of brown could be seen on the backs of the heads of males, but it was not until the very end of June in 1985, and the second week of July in 1986, that the winter plumage of the majority

Table 3.1. Numbers of territorial male ptarmigan counted on census plots at Kilgavik, N.W.T., 1983 to 1986.

	Mean no. of male ptarmigan (no. of censuses)			
Plot	1983	1984	1985	1986
A	4.5(2)	--	7(1)	5(1)
B	7(1)	8(5)	8(2)	10.5(2)
C	3(2)	--	5(1)	6(1)
D	2.5(2)	--	4(2)	1(1)
E	5(1)	--	--	6(1)
F	--	1.2(5)	2(2)	3(1)
Sum B	7.0	8.0(14%)[a]		
Sum A-D	17.0		24.0(41%)	
Sum A-E	22.0			28.5(30%)

[a] Numbers obtained from plots censused in 1984-1986 were compared to the same plots in 1983. Percentages in parentheses are the increases in numbers over those recorded in 1983.

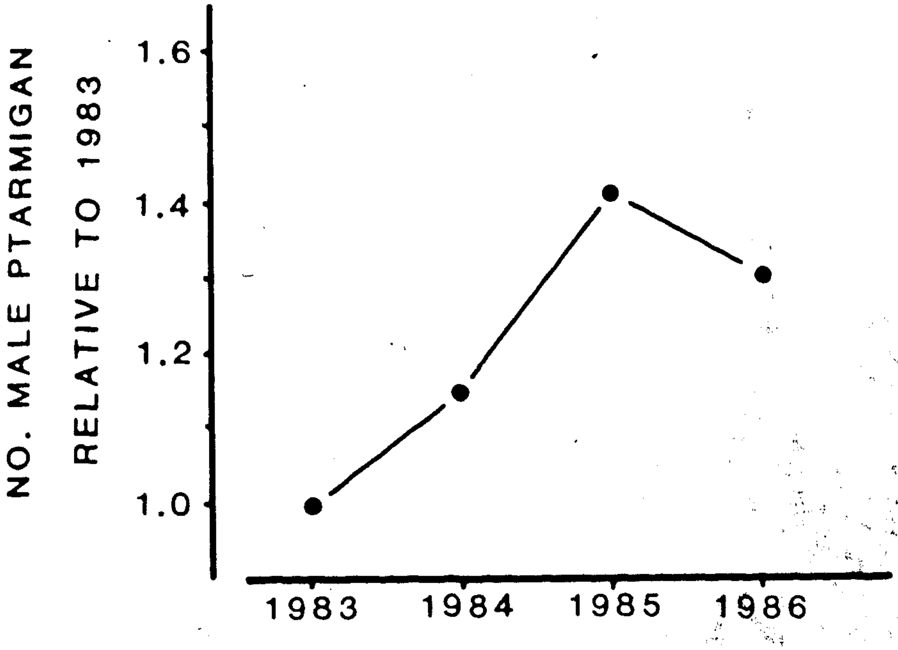

Figure 3.1 Index of density for male ptarmigan breeding at Kilgavik, N.W.T., 1983 to 1986. See text for explanation.

of the males had been moulted. Behavioural changes were noted well before summer plumage was attained; males reduced the frequency of displays and became more inconspicuous by mid- to late June. Some male ptarmigan were observed to dust bathe at this time which tended to dull the whiteness of the winter plumage, enhancing camouflage. Those male ptarmigan seen after late June were reluctant to take flight, and generally were observed only when flushed from hiding places in the bushes and rocks. The chronology of moult and behavioural changes varied with spring phenology; a severe and late spring in 1986 apparently caused timing of moult to be delayed up to a week relative to 1985.

Subjectively, the size of spring populations of adult arctic ground squirrels observed from 1984 to 1986 appeared similar. Adults emerged in late April or early May, often digging through over a metre of snow from their burrows. Presence of squirrels above ground was heavily dependent upon weather, with few seen on cool, overcast days, or days with precipitation.

Juvenile squirrels emerged from their natal burrows around 1 July, and were plentiful in 1984 and 1985. However, in 1986 no juvenile squirrels were seen during July, and only one was detected among the prey remains collected at gyrfalcon sites. This apparent almost complete failure of ground squirrels to produce young was probably a direct result of the severe, late spring in 1986, which may have curtailed breeding activities and diminished availability of food.

Densities of passerines, in the years 1985 and 1986 combined, averaged 6.2±4.2 birds per transect, and ranged from 1 to 13 birds. Lapland longspurs (Calcarius lapponicus) and horned larks (Eremophila alpestris) were the most abundant species identified, comprising 56 and 30% of all birds, respectively. The late spring in 1986 affected the chronology of passerine breeding. In 1985 the first fledglings were seen 22 June; in 1986 it was 16 July before fledglings were observed.

Microtine numbers, as indexed by snap-trapping, dropped dramatically from 1984 to 1986 (Fig. 3.2). No microtines were trapped in 1986, despite efforts on six different grids. Because the location of base camp, and hence that of traps, was different from year to year, the results were not directly comparable; however, a trend was evident. Strengthening this conclusion was the number of nests occupied by rough-legged hawks (Buteo lagopus) each year (Fig. 3.2). Rough-legged hawk numbers usually follow local microtine cycles (Hagen 1969, Newton 1979); at Kilgavik they closely tracked the microtine trapping results. Two species of both voles and lemmings were identified (Appendix 1).

Subjectively, numbers of arctic hare seemed much greater in 1986 than in previous years. Population levels of waterfowl and shorebirds appeared similar over the 3 years, although arrival dates, and chronology and success of breeding were heavily weather dependent. Large numbers of eiders (Somateria spp.) were present along the coast each year, and at least a dozen colonies of glaucous (Larus hyperboreus) and Thayer's gulls (L. glaucoides thayeri) were located in Melville Sound and Elu Inlet; population size of these species appeared to remain relatively constant.

Food Habits

Results from prey remains and pellet collections were combined with direct observations for all years to examine the general food habits of

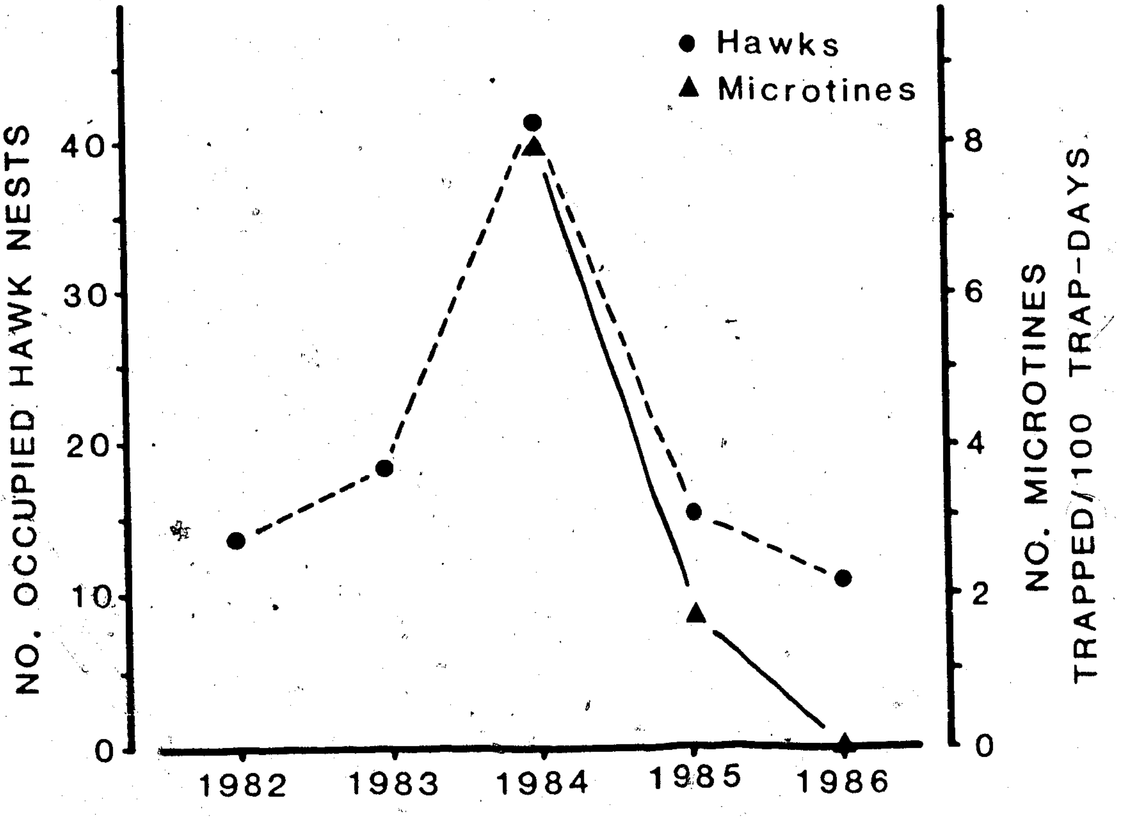

Figure 3.2 Index of microtine population size and number of rough-legged hawks breeding at Kilgavik, N.W.T., 1982 to 1986. Data from 1982 and 1983 are from Poole and Bromley (1985).

the gyrfalcon at Kilgavik (year to year differences in food habits did exist, and will be discussed later). Summing data from collections, 1998 prey remains and 467 pellets containing at least 925 individual prey items were recorded. During direct observations at nest sites, 174 individual prey items (96% identified) were brought to the nest area or fed to the nestlings. From these three sources 1003 individual prey items, representing over 463 kg of prey, were identified to species (Table 3.2).

Eleven species of birds and five species of mammals were identified among the prey (Table 3.2). Rock ptarmigan were by far the most common species identified, accounting for 64.5% of all individuals and 73.2% of total prey biomass. The vast majority (99.2%) of ptarmigan taken before the young gyrfalcons fledged (late July, early August) were adults; only 5 of 647 ptarmigan, all taken in late July or early August, were identified as young of the year. Ptarmigan eggs hatched in the first half of July, and by late July were two thirds grown. Passerines accounted for a relatively large number of prey (11.1% of all prey individuals) but were of minor importance (0.6%) in terms of total biomass. Avian species accounted for about three quarters of the diet based on both numbers of individual prey items and total biomass of prey.

Two species made up the bulk of prey from mammalian sources. Arctic ground squirrels, usually juveniles, were used heavily. Roughly equal numbers of juvenile and adult arctic hares were killed. As with passerines, microtines were taken in fair numbers, but made a very small contribution to total prey biomass (0.4%).

Table 3.2. Species of prey recorded in prey remains and pellets, and observed brought to the nest site by gyrfalcons at Kilgavik, 1984 to 1986.

		Prey Numbers					
Species	Average weight(g)[a]	Remains & Pellets	Observed[b]	Total	%TPI[c]	Prey Biomass(g)	%TPB[d]
Rock ptarmigan							
ad	525	640	45(2)	642	64.0	337,000	72.8
juv	400	5	2(0)	5	0.5	2,000	0.4
Total		645	47(2)	647	64.5	339,050	73.2
Lapland longspur	27	48	0	48	4.8	1,296	0.3
Savannah sparrow	20	4	0	4	0.4	80	Tr
Snow bunting	42	3	1(1)	4	0.4	168	Tr
Redpoll sp.	13	1	0	1	0.1	13	Tr
Horned lark	32	11	0	11	1.1	352	0.1
Unid. passerine	20	9	45(34)	43	4.3	860	0.2
Total		76	46(35)	111	11.1	2,769	0.6
Oldsquaw	650	12	1(0)	12	1.2	7,800	1.7
Pintail	1000	3	0	3	0.3	3,000	0.6
Total		15	1(0)	15	1.5	10,800	2.3
Baird's sdpiper	39	2	0	2	0.2	78	Tr
Pectoral sdpr	70	1	0	1	0.1	70	Tr
Lesser golden pl.	145	2	0	2	0.2	290	0.1
Shorebird sp.	50	1	0	1	0.1	50	Tr
Total		6	0	6	0.6	488	0.1
Avian total		742	94(37)	779	77.7	353,107	76.2
Arc grd squirrel							
ad	830	9	0	9	0.9	830	1.6
juv	350	98	61(36)	134	13.4	55,600	12.0
Total		107	61(36)	143	14.3	63,070	13.6
Arctic hare							
ad	2000	15	1(1)	16	1.6	32,000	6.9
juv	500	15	1(0)	15	1.5	13,150	2.8
Total		30	2(1)	31	3.1	45,150	9.7
Brown lemming	70	4	1(0)	4	0.4	280	0.1
Collared lemming	73	3	0	3	0.3	219	Tr
Red-backed vole	22	19	1(1)	20	2.0	440	0.1
Lemming sp.	70	2	0	2	0.2	140	Tr
Vole sp.	25	2	0	2	0.2	50	Tr
Microtine sp.	40	14	5(3)	17	1.7	680	0.1
Total		44	7(4)	48	4.8	1,809	0.4
Mammal total		181	70(41)	222	22.1	110,029	23.8
Unidentified sp.		2	10(0)	2	0.2		
Total all species		925	174(78)	1003		463,136	

---

[a] Weights after Banfield 1974, Dunning 1984, K. Poole unpubl. data.

[b] Figures in parentheses are the number not subsequently found as prey remains at the nest.

[c] %TPI = % total prey individuals.

[d] %TPB = % total prey biomass.

The simplicity of the breeding season diet of gyrfalcons at Kilgavik was evident. Only three species, ptarmigan, ground squirrels and hares, provided 81.9% of all individuals, and 96.5% of the entire prey biomass during the breeding season.

Yearly and monthly variation in gyrfalcon diet were analyzed for 1985 and 1986, when collections were conducted continually throughout the field season (Fig. 3.3). Diet between years differed significantly (G-test, G=22.5, P<0.001). In May and June of both years, rock ptarmigan and arctic hare accounted for 98.2% of the total identified biomass. Adults (at least 11 months old) of both species were the sole component of the kill. Ptarmigan represented a smaller proportion of the kill in July 1985 than in July 1986 (G=50.4, P<0.01), although the use of ptarmigan in both years decreased from May through early August. In 1985 juvenile ground squirrels were preyed upon immediately after they emerged, contributing 32.0% of the total prey biomass in July. No adult ground squirrels were detected in prey remains in 1985. In 1986, however, only five adult and one juvenile ground squirrels were identified in collections from July, contributing 3.2% to total prey biomass. Use of ptarmigan continued throughout July (79.9% of biomass versus 60.7% in 1985), with arctic hare (10.6%) and ducks (5.6%) contributing the bulk of the remainder.

I measured the right humeri from 172 ptarmigan collected in prey remains. The humeri were divided into those collected before (n=74) and after (n=98) 1 July, the approximate date when male ptarmigan acquired cryptic plumage and behaviour. The length of humeri in the two samples did not differ significantly in their means (spring 58.3 mm; summer 58.5 mm; t-test, t=-0.47, df=170, P=0.64) or in their distribution

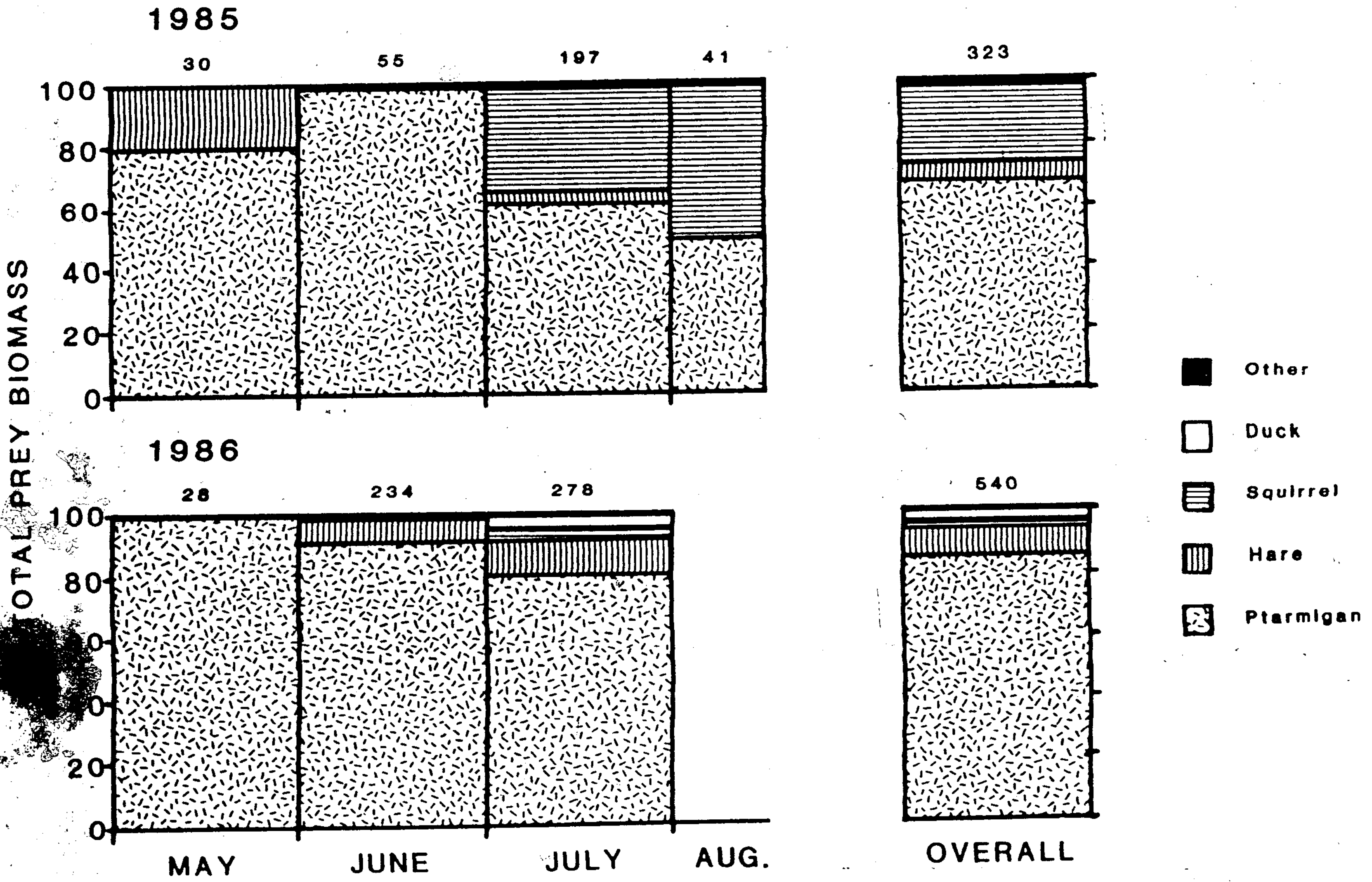

Figure 3.3 Prey taken by gyrfalcons (% biomass) by month at Kilgavik, N.W.T., 1985 and 1986, based on prey remains, pellets, and direct observations. Numbers above columns are number of individual prey items. Column width correspond to period covered by collections.

(Kolmogorov-Smirnov two-sample test, D=0.145, P>0.20), suggesting no selection for one sex over the other during these two periods. However, if differences in humeri length existed between juvenile and adult birds within each sex, selection of specific age and sex classes could confound the analyses. Insufficient data were available to examine this question.

The gyrfalcon nest sites situated closest to base camp in 1985 (site 112) and 1986 (site 122) were studied in the greatest detail and were visited almost daily. At site 112 in 1985, ptarmigan accounted for most prey taken until the end of June (Fig. 3.4). In the last days of June juvenile ground squirrels emerged, and were detected immediately in the prey remains. Use of ground squirrels increased throughout July to a high of 83.5% of the total prey biomass. By contrast, because of near failure of ground squirrel production, ptarmigan were taken at site 122 throughout July 1986. Arctic hares and ducks were taken in larger numbers than previously noted. A few ground squirrels were killed, mainly adults, but not nearly to the extent seen in previous years.

As shown schematically (Fig. 3.5), of the three main prey species, only adults were available to gyrfalcons during the incubation period. In years of successful production of arctic ground squirrels (e.g., 1984 and 1985), most gyrfalcon eggs hatched about 1 week prior to emergence of juvenile squirrels. Emergence of young squirrels also coincided with the period when male ptarmigan began to be cryptic in plumage and behaviour.

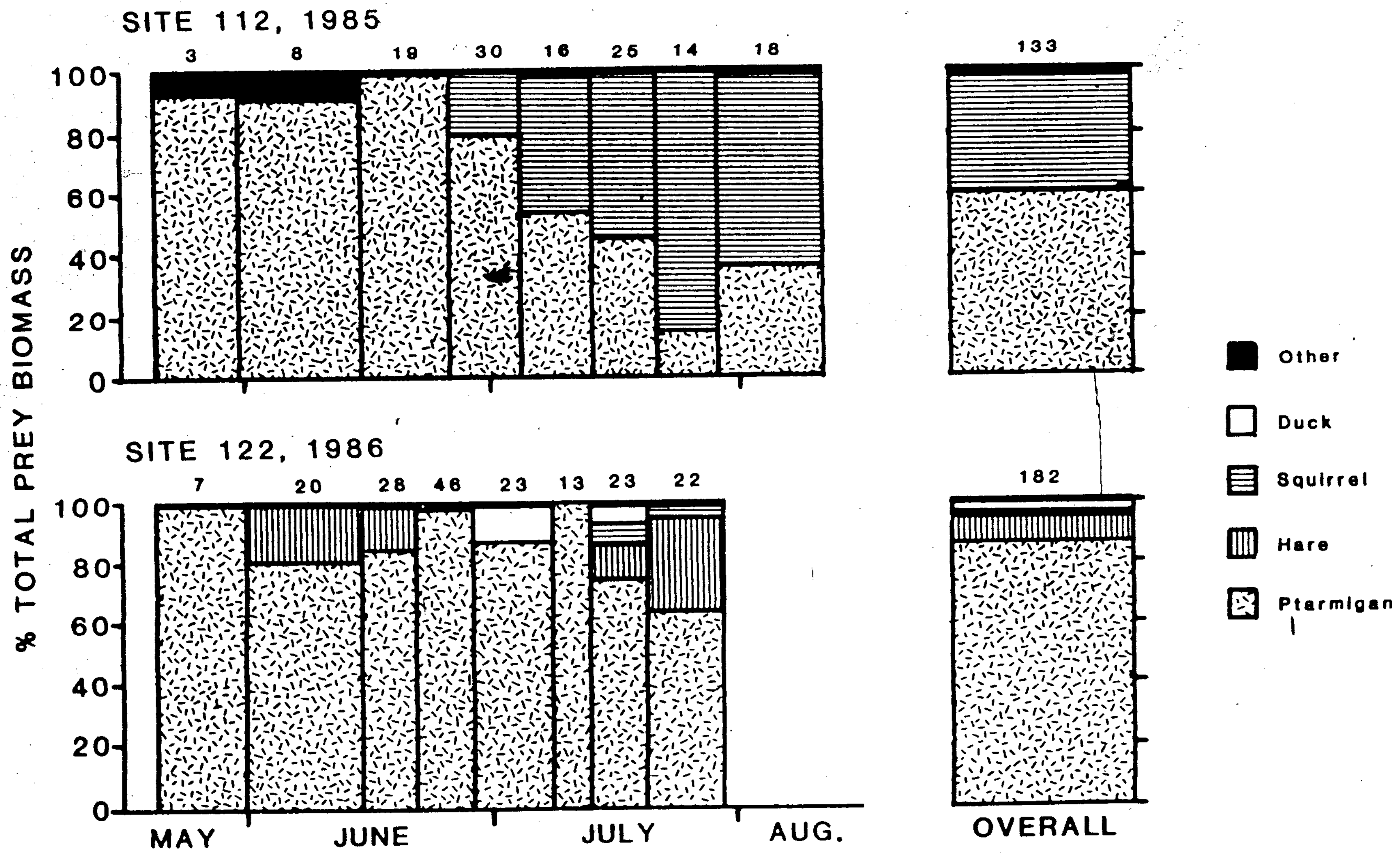

Figure 3.4 Prey taken by gyrfalcons (% biomass) at two sites (112 and 122), N.W.T., 1985 and 1986. Numbers above columns are number of individual prey items. Column width correspond to period covered by collections.

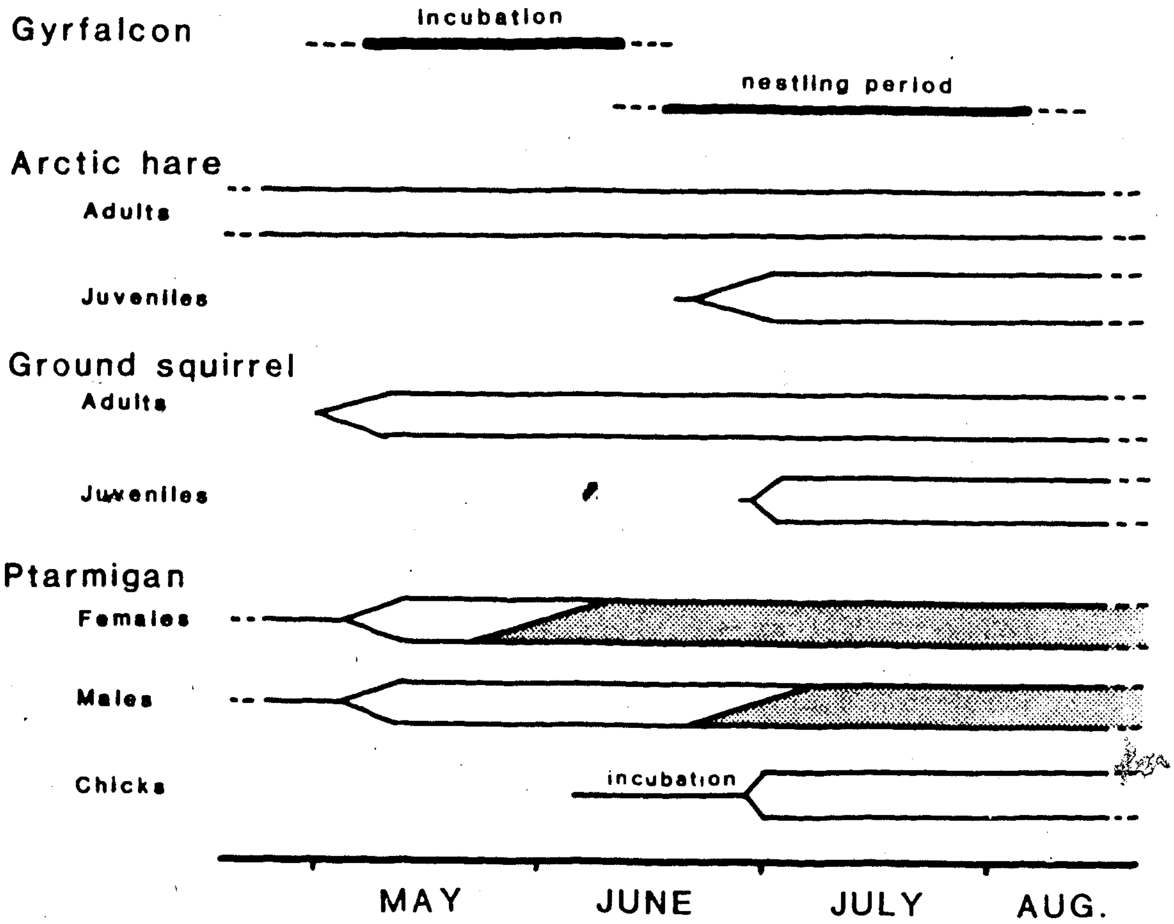

Figure 3.5 The breeding cycle of gyrfalcons in relation to availability of their major prey species. Shading in ptarmigan bars indicate progression to summer plumage.

Prey Biomass

Prey representing 22 to 85 kg biomass per nest were documented in collections and observations at seven gyrfalcon nest sites (Table 3.3). Within each year, more prey biomass was collected at sites with broods of four than broods of two by approximately a 2:1 ratio. The adult female gyrfalcons were observed to eat occasionally at the nest and perches where prey remains were collected, therefore, the female was counted as one 'chick' for calculations. When the mean prey biomass per 'chick' (nestlings and female) was calculated, the difference between broods of two and four was small. Small sample sizes and the difficulty of ensuring that prey remains were collected equally at all sites precluded detailed analysis of these differences.

The pattern of use of prey over the course of the breeding season was exemplified by sites 112 and 122, each of which fledged four young (Fig. 3.6). Prey biomass delivered per day generally peaked in the second and third week after hatch and tapered off to lower levels as the date of fledging approached. However, at each site mean prey biomass per day among the collection periods did not differ from an equal distribution (site 112 $X^2=6.85$, df=6, $P>0.25$; site 122 $X^2=11.52$, df=6, $0.05<P<0.1$).

Feeding Rate and Behaviour

The pattern of occurrence of daily feeding events was similar within each year, but differed between years (G-test, G=35.34, df=23, $P<0.05$). For example, the number of feedings at site 1191, from which two young fledged in 1985, peaked around 1800 hours, with a smaller peak mid-morning between 0800 and 0900 hours (Fig. 3.7a). Feedings occurred

Table 3.3. Total number and biomass of prey items recorded at seven gyrfalcon nest sites, Kilgavik, N.W.T., 1985 and 1986.

Year	Nest site	No. young	No. prey items	Biomass (g)	No. items/ chick[a]	Biomass/ chick[a]
1985	922	2	66	33,473	22	11,158
	1191	2	63	22,020	21	7,340
	112	4	133	50,469	27	10,094
1986	1347	2	93	45,932	31	15,311
	122	4	182	85,225	36	17,045
	113[b]	2-5	99	50,673	--	--
	119[b]	4-1	101	46,527	--	--
Mean (excluding sites 113 and 119)		2	74	33,808		
		4	158	67,847		

[a] The adult female was counted as one chick at each nest (see text).

[b] Brood size at sites 113 and 119 were manipulated in 1986 (see Chapter 4).

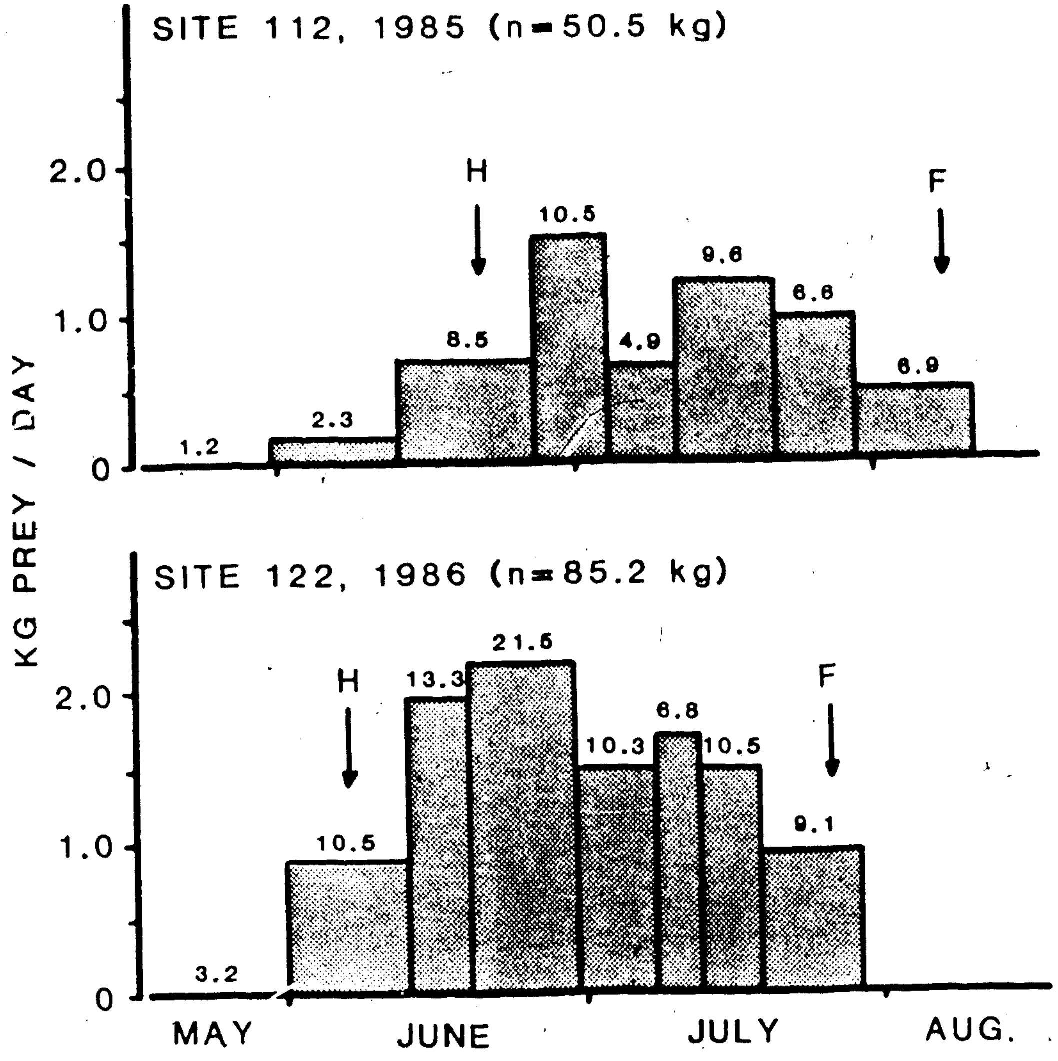

Figure 3.6 Weight (kg per day) of prey used at two nest sites where four chicks fledged, Kilgavik, N.W.T., 1985 and 1986. H=hatch; F=fledging date; numbers above columns are kg prey collected for time period indicated.

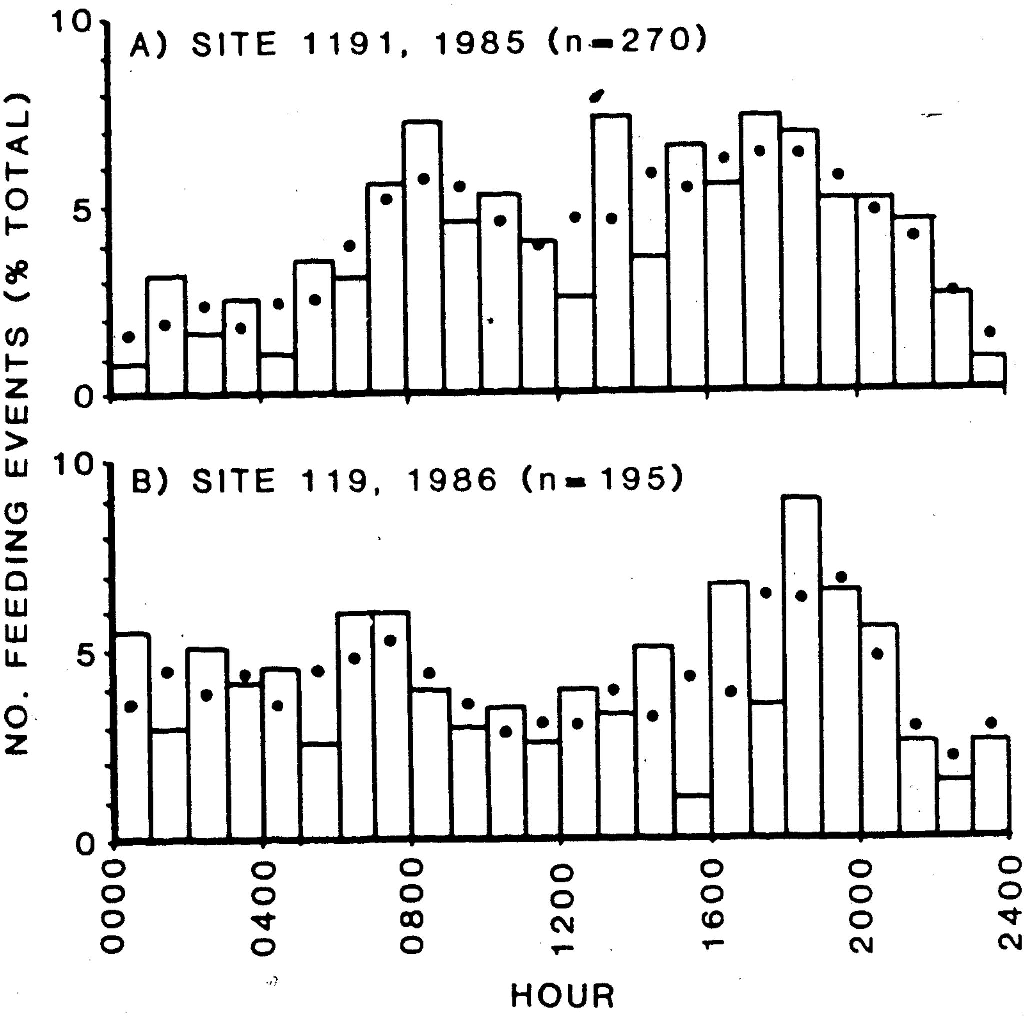

Figure 3.7 Hourly distribution of feeding events at A) site 1191 in 1985 and B) site 119 in 1986, Kilgavik, N.W.T. Dots are 3-hour moving averages; n=number of events recorded.

at all hours of the day, with a minimum frequency around midnight. The number of feedings recorded each hour differed significantly from an even distribution (X^2=42.88, df=23, P<0.01). What I assumed to be the same pair nested at site 119 in 1986, an alternative nest 800 m from site 1191. Four nestlings were fledged in 1986, although I removed three young for 2 1/2 weeks (14-32 days old) during brood manipulation experiments (Chapter 4). The daily pattern of feeding continued to show a slight morning and evening peak, but the overall pattern was much more even because of a greater frequency of feeding events after midnight (Fig. 3.7b). The feeding rate over the 24 hours did not differ from an equal distribution (X^2=15.27, df=23, P>0.5). A similar pattern of evenly distributed feedings also prevailed at the three other sites monitored by cameras in 1986 (X^2, all P>0.9).

When the number of feedings per day (feeding rate) was plotted over the nestling period a pattern emerged, exemplified by site 1191 in 1985 (Fig. 3.8a), that was typical of all nests observed with cameras. The feeding rate increased from hatch to about 10 to 12 days of age, reached a plateau, and slowly decreased after the young were about 25 days of age. A maximum of 12 feedings per day was recorded. Feedings were observed the day of hatch; at one site I saw the female trying to feed pipping eggs. As determined from analysis of time-lapse photographs, the pooled mean length of feeding for all sites was 11.8 minutes (n=923) and at different sites ranged from 10.0 to 13.0 minutes. There was no relationship between brood size and mean length of a feeding (r=-0.02, P=0.48, n=6). Feedings took 1 to 37 minutes to complete. The mean interval between successive feedings ranged from 118.8 to 235.5 minutes

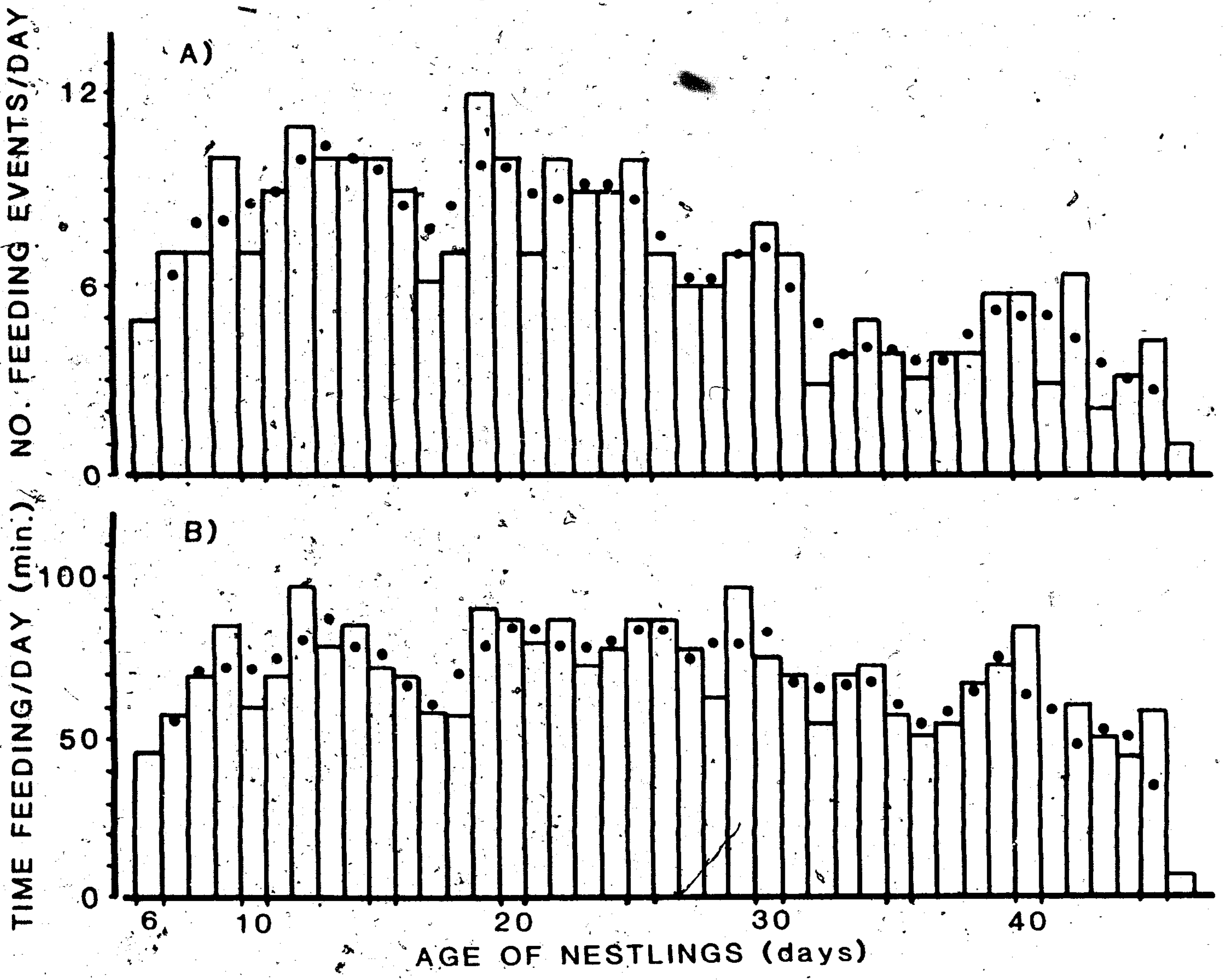

Figure 3.8 A) Feedings per day and B) total time feeding per day at site 1191, Kilgavik, N.W.T., 1985. Dots are 3-day moving averages.

(pooled mean 217.8 minutes, n=850). Again, there was no clear relationship with brood size (r=-0.29, P=0.29, n=6).

Assuming that larger prey required longer periods of time to consume, I also plotted the total time spent feeding per day (Fig. 3.8b). Time spent feeding each day remained relatively constant throughout the nestling period, and did not fall off until a week or two before fledging. When total time spent feeding each day, at each of the seven nests, was plotted against the daily maximum temperature and an index of precipitation (1=sunshine to 4=severe storm), no relationship emerged.

Data were examined to determine feeding rate and total time feeding per day in broods of two (n=3) and four (n=2)(Fig. 3.9). There was no relationship between brood size and feeding rate; however, broods with four nestlings spent more time feeding each day than did broods of two. The difference in means, however, was not proportionately equal to the difference in brood size, indicating that although broods of four ate for longer time periods as a group, nestlings in broods of two had more food available to them and fed for longer on a per capita basis (mean 41.1 versus 28.0 minutes per day per chick). Small sample size precluded statistical analysis of these differences. Comparison of the slope of the linear portion of the nestling's growth between chicks in broods of two and broods of four revealed no significant difference within each sex (Analysis of Covariance: males F=0.01, P=0.93; females F=0.24, P=0.63).

About 6% of feedings recorded on film were in response to food dropped off at the nest by one of the adults. The average age of the chicks when food deliveries of this sort were first detected was 35 days

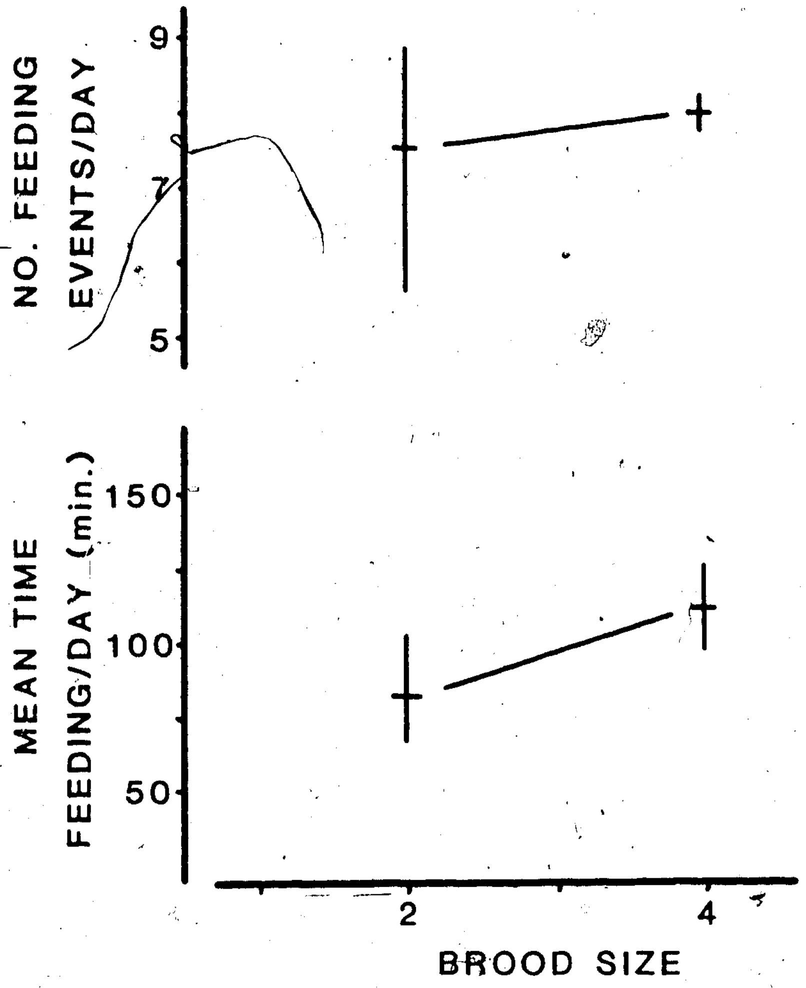

Figure 3.9 Relationship of brood size with feeding rate and mean total time feeding during the second week post-hatch. Mean and range for broods of two nestlings (n=3) and four nestlings (n=2).

(range 29 to 43 days). From direct observations, food deliveries involved prey of all sizes.

Caching

Partial consumption occurred in all cases when prey were observed brought to the nest by an adult. Partially consumed prey were usually cached, such that uneaten prey never accumulated at the nest itself. Fifty-eight instances of caching were observed at gyrfalcon nest sites during 1985 and 1986. Caching occurred when partially consumed, but occasionally uneaten (prey brought to the nest area but not to the nest itself), prey were deposited along the cliff face. These caches were retrieved later and eaten by the adults or fed to the nestlings. Caching involved the remains of large prey items; no caching of microtines or passerines was observed. Almost all (93%) caching was carried out by females; males were recorded caching on only four occasions, all cache retrievals.

Caching was not recorded at any gyrfalcon nest site before the eggs hatched. The frequency of caching was greatest when the chicks were young, and decreased as the nestlings grew (Fig. 3.10), No caching was observed after nestlings reached 29 days of age.

A typical cache site was a small vegetated ledge on the cliff face, with the prey item tucked with great care at the back of the ledge or beside a clump of vegetation. Most instances of caching (43 of 49 (88%) in 1985 and 1986 where the exact location of the cache was determined) were within 100 m of the nest along the cliff face, and the furthest recorded was 200 m from the nest. The distribution of cache sites used within 100 m of the nest, in 25 m increments, did not differ from

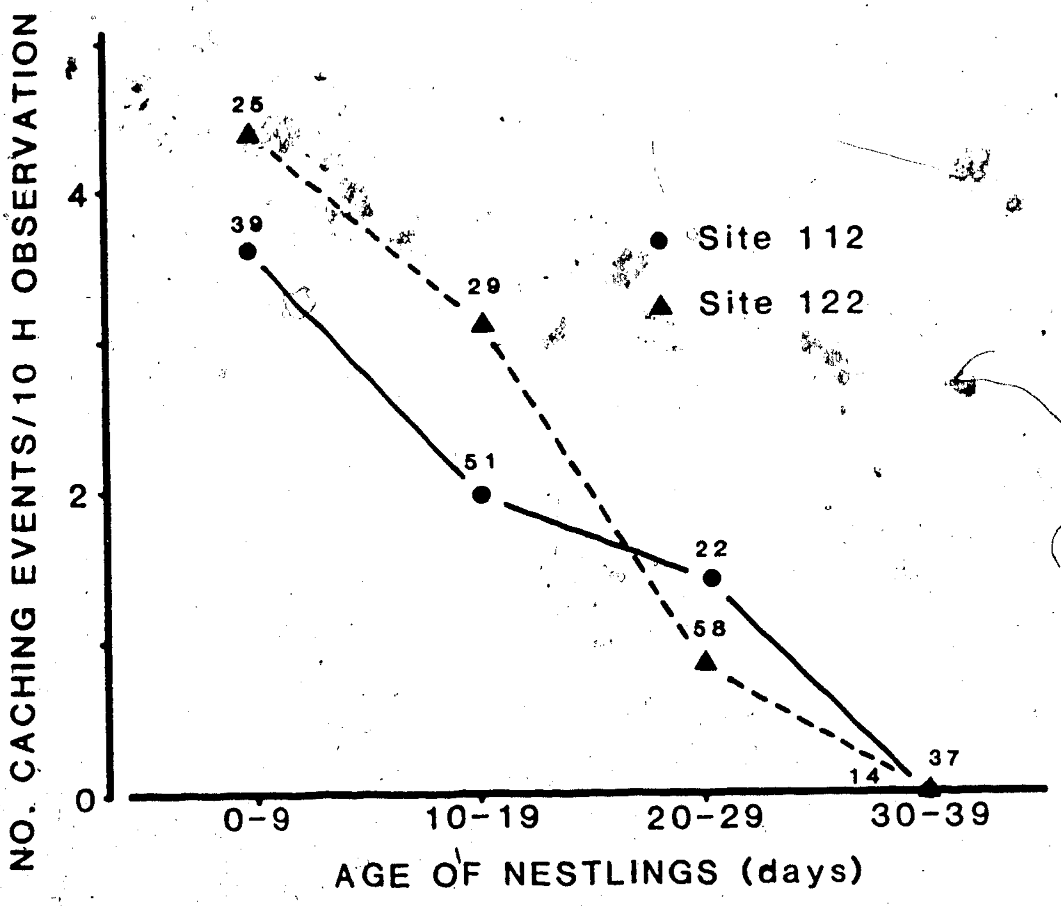

Figure 3.10 Number of times caching events observed at nest sites 112 and 122, Kilgavik, N.W.T. Numbers above symbols denote hours observed for given time period.

equality ($X^2=1.2$, df=3, P>0.5). Reuse of cache sites was infrequent. At gyrfalcon nest site 112 in 1985, 11 cache sites were used for 26 caching events, and 13 sites were used for 25 events at gyrfalcon site 122 in 1986.

Role of Sexes

On average males participated in 5.7% (range 3.1 to [illegible]%) of the direct feedings (n=932) recorded on time-lapse [illegible] at five gyrfalcon nests. Nevertheless, when results of direct [illegible] from 1984 to 1986 were combined, using [illegible]e instances when the identity of the adults that actually kill[illegible]y item was known, male gyrfalcons provided 73% of the prey it[illegible]rought to the nest site (n=125). In many instances, particularly when older nestlings were present, the female flew up to 2 km to meet the incoming male and received the prey item from it. Often the female returned directly to the nest to feed the chicks, but on occasion she perched for up to 30 minutes near the transfer point and vocalized (using the wail, Platt 1977) before returning. At times, therefore, the identity of the adult that actually killed the prey was in question; these instances were removed from the calculation.

The male provided all the prey brought to the female during incubation, and to the female and chicks during the first 2 to 3 weeks of the nestling period. The female began foraging trips when the chicks were about 18 to 25 days of age. Initial absences were for short periods, but their length increased as the young grew older.

Prey Size

The mean weight of prey (250.2 g, $n=91$) supplied to the nest site by male gyrfalcons was significantly less (1-tailed t-test $t=-1.81$, $P=0.036$) than the weight of prey (330.5 g, $n=33$) captured by females. The lower mean weight of prey resulted primarily from a greater proportion (39 of 46, 85%) of passerines taken by males. Male gyrfalcons supplied most (95%) of the ptarmigan taken, which was expected since ptarmigan comprised the bulk of the diet at the time when males were the sole provider of food to the nest site. The harvest of ground squirrels was divided about equally between sexes (27 by males:23 by females).

During 801 observation hours at gyrfalcon nest sites from 1984 to 1986, both the departure and return times for 83 individual foraging trips were recorded when both the sex of the adult killing the prey item and the identity of the prey were discerned. No relationship was found between date and time away from the nest site for ptarmigan or ground squirrels within each year (all $r<0.30$, $P>0.25$). However, a trend existed for larger prey items to be brought when time absent was longer, although there was a great deal of variation within each prey class (Table 3.4). All smaller prey items (passerines and microtines) were brought to the nest after absences of 90 minutes or less, whereas in 19% of the cases when ground squirrels and ptarmigan were taken, the time exceeded 90 minutes. The relationship between these two variables was highly significant ($P=0.001$), however, it only explains a low proportion of the total variance ($r^2=0.09$), implying that other factors were also operative. It is also apparent that the benefit, in terms of biomass

Table 3.4. Prey size and time away from the nest for gyrfalcons at Kilgavik, N.W.T., 1985 and 1986.

Prey item	n	Weight[a] (g)	Mean time (min)	SD	Range (min)	Mean weight/min (g/min)
Passerine	38	20	26.8	22.2	1-84	0.7
Microtine	5	40	33.0	33.5	1-90	1.2
Ground squirrel	39	400±	54.3	60.7	1-286	7.4
Ptarmigan	15	525	79.9	76.1	1-227	6.6
Arctic hare	1	1000	15.0	--	--	66.7

[a] Weights after Banfield 1974, Dunning 1984, K. Poole unpubl. data.

taken per unit time of assumed hunting, was greater the larger the prey item.

Handling time was likely greater for the larger prey items. Ptarmigan were brought to the nest eviscerated, almost always decapitated, and with most of the body feathers removed. Ground squirrels were decapitated on most occasions, but were not plucked. When fed to nestlings, squirrels were eaten from the neck region posteriorly with the stomach and intestines pulled out and left on the nest. Passerines and microtines, on the other hand, were usually eaten without pre-processing, with the exception of occasional plucking of primaries or fur at the nest.

Discussion

Prey Availability

Weather factors at Kilgavik appeared to have a significant influence on the availability of avian prey. The dates of arrival of large numbers of migrating rock ptarmigan and their dispersal onto breeding territories was apparently influenced by ambient conditions. Myrberget (1986) found the timing of snow-melt most closely correlated with variations in laying dates in L. <u>lagopus</u> in northern Norway. Air temperature has an important effect on the gonadal cycle in ptarmigan (Stokkan et al. 1986). Low temperatures or severe storms in the spring may delay both the timing of gonadal growth and the development of vegetation used as food, and may also influence migratory behaviour of ptarmigan, including distances covered during migration. Once begun, breeding activities were readily depressed by inclement weather, as clearly demonstrated in the spring of 1986.

The densities of rock ptarmigan observed at Kilgavik (2.2-2.9 males per km^2) appear to be within the published range for the species, which varies from about 0.4 territorial males per km^2 on Bathurst Island, N.W.T. (MacDonald 1970), to 3.2 to 8.3 ptarmigan (both males and females) per km^2 in central Alaska (Weeden and Theberge 1972). The 41% difference among years in densities of breeding male ptarmigan at Kilgavik cannot be considered significant because of the low density present and relatively small area censused. The proportion of yearlings in the spring population remained relatively constant from 1984 to 1986, suggesting some stability in the population (Weeden and Theberge 1972). From a review of the literature on cycles in ptarmigan, it is difficult to determine whether the population is actually cyclic. No long term studies have been carried out on rock ptarmigan in the central Canadian arctic to determine if they are cyclic, and if so, what is the amplitude of their cycles. Data on population cycles in L. mutus in other parts of the world are equivocal; cycles of 3 to 10 years with increases of 2.6- to 6.5-fold have been reported (Bengtson 1971, Weeden and Theberge 1972, Watson and Moss 1979), but there is little evidence for fluctuations in mainland populations of Scandinavian rock ptarmigan (Langvatn and Moksnes 1979).

My observations and those of other researchers (Cade 1960, Woodin 1980, Nielsen 1986) suggest that the vulnerability of ptarmigan to gyrfalcon predation varies over the course of the breeding season, and is related to territorial activity and progression of moult. Ptarmigan numbers on the study area rose dramatically with the influx of migrating birds, and vulnerability probably increased with the onset of territorial activity. Because the moult in male ptarmigan is delayed until later in the season than in females, and their display flights persist until late June, the vulnerability of males to predation did not diminish until late June or early July. At that time behavioural changes and the attainment of more cryptic summer plumage decreased their conspicuousness and their vulnerability.

Production of juvenile ground squirrels was reduced significantly at Kilgavik in 1986, apparently as a result of inclement spring weather. In examination of an arctic ground squirrel population in northwestern Alaska, Carl (1971) stated that they "maintain a relatively constant population", but made no mention of disruption of the breeding season because of poor spring weather. However, late spring snowstorms have been shown to have a negative impact on ground squirrel reproduction (Morton and Sherman 1978). The impact of th[illegible] of one year's production on the size of the subsequent year's population of ground squirrels at Kilgavik is unknown, but may be significant.

Densities of passerines at Kilgavik averaged 6.2 birds per 1 km transect (5.6 birds per 900 m), similar to the average of 5.8 birds per 900 m transect observed in northwestern Greenland (Burnham and Mattox 1984), but much below the average of 32 birds per 900 m transect found in Alaska (C. White et al. unpubl., cited in Burnham and Mattox 1984). No trend among years could be detected in density of breeding birds at Kilgavik, but the timing and success of passerine reproduction was apparently dependent upon spring and early summer weather conditions.

To summarize, the density of ptarmigan from 1983 to 1986 increased slightly, and the availability of ptarmigan to gyrfalcons varied fairly predictably during each breeding season, influenced to some degree by spring weather conditions. Nearly complete failure of production of juvenile arctic ground squirrels meant the loss of a readily available source of prey in 1986.

Food Habits

I believe the use of a combination of prey remains, pellet collections, and direct observations reliably reflected the actual diet of nesting gyrfalcons at Kilgavik. There was no evidence that prey remains were removed from the nest cliff area by the adults, as suggested by some authors (Bengtson 1971, Jenkins 1974). Loss of remains to scavengers, a potential bias in some areas (Weir 1967), was minimized through frequent collections at most nests.

Fewer pellets than expected were collected, partly because at some sites the pellets were rapidly broken up and lost into the nest substrate through the activities of the young gyrfalcons. Pellets are an important source for detecting smaller prey items that are often underestimated in collections of prey remains alone (Errington 1932, Langvatn 1977, K. Poole unpubl. data). Small prey items such as passerines and microtines made up a very small proportion of the total biomass detected at nests. Even if small prey items were of critical importance in the diet for brief periods during the nestling phase, their underestimation would have a minimal impact on the calculated diet in terms of total prey biomass. Pellets were less useful in determining the number of large prey items in the diet. The main bones of most large prey, such as the sterna of ptarmigan, were not ingested. Furthermore, gastric digestion of bones by the Falconiformes is [illegible] thorough than it is in the Strigiformes, resulting in a smaller proportion of bone in falcon pellets (Duke et al. 1975).

Direct observations alone can be used to determine prey use over the entire breeding season only if observations cover the entire feeding period every day. The timing of periods of observation, usually between 0900 and 1800 hours from mid-June to mid-July, may have biased the results. If different prey species were taken more often during other periods, they would be underrepresented. Consequently, I believe a more accurate and complete picture of the diet was obtained by combining techniques to examine prey use.

The time-lapse camera units proved useful for examining aspects of feeding behaviour at nest sites. The accuracy of detecting feedings was good, as only one of 25 feedings was missed when 93 hours of time-lapse film were checked against direct observations at sites with chicks less than 24 days of age. Nestlings began to be more mobile at about 25 days of age, and at some sites moved out of camera view for periods of time, thereby diminishing the reliability of the films as the nestlings neared fledging age.

Diversity of Prey

The narrow spectrum of prey species used by gyrfalcons at Kilgavik from 1984 to 1986 reaffirm the comment made by Cade (1960), that gyrfalcons are much more specialized than peregrines (Falco peregrinus) in their food habits, depending primarily upon resident species of prey. Even so, the diet of gyrfalcons at Kilgavik was simplistic in the extreme. The Shannon-Wiener function (Krebs 1978) was used to measure diversity in the composition of the diet. From the overall diet (Table 3.2) I calculated a value of H=0.47 (1985 H=0.52, 1986 H=0.37). Nielsen (1986:111) calculated H-values for gyrfalcon diets published in the literature (18 studies) and found a range of 0.44 to 3.03 (mean 1.77). Only one study (Haftorn 1971, cited in Nielsen 1986) had a lower diversity of dietary prey than that at Kilgavik. The mean number of species taken in these studies was 16 (range 4 to 40 species), identical to the 16 species taken at Kilgavik. Thus, although gyrfalcons at Kilgavik killed a moderate variety of species, they depended mainly on only a few.

Some potential prey species were not used by gyrfalcons at Kilgavik. Eiders were plentiful along Melville Sound and Elu Inlet, arriving about 1 June. Gulls nested in colonies along the ocean and were seen often far inland. No use of these species was detected, despite some gyrfalcon nest sites being located within several hundred metres of colonies of gulls and groups of eiders. Although seabirds and gulls have been used heavily by some populations of gyrfalcons (Dement'ev and Gortchakovskaya 1945, Dement'ev 1960, R. Bromley pers. comm.), sufficient numbers of more preferred prey species were probably present at Kilgavik, and hence were selected.

Yearly and Seasonal Diet

Ptarmigan formed the majority of the diet from the onset of breeding activities by gyrfalcons until late June in both 1985 and 1986. Despite higher vulnerability of male ptarmigan compared with females, related to territorial activities and delayed moult, gyrfalcons at Kilgavik did not appear to take male ptarmigan more often than females, contrary to the findings of previous authors (Cade 1960, Woodin 1980, Nielsen 1986).

Adult arctic hares were killed as well, an impressive feat considering that they weigh up to 4 kg (Banfield 1974) and the adult gyrfalcons weigh from 1.2 to 1.8 kg. Extensive use of juvenile hares by gyrfalcons on Ellesmere Island has been reported by Muir and Bird (1984), but they doubted that a gyrfalcon could kill an adult hare. However, the evidence collected at Kilgavik suggests that even male gyrfalcons are capable of dispatching and transporting (in pieces) an adult hare to the nest.

Although adult arctic ground squirrels were present above ground after early May, depending upon the vagaries of weather, very few were taken. The reason for low use of this potential prey source was unclear. Gyrfalcons take adult hares, thus it is difficult to believe that an adult squirrel, weighing from 700 to 1,300 g at emergence (K. Poole unpubl. data), was too large for a male gyrfalcon to kill. However, ground squirrels may have some ability to injure falcons, as fall-captured juveniles often have foot and beak scars that may result from interactions with squirrels (R. Bromley pers. comm.). It cannot be argued that colonial squirrels are too wary to allow many being taken by aerial predators, because adults were used extensively in May and June by golden eagles (Aquila chrysaetos) nesting at Kilgavik (K. Poole unpubl. data). I suspect that in the spring gyrfalcons have a fixed preference for ptarmigan and hare, and during my study these species were present in sufficient numbers that gyrfalcons did not have to switch to less preferred prey such as adult ground squirrels. Arctic ground squirrels are taken in large numbers in other areas where they and gyrfalcons are sympatric (Cade 1960, Roseneau 1972, Platt 1977, Bente 1981, N. Barichello pers. comm.), although it is unclear whether adults formed a large portion of the kill in these studies.

The pattern of prey use in early July in years of successful production of ground squirrels corresponded to an increase in availability of juvenile squirrels and the onset of cryptic behaviour and plumage in ptarmigan. Decreased use of Lagopus with the waning of territorial activity has been noted in other gyrfalcon populations, where gyrfalcons switched to other prey such as waterfowl (Woodin 1980, Nielsen 1986), and rodents and rodent-eating birds (Cade 1960, Roseneau 1972, Bente 1981).

In most populations of gyrfalcons that rely upon Lagopus spp. for a majority of their diet, nestlings were fed primarily adult ptarmigan (Hagen 1952, Cade 1960, Pulliainen 1975, Langvatn and Moksnes 1979, Nielsen 1986). This is in contrast to many other raptors, the nestling periods of which correspond with the time when their main prey populations have increased with the flush of immature individuals (Newton 1979). Although ptarmigan formed a majority of the diet, the gyrfalcons at Kilgavik appeared able to exploit a source of naive immature ground squirrels during the nestling period, as shown in 1984 and 1985. A benefit of using adult ptarmigan during the nestling period is that the gyrfalcon fledglings gain independence in the presence of vulnerable, newly-fledged ptarmigan.

Nutritional demands of the gyrfalcon family peak when the rate of growth of nestlings is maximum and almost linear (Ricklefs 1968, Brown 1976, Newton 1979). This occurred at between about 6 and 26 days of age in male gyrfalcons, ending 1 or 2 days later in females (Chapter 2). Emergence of juvenile ground squirrels at the end of June in 1985 coincided with the beginning of this stage of rapid growth (Fig. 3.5). Thus, an abundant and vulnerable prey was successfully exploited almost precisely at the time when energy demands on the adults, primarily the males, were greatest. Similar synchrony of the nestling period with the emergence of juvenile ground squirrels (Spermophilus spp.) has been demonstrated in other raptors (Schmutz et al. 1980, Haak 1983). In years of successful squirrel production, use of young squirrels could probably carry the gyrfalcon family through this period of high energy needs even if ptarmigan numbers were much reduced.

By contrast, although most gyrfalcon nestlings in 1986 were fed through the period of rapid growth almost exclusively on adult ptarmigan, no cases of reduced growth rate or starvation of nestlings were noted. Indeed, in 1986 the mean brood size per successful nest was the highest observed during 5 years of survey. At site 122 a mean of 3.2 ptarmigan per day was recorded in prey remains collected during the time nestlings were 11 to 24 days of age. Clearly, the adults were able to provide sufficient food during this period of high energy demands despite restricting themselves to ptarmigan.

Densities of ptarmigan were similar in 1985 and 1986, but juvenile squirrels were preyed upon heavily in 1985 when they were widely available. Why one prey is selected over another depends upon many factors, including availability (prey density), vulnerability, search time and handling time (Krebs et al. 1983). In 1985, young ground squirrels were present in large numbers, and appeared highly vulnerable to predation. By the time young squirrels emerged, ptarmigan had been harvested for over 2 months, possibly depleting densities in the vicinity of the gyrfalcon nests. Thus, the density of ground squirrels within a prescribed radius of the nest was likely much higher than the density of ptarmigan. There was little lag time between emergence of juveniles and frequent use of them by gyrfalcons. Handling time for squirrels was also probably shorter than for ptarmigan. All these factors could enhance the appeal of juvenile squirrels to gyrfalcons.

Gyrfalcons frequently respond to high densities of a new prey source. For example, Cade (1960) reported that microtines and rodent-eating birds were used heavily in northern Alaska, despite the presence of "good numbers" of ptarmigan. Investigators have also recorded gyrfalcons responding to experimental releases of prey (Bente 1981). No numerical response to changing density of prey was detected at Kilgavik, probably because of the relative stability in ptarmigan numbers from year to year. However, the gyrfalcons at Kilgavik clearly showed a functional response to increased prey density by changing the proportions of prey used. In 1985 gyrfalcons responded to the emergence of juvenile ground squirrels by increasing use of this species and killing fewer ptarmigan. In 1986 little change in diet was noted at the end of June as the proportion of ptarmigan in the diet remained high, apparently because of a lack of juvenile squirrels.

Biomass of Prey

Based upon the number of ptarmigan and other large prey identified at nest sites, and assuming some prey remains were missed, an estimated 120 to 170 adult ptarmigan or equivalent were required to successfully raise four chicks from initiation of incubation to fledging. Fewer young required fewer prey (Table 3.3). Similar estimates of 150 to 200 ptarmigan units as the requirement for the nesting season (lengths vary) have been published (Hagen 1952, Cade 1960, Bengtson 1971, Langvatn 1977).

The maximum prey biomass consumed per day by the nestlings and female (Fig. 3.6) coincided closely with the period of rapid growth by the nestlings. To fledge young successfully an average of 1.0 to 1.5 kg of prey per day were required over the 47-day nestling period. Kishchinskii (1957) estimated that a family with two nestlings consumed about 1.1 kg of prey per day over a 12-day period, but did not mention the stage of the nestling period.

The determination of biomass used at site 112 in 1985 and site 122 in 1986 (Table 3.3) permitted a rough estimation of the efficiency of conversion from prey to chick biomass. Using average weights of 1.2 kg and 1.5 kg for male and female nestlings at fledging, respectively, and counting the adult female as one average chick (1.35 kg), a 12.3% efficiency was calculated from data obtained at site 112, and an 8.3% efficiency for site 122. Comparison of these efficiencies raises the question of the impact of the different proportions of prey species used at each site. Forty-five percent of the nestling's diet at site 112 came from juvenile arctic ground squirrels. No ground squirrels were detected in the diet at site 122, where ptarmigan contributed 86% of the biomass of the diet. The higher efficiency calculated for site 112 may have resulted from a higher fat, and hence caloric, content associated with these juvenile ground squirrels, when compared with adult ptarmigan, possibly an important reason why gyrfalcons switched rapidly to juvenile squirrels when they became available.

Impact on Ptarmigan

What impact did gyrfalcon predation have on the rock ptarmigan population breeding at Kilgavik? In 1986, the density of ptarmigan averaged 2.85 males per km^2 (Table 3.1). Assuming an even sex ratio among ptarmigan in the spring (Weeden and Theberge 1972), approximately 11,400 ptarmigan were present on the 2,000 km^2 study area in late May. The sex ratio of ptarmigan killed by gyrfalcons over the entire breeding season likely approached equality. In Iceland, Nielsen (1986) found 56% of ptarmigan killed by gyrfalcons to be male, with proportionately more males killed earlier in the season and females later.

Assuming 140 ptarmigan were used by each pair of gyrfalcons, and 10 pairs of breeding gyrfalcons were present, then 1,400 ptarmigan, or 12.3% of the entire population was killed by gyrfalcons. Assuming the gyrfalcon kill was restricted to within 5 km of the nest (no overlap in hunting areas), 31.3% of the ptarmigan would have been removed from that area; within 10 km this figure falls to 7.8%. Little evidence exists on the distance gyrfalcons travel to hunt, although they may regularly fly up to 10 km to find prey (Kishchinskii 1957, Nielsen 1986).

Therefore, depending upon how far gyrfalcons fly to hunt, gyrfalcon predation alone could remove a large number of ptarmigan, at least within 5 km of the nest. Additional pressure is exerted by other predators, such as golden eagles. Whether predation has a major impact in determining spring ptarmigan numbers at Kilgavik is conjecture (Cade 1960), but the density of ptarmigan in some areas, including close to gyrfalcon nests, did appear subjectively to be reduced significantly over the course of the breeding season. Presence of juvenile arctic ground squirrels probably deflects some predation pressure away from the ptarmigan, possibly resulting in a higher density of ptarmigan the subsequent year.

Feeding Patterns

The difference in daily feeding pattern observed between 1985 and 1986 may be related to a number of factors. Inherent differences in foraging behaviour between pairs is not likely a reason, because the results illustrated (Fig. 3.7) were from the same pair over two breeding seasons. Availability of prey varied greatly between years, and the foraging success may have been linked to prey activity cycles. In 1985 arctic ground squirrels comprised a significant part of the diet during the nestling period, while in 1986 ptarmigan formed the majority of prey items. Possibly the activity of squirrels above ground peaked mid-morning and late afternoon to result in the activity pattern observed in 1985. Jenkins (1974) observed a pattern similar to that seen in 1985 at a nest in Greenland where non-ptarmigan prey predominated (primarily Lapland longspur, oldsquaw (<u>Clangula hyemalis</u>) and arctic hare).

It might be argued that the gyrfalcons were more food-stressed in 1986, because few juvenile ground squirrels were present and the adults had to feed four young, as opposed to two in 1985, for most of the nestling period. Under conditions of relative food scarcity the adults, primarily the male, would presumably have had to have worked harder and longer to supply adequate food to the family. Nevertheless, despite a similar pattern of relatively even feeding throughout the day being recorded at all four gyrfalcon sites under camera observation in 1986, total prey biomass per nest appeared greater in 1986 than 1985 (Table

3.3), suggesting no shortage of prey. Thus, I suspect that the differences between years in the activity cycle of the main prey used caused the observed feeding patterns.

Feeding Behaviour

During many hours of observation at nest sites it became apparent that in general the youngest member of a brood received less "bites" of prey than its older siblings, and consequently experienced a slightly retarded weight gain (Chapter 2). Larger siblings were simply quicker to line up in front of the adult providing food, and were capable of stretching a little further to be fed. These differences were apparent despite the hatch being relatively synchronous. With large prey items the older nestlings would eventually collapse with bulging crops, enabling the youngest sibling to feed undisturbed. Frequently, only one or two chicks from a brood of four would be fed bites from smaller items. Despite the slightly retarded growth of some younger siblings, I found no evidence that last-hatched chicks succumbed to starvation, although some may have died at a very young age and left no evidence of their demise. Last-hatched chicks usually caught up to their siblings in weight at about 3 weeks of age and fledged at normal weights (Chapter 2). Other authors have also noted an unequal division of prey fed to nestlings in wild gyrfalcons (Muir 1975, Platt 1977, Fletcher and Webby 1977).

Caching enabled large prey items, not entirely consumed by the chicks and female early in the nestling period, to be reused, a form of insurance in the event that the male was unsuccessful in providing food for a period of time. I observed some prey items used three times before all the meat was removed. Caching involves defense of the cache sites from scavengers (Weir 1967). On a few occasions I saw either gulls or common ravens (Corvus corax) approach a gyrfalcon nest and take a cached item. Often the male gyrfalcon attacked the intruder and drove it off. In one instance a male reclaimed a ptarmigan from a glaucous gull 400 m from the nest. Caching items close to the nest would seem to be a good strategy to dissuade scavenging. The incidence of caching at gyrfalcon sites is well reported (Muir 1975, Nielsen 1986), with females involved in most (94%, Bente 1981) or all (Platt 1977, Jenkins 1978) of the caching activities.

Males took on average smaller prey than females, which conforms to the general pattern found in most sexually dimorphic raptors (reviewed by Newton 1979). At Kilgavik there was a lack of readily available prey of different weight classes. Most prey were either fairly light (<70 g) or heavy (>400 g). The male gyrfalcons took proportionately more of the lighter prey, which may reflect their increased agility resulting from lighter wing loading than females (Cade 1982) and their lower weight making hunting of lighter prey more energetically efficient.

Optimal foraging models propose that predators select the most profitable prey items (Krebs et al. 1983). Within the framework of this theory, the central place foraging model predicts prey size as a function of distance, e.g., greater selectivity (larger prey) at greater distances (Orians and Pearson 1979). It was impossible to visually follow adults on their foraging trips to determine distance travelled. The question can still be examined if we assume that time away from the nest site reflected distance travelled (Orians and Pearson 1979).

Although much variation was detected, prey size did increase as time away from the nest increased (Table 3.4), in conformation with optimal foraging theory. However, when energy per unit time for each prey type was calculated, the larger prey items were on average vastly superior to smaller items in providing a high return per trip. In some instances passerines and microtines provided similarly high rates of return, but only when the foraging trip took less than 10 minutes to complete. Thus, it may not have been energetically profitable for gyrfalcons to take smaller prey items on trips of greater than 10-minutes duration.

Effects of Prey on Breeding Ecology

The evidence presented encourages examination of the factors that might influence density of breeding pairs, timing of breeding and productivity of gyrfalcons at Kilgavik. Access to two resources, nest sites and food, usually limit the number of pairs that attempt to breed in a given area (Newton 1979). As demonstrated earlier (Chapter 2), with the abundance of stick nests and ledges present throughout the study area, nest sites cannot be considered to be in short supply. Over the contiguous portion of the study area spacing of pairs tended to be regular, a pattern often seen where an abundance of nest sites is available (Newton 1979).

If food supply is the ultimate factor limiting the density of gyrfalcons at Kilgavik, when does this limitation take place? I conclude that food was not limiting during the nestling period since consumption increased during that period (Fig. 3.8), prey biomass increased with larger broods (Table 3.3), females did little hunting until well into the nestling period, and no cases of nestlings starving from lack of food were detected. These observations reflect the conditions of food abundance proposed by Newton (1979).

Food stress in the breeding cycle of raptors, however, usually occurs during both the prelaying/laying period and the early nestling period (Brown 1976). Thus, the food supply during prelaying and laying may determine pair spacing. The importance of sufficient food to the breeding female during prelaying has been demonstrated clearly (Newton 1979, Drent and Daan 1980, Newton et al. 1983, N. Barichello pers. comm.). The prelaying period coincided with the yearly low in prey availability at Kilgavik; only arctic hares and small scattered groups of ptarmigan were present. Since food may limit population levels only during certain times of the year (Newton 1980), I suspect it is during the critical prelaying period that the spacing of pairs is determined. The mechanism used to achieve spacing is unknown, but may relate to intraspecific interactions at the onset of breeding activities, as appears to be the case in arctic breeding peregrines (Court 1986).

Timing of breeding, and production and productivity are affected to a large degree by similar factors. Much of the variation in both laying dates and productivity of a species can be related to differences in food supply (Newton 1979, 1980). Adequate supplies of food are essential to the reproducing female. Most pairs of gyrfalcons at Kilgavik initiated laying coincidentally with the main influx of migrating ptarmigan. The timing here appeared critical; when the ptarmigan migration was delayed, so was laying in gyrfalcons. In an arctic species needing about 120 days to raise young, it would be selectively advantageous to begin laying as early as possible, thereby giving the young as much time as possible to perfect their hunting skills before the onset of winter and the resulting low densities of potential prey. This phenomenon has been recorded in many species; those individuals that lay early are more successful reproductively (Perrins 1970, Newton 1979, Drent and Daan 1980, Chapter 2). Nevertheless, as pointed out by Perrins (1970), this strong tendency to breed early usually is delayed until sufficient food is available.

Productivity at Kilgavik varied among years (Chapter 2), despite relatively constant spring densities of ptarmigan (Fig. 3.1), the main prey species. The density of yearling ptarmigan in spring, closely correlated with productivity of gyrfalcons in some populations (Barichello 1983), was also similar over the last 3 years of the study. Production of juvenile ground squirrels was extremely low in 1986, but this lack produced no impact on mean brood size, which in 1986 was the highest recorded. Thus, in the 3 years of this study, food supply during the nestling period did not directly influence fluctuations in gyrfalcon production and productivity.

Thus, if food is the ultimate factor influencing reproduction, its influence must be felt early in the annual reproductive cycle. The availability of prey appeared to be modified to a large extent by weather, especially early spring weather. Severe spring weather correlated negatively with gyrfalcon reproductive success (Chapter 2). Therefore, although food supply may be the ultimate determinant of productivity of gyrfalcons at Kilgavik, spring weather was probably a major proximate determinant.

Literature Cited

Banfield, A.W.F. 1974. The Mammals of Canada. Nat. Mus. of Canada. Univ. of Toronto Press.

Barichello, N. 1983. Productivity of gyrfalcons (Falco rusticolus) as a response to changes in the ptarmigan (Lagopus) abundance over a five year period. Paper presented to the 34th Alaska Sci. Conf., Whitehorse, 1983.

Bengtson, S.-A. 1971. Hunting methods and choice of prey of gyrfalcons Falco rusticolus at Myvatn in northeast Iceland. Ibis 113:468-476.

Bente, P.J. 1981. Nesting behavior and hunting activity of the gyrfalcon Falco rusticolus, in south central Alaska. Unpubl. M.Sc. thesis, Univ. of Alaska, Fairbanks.

Brown, L.H. 1976. Birds of Prey: Their Biology and Ecology. Hamlyn, London.

Burnham, W.A., and W.G. Mattox. 1984. Biology of the peregrine and gyrfalcon in Greenland Meddel. om Grønland, Bioscience 14:1-25.

Cade, T.J. 1960. Ecology of the peregrine and gyrfalcon populations in Alaska. Univ. Calif. Publ. Zool. 63:151-290.

Cade, T.J. 1982. The Falcons of the World. Cornell Univ. Press, Ithaca, N.Y.

Carl, E.A. 1971. Population control in arctic ground squirrels. Ecology 52:395-413.

Court, G.S. 1986. Some aspects of the reproductive biology of tundra peregrine falcons. Unpubl. M.Sc. thesis, Univ. of Alberta, Edmonton.

Craighead, J.J., and F.C. Craighead. 1956. Hawks, Owls, and Wildlife. Stackpole Co., Harrisburg, Penn.

Dement'ev, G.P. 1960. The Gyrfalcon (Trans. from Russian). Franch'sche Verlangshandlung, Stuttgart.

Dement'ev, G.P., and N.N. Gortchakovskaya. 1945. On the biology of the Norwegian gyrfalcon. Ibis 87:559-565.

Drent, R.H., and S. Daan. 1980. The prudent parent: energetic adjustments in avian breeding. Ardea 68:225-252.

Duke, G.E., A.A. Jegers, G. Loff and O.A. Evanson. 1975. Gastric digestion in some raptors. Comp. Biochem. Physiol. 50:649-656.

Dunning, J.B.,Jr. 1984. Body weights of 686 species of North American birds. Western Bird Banding Assoc. Monogr. No. 1.

Errington, P.L. 1932. Technique of raptor food habits study. Condor 34:75-86.

Fletcher, D.J., and K. Webby. 1977. Observations on gyrfalcons Falco rusticolus in Northeastern Greenland. Dansk Orn. Foren. Tidsskr. 71:29-35.

Haak, B.A. 1983. Foraging ecology of prairie falcons in northern California. Unpubl. M.Sc. thesis. Oregon State Univ., Corvallis.

Haftorn, S. 1971. Norges fugler. Universitetsforlaget, Oslo, Norway. (cited in Nielsen 1986)

Hagen, Y. 1952. The gyrfalcon (Falco rusticolus) in Dovre, Norway. Skrifter utgitt av det Norske Videnskap-Akademi. I. Mat.-Naturv: Klasse, 4:1-37.

Hagen, Y. 1969. Norwegian studies on the reproduction of birds of prey and owls in relation to micro-rodent fluctuations. Fauna 22:73-126.

Jenkins, M.A. 1974. Behavior of the gyrfalcon (Falco rusticolus) from hatching to fledging: a time-lapse photographic study. Unpubl. M.Sc. thesis, Brigham Young Univ., Provo.

Jenkins, M.A. 1978. Gyrfalcon nesting behavior from hatching to fledging. Auk 95:122-127.

Kishchinskii, A.A. 1957. On the biology of the gyrfalcon (Falco gyrfalco gyrfalco) in the Kola Peninsula. Ornithologiia (U.S.S.R.) 1:1-31.

Krebs, C.J. 1978. Ecology: the Experimental Analysis of Distribution and Abundance, 2nd ed. Harper & Row Publ., New York.

Krebs, J.R., D.W. Stephens and W.J. Sutherland. 1983. Perspectives in optimal foraging. Pp. 165-213. In: A.H. Brush and G.A. Clark, Jr. (eds.). Perspectives in Ornithology. Cambridge Univ. Press, Cambridge.

Langvatn, R. 1977. Characteristics and relative occurrence of prey found at nesting places of gyrfalcons Falco rusticolus in Central Norway. Ornis Scand. 8:113-125.

Langvatn, R., and A. Moksnes. 1979. On the breeding ecology of the gyrfalcon Falco rusticolus in central Norway. Fauna Norv. Ser. C, Cinclus 2:27-39.

MacDonald, S.D. 1970. The breeding behavior of the rock ptarmigan. Living Bird 9:195-238.

Morton, M.L., and P.W. Sherman. 1978. Effects of a spring snowstorm on behavior, reproduction, and survival of Belding's ground squirrels. Can. J. Zool. 56:2578-2590.

Muir, R.D. 1975. A study of the breeding biology of arctic gyrfalcons. Can. Wildl. Serv. unpubl. rep.

Muir, R.D., and D.M. Bird. 1984. Food of gyrfalcons at a nest site on Ellesmere Island. Wilson Bull. 96:464-467.

Myrberget, S. 1986. Annual variation in timing of egg-laying in a population of willow grouse Lagopus lagopus. Fauna Norv. Ser. C, Cinclus 9:1-6.

Newton, I. 1979. Population Ecology of Raptors. Buteo Books, Vermillion, S. Dakota.

Newton, I. 1980. The role of food in limiting bird numbers. Ardea 68;11-30.

Newton, I, M. Marquiss and A. Village. 1983. Weights, breeding and survival in European sparrowhawks. Auk 100:344-354.

Nielsen, Ó.K. 1986. Population ecology of the gyrfalcon in Iceland, with comparative notes on the merlin and the raven. Unpubl. Ph.D. thesis, Cornell Univ., Ithaca, N.Y.

Orians, G.H., and N.E. Pearson. 1979. On the theory of central place foraging. Pp. 155-177. In: D.H. Horn, G.R. Stairs and R. Mitchell (eds.). Analysis of Ecological Systems. Ohio State Press, Columbus.

Parker, H., H. Ottesen and E. Knudsen. 1985. Age determination in Svalbard ptarmigan Lagopus mutus hyperboreus. Polar Research 3n.s.:125-126.

Perrins, C.M. 1970. The timing of birds' breeding seasons. Ibis 112:242-255.

Platt, J.B. 1977. The breeding behavior of wild and captive gyrfalcons in relation to their environment and human disturbance. Unpubl. Ph.D. thesis, Cornell Univ., Ithaca, N.Y.

Poole, K.G., and R.G. Bromley. 1985. Aspects of the ecology of the gyrfalcon in the central arctic, Northwest Territories, 1983 and 1984. N.W.T. Dept. Ren. Res. File Rep. No. 52, Yellowknife.

Pulliainen, E. 1975. Choice of prey by a pair of gyrfalcons *Falco rusticolus* during the nestling period in Forest-Lapland. Ornis Fenn. 52:19-22.

Ricklefs, R.E. 1968. Patterns of growth in birds. Ibis 110:419-451.

Roseneau, D.G. 1972. Summer distribution, numbers, and food habits of the gyrfalcon (*Falco rusticolus* L.) on the Seward Peninsula, Alaska. Unpubl. M.Sc. thesis, Univ. Alaska, College, Alaska.

Schmutz, J.K., S.M. Schmutz and D.A. Boag. 1980. Coexistence of three species of hawks (*Buteo* spp.) in the prairie-parkland ecotone. Can. J. Zool. 58:1075-1089.

Solomon, M.E. 1949. The natural control of animal populations. J. Anim. Ecol. 18:1-35.

Steenhof, K. 1983. Prey weights for computing percent biomass in raptor diets. Raptor Research 17:15-27.

Stokkan, K.-A., P.J. Sharp and S. Unander. 1986. The annual breeding cycle of the High-arctic Svalbard ptarmigan (*Lagopus mutus hyperboreus*). Gen. and Comp. Endocrin. 61:446-451.

Temple, S.A. 1972. A portable time-lapse camera for recording wildlife activity. J. Wildl. Manage. 36:944-947.

Watson, A., and R. Moss. 1979. Population cycles in the Tetraonidae. Ornis Fennica 56:87-109.

Weeden, R.B., and J.B. Theberge. 1972. The dynamics of a fluctuating population of rock ptarmigan in Alaska. Proceed. Inter. Ornith. Cong. 15:90-106.

Weeden, R.B., and A. Watson. 1967. Determining the age of rock ptarmigan in Alaska and Scotland. J. Wildl. Manage. 31:825-82[illegible]

Weir, D.N. 1967. A possible source of error in raptor food analysis. Bird Study 14:194.

Woodin, N. 1980. Observations on gyrfalcons (*Falco rusticolus*) breeding near Lake Myvatn, Iceland, 1967. Raptor Research 14:97-124.

IV. FORAGING RESPONSES BY GYRFALCONS TO MANIPULATIONS OF BROOD SIZE

Introduction

A central question in avian ecology concerns the evolution of brood size. Lack (1968) postulated that parents work to capacity in feeding their young, and that brood size is adjusted, mainly through clutch size, to produce the largest number of surviving young. However, studies of food consumption by raptors with natural broods of varying sizes have produced equivocal results. Some workers reported little or no difference in food consumption among broods of varying sizes (Snyder and Wiley 1976, Newton 1978), whereas others found the amount of biomass consumed was greater in larger broods, although not proportional to the increase in number of young (Enderson et al. 1973, Snyder and Snyder 1973, Green 1976, Drent and Daan 1980, Nielsen 1986). It is difficult to evaluate Lack's (1968) hypothesis on the basis of naturalistic studies alone, because it is unclear whether brood size has been adjusted to the capacity of the adults to obtain food in a particular environment, or whether the adults are adjusting food consumption to the demands of the brood. Experimental studies that involve altering brood size circumvent these problems and allow a direct test of the question. Lack's hypothesis may be falsified if addition of young, when nestling growth is maximal and linear - presumably the period of greatest food demands faced by the parents (Brown 1976) - elicits an increase in foraging rate or in the amount of prey brought to the nest.

From 1984 to 1986, I examined food habits and foraging behaviour of gyrfalcons (<u>Falco rusticolus</u>) in the central Canadian arctic (Chapter 3). In natural broods I found that biomass of prey delivered per nest varied directly with the number of chicks (Chapter 3:Table 3.3) and that time spent by the nestlings feeding each day (total time feeding) was slightly longer for larger broods (Chapter 3:Fig. 3.9), but that the number of feeding events per day (feeding rate) did not vary with brood size (Chapter 3:Fig. 3.9). Feeding events included direct feedings of nestlings by one of the adults, and unaided consumption of prey by chicks following delivery of prey to the nest by the adults (food delivery; Jenkins 1978). In an attempt to clarify the reasons for these results, and to test Lack's (1968) hypothesis, I manipulated brood size in two gyrfalcon nests in 1986, and recorded the foraging response of the adults.

Methods

The two gyrfalcon nests used in these experiments were located on the Kilgavik study area (68°10'N, 106°15'W) (Chapter 2). The nests selected were those in which the broods were approximately the same age (the first egg in both hatched on the same day - 11 June). Both nests were also large enough (4 x 1.5 m ledges) to physically accommodate additional young. At site 113, two female nestlings hatched a day apart from a clutch of four eggs (two eggs did not hatch). At site 119, 30 km to the east, three females hatched on 11 and 12 June and one male hatched on 14 June.

When the oldest nestlings were 14 days old, the one male and two females from site 119 were moved by helicopter to site 113, changing brood sizes from the original four and two, to one and five, respectively. During the experiment the nests were visited three times: at the original switch, when the young were 25 days old, and when the three young were returned to their natal site at 32 days of age. Data were collected throughout the nestling period by a number of methods, detailed in Chapter 3. Time-lapse 8 mm movie cameras (Temple 1972) provided a sampled documentation of activities at the nest, including attendance by adults, and frequency and duration of feeding bouts before, during, and after manipulation of brood size. A period of 5 days before and after each change in brood size was used for examination of response in feeding rates and total time feeding each day. This period was chosen as the best compromise between too short a time with possible biases associated with any lag time in foraging response after manipulation (Snyder and Snyder 1973), yet sufficiently short a time so as to remain within similar periods of growth (linear growth approximately 6 to 27 days of age, Chapter 2:Figs. 2.3, 2.4) in the nestling's growth curves.

On each visit to a site, prey remains and pellets were collected to determine the species and biomass of prey used since the previous visit, and weights and morphometric measurements of the chicks were obtained. Mean prey biomass used per day was examined for approximately 1 week before, during, and 1 week after the manipulation experiment, corresponding to the timing of prey collections. Each site was visited 10 times during the entire nestling period. Distance from base camp and the difficulty of travel because of spring thaw during the period of the experiment precluded extended periods of direct observation and more frequent visits. This was compensated for in part by the film records from the time-lapse cameras.

Results

Brood size was artificially increased at site 113 when the age of the oldest chick was 14 days, and at site 119 at 32 days when original brood size was restored (Fig. 4.1). Following addition of three nestlings to site 113 the feeding rate declined, rather than increasing as predicted. The post-manipulative feeding rate was significantly lower (t-test, t=3.77, P=0.02), when the 5-day pre- and post-manipulation periods were compared. Total time feeding increased slightly, but the difference was not significant (t=0.90, P>0.5) (Fig. 4.2). A similar comparison was not possible at site 119 because of camera malfunction. Nevertheless, I did not suspect a major increase in feeding rate or total time feeding per day following return of the nestlings.

The artificially imposed reduction in brood size at site 119 (at age 14 days) was followed by a significant decline in ~~both~~ feeding rate (t=2.75, P=0.05) (Fig. 4.1) and total time feeding per day (t=9.02, P<0.01) (Fig. 4.2). At site 113, however, there was no change in either feeding rate (t=0.11, P>0.5) or total time feeding (t=0.05, P>0.5) subsequent to the reduction in brood size on day 32.

Mean biomass of prey used per day at each site for 6-7 days before, 18 days during, and 6-8 days after the experiment increased with larger brood size (Fig. 4.3, Table 4.1; comparing mean biomass (BM) used per day in each period with brood size (BS), combining sites: BM=153BS+525, r=0.98, P=0.001, n=6). Adult female gyrfalcons were observed to eat occasionally at the nest and perches where prey remains were collected, therefore, the adult female was counted as one 'chick' for calculations. When the mean biomass of prey per 'chick' (nestlings and female) per day

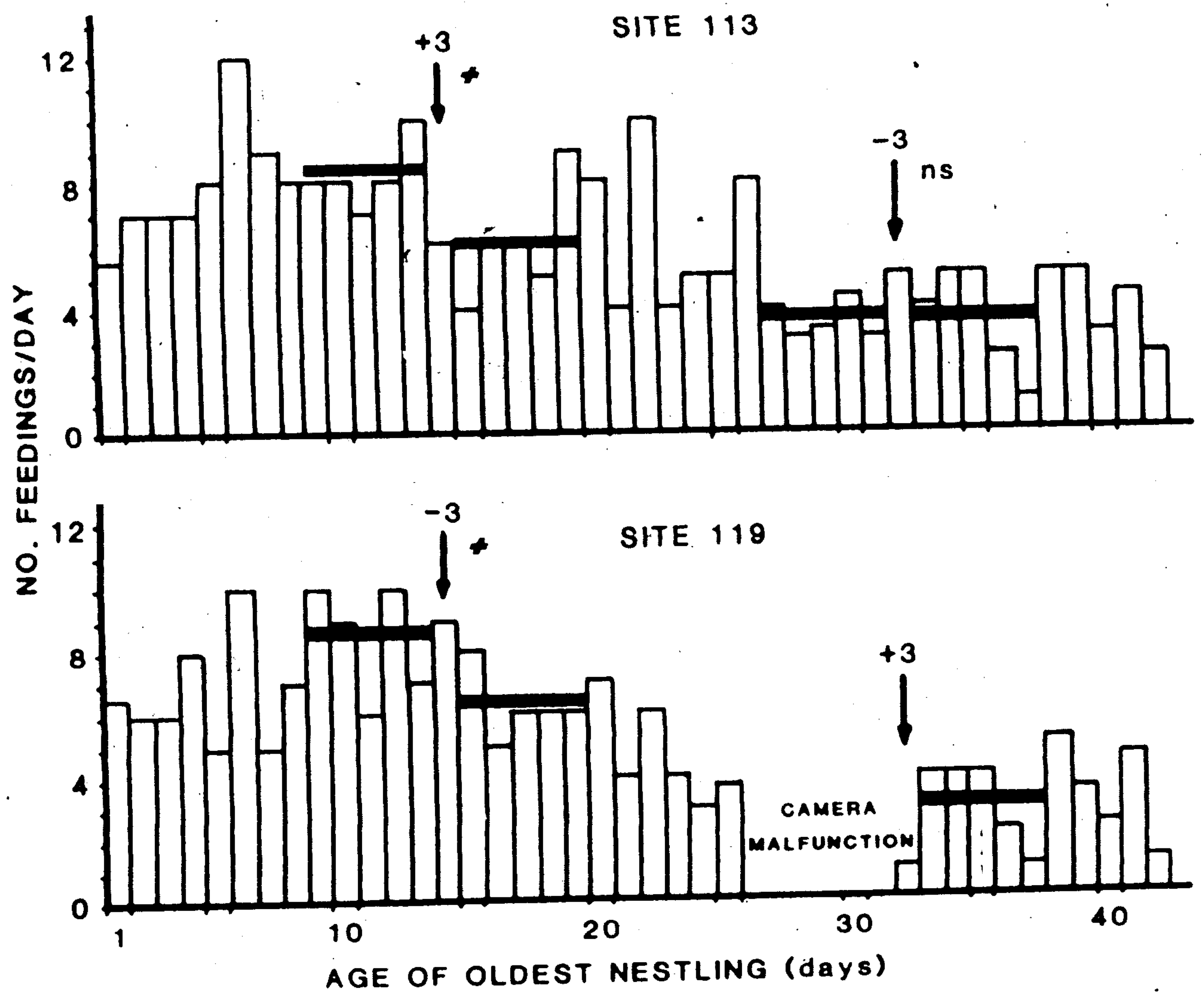

Figure 4.1 Feedings rate at sites 113 and 119, at which brood sizes were experimentally manipulated, Kilgavik, N.W.T., 1986. Arrows denote addition (+3) or removal (-3) of three chicks. Horizontal bars indicate 5-day means before and after manipulation; t-test between means, # - P≤0.05, ns - P>0.05.

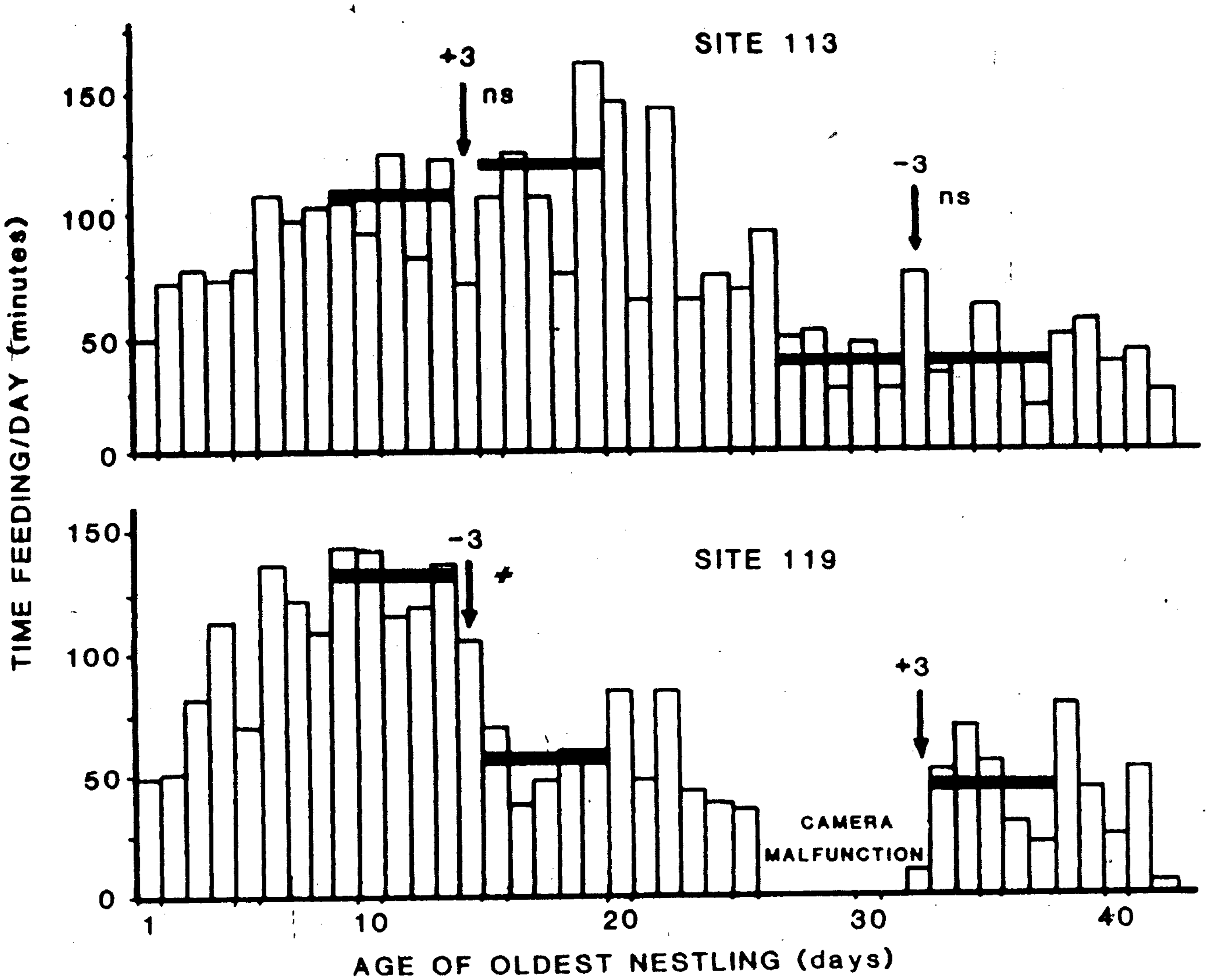

Figure 4.2 Time feeding per day at site 113 and 119, at which brood sizes were experimentally manipulated, Kilgavik, N.W.T., 1986. Arrows denote addition (+3) or removal (-3) of three chicks. Horizontal bars indicate 5-day means before and after manipulation; t-test between means, # - $P \leq 0.05$, ns - $P > 0.05$.

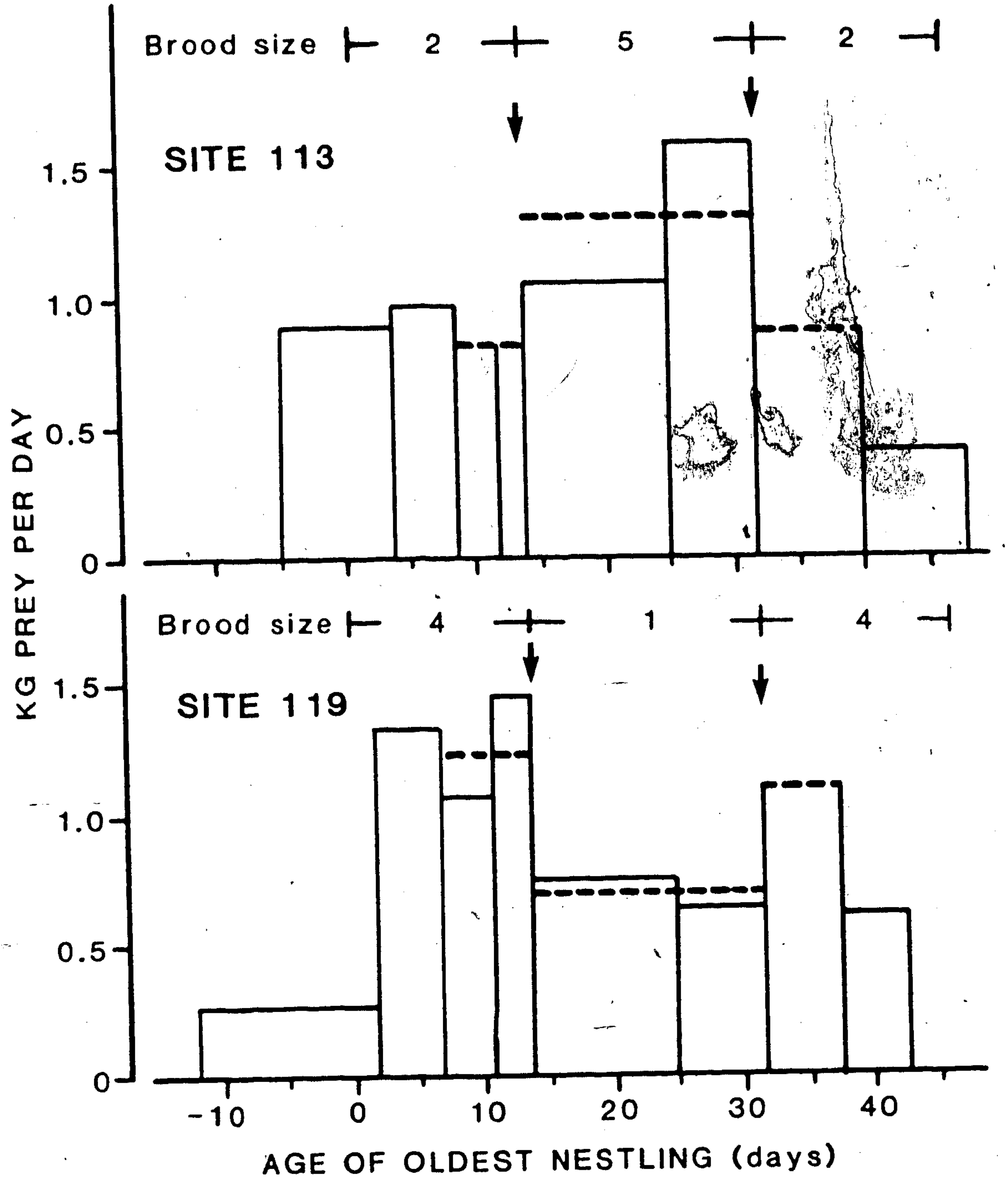

Figure 4.3 Weight (kg per day) of prey used at sites 113 and 119, at which brood sizes were experimentally manipulated, Kilgavik, N.W.T., 1986. Arrows indicate timing manipulations; width of bars indicates period covered by collections; dashed lines indicate means for period covered (see text).

Table 4.1. Mean biomass of prey per day and prey per chick per day, and mean prey weight at sites 113 and 119, at which brood sizes were experimentally manipulated, Kilgavik, N.W.T., 1986.

	Site 113			Site 119		
No. chicks	2	5	2	4	1	4
Age of oldest chick (days)	8-14	14-32	32-40	7-14	14-32	32-38
Mean prey biomass/day (g)	803	1269	841	1221	684	1092
Mean prey biomass/ 'chick'/day (g)[a]	268	212	280	244	342	218
Mean prey weight (g)	438	544	560	389	456	546

[a] 'Chick' includes nestlings and adult female; see text.

was calculated for these periods, the chicks in the larger broods received less on a per capita basis (Table 4.1; combining sites: BM=-29BS+347, r=-0.93, P<0.01, n=6). Mean prey weight increased throughout the nestling period at both sites (Table 4.1).

Too few weights of chicks were obtained during the manipulation experiment to enable comparison of growth rates in large and small broods. However, comparison of weights of the female that stayed alone at site 119 (chick A) and the female sibling that was transferred to site 113 (chick B), which were hatched on the same day, indicates the impact of the availability of different amounts of prey biomass on growth rates. Chick A was 40 to 65 g (12 to 26%) lighter than its sibling during the 7 days prior to the initial switch. By the middle of the manipulation experiment the weights of both chicks were virtually identical (5 g difference), and when the original brood sizes were restored chick A was 185 g (15%) heavier than its sibling, indicating that once alone, chick A grew faster. Chick B's weight increased to within 45 g (3%) of chick A's weight when the final measurements were made 6 days after the last manipulation.

Brooding patterns also showed a strong response to brood size alteration (Fig. 4.4). At two unmanipulated gyrfalcon sites (122 and 1347) monitored by camera in 1986, the time spent brooding dropped off substantially when the chicks were 13 to 15 days old. A similar pattern began to appear at sites 113 and 119 before the initial manipulation of brood size; however, once brood size was lowered to one at site 119, brooding increased again, ending at about 20 days. The pattern at site 113 when five chicks were present was similar to that observed in unmanipulated nests.

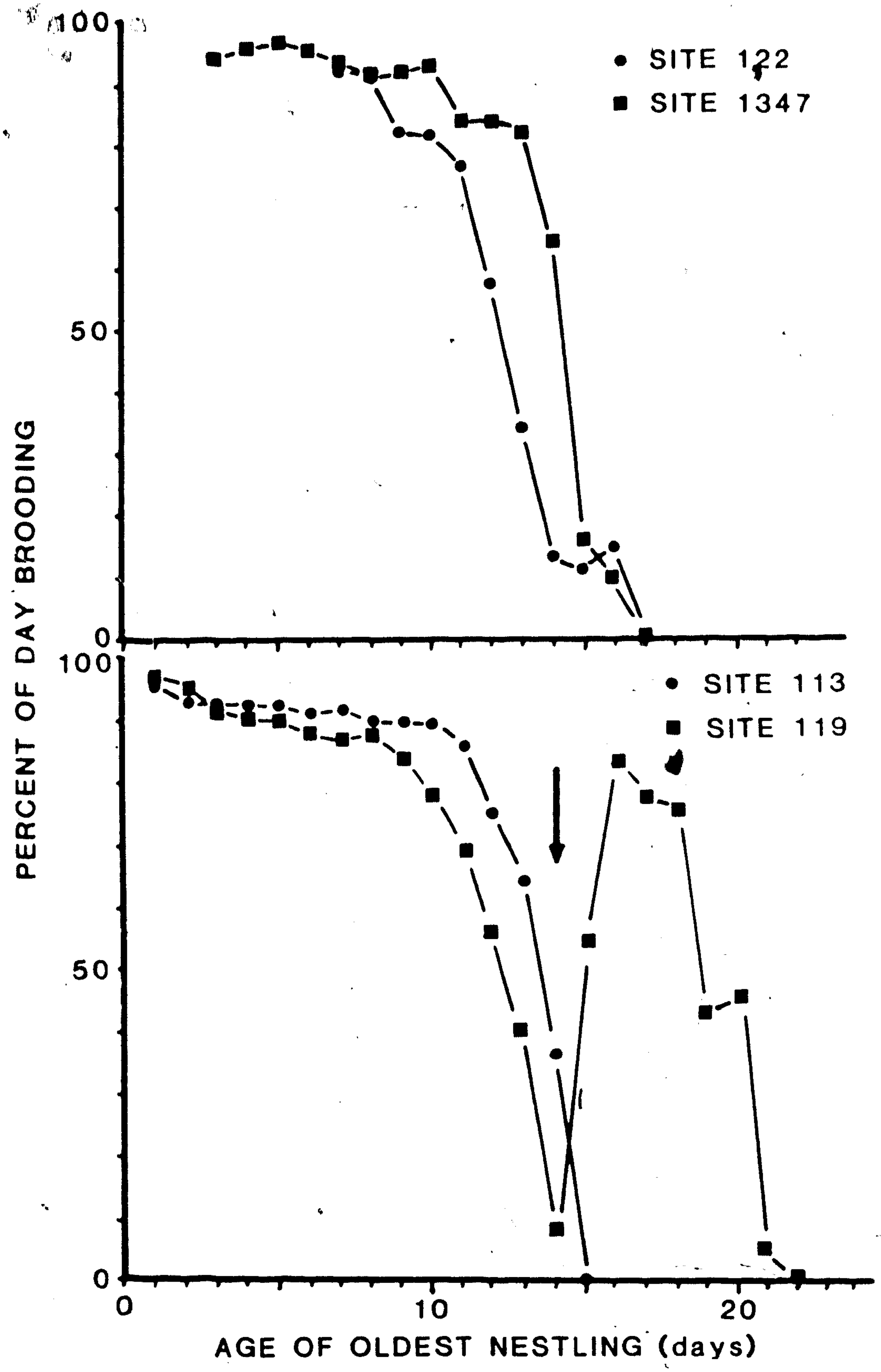

Figure 4.4 Frequency of brooding at sites 113 and 119, at which brood sizes were experimentally manipulated, and two control sites (122 and 1347), Kilgavik, N.W.T., 1986. Arrows indicate timing of manipulation of brood size.

Discussion

Adult gyrfalcons at each nest appeared to respond to alterations in brood size by compensatory changes in total prey biomass fed to the nestlings and, to a lesser degree, in total time spent feeding the nestlings each day. However, the feeding rates did not vary in a similar manner. Two reasons may account for this discrepancy. Five passerine birds eaten in one day would give the same rate as five rock ptarmigan (Lagopus mutus), but with vastly different total time spent feeding and biomass used. Secondly, caching, observed regularly into the fourth week post-hatch (Chapter 3), would also confound analysis based on rate alone. The same rate could result from one ptarmigan fed to one nestling three times, or a whole ptarmigan fed to a larger brood on each of three occasions. Thus, feeding rate must be used cautiously when prey of greatly differing sizes are taken or are too large to be consumed completely in one feeding. Examination of biomass of prey used may be more appropriate in these cases.

Despite the evidence that the adults were able to adjust the biomass of prey killed, the changes were not in the 2:5 or 4:1 ratio expected if the adults were responding simply to the number of young in the nest. According to von Haartman (1954 cited in Drent and Daan 1980), food consumption by each brood is a compromise between the demands of the nestlings and the effort required by the parents to supply food. Nestlings in smaller broods received more biomass per day than their counterparts in larger broods, such that in smaller broods the nestlings may have been 'overfed' to some degree (Newton 1979). All quantities of food were apparently sufficient for normal growth and development to occur, although comparison of chicks A and B at site 119 indicated that the rate of growth did vary somewhat with the amount of food provided. When transferring the nestlings on the first manipulation I was concerned about the survival of the male, which I anticipated would be disadvantaged by having to compete for food with four female nest-mates 2 to 3 days older and 155 to 340 g (39 to 86%) heavier. My concerns proved unfounded and the male fledged successfully, suggesting no significant lack of food.

The extended period of brooding observed at site 119 when one chick was left may have resulted from the inability of the single young to thermoregulate adequately, or from a decreased need for the adult female to hunt for food for the now depleted brood. Newton (1978) found extended brooding at sparrowhawk (Accipiter nisus) sites where food consumption was the greatest, suggesting that the female was needed to hunt only when the take by the male was not sufficient for herself and the brood. Thus, attentive behaviour by the female gyrfalcon may have occurred whether the nestling really needed it or not.

The results of these manipulations suggest that the pairs were not operating at maximal capacity in supplying food during the nestling period. The adults were able to adjust prey consumption, at least partially, to the number of young. Such adjustments may be made in response to the begging calls of the chicks (Newton 1978), an indication of their state of hunger. The results of this study suggest that brood size was not an adjustment to the quality of the environment or the hunting abilities of the adults.

These results do not refute Lack's (1968) suggestion that brood size is adjusted by the parent's ability to feed the young because Lack defined reproductive success based on number of surviving offspring rather than fledged young. Newton's (1985) observations suggest that less than 24% of young sparrowhawks that fledge enter the breeding population. Some studies of raptors have shown lower fledging weights as a result of lower prey biomass per chick (Newton 1978, Schmutz et al. 1980). Young gyrfalcons fledged at lower weights may have a decreased capacity to survive the initial period of independence, thus a compromise between quality and quantity of nestlings must be reached. In addition, increased foraging activities in response to larger broods may reduce the adult's chanc of surviving to breed again, diminishing lifetime reproductive output (Drent and Daan 1980). A full examination of Lack's (1968) hypothesis requires quantifying early mortality of juvenile gyrfalcons and determining lifetime reproductive success of individuals.

Literature Cited

Brown, L.H. 1976. Birds of Prey: Their Biology and Ecology. Hamlyn, London.

Drent, R.H., and S. Daan. 1980. The prudent parent: energetic adjustments in avian breeding. Ardea 68:225-252.

Enderson, J.H., S.A. Temple and L.G. Swartz. 1973. Time-lapse photographic records of nesting peregrine falcons. Living Bird 11:113-128.

Green, R. 1976. Breeding behaviour of ospreys Pandion haliaetus in Scotland. Ibis 118:475-490.

Haartman, L. von. 1954. Der Trauerfliegenschnapper. III. Die Nahrungsbiologie. Acta Zool. Fenn. 83:1-96. (Cited in Drent and Daan 1980)

Jenkins, M.A. 1978. Gyrfalcon nesting behavior from hatching to fledging. Auk 95:122-127.

Lack, D. 1968. Ecological Adaptations for Breeding in Birds. Methuen & Co., London.

Newton, I. 1978. Feeding and development of sparrowhawk Accipiter nisus nestlings. J. Zool., Lond. 184:465-487.

Newton, I. 1979. Population Ecology of Raptors. Buteo Books, Vermillion, S. Dakota.

Newton, I. 1985. Lifetime reproductive output of female sparrowhawks. J. Anim. Ecol. 54:241-253.

Nielsen, O.K. 1986. Population ecology of the gyrfalcon in Iceland, with comparative notes on the merlin and the raven. Unpubl. Ph.D. thesis, Cornell Univ., Ithaca, N.Y.

Schmutz, J.K., S.M. Schmutz and D.A. Boag. 1980. Coexistence of three species of hawks (Buteo spp.) in the prairie-parkland ecotone. Can. J. Zool. 58:1075-1089.

Snyder, N.F.R., and H.A. Snyder. 1973. Experimental study of feeding rates of nesting Cooper's hawks. Condor 75:461-463.

Snyder, N.F., and J.W. Wiley. 1976. Sexual size dimorphism in hawks and owls of North America. Ornith. Monogr. No. 20.

Temple, S.A. 1972. A portable time-lapse camera for recording wildlife activity. J. Wildl. Manage. 36:944-947.

V. CONCLUSION

This study of the ecology of gyrfalcons (Falco rusticolus) at Kilgavik began as a feasibility study to examine whether or not useful information could be collected on the species. Despite great distances between nest sites and many other factors that could have inhibited data collection, research on gyrfalcons at Kilgavik produced valuable results that elucidated many interesting and unique aspects of their foraging ecology. In this closing section of the thesis I highlight some of these findings, and suggest several areas for further research.

The density of breeding pairs of gyrfalcons recorded at Kilgavik is one of the highest in the world. This high density appeared to result from a combination of factors. Many potential nest sites were available, the result of both an abundance of cliffs and relatively high densities of sympatric species that build stick nests, particularly ravens (Corvus corax) and golden eagles (Aquila chrysaetos). In addition, large numbers of potential prey were available to the nesting gyrfalcons, some of them early in the breeding season. Indeed, the evidence indicated that inclement weather had a greater impact on some aspects of gyrfalcon reproduction than varying availability and vulnerability of key prey species. Food availability during the nestling period did not appear to be limiting the population, as the conditions indicating food abundance, as proposed by Newton (1979), were generally fulfilled. The density of breeding pairs may be determined during courtship and prelaying, a period that coincides with the yearly low in availability of prey, when the male must provide food for itself and the female (Platt 1977). Most pairs did not initiate laying until the arrival of the major spring migration of rock ptarmigan (Lagopus mutus), their principal prey, underlining the importance of food during this period for successful reproduction.

The diet of gyrfalcons breeding at Kilgavik was one of the least diverse recorded in terms of number of species (Nielsen 1986), which suggests that despite the availability of many species of potential prey, the gyrfalcons were almost always able to exercise food preference. The period of rapid growth of gyrfalcon nestlings in 1984 and 1985 coincided closely with the emergence of naive juvenile arctic ground squirrels (Spermophilus parryii), which formed a large portion of the diet during the nestling period. Because of the nearly complete failure of ground squirrel production in 1986, ptarmigan were killed by gyrfalcons in larger numbers throughout that summer, even though the apparent vulnerability of ptarmigan decreased significantly as in previous years. These results emphasize two points. Because spring densities of ptarmigan were relatively similar during the study, when juvenile squirrels were present during the nestling period they were preferred more than ptarmigan. However, the successful exploitation of ptarmigan in the summer of 1986 indicated that, despite assumed decreased vulnerablility, the gyrfalcons were able to detect and kill ptarmigan with relative ease. Indeed, the actual vulnerability of ptarmigan apparently did not fall to a level that caused the gyrfalcons to switch to other (less preferred) prey for the majority of their diet.

The commercial harvest of gyrfalcons by Inuit was the primary factor driving recent research efforts in the N.W.T. (Bromley 1983). Should a commercial harvest be reinstated at some point in the future, the size of the breeding population of gyrfalcons and their productivity must be monitored annually, probably in two or three regions of the

N.W.T. Late winter and spring weather conditions were correlated with gyrfalcon production at Kilgavik (Chapter 2), and could be used to predict overall production for that region - the level of confidence in the prediction could rise with additional data. To ensure that any harvest errs well on the conservative side, production of birds in a given region should be determined to decide where and if harvests should occur. The foregoing is based on the assumptions that fledging birds that survive return to breed in or reasonably near their natal area (Mearns and Newton 1984, Nielsen 1986, G. Court pers. comm.), and that fall harvest efforts would trap young birds (in their first year) that originated within a few hundred kilometers of the point of harvest effort. These assumptions need to be tested for gyrfalcons. Use of late winter and spring weather conditions for predicting gyrfalcon reproductive success also assumes an impact of weather on the birds throughout the N.W.T. similar to that recorded at Kilgavik. Such regional indices of weather severity might prove to be reliable caution flags for potential harvests in years of poor reproduction.

The research undertaken in this study has identified several important questions that need to be addressed in the future. 1. Rock ptarmigan are a key prey species of gyrfalcons in the central arctic. Their importance as an early season food source, upon which reproductive output seemed to be based, could only be replaced by arctic hares (Lepus arcticus). Thus, the availability of these two species over time is central to understanding long-term productivity in the gyrfalcon. Therefore, research into spring densities of breeding ptarmigan, begun in 1983, should be continued and expanded to examine the extent of fluctuations/cycles in these birds and the impact of predation upon ptarmigan populations. The factors affecting the timing of migration should also be explored, since they determine the availability of this prey source early in the reproductive cycle of the gyrfalcons. Such studies of rock ptarmigan in other regions of the N.W.T. have not and are not being carried out. Examination of the extent of fluctuations/cycles in the resident arctic hares should also be undertaken. 2. From 1983 to 1986, over 95% of the young gyrfalcons known to have fledged at Kilgavik were banded. The proportion returning to establish territories in their natal or adjacent areas, and the age at which they return, should be determined. Trapping efforts directed at breeding pairs should be intensified. If successful, these efforts could provide much valuable data on the population turnover of gyrfalcons, the extent of movement between sites, and phenomena such as mate switching. 3. We know little about fledgling gyrfalcons once they leave the nest area, including overwintering locations, survival rates, and whether they return to their natal area in their first breeding season. Telemetry studies are required to examine these questions as technology permits. Telemetry should also be used to determine home range and foraging areas of adults during the nestling period. 4. Studies are needed to examine weather in other regions of the N.W.T., to aid in predicting the productivity of gyrfalcons in these regions.

Fruitful results of these research efforts will not come easily. Field work on gyrfalcons is demanding, with relatively small pieces of information obtained only after great effort. Nevertheless, the population breeding at Kilgavik is one of the best documented in the world, and the return on effort and investment will likely increase exponentially as research continues.

Literature Cited

Bromley, R.G. 1983. 1982 raptor survey. N.W.T. Dept. Ren. Res. File Rep. No. 35, Yellowknife.

Mearns, R., and I. Newton. 1984. Turnover and dispersal in a peregrine _Falco peregrinus_ population. Ibis 126:347-355.

Newton, I. 1979. Population Ecology of Raptors. Buteo Books, Vermillion, S. Dakota.

Nielsen, Ó.K. 1986. Population ecology of the gyrfalcon in Iceland, with comparative notes on the merlin and the raven. Unpubl. Ph.D. thesis, Cornell Univ., Ithaca, N.Y.

Platt, J.B. 1977. The breeding behavior of wild and captive gyrfalcons in relation to their environment and human disturbance. Unpubl. Ph.D. thesis, Cornell Univ., Ithaca, N.Y.

APPENDIX 1. List of birds and mammals recorded on the Kilgavik study area, N.W.T., 1983-1986.[a]

Birds		Status[b]	Abundance[c]
Red-throated loon	Gavia stellata	BL	FC
Pacific loon	G. pacifica	BL	C
Common loon	G. immer	? *	R
Yellow-billed loon	G. adamsii	BL	FC
Tundra swan	Cygnus columbianus	BL	FC
Greater white-fronted goose	Anser albifrons	BL	C
Snow goose	A. caerulescens	M	FC
Brant	Branta bernicla	M	R
Canada goose	B. canadensis	BL	C
Green-winged teal	Anas crecca	? *	R
Northern pintail	A. acuta	BL	FC
Lesser scaup	Aythya affinis	BL*	R
Common eider	Somateria mollissima	BL*	FC
King eider	S. spectabilis	BL	FC
Oldsquaw	Clangula hyemalis	BL	C
Surf scoter	Melanitta perspicillata	BL*	R
White-winged scoter	M. fusca	BL*	R
Red-breasted merganser	Mergus serrator	BL	FC
Rough-legged hawk	Buteo lagopus	BL	C
Golden eagle	Aquila chrysaetos	BL*	FC
Peregrine falcon	Falco peregrinus	BL	FC
Gyrfalcon	F. rusticolus	BL	FC
Willow ptarmigan	Lagopus lagopus	M	R
Rock ptarmigan	L. mutus	BL	C
Sandhill crane	Grus canadensis	BL	FC
Lesser golden-plover	Pluvialis dominica	BL	R
Semipalmated plover	Charadrius semipalmatus	BL	FC
Semipalmated sandpiper	Calidris pusilla	BL	FC
Least sandpiper	C. minutilla	BL	R
White-rumped sandpiper	C. fuscicollis	BL	R
Baird's sandpiper	C. bairdii	BL	FC
Pectoral sandpiper	C. melanotos	BL	C
Common snipe	Gallinago gallinago	BL*	O
Red-necked phalarope	Phalaropus lobatus	BL	R
Pomarine jaeger	Stercorarius pomarinus	?	R
Parasitic jaeger	S. parasiticus	?	R
Long-tailed jaeger	S. longicaudus	?	R
Iceland (Thayer's) gull	Larus glaucoides thayeri	BL	C
Glaucous gull	L. hyperboreus	BL	C
Arctic tern	Sterna paradisaea	BL	C
Snowy owl	Nyctea scandiaca	BL	O
Short-eared owl	Asio flammeus	BL*	O
Horned lark	Eremophila alpestris	BL	C
Common raven	Corvus corax	BL	FC
Gray-cheeked thrush	Catharus minimus	BL*	O
Water pipit	Anthus spinoletta	BL	C

American tree sparrow	*Spizella arborea*	BL*	C
Savannah sparrow	*Passerculus sandwichensis*	BL	C
White-crowned sparrow	*Zonotrichia leucophrys*	BL	R
Harris's sparrow	*Z. querula*	BL*	R
Lapland longspur	*Calcarius lapponicus*	BL	C
Snow bunting	*Plectrophenax nivalis*	BL	C
Redpoll	*Cardruelis* sp.	BL	FC
Mammals			
Arctic hare	*Lepus arcticus*		FC
Arctic ground squirrel	*Spermophilus parryii*		C
Northern red-backed vole	*Clethrionomys rutilus*		
Tundra vole	*Microtus oeconomus*	*	
Brown lemming	*Lemmus sibiricus*		
Collared lemming	*Dicrostonyx groenlandicus*		
Gray wolf	*Canis lupus*		O
Arctic fox	*Alopex lagopus*		R
Red fox	*Vulpes vulpes*		FC
Grizzly bear	*Ursus arctos*		O
Ermine	*Mustela erminea*		R
Wolverine	*Gulo gulo*		O
Ringed seal	*Pusa hispida*		C
Bearded seal	*Erignathus barbatus*		FC
Moose	*Alces alces*	(tracks only)	R
Barren-ground caribou	*Rangifer tarandus*		C
Muskoxen	*Ovibos moschatus*		FC

---

[a] Nomemclature and range extensions after Godfrey 1986, Hall 1981.

[b] Status - BL=breeds locally, M=migrant, ?=unknown, *=range extension

[c] Abundance - C=common, FC=fairly common, O=occasional, R=rare